A number of taxonomic changes and observations have resulted from a study of Panamanian *Columnea* and these are discussed below.

1. Recognition of taxonomic sections within *Columnea* sens. lat.—Experimental work on cultivated *Columnea* and herbarium work have led me to regard leaf anisophylly as an unreliable taxonomic character for all but a few large-leaved species, and for this reason I do not recognize the differences between sections *Collandra* and *Stygnanthe* or *Columnea* and *Cryptocolumnea*.

The differences between sections *Stenanthus* and *Ortholoma*, based on sepal shape and adaxial leaf vestiture, are also unreliable and arbitrary in my opinion and are not followed here. There is much work needed on the floral morphology of *Columnea*, but I think that present knowledge will allow the construction of a sectional classification based on corolla morphology, despite the views of those suggesting that such a classification is simply a classification of the pollen vectors associated with different corolla shapes. Breeding relationships suggest that corolla morphology is more than simply an indicator of the type of pollinator which visits the flowers (Morley, in press). On the basis of corolla morphology I have transferred some species usually placed in sections *Collandra* and *Stygnanthe* into sect. *Pterygoloma*, which hitherto contained only one species. Figure 1 shows representative corollas from the sections recognized in Panama and listed below with synonymy.


I wish to thank the late C. V. Morton for help with nomenclatural problems and Professor John O'Meara and R. D. Meikle for correcting the Latin diagnoses.

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Figure 1. Corolla morphology in sections of Cohimnea.—Sect. Collandra: a, C. aureonitens Hook. (Colombia); b, C. dissimilis Morton (Panama); d, C. segregata Morley (Panama).—Sect. Pterygoloma: c, C. silvarum Morton var. butcheri Morley (Panama); e, C. moorei Morton (Panama).—Sect. Ortholoma: f, C. mira Morley (Panama); g, C. sanguino-
Section Collandra

2. Columnea consanguinea Hanst. from Panama has adpressed abaxial leaf vestiture unlike the more erect abaxial vestiture of Costa Rican plants. As C. consanguinea was originally described from Costa Rica, and all Panama material has adpressed vestiture, it is proposed to recognize a new variety in Panama.

Columnea consanguinea Hanst. var. adpressa var. nov.

A var. consanguinea differt foliis subtus pilis adpressis.

Differing from var. consanguinea by the adpressed hairs on the leaf undersides.


3. There are few morphological discontinuities between Columnea darienensis Morton and C. consanguinea var. adpressa. The flower of the type of C. darienensis (Pittier 5660, US) is damaged with one of the corolla lobes appearing to spread, but the other two undamaged lobes have a typical incurved appearance of many species in sect. Collandra. Pittier 5660 has corolla vestiture and dimensions close to those of C. consanguinea, and as C. darienensis have poorly serrate sepals (Duke & Elias El3694, MO) and some C. consanguinea do not have entire sepals (Allen 4788, 4924, US), this distinction breaks down. Some C. darienensis (Terry 1547, GH) are reported with the same yellow corollas which are supposed to characterize C. consanguinea, instead of orange-scarlet. Columnea darienensis has not yet been found with red abaxial leaf coloring which is common in C. consanguinea, and furthermore the leaf vestiture of C. darienensis is more sparsely strigose, corollas less sericeous, and sepals tend to be more often serrate. In order to relate the variation of C. darienensis more closely with C. consanguinea I propose to make C. darienensis a variety of C. consanguinea.

Columnea consanguinea Hanst. var. darienensis (Morton) Morley, comb. nov.


4. Columnea dissimilis Morton was described in 1942 from El Valle de Anton, Prov. Coclé (Allen 2483, US) and is thought to be endemic to the area. Comparison between C. dissimilis and C. translucens Raymond, known only in cultivation and from an unknown source, shows the latter to be almost identical with C. dissimilis.

C. translucens (Soulier s. n., US) has reddish sepals which breaks down the distinction with C. dissimilis based on sepal colour. Likewise the appearance
of orange corollas in *C. translucens* can be explained by less dense red hairs superimposed upon yellow corolla tissues; in *C. dissimilis* the yellow corolla tissue does not show through a thick covering of red hairs on the tube. The only notable difference which *C. translucens* exhibits is the possession of glandular hairs in all parts, although the type of *C. dissimilis* (Allen 2483) is not devoid of them. Possession of glandular hairs is thought insufficient reason to maintain *C. translucens* at specific level, and lack of provenance of *C. translucens* material leads me to reduce the taxon to synonymy with *C. dissimilis* pending further information on the distribution of *C. translucens*.


Section **Columnea**.

5. *Columnea conferta* Morton was described in synonymy with *C. citrina* Morton if the isotype (*Terry & Terry 1554, GH*) of *C. conferta* is identical to the holotype (*F*, not seen). A fundamental similarity between the type descriptions led to closer examination of the corolla morphology of *C. conferta*, and was found to place the taxon in sect. *Columnea* and not *Collandra*. The isotype of *C. conferta* has a bilabiate corolla in the bud burst condition. Detailed examination of calyx lobe shape and margin, abaxial leaf vestiture and pigmentation and corolla pigmentation of the types of both taxa confirm that *C. conferta* is a synonym of *C. citrina*. It is therefore not surprising that *C. conferta* is known only from the type collection but *C. citrina* has been collected on several occasions.

It may be that *C. conferta* was mistakenly described as belonging to sect. *Collandra* by the use of immature flowering material as the young buds of *C. citrina* (Allen 2404, US) bear some resemblance to fully opened flowers of species in sect. *Collandra*. To support this view the type description of *C. conferta* states the corolla is “verisimiliter paullo bilabiato” indicating some doubt in the interpretation of corolla shape.


6. *Columnea nicaraguensis* Oersted was found to exhibit much variation in leaf shape, but sepal shape and sepal, leaf and corolla vestiture made it possible to identify specimens without difficulty. Figure 2 shows the scatter diagram for a plot of leaf length against leaf width at the widest part for large leaves of the Panamanian specimens seen.

7. *Columnea microcalyx* Hanst. was described in 1865 from Costa Rica, and in 1901 Donnell Smith described the variety *macrophylla* also from Costa Rica. In 1938, Morton, wishing to raise var. *macrophylla* to specific rank found it necessary to use a new epithet “localis,” *C. localis* Morton, because of the existence of *C. macrophylla* Kuntze (1891). Study of the variation of *C. microcalyx* and *C. localis* has led me to regard the latter as a variety of the former, so that Donnell Smith’s var. *macrophylla* should be reinstated.
The example of variation in *C. localis* and *C. microcalyx* shown in Table 1 concerns three collections. *Allen 1428* (GH, US, MO) are all identified as *C. localis* by Morton; *Davidson 76* (MO) is misidentified as *C. tomentosa*, while *Skutch 3215* (MO) is identified as *C. microcalyx* by Morton. It can be seen that the three specimens collected by Allen, presumably from the same site, each show a different combination of *C. localis* and *C. microcalyx* characters.

*Columnnea microcalyx* and *C. localis* can only be consistently distinguished by the use of leaf and stem vestiture and leaf length. Differences based on sepal shape and pedicel length intergrade; for example *Allen 4381* (US), identified by Morton as *C. localis*, agrees with the description of that taxon, but the same collection (MO) has sepals with a blunt tip and short pedicels, both characters characterizing *C. microcalyx*. Likewise, *Pittier 5625* (US) is like *C. localis* apart...
Columnea microcalyx Hanst. var. microcalyx, Linnaea 34: 408. 1865.


8. Columnea billbergiana Beurl. was described in 1854, being based on material collected by Billberg from Porto Bello, Prov. Colón, Panama. The species is found only in Panama and is held to differ from C. percrassa Morton by having red sepals (but the type of C. percrassa (US) and a topotype have sepals with traces of red pigment), by having scarlet corollas (but as with C. percrassa there is sometimes a small yellow area at the throat of the corolla), and by having brown instead of olive stems as in C. percrassa (but some old C. percrassa plants with dappled axes suggest that these also turn brown, i.e. become non-photo-synthetic).

All known Columnea percrassa herbarium material comes from the type locality of Cerro Campana, Prov. Panamá, altitude 400 m, and all cultivated material from an unknown locality, so there was reason to examine the validity of C. percrassa as a species. Columnea billbergiana also grows on Cerro Campana and comparison of C. percrassa with this material has shown the two are the same. The type of C. percrassa (Allen 2432, US) has sepals only slightly less hairy than those of C. billbergiana (Allen 2428, US, MO), which have densely hairy sepals and pedicels. Sepal margins in C. percrassa type show as much basal toothing as certain C. billbergiana specimens (Allen 1651, US). The shape of the leaves of type C. percrassa is indistinguishable from certain C. billbergiana specimens (Allen 2428; Porter 4273, and 4948, all MO), instead of being less acute than in C. billbergiana. Columnea percrassa as identified by Morton (Hutchison & Dressler 2952, MO) has traces of red pigment on the undersides of the leaves yet the pigment is held to occur only in C. billbergiana. These observations lead me to reduce C. percrassa to synonymy with C. billbergiana.


9. *Columnea tenuis* Kl. ex Oerst. was described from material collected in Prov. Veraguas, Panama, by Julius von Warscewicz. *Columnea obliqua* Morton is held to differ from *C. tenuis* in having entire sepals (but type *C. obliqua* has slightly toothed sepals like some *C. tenuis*), in having green sepals (but sepals are reddish in type *C. obliqua*), in having leaves which are oblique at the base (also seen in some *C. tenuis*), and in having different leaf and corolla dimensions (dimensions which are found to overlap). The corolla color of the two taxa is the same in some specimens, and both sometimes show red abaxial leaf surfaces. These observations lead me to reduce *C. obliqua* to synonymy with *C. tenuis*. The difference of leaf shape between *C. tenuis* and the closely related *C. oerstediana* Kl. ex Oerst. was seen to be constant.

*Columnea tenuis* Kl. ex Oerst., Centralamer. Gesner. 63. 1858.


10. *Columnea hirta* Kl. & Hanst. was described from material collected in Prov. Veraguas, Panama, by Warscewicz, but the type has probably been destroyed in Berlin. I have seen no Panamanian collection of this species, but the closely similar *C. mortonii* Raymond is Panamanian. *Columnea hirta* and *C. mortonii* are said to differ in the color of the stem hairs, leaf shape, bract shape, calyx lobe toothing, and hairiness of the filaments. However, *C. mortonii* identified by Raymond (Soulier s. n., US) has oblong leaves, reddish stem hairs, lacks red-based calyx hairs (all of which are *C. hirta* characters), and has no sepal teeth unlike both *C. hirta* and *C. mortonii*. This material was apparently from the same source as the type material, from the Fairchild Tropical Garden, Miami, Florida. Peele 111 (US), from Longwood Gardens, also has traces of red stem hairs and lacks red-based calyx hairs, yet Longwood plants are stated to represent *C. mortonii* by Morton (1971). I have not seen specimens of Dressler 3469 and 3848 from Cerro Jefe, Prov. Panamá, which Wiehler (1970) refers to *C. mortonii*.

Until further material of *C. hirta* is collected from Panama I propose to make *C. mortonii* a Panamanian variety of *C. hirta*, which is known to occur in Costa Rica. Subsequent collections may require that *C. mortonii* be made synonymous with *C. hirta*.

*Columnea hirta* Kl. & Hanst. var. *hirta* Linnaea 34: 403. 1865.

Syn. C. hirsuta Kl. ex Oerst., Centralamer. Gesner. 61. 1858, non Swartz.

*C. hirta* Kl. & Hanst. var. *mortonii* (Raymond) Morley, comb. nov.


11. *Columnea tomentulosa* Morton was described in 1938 to replace the later homonym of *C. tomentosa* Roxb. (1814), *C. tomentosa* Oerst. (1858). Comparison of *C. tomentulosa* with *C. tulae* Urb. from Puerto Rico and Hispaniola shows that apart from possessing more highly toothed sepals and being smaller
Table 2. Comparison of pedicel length and sepal tooth length in *Columnea grata* and *C. sanguinolenta*.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Pedicel length (cm)</th>
<th>Sepal tooth length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Columnea grata</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oersted 9288 i</td>
<td>11.1</td>
<td>2</td>
</tr>
<tr>
<td>Oersted 9288 ii</td>
<td>10.0</td>
<td>2</td>
</tr>
<tr>
<td><em>C. sanguinolenta</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Siebert 1562</td>
<td>4.5</td>
<td>10</td>
</tr>
<tr>
<td>Wedel 942</td>
<td>3.0</td>
<td>7</td>
</tr>
<tr>
<td>Wedel 1513</td>
<td>3.4</td>
<td>8</td>
</tr>
<tr>
<td>Wedel 2325</td>
<td>2.7</td>
<td>4</td>
</tr>
<tr>
<td>Kirkbride et al. 567</td>
<td>3.4</td>
<td>8</td>
</tr>
<tr>
<td>Standley et al. 45757</td>
<td>3.9</td>
<td>12</td>
</tr>
<tr>
<td>Dunlap 449</td>
<td>2.5</td>
<td>5</td>
</tr>
</tbody>
</table>

In all parts, *C. tomentulosa* is very close to *C. tulae*. It is proposed to relate Central American *tomentulosa* to the variation pattern of *C. tulae* by making the latter a variety of the former. (There is a parallel variation pattern found in *C. scandens* L. where certain Lesser Antillean populations of var. *scandens* have variously toothed sepals and differ in leaf size from mainland populations of var. *fendleri* (Sprague) Morley from Venezuela.) Conspecificity of *C. tulae* with *C. tomentulosa* supports the independently arrived at conclusion that *C. tulae* probably arose from Central American ancestors rather than South American as is the case in *C. scandens* (Morley, 1972). The distribution of var. *tomentulosa* along the Atlantic side of Central America supports relationship with the Greater Antillean var. *tulae*.


Syn. *C. tomentosa* Oerst., Centralamer. Gesner. 64. 1858.

*Columnea tomentulosa* Morton var. *tulae* (Urban) Morley, comb. nov.


*C. tulae* var. *flava* Urban, Symb Antill. 1: 409. 1899.

12. A loan of Oersted material from Copenhagen included some Panamanian specimens, the details of the sheets being as follows.

*Columnea* sp. (as *Stenanthus serratus*), one sheet, single shoot, no corolla, no fruit; “No. 188, *Columnea serrata, Stenosactanuthus serratus, Stenanthus* Oersted, Cult.”—This specimen was clearly not *C. serrata* (KL.) Hanst., the type of which is probably destroyed in Berlin.

*Columnea tomentulosa* Mort. var. *tomentulosa* (as *Columnea tomentosa*), one sheet, single shoot, no corolla, no fruit; “Oersted 9293, Nicaragua: River (?) S. Juan, det. Kränzlein.”—Isotype.
Columnea magnifica Kl. & Hanst. ex Oerst. (as C. magnifica), one sheet, one shoot tip, leaves and two damaged corollas in packet; "Columnea magnifica Kl. Costa Rica, Warscewicz, Spec. Orig. 22700."

Although Columnea grata Morton is not recorded from Panama, it is similar to C. sanguinolenta (Kl.) Hanst. which does, so that the two can be compared. Columnea grata Morton (as Stenanthus heterophyllus), 3 sheets, all organs present except fruit; “Oersted Pl. Centram. 9288, Columnea heterophylla, Stenanthus heterophyllus Oerst., prope Naranjo 5/49.”—holotype. Table 2 compares pedicel length and sepal tooth length in C. grata and C. sanguinolenta, showing the two are distinct.

New Taxa.

13. Columnea silvarum Morton var. butcheri var. nov. (Sect. Pterygoloma)

Differt a var. silvarum sepalis brevioribus et sepalis et pedicellis pilis fuscis vestita.

Differing from var. silvarum by the shorter sepals and sepal and pedicel hairs dull brown.

Woody herb; stems about 7 mm in diameter, purplish-dull brown tomentose. Leaves of a pair unequal, the larger oblanceolate, acuminate, oblique at base, serrate, about 10.3 cm long and 2.3 cm wide at widest point, adaxially hirsute-tomentose with 2–3-celled white adpressed hairs and 7–10-celled reddish erect fine hairs, abaxially hirsute-tomentose with 5–8-celled reddish erect fine hairs, blades green above and beneath but with reddish cast produced by indumentum, petioles about 2 mm long, the smaller leaves about 2.1 cm long and 5 mm wide, lanceolate, acuminate, serrate, green above and beneath, vestiture as in larger leaves. Flowers in clusters of 3 or more, bracteate, bracts about 5 mm long, linear, dull brown tomentose, pedicels to about 2 cm long, dull brown long tomentose; sepals lanceolate, acuminate, 3–4 toothed, teeth linear, to 1 mm long, sepals green, about 8 mm long and 1 mm wide at middle, externally dull brown tomentose; corollas tubular, slightly zygomorphic, yellow with lobes having reddish crescent marks, about 3.7 cm long, about 3 mm in diameter at base, becoming about 7 mm in diameter in middle then 5 mm in diameter at throat, lobes slightly unequal, lobed portion about 4 mm long, spreading, corolla externally pilose, hairs transparent, filaments glabrous, yellow, anthers included, 1 mm long and 1.5 mm wide, style glabrous, yellow, stigma stomatomorphic, ovary white pilose, disk gland bilobed, fruit not seen.

Holotype: Panama. prov. chiriquí: Near village Cuesta de Piedra, near Río Escarria, altitude 3600 feet, Butcher s. n., March 1962 (US).

This variety is known also from Costa Rica (Pittier JJ196, US). It is close to C. silvarum in its characters.

14. Columnea mira sp. nov. (Sect. Ortholoma)

A Columnea ochroleuca (Kl. ex Oerst.) Hanst. differt corollis flavis et rubris, foliis oblanceolate et caulisibus rutilis et hispidis.

Differing from Columnea ochroleuca (Kl. ex Oerst.) Hanst. by the yellow and red corollas, oblanceolate leaves and reddish purple hirsid stems.
Woody herb; epiphytic, stems 3-4 mm in diameter, red-purple hispid when young. Leaves of a pair unequal, the larger oblanceolate: acute, oblique at base, crenate-serrate, about 5.3-8.1 cm long and 2.1-2.8 cm wide at widest point, adaxially densely hirsute with 2-3-celled white adpressed hairs and 4-8-celled reddish or red erect hairs, abaxially densely hirsute with 2-3-celled white adpressed hairs and 5-9-celled red erect hairs, blades green above but conspicuously red hirsute, blades concolorous red-purple beneath, petioles absent or to 2 mm long, the smaller leaves lanceolate, acuminate, serrate, about 8 mm long and 3 mm wide, green above, red purple beneath, indument as larger leaves. Flowers solitary or paired, bracteate, bracts about 4 mm long, linear, brown reddish pilose, pedicels 1.1-1.6 cm long, dull brown-red pilose; sepals lanceolate, acuminate, 2-3 toothed, teeth linear, to 2 mm long, sepals green, about 8-10 mm long and 1.5 mm wide in middle, externally red-purple-brown hirsute; corollas tubular, zygomorphic, yellow with two long brownish red stripes running from sinuses of anterior lobe and two shorter paler red stripes running from sinuses between lateral and posterior lobes, about 4.6 cm long, about 3 mm in diameter at base becoming about 11 mm in diameter in middle then 8 mm in diameter at throat, lobes unequal, posterior lobes about 7 mm long, bilobed at apex, lobed portion of corolla about 9 mm long, anterior lobe about 6 mm long, all lobes spreading and narrow, corolla externally reddish pilose, filaments glabrous, yellow, anthers exerted, 1 mm long and 1.2 mm wide, style glabrous, reddish, stigma stomatomorphic, ovary reddish pilose, disk gland bilobed, fruits not seen.


This species will make a most ornamental addition to cultivated Columneas. The type of C. ochroleuca I have not seen, as it was destroyed in Berlin together with other type material of C. ochroleuca it is difficult to know whether C. mira should be given specific rank. In the absence of other data I have given C. mira specific rank.

15. *Columnea cruenta* sp. nov. (Sect. *Pterygoloma*)

A *Columnea perpulchra* Morton differs in sepals brevioribus, foliis angustioribus, caulibus indumento pilorum rutiliorum densius vestitis.

Differing from *Columnea perpulchra* Morton by the shorter sepals, narrower leaves, red stem hairs, and denser indumentum.

Woody herbs; epiphytic, stems about 5 mm in diameter, brown-purple hirsute. Leaves of a pair unequal, the larger oblanceolate, acuminate, oblique at base, serrate, about 13 cm long and 3.5 cm wide at widest point, adaxially pilose with 4-5-celled reddish erect hairs, abaxially pilose with 2-3-celled white adpressed hairs and 5-6-celled reddish erect hairs, blades green above but suffused red-purple at margins and tip, blotched red-purple at tip, margins and in center of blade beneath, petioles about 6 mm long, the smaller leaves ovate, acuminate, serrate, about 10 mm long and 6 mm wide, green above, purple tipped beneath, vestiture as larger leaves. Flowers at least paired, bracts not seen; pedicels about
9 mm long, dull brown pilose; sepals lanceolate, acuminate, 3–4 toothed, teeth linear, to 3 mm long, sepals green, about 9 mm long and 1.5 mm wide at middle, externally dull brown pilose; corollas tubular, slightly zygomorphic, yellow with lower parts of the lobes red (producing a red ring around the dissected part of the corolla), about 4.6 cm long, about 3 mm in diameter at base becoming about 7 mm in diameter in middle then 5.5 mm in diameter at throat, lobes slightly unequal, lobed portion 6 mm long, spreading, corolla externally dull brown pilose, filaments remotely pilose at base otherwise glabrous, yellow, anthers included, 1 mm long and 1.5 mm wide, style glabrous, yellow, stigma not seen, ovary pilose, disk gland bilobed, fruits not seen.

Holotype: Panama. Prov. Panama: Cerro Jefe summit, altitude 2900 feet, Dwyer et al. 7235, March 12, 1967 (MO).

Columnea omenta is not to be confused with C. pectinata Morton which has somewhat similar leaf coloration, but differently colored and shaped corollas, which place C. pectinata in sect. Collandra. Columnea omenta is most closely related to C. perpulchra but differs in a number of characters, the most easily seen being the possession of red hirsute stems, shorter sepals and a more dense vestiture in all parts.

16. **Columnea segregata** sp. nov. (Sect. Collandra)

A **Columnea florida** Morton differs from foliis brevioribus, sepalarum dentibus longioribus, et sepalorum pilis rubellis; a **Columnea serrata** (Kl. ex Oerst.) Hanstein differs from **Columnea tubiformis** pro parte majore flavis, et foliis inferioribus maculis rubris notatis.

Differing from **Columnea florida** Morton by the shorter leaves, longer sepal teeth, and reddish sepal hairs; differing from **Columnea serrata** (Kl. ex Oerst.) Hanstein notably by the tubular mainly yellow corolla and red blotched leaves.

Woody herbs, epiphytic, stems 4–5 mm in diameter, brown-purple villous. **Leaves** of a pair unequal, the larger lanceolate, abruptly acuminate, oblique at base, serrulate-crenulate, 11.3–13.6 cm long and about 3.5 cm wide at widest point, adaxially glabrous, abaxially sericeo-stribose, hairs 2–3-celled transparent adpressed, also 4–5-celled especially on veins, blades green above, red spotted or blotched to nearly concolorous beneath, petioles to 2 mm long, the smaller leaves lanceolate, acuminate, remotely serrate, 1.2–1.8 cm long and about 5 mm wide, green above and beneath, vestiture as larger leaves. **Flowers** solitary, bracteate, bracts 6–8 mm long, lanceolate, sericeo-stribose; pedicels about 2.3 cm long, transparent to reddish pilose; sepals pectinate, 6–7 toothed, teeth linear, to 6 mm long, sepals reddish, about 2 cm long and 2 mm wide excluding teeth at middle, externally reddish pilose; corollas tubular, slightly zygomorphic, yellow with reddish lobes, about 2 cm long when fully expanded, about 3 mm diameter at base, becoming about 5 mm in diameter at throat, lobes slightly unequal, lobed portion 2 mm long, spreading, corolla externally red pilose, filaments not seen, anthers included, style glandular papillose, stigma stomatomorphic, ovary pilose, disk gland not seen. **Fruit** about 7 mm in diameter (immature).


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