

***COLUMNEA CAUDATA* AND *COLUMNEA MEGAFOLIA*,  
TWO NEW SPECIES OF GESNERIACEAE**  
***Columnnea caudata* y *Columnnea megafolia*, dos especies nuevas de  
Gesneriaceae**

**MARISOL AMAYA MÁRQUEZ**

*Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado 7495, Bogotá D.C., Colombia. mamayam@unal.edu.co*

**LAURENCE E. SKOG**

*Department of Botany MRC-166, PO Box 37012, Smithsonian Institution, Washington, DC 20013-7012 U.S.A. SKOGL@si.edu*

**LARS PETER KVIST**

*Institute of Biological Sciences, University of Aarhus, Building 540, Ny Munkegade, DK-8000, Aarhus C., Denmark. larskvist@biology.au.dk*

**ABSTRACT**

Two new species of *Columnnea* belonging to section *Collandra* (Gesneriaceae) from the “cordillera Occidental” in the Colombian Andes are described and illustrated. *Columnnea caudata* is distributed along the Biogeographical Chocó in the Departments of Antioquia, Chocó, Risaralda, and Valle del Cauca, whereas *Columnnea megafolia* is restricted to Antioquia, and probably is an endemic species of the National Natural Park Las Orquídeas.

**Key words.** *Collandra*, *Columnnea*, Colombia, Flora of Colombia, Gesneriaceae, Biogeographical Chocó, Plant Taxonomy.

**RESUMEN**

Se describen e ilustran dos nuevas especies de *Columnnea* pertenecientes a la sección *Collandra* (Gesneriaceae) en la Cordillera Occidental en Colombia. *Columnnea caudata* se distribuye en el Chocó Biogeográfico Colombiano, en los departamentos de Antioquia, Chocó, Risaralda, y Valle del Cauca, mientras que *Columnnea megafolia* tiene una distribución restringida a los bosques montanos en Antioquia, siendo probablemente endémica del Parque Nacional Natural Las Orquídeas.

**Palabras clave.** *Collandra*, *Columnnea*, Colombia, Flora de Colombia, Gesneriaceae, Chocó biogeográfico, Taxonomía Vegetal.

**INTRODUCTION**

The taxonomic revision of section *Collandra* (Lem.) Benth. & Hook.f. (*Columnnea* L., Gesneriaceae) has revealed that our knowledge about this lineage of plants is far from complete. Several new species of *Columnnea*, most of them from Colombia, have been published in

the last ten years (e.g., Amaya-Márquez *et al.* 2004; Kriebel 2005; Amaya-Márquez 2010a, b; Amaya-Márquez & Clark 2011; Amaya-Márquez & Marín-Gómez 2012; Amaya-Márquez & Smith 2012; Clark & Clavijo 2012). The species of the genus *Columnnea* play an important role in maintaining biodiversity due to the specialized system

of pollination by hummingbirds (Morley 1971; Jones & Rich 1972; Stiles & Freeman 1993; Amaya-Márquez 1996; Kastinger & Weber 2000). Biotic specialization, (*e.g.*, the Neotropical interaction hummingbird-*Columnea*) is known to promote coexistence and speciation (Thompson 1994; Dyer *et al.* 2007; Schemske 2009) and therefore these ecological interactions may determine local and global biodiversity patterns (Schemske 2002, Schemske *et al.* 2009). Colombia is the country with the highest number of species of *Columnea* (Kvist & Skog 1993; Skog & Boggan 2007) as well as of hummingbird species (Schuchman 1999), which may be the result of selection driven by interactions between these two groups. These facts call for a great responsibility to preserve the biodiversity and the ecological interactions among species (Schemske 2002) and a precondition for this, is to document the species that exist and investigate the ecology including their coevolution with pollinators, dispersers, and other organisms; one limitation to go farther in building this type of knowledge is the lack of taxonomic tools available to identify species. As part of the effort to overcome taxonomic limitations in the knowledge of the genus *Columnea*, we report in this paper two new species of *Columnea* from the Biogeographical Chocó, one of the most biodiverse regions in Colombia and in the world (Myers *et al.* 2000; Rangel-Ch. & Rivera-Díaz 2004).

*Columnea caudata* and *C. megafolia* are assigned to section *Collandra* on the basis of having dorsiventral shoots typical for the species of the section, and by having a solitary bilobate or tridentate nectar gland. Additionally, these species have a great similarity to *C. ericae* Mansf. and *C. purpurata* Hanst. respectively, two well-known species belonging to section *Collandra*. *Columnea caudata* is unique among the species of section *Collandra* by having a long tubular corolla with a bilateral limb, with two lateral lobes and four appendages inside the corolla, as well as having the larger leaf at each

node on the stem present a long caudate apex. *C. megafolia* has large membranous leaves lacking red spots, but having conspicuous inflorescences crowded with several flowers and bracts. The corolla tube is sigmoid and the limb has a marked bilateral symmetry.

***Columnea caudata*** M. Amaya & L. P. Kvist sp. nov. Figure 1

TYPE: COLOMBIA: Valle del Cauca, trail uphill from Río Calima immediately across river from encampment Cuzumbu, 400-1000 m, 21 Feb. 1989, *Smith, J. F. et al. 1443* (Holotype: COL, Isotypes: MO, WIS, US).

*Columnea caudata* differs from *C. ericae* by the larger leaf of a pair having a long caudate apex and long narrow corollas with a constricted zygomorphic limb.

**Suffrutescent** woody climber. Stem subterete, 0.5-0.7 cm in diam., sericeous; internodes 1-2 cm long. **Leaves** opposite, strongly anisophyllous in a pair, papyraceous; larger leaf sessile; blade asymmetric, narrow oblanceolate to falcate, 8.5-23.5 x 1.3-3.5 cm, base truncate and slightly oblique, apex long caudate, margin serrate; adaxially green and densely sericeous, veins obscure, abaxially green and red-purple apically (ca. 1/5th of the leaf length), sometimes the margins are red-colored, densely sericeous (10- to 14-celled trichomes) and with setulose unicellular trichomes sparsely distributed, 13-17 veins on the larger side of the midrib, veining mixed craspedodromous; smaller leaf sessile, linear, 5-7 x 0.5 mm. **Inflorescence** fasciculate of 1-2 flowers in the larger leaf axil; 1-2 bracts, lanceolate 2.3 x 0.3 cm or reduced linear 4.0 x 0.5 mm, caduceous. **Flowers** pedicellate, pedicel 2.5-3.5 cm, pilose glandular (uniseriate 6- to 10-celled trichomes ending in a glandular head). **Calyx** green or pale yellow, lobes almost free, connate basally for about 1 mm, subequal, very narrowly elliptic, 2-2.8 x 0.1-0.3 cm, abaxially glandular (uniseriate 6- to 10-celled trichomes with a glandular head), adaxially glabrescent; margin

dentate with 3 subulate teeth per side. **Corolla** bright orange or yellow, tube cylindrical, dorsally slightly recurved, 4.3-5.5 cm long, 0.6-0.8 cm wide along the tube, 2.7-3.0 cm wide at the limb, slightly constricted basally 0.5-0.6 cm wide; base dorsally gibbous 0.3 x 0.4 cm; limb bilabiate, upper lip formed by the two dorsal lobes, lower lip formed by the other three; lobes unequal, two dorsal connate, erect, acuminate, 0.5 x 0.3 cm; two lateral spreading, acute, 1.2 x 0.3 cm; the ventral lobe slightly reflexed, acute, 1.0 x 0.3 cm; corolla outside pilose glandular (uniseriate 6- to 10-celled trichomes ending in a glandular head), with a tuft of hairs outside apically crowded in the lateral lobes, inside glabrous and with 4 appendages. **Androecium** of 4 stamens, filament 4.0-4.8 cm long, with short trichomes at the base of the filaments, basally connate for 1.0-1.2 cm of their length forming a staminal blade folded and open dorsally, anther rectangular 2.5 x 1.5 mm. **Gynoecium** with ovary conical, 0.5 x 0.3 cm, setulose, apically densely sericeous (uniseriate 3-to 6-celled trichomes); style 4.4-5.0 cm long, glabrous; stigma bilobate. **Nectary** of one bilobulate dorsal gland, 3 x 3 mm. **Fruit** a green, ovoid berry, 1.2-1.5 x 0.7-1 cm. **Seeds** brown, elliptic, obliquely striated, 1.5 x 0.5 mm.

**Etymology.** The species name makes reference to the long caudate apex of the larger leaf at each stem node.

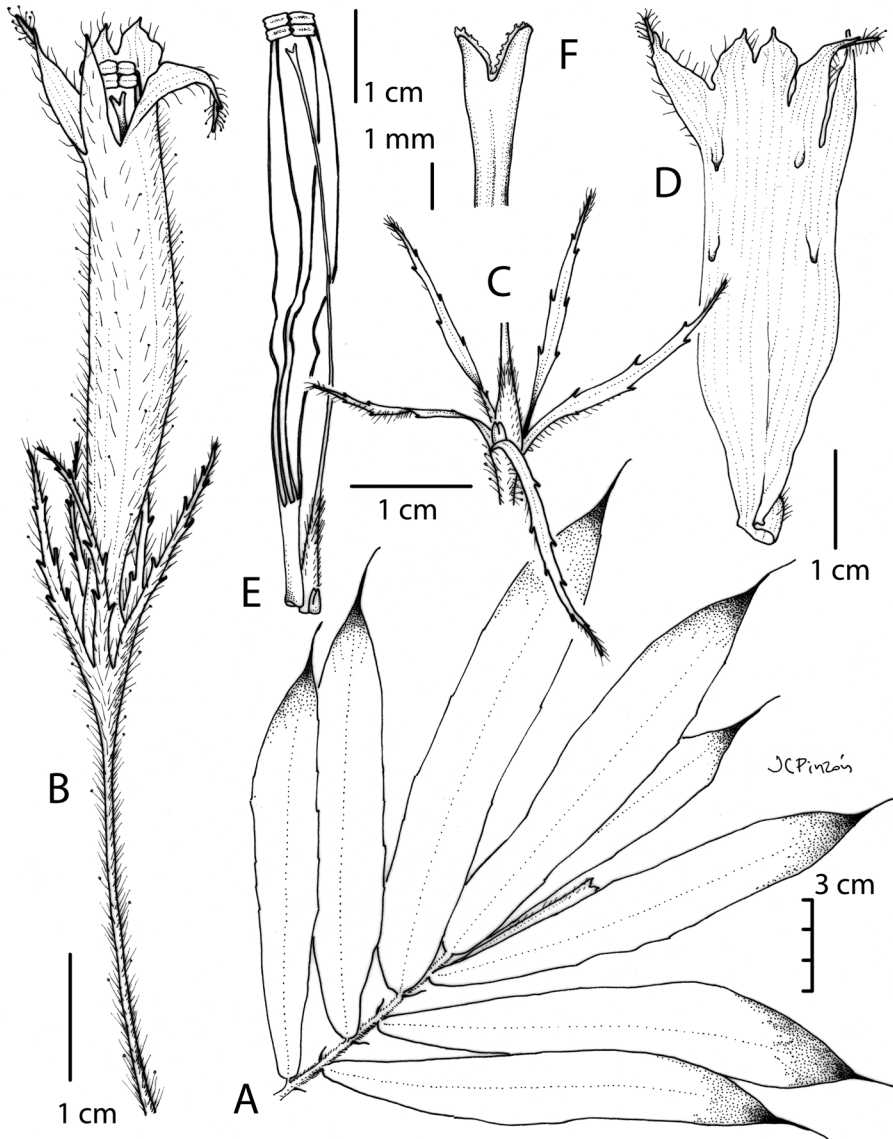
**Phenology:** Flowers have been recorded on the specimens collected in February, March and November. Fruits were recorded from two specimens collected in February and March.

**Distribution:** Colombia (Antioquia, Chocó, Risaralda, Valle del Cauca), 400-1900 m alt. This species is distributed along a large part of the Colombian biogeographical Chocó region. The species seems to be distributed through a corridor of wet and cloud forest on the mountains in the “Cordillera Occidental” of Colombia in the Departments of Antioquia, Chocó, Risaralda, and Valle del Cauca.

**Representative specimens:** COLOMBIA. **Antioquia:** Parque Nacional Natural Las

Orquídeas, trail from Venados to Carauta on the margin of the Río Venados, 1300-1350 m, Feb. 15, 1989, *Cogollo, A. et al. 4031* (JAUM). Area around community called La Madrona, 6-8 hrs walk from La Clara which is 3 hrs from El Sireno, which is 2 hrs on bus north of Urrao, 1050-1200 m, Nov. 10, 1982, *Folsom, J. P. 10582* (US). **Chocó:** Municipio San José del Palmar, river basin of river Torito, tributary of the river Hábita, 850-950 m, Mar. 16, 1980, *Forero, E. et al. 7398* (COL). Municipio of Nóvita, north slope of Cerro Torrá, western edge of the river Surama, trail to the Alto del Oso, 600-900 m, Feb. 22, 1977, *Forero, E. et al. 3128* (COL). **Risaralda:** Municipio of Mistrató, 12 Km NE from the municipality headwaters, 1800-1900m, Mar. 7, 1991, *Galeano, G. et al. 2575* (COL). On the road San Antonio de Chami and Mistrató, Quebrada Sutu, 1750 m, Apr. 27, 1992, *Fernández, A. et al. 10214* (COL).

**Distinctive features:** *Columnea caudata* is easily recognized by having a dorsiventral vegetative shoot, the pair of leaves at each node are strongly anisophyllous, the smaller leaf being an inconspicuous linear scale leaf of 0.5-0.7 x 0.1 cm is the smallest leaf known in any species of *Columnea* section *Collandra*. The apex of the larger leaf is long acuminate and 1.4-2.8 cm long giving to the plant a characteristic appearance making it easy to recognize the species. The bracts are reduced, lanceolate to linear, most of the time absent, suggesting that they are caducous. Unlike other species in section *Collandra* in which the flowers are covered and protected by the bracts and are kept very close to the vegetative shoot, in this species the reduced bracts and long pedicels allow the flowers to be exerted from the vegetative shoot. The corolla limb is bilabiate but narrow, which points out a specialization to restrict the nectar only to hummingbirds with long bills. It is interesting that a narrow bilabiate limb neither allows hummingbirds with short bills (*e.g. C. ericae*) nor bees to access the nectar. Besides, the flowers of *C. caudata* present trichomes at the edges of the lateral limbs, adding to



**Figure 1.** *Columnnea caudata* M. Amaya & L. P. Kvist

A. Habit, showing the marked anisophylly, the smaller leaf at each node looks like an inconspicuous scale, the long acuminate apex of the larger leaf gives the vegetative shoot a characteristic appearance. B. Flower showing pedicel, calyx and corolla outside pilose-glandular; the long pedicel and the reduced caducous bracts expose the flowers outside the foliage; the corolla limb bilabiate, the upper limb formed by the two connate dorsal lobes, the lower lip formed by the other three lobes, the two lateral lobes have outside and apically a tuft of trichomes increasing the bilateral symmetry of the limb. C. Calyx showing the lobes almost free, connate basally only by 1 mm of their length, margin dentate with three subulate teeth, outside pilose glandular, inside glabrescent. D. Corolla opened to show internal surface glabrous, four internal appendages located at two heights, and the corolla lobes. E. Androecium showing the connivent anthers and the staminal basal blade folded around the ovary. Pistil showing ovary conic apically densely sericeous, style glabrous, and stigma bilobate. Nectary glands outside the ovary F. Bilobate stigma. (Smith, J. F. et al. 1443).

the zygomorphic symmetry of the limb; the long and narrow corolla suggests pollination exclusively by a long-billed hummingbird, and the limb design might indicate a visual signal directed to a specific species of hummingbird. This conjecture might be found to be true if the species is a plentiful nectar producer and has other ornithophilous plants competing for the same bird pollinator in the same area. A reliable nectar producing plant might increase its fitness (in, for example, pollinator visits, temporal flower fidelity, fertilization, and outcrossing) by being distinctive from other congeners which may be less competitive. Another morphological novelty reported in *C. caudata* is the four internal appendages, of unknown function, located inside the corolla at two heights (Fig. 1). All of these floral traits broaden the diversity of floral architectures known for the genus *Columnea* and pose the question about their functional value.

***Columnea megafolia*** L. E. Skog & M. Amaya, sp. nov. Figure 2

TYPE: COLOMBIA: Antioquia, municipio Urrao: Vereda Calles, Alto de Palmitas 1 km from the Inderena's cabin at Calles, 76°19' W, 6°32' N, 1300-1400 m, *Pipoly, J. et al.* 17497 (Holotype: US, Isotype: MO).

*Columnea megafolia* differs from *C. purpurata* by having larger leaves and flowers, corolla red or apically red and yellow, with a marked zygomorphic limb.

**Suffrutescent** terrestrial, 1 m tall or woody climber  $\geq 1.5$  m. Stem subterete, 1 cm diam., indument lanate (trichomes 10-celled), internodes 1-7 cm long. **Leaves** opposite, strongly anisophyllous in a pair, membranous, large leaf petiolate, petioles 0.2-1.8 cm, villous (9- to 11-celled trichomes); blade asymmetrical, oblanceolate to narrowly oblong, 31-51 x 10-16 cm, base oblique, shorter side cuneate, longer side rounded, apex acuminate, margin serrate; adaxially green, sparsely strigose (trichomes 5- to 12-celled trichomes); abaxially pale green,

sparsely strigose (5- to 12-celled trichomes), 13-16 secondary veins, the tertiary veins forming a reticulate pattern; smaller leaf in a pair sessile, blade notably asymmetric, lanceolate, 2-3 x 0.4-1.2 cm, base oblique, shorter side obtuse, longer side auriculate, apex acuminate, margin dentate, adaxially green, sparsely strigose (9- to 12-celled trichomes), abaxially pale green, sparsely strigose (10- to 12-celled trichomes).

**Inflorescence** fasciculate, of 4-5 flowers in the axil of larger leaf; bracts 8-12, lanceolate, 1.8-5 x 0.3-1.1 cm, abaxially red, villous (8- to 12-celled trichomes), adaxially glabrous, margin dentate.

**Flower** shortly pedicellate, pedicels 0.1-0.8 cm long, villous, glandular near the calyx. **Calyx** red, sepals free, subequal, lanceolate, 1.5-2 x 0.1-0.4 cm, abaxially villous (8- to 12-celled trichomes), adaxially glabrous, margin dentate (sometimes with three subulate teeth per side).

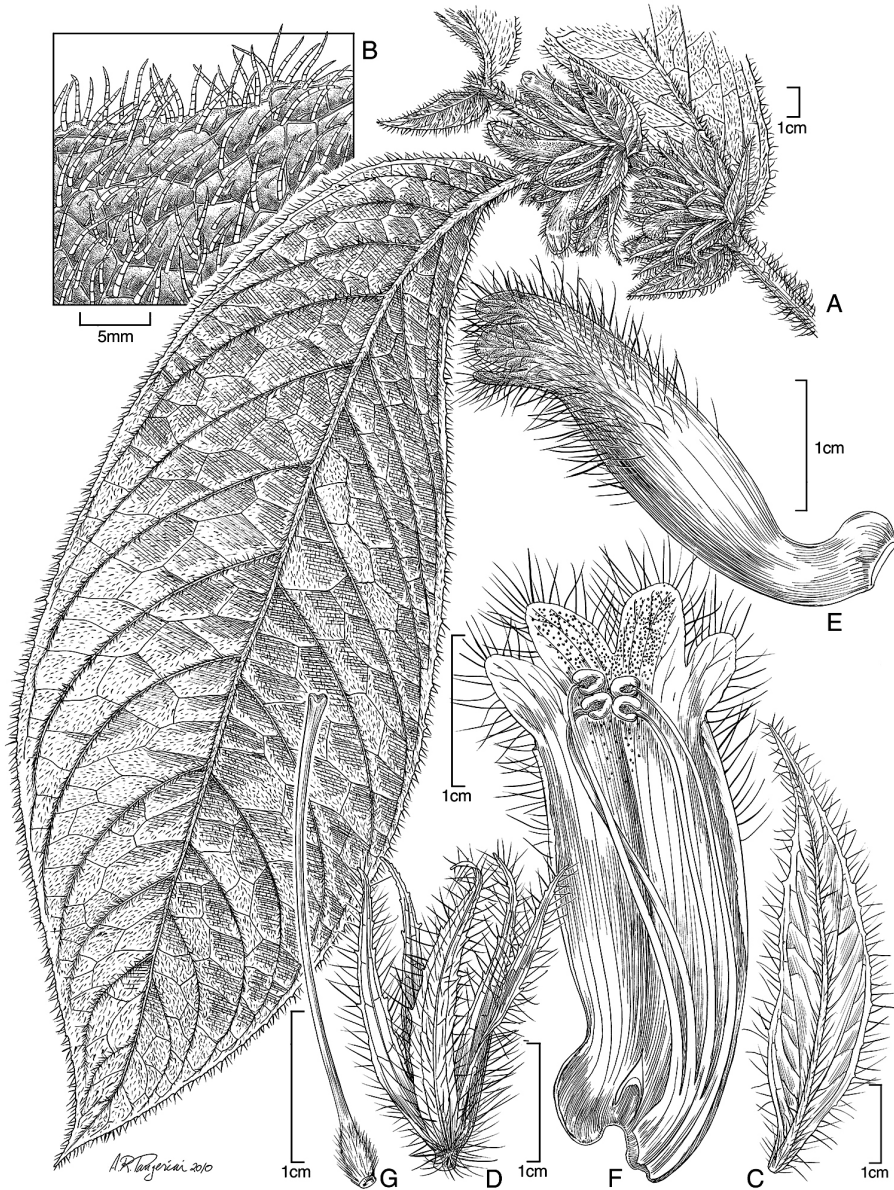
**Corolla** red, or red and apically yellow, corolla tube sigmoid, 3.5-3.8 cm long, 0.7-0.8 cm wide at the middle, constricted at base 0.4-0.5 cm, base dorsally gibbous, gibbosity 0.3-0.5 x 0.5-0.7 cm; zygomorphic, curved downward, lobes subequal, the two dorsal obtuse, slightly hooded, imbricate and curved down, 3 x 2 mm; the two lateral obtuse, 3 x 2 mm; and the ventral rounded 2 x 2 mm; corolla outside villous more dense apically (trichomes 10- to 12-celled), inside glabrous, except on the two dorsal lobes that are densely glandular (with unicellular trichomes).

**Androecium** of 4 stamens, filament 3-3.4 cm long, glabrous basally connate by 0.5-0.7 cm of their length and forming a staminal blade; anther rectangular 2.5 x 1.5 mm, connective rectangular. **Gynoeceum** with ovary conical, 0.4-0.5 x 0.1-0.2 cm, villous (trichomes 10-celled) and basally setulose (unicellular trichomes); style 3.3 cm long, basally glandular (2-celled trichomes); stigma bilobate. **Nectary** of one tridentate dorsal gland, 1.5 x 3 mm. **Fruit** and **Seeds** not seen.

**Etymology:** The species name refers to the large size of the larger leaf at each node.

**Phenology:** Flowers have been recorded from specimens collected in February, March, May, June, July and December.





**Figure 2.** *Columnnea megafolia* L. E. Skog & M. Amaya

A. Habit showing the vegetative shoot anisophyllous at each node, and the conspicuous inflorescences, with an apparent verticillate distribution, formed by several bracts of different sizes and flowers. B. Detail of the abaxial surface of the larger leaf showing the reticulate venation formed by the tertiary veins, and the strigose indumenta. C. Bract, adaxially glabrescent, abaxially densely villous. D. Short pedicel, and calyx with free sepals; the sepals outside villous, inside glabrescent. E. Sigmoid corolla, the external indumenta is localized apically; the two curvatures with contrary concavities are shown; the lobes are curved down closing the corolla entrance. F. Corolla opened to show the corolla inside glabrous, except at the limb level with unicellular glandular trichomes on the two dorsal lobes, and the androecium with the basal staminal blade; this dissection does not show the ventral lobe. G. Pistil showing the conic ovary with villous indumenta; the style has basally glandular two-celled trichomes that are not observed at the drawing's scale; the stigma is bilobate. (*Pipoly, J. et al. 17497*).

**Distribution:** Colombia (Antioquia) at 1240-1460 m alt. in Andean Premontane Wet Forest on the western slopes of the “Cordillera Occidental”. This species seems to be endemic to the National Natural Park Las Orquídeas.

**Representative specimens:** COLOMBIA.

**Antioquia:** Municipio de Urrao Parque Nacional Natural Las Orquídeas, sector Calles, 1240 m, 29 May 1988, *Cogollo, A. & J. G. Ramírez 3037* (COL, JAUM); margin of river Calles, 1 km ahead from the confluence of the rivers Polo and Calles, 76°19' W, 6°32' N: 1460 m, Feb. 11 1989, *Cogollo, A. et al. 3896* (JAUM); 1380 m, Mar. 26 1988, *Cogollo, A. et al. 2622* (COL, JAUM); 1350-1450 m, Jul. 6 1991, *Cogollo, A. et al. 5009* (MO); 76°19' W, 6°31' N: 1300-1320 m, Mar. 27 1991, *Ramírez, J. & E. Muñoz 4045* (MO); river Calles, 77°4'51" W, 4°35'56" N, 1400-1500 m, May 3 1995, *Fonnegra, R. et al. 5536* (HUA); 1400 m, Jun. 15 1981, *Albert de Escobar, L. 1714* (HUA).

**Distinctive features:** *Columnea megafolia* is close to *C. purpurata*, and both species have conspicuous orange bracts that usually dry purplish, both species do not have red spots on the larger leaves, which is unusual for species of section *Collandra*. Also both species have a tridentate dorsal nectary gland. However *C. megafolia* can be recognized by having robust shoots and villous indumenta on the surface of almost all organs. The larger leaf at each node is very large, 31-51 x 10-16 cm (vs. 11-30 x 3-12 cm in *C. purpurata*), usually with 15 veins on the larger side of the blade (vs. 9-12 in *C. purpurata*); short petioles give the appearance of the leaves being sessile; the margin is serrate with glandular teeth, whose function might be to release excess water. The inflorescences are very conspicuous both in color which is red, and size; although the inflorescence buds are located in the axils of the larger leaf of each node, their size makes their distribution around the node appear verticillate; the bracts are numerous and of different sizes, having the same red color of the calyx and corolla, increasing the visual signal for pollinators. The corolla tube is sigmoid presenting two marked curvatures along the tube, *i.e.*, one concave up,

basally just before the gibbous, the other concave down, apically before the corolla limb; the corolla limb is curved downward closing the corolla entrance (vs. an open corolla in *C. purpurata*). This trait might be a trait to deter the entrance of certain floriverous insect - larvae of an unknown insect were found inside the corolla of several dissected flowers. The corolla limb is clearly zygomorphic (vs. an actinomorphic limb in *C. purpurata*), however the limb is not bilabiate as all the lobes are recurved down to close the corolla entrance, instead of forming upper and lower lips (Fig. 2). As mentioned before, *C. megafolia* has been found only in Colombia (Antioquia) at 1200-1460 m, while *C. purpurata* has a Neotropical distribution and has been collected in Mexico, Nicaragua, Costa Rica, Panama, Venezuela, and Colombia at 80-1750 m.

## ACKNOWLEDGMENTS

The authors thank National University of Colombia, University of Aarhus, and Smithsonian Institution for the opportunity to do research, Juan Carlos Pinzón and Alice Tangerini for the elaboration of the drawings, and to the directors of the herbaria of COL, HUA, JAUM, MO, and US for their support and collaboration to consult the collections deposited in those herbaria. To Jim Smith and another anonymous reviewer whose valuable comments helped to improve the manuscript.

## LITERATURE CITED

- AMAYA-MÁRQUEZ, M. 1996. Sistemática y polinización del género *Columnea* (Gesneriaceae) en la Reserva Natural la Planada (Nariño). Tesis de maestría, Universidad Nacional de Colombia, Bogotá, Colombia.
- AMAYA-MÁRQUEZ, M. 2010a. Una nueva especie de *Columnea* (Gesneriaceae) de la cordillera Oriental en los Andes Colombianos. *Caldasia* 32 (1): 113-116.
- AMAYA-MÁRQUEZ, M. 2010b. Novedades Taxonómicas en el género *Columnea* (Gesneriaceae). *Rev. Acad. Colomb. Ci. Ex. Fis. Nat.* 34 (132): 301-307.

- AMAYA-MÁRQUEZ, M. & J. L. CLARK. 2011. *Columnnea bivalvis* (Gesneriaceae), a new species from the eastern slopes of the Ecuadorian Andes. *J. Bot. Res. Inst. Texas* 5 (1):75-79.
- AMAYA-MÁRQUEZ, M. & O.H. MARÍN-GÓMEZ. 2012. *Columnnea rangelii* (Gesneriaceae), a new species from the Serranía de los Paraguas in the Colombian Andes. *Caldasia* 34 (1): 69-74.
- AMAYA-MÁRQUEZ, M. & J.F. SMITH. 2012. A rare new species of *Columnnea* (Gesneriaceae) from "Cordillera Occidental" in the Colombian Andes. *Rev. Acad. Colomb. Ci. Ex. Fis. Nat.* 23 (139): 13-16.
- AMAYA-M, M, L.E. SKOG & L.P. KVIST. 2004. Novae Gesneriaceae Neotropiarium XIII: Four New Species of *Columnnea* (Gesneriaceae) Section *Collandra* from Colombia. *Edinburgh J. Bot.* 60: 415-424.
- CLARK, J.L. & L. CLAVIJO. 2012. *Columnnea antennifera*, a new species of Gesneriaceae from the Cordillera Central of the Colombian Andes. *J. Bot. Res. Inst. Texas* 6(2):385-389.
- DYER, L.A., M.S. SINGER, J.T. LILL, J.O. STIREMAN, G.L. GENTRY, R.J. MARQUIS, R.E. RICKLEFS, H.F. GREENEY, D.L. WAGNER, H.C. MORAIS, I.R. DINIZ, T.A. KURSAR & P.D. COLEY. 2007. Host specificity of Lepidoptera in tropical and temperate forest. *Nature* 448: 696-699.
- JONES, C.E. & P.V. RICH 1972. Ornithophily and extrafloral color patterns in *Columnnea florida* (Morton) Morton (Gesneriaceae). *Bull. S. Calif. Acad. Sci.* 7: 220-243.
- KASTINGER, C. & A. WEBER. 2000. Attraction of hummingbirds by extrafloral cues in some Costa Rican Species of *Columnnea* (Gesneriaceae) *Linzer Biol. Beitr.* 32(2): 652-653.
- KRIEBEL, R. 2005. A new species of *Columnnea* and range extension in the Gesneriaceae from Costa Rica. *Brittonia* 57(1): 39-42.
- KVIST, L.P. & L.E. SKOG. 1993. The genus *Columnnea* (Gesneriaceae) in Ecuador. *Allertonia* 6: 327-400.
- MYERS, N., R.A. MITTERMEIER, C.G. MITTERMEIER, G.A.B. DE FONSECA & J. KENT. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.
- MORLEY, B.D. 1971. A hybrid swarm between two hummingbird-pollinated species of *Columnnea* (Gesneriaceae) in Jamaica. *J. Linn. Soc. Bot.* 64: 81-96.
- RANGEL-CH., J.O & O. RIVERA-DÍAZ. 2004. Diversidad y riqueza de espermatófitos en el Chocó Biogeográfico: 83-99. In: Rangel-Ch., J.O. (ed.). *Colombia Diversidad Biótica IV. El Chocó Biogeográfico/Costa Pacífica*. Universidad Nacional de Colombia. Bogotá.
- SCHEMSKE, D.W. 2002. Ecological and evolutionary perspectives on the origins of tropical diversity. pp. 163-173. In: Chazdon, R.I. & T.C. Whitmore (eds.). *Foundations of Tropical Forest Biology*. Univ. Chicago Press. Chicago, Illinois, USA.
- SCHEMSKE, D.W. 2009. Biotic interactions and speciation in the tropics: 219-239. In: Butlin, R.K., J.R. Bridle & D. Schluter (eds.). *Speciation and patterns of diversity*. Cambridge University Press, Cambridge.
- SCHEMSKE, D.W., G.G. MITTELBAACH, H.V. CORNELL, J.M. SOBEL & J.M. ROY. 2009. Is there a latitudinal gradient in the importance of biotic interactions? *Ann. Rev. Ecol. Evol. Syst.* 40: 245-269.
- SCHUCHMAN, K.L. 1999. Trochilidae. *Handbook of the Birds of the World. Volume 5*. Lynx Editions.
- SKOG, L.E. & J.K. BOGGAN. 2007. World Checklist of Gesneriaceae. Washington, DC: Dept. of Botany, Smithsonian Institution Washington, DC. <http://botany.si.edu/Gesneriaceae/Checklist>
- STILES, F.G. & C.E. FREEMAN. 1993. Patterns in floral nectar characteristics of some bird-visited plant species from Costa Rica. *Biotropica* 25:191-205
- THOMPSON, J.N. 1994. *The Coevolutionary Process*. Univ. Chicago Press, Chicago, Illinois, USA.

Recibido: 16/05/2013

Aceptado: 06/08/2013