

An addition to the diversity of dendrobatid frogs in Venezuela: description of three new collared frogs (Anura: Dendrobatidae: *Mannophryne*)

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Abstract

An addition to the diversity of dendrobatid frogs in Venezuela: description of three new collared frogs (Anura: Dendrobatidae: *Mannophryne*). Three new species of collared frogs of the genus *Mannophryne* are described from Venezuela. Two are newly discovered taxa from the Venezuelan Andes, whereas the third species, previously confused with *M. trinitatis*, is from the Caracas area in the Cordillera de la Costa. The call of the three new species and that of *Mannophryne collaris* are described. Taxonomic, zoogeographic, and conservation issues are discussed.

Keywords: Anura, Dendrobatidae, *Mannophryne*, new species, Colombia, conservation.

Resumen

Adición a la diversidad de dendrobátidos en Venezuela: descripción de tres nuevas ranas acollaradas (Anura: Dendrobatidae: *Mannophryne*). Describimos tres nuevas especies de sapitos acollarados del género *Mannophryne* de Venezuela. Dos corresponden con nuevos descubrimientos y provienen de los Andes venezolanos, mientras que la otra especie es la que desde antiguo se venía confundiendo con *M. trinitatis* del área de Caracas en la Cordillera de la Costa. Se describen los cantos de las tres nuevas especies y el de *Mannophryne collaris*. Se discuten temas de taxonomía, zoogeografía, y conservación relacionadas con el género.

Palabras clave: Anura, Dendrobatidae, *Mannophryne*, especies nuevas, Colombia, conservación.

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Resumo

Adição à diversidade de dendrobatídeos da Venezuela: descrição de três novas espécies de *Mannophryne* (Anura: Dendrobatidae). Descrevemos aqui três novas espécies de anuros do gênero *Mannophryne* da Venezuela. Duas delas correspondem a novas descobertas e são provenientes dos Andes venezuelanos, enquanto a outra vinha sendo confundida há muito tempo com *M. trinitatis* da região de Caracas, na Cordilheira da Costa. Descrevemos a vocalização das três novas espécies e também a de *Mannophryne collaris*. Discutimos temas da taxonomia, da zoogeografia e da conservação relacionados ao gênero.

Palavras-chave: Anura, Dendrobatidae, *Mannophryne*, espécies novas, Colômbia, conservação.

Introduction

Mannophryne La Marca, 1992 is a nearly endemic dendrobatid genus from Venezuela. It has been somewhat problematic for dendrobatid systematics because the original description is cursory (La Marca 1992, Kaiser *et al.* 1994, Coloma 1995, Grant *et al.* 1997, Barrio-Amorós 2001). Recent molecular data supported its monophyly and provided evidence of cryptic diversity within this genus (Vences *et al.* 2003, Grant *et al.* 2006, Manzanilla *et al.* 2009). La Marca (1992, 1994) described three apparent synapomorphies for the genus, (1) a black collar in both sexes, (2) a yellow throat mostly on females, and (3) social behavior that includes female combat displays. Furthermore Grant *et al.* (2006) noted another putative synapomorphy, an evenly stippled abdomen. Grant *et al.* (2006) included *Mannophryne* in their family Aromobatidae, nested closely with *Aromobates*. Santos *et al.* (2009) noted that there is no evidence for the recognition of Aromobatidae, and returned to a comprehensive Dendrobatidae that includes Aromobatinae as a subfamily.

Recent expeditions to several parts of Venezuela revealed an extraordinary diversity of species in different genera of dendrobatids (*Allobates*, *Aromobates*, and *Mannophryne*). *Mannophryne* currently includes 16 species, 14 of which occur in Venezuela (Barrio-Amorós 2009, La Marca 2009). Only two species occur out of Venezuela—*M. trinitatis* (endemic on Trinidad; Barrio-Amorós *et al.* 2006) and *M. olmonae* (endemic on Tobago).

In Venezuela, collared frogs (sensu Barrio-Amorós 2010) are known from the Cordillera de Mérida in the Andes and the Coastal Range; they are most diverse in the Coastal Range (Manzanilla *et al.* 2009).

The first *Mannophryne* to be described was *M. trinitatis* from Trinidad (Garman 1887). Subsequently, Boettger (1896) named *M. herminae* from the port town of Puerto Cabello in Caribbean Venezuela. Until recently, all collared dendrobatids from the Coastal Range have been assigned to one of these two species (La Marca 1994). Test (1956) described *M. neblina* from Rancho Grande and Donoso-Barros (1964) *M. riveroi* from Península de Paria. *Mannophryne oblitterata* was named from Guatopo (Rivero 1984); more recently, two species were described from Estado Falcón—*M. caquetio* (Mijares-Urrutia and Arends 1999a) and *M. lamarcai* (Mijares-Urrutia and Arends 1999b). Manzanilla *et al.* (2005) described *M. leonardoi* from the northeastern area of Venezuela and Manzanilla *et al.* (2007) named *M. venezuelensis* from Península de Paria. For many years, only one species of collared frog was known from the Andes—*M. collaris* described by Boulenger (1912) from Mérida. Recently, a diverse fauna of these frogs has been revealed. La Marca (1989) described *M. yustizi* from the Yacambú area; Yústiz (1991) and La Marca (1994) then described *M. larandina* and *M. cordilleriana*, respectively, and most recently, Vargas and La Marca (2007) and La Marca (2009) named *M. trujillensis* and *M. speeri*, respectively. See Appendix I for color photographs of most of the Venezuelan species.

Herein we describe three new species from Venezuela—two from the Andes, and another from the Coastal Range in the region of Caracas; the latter species corresponds to a taxon that has been confused for many years with *M. trinitatis* from this region.

Materials and Methods

Specimens examined are housed in the following collections: Colección de Vertebrados, Universidad de los Andes, Mérida (CVULA); Museo de la Estación Biológica de Rancho Grande, Maracay (EBRG); Colección de Herpetología del Museo de Biología de la Universidad Central de Venezuela, Caracas (MBUCV); Museo de Historia Natural La Salle, Caracas (MHNLS); and University of Michigan, Museum of Zoology, Ann Arbor, Michigan, U.S.A. (UMMZ).

The species diagnoses and descriptions follow those of Barrio-Amorós and Santos (2009). We apply the web formula proposed by Myers and Duellman (1982). Comparative data were taken from Test (1956), Dixon and Rivero-Blanco (1985), Rivero (1984), La Marca (1994, 1995), Manzanilla *et al.* (2005, 2007), and Mijares-Urrutia and Arends (1999a, b). We include data that we recorded from direct examination of representatives of the following species (detailed in Appendix II): *Mannophryne collaris*, *M. cordilleriana*, *M. herminae*, *M. leonardo*, *M. oblitterata*, *M. neblina*, *M. riveroi*, *M. speeri*, *M. trinitatis*, *M. venezuelensis*, and *M. yustizi*. Sex determination was based on the presence of mature testes or oviducts, presence of vocal slits, sexual color dimorphism in adult specimens, and direct observation of calling males. Measurements of adult frogs were taken to the nearest 0.01 mm using digital calipers. Measurements are defined and abbreviated as follow: SVL—straight length from tip of snout to vent; SL—shank length from outer edge of flexed knee to heel; FL—length of the (left if not damaged) foot from the tip of the Toe IV to the

inferior edge of the inner metatarsal tubercle; HeL—head length from tip of snout to the posterior border of skull (posterior edge of prootic); HW—head width between angle of jaws; InD—internarial distance, taken between centers of nares; IOD—interorbital distance, measured from shortest distance between the medial edges of the orbits across the skull; EN—distance of anterior edge of eye to posterior edge of naris measured on the same side of the head; ED—horizontal eye diameter; TD—horizontal tympanum diameter estimated of a circular tympanum; ETS—distance between the anterior edge of the eye to the tip of snout; FD—disc width of Finger III; T4D—disc width of Toe IV; 1FiL—length of Finger I from inner edge of thenar tubercle to tip of disc; 2FiL—length of Finger II from the junction of Fingers I and III to the tip of finger disc. F refers to finger; T refers to toe. We use the traditional taxonomic terminology in numbering the digits (as Fingers I, II, III, and IV) to be more consistent with previous and generalized descriptions. However, as Alberch and Gale (1985) pointed out, Digit I was lost in anurans, and therefore the correct numbering should be FII, III, IV and V.

Results

Mannophryne was diagnosed by the presence of a black collar and yellow throat by La Marca (1992), and by male abdomen being evenly stippled (Grant *et al.* 2006). Other diagnostic characters include: presence of a pale, oblique lateral stripe; absence of a pale ventrolateral stripe; Finger III not swollen in males; and Finger I shorter than II.

Mannophryne orellana sp. nov.

(Figures 1, 2)

Spanish name: Ranita acollarada de Orellana

English name: Orellana's Collared Frog

Holotype.—CVULA 7165, an adult male from the Pregonero–La Trampa Road, Estado Táchira, Venezuela (08°01' N, 71°43' W), elevation

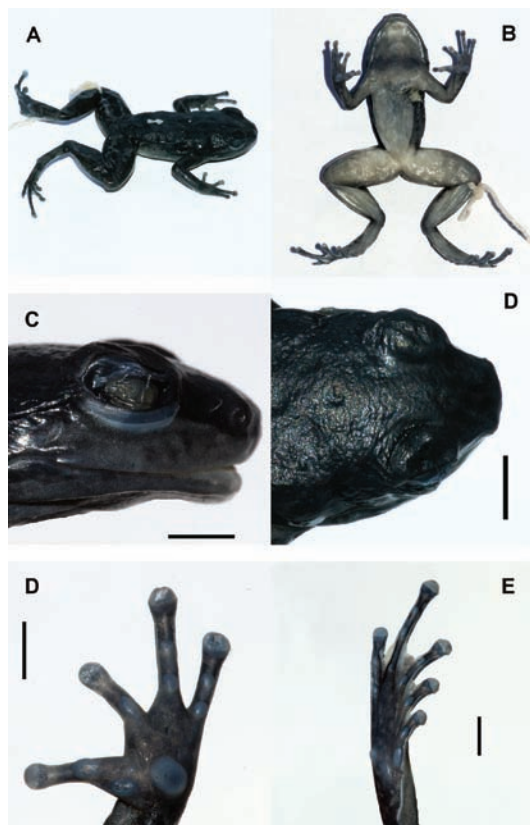


Figure 1. Holotype of *Mannophryne orellana* sp. nov. Dorsolateral (A), ventral (B), and lateral (C) views of the head. (D) Dorsal view of the head. (E) Ventral view of left hand. (F) Ventral view of right foot. Scale bars = 2 mm.



Figure 2. *Mannophryne orellana* sp. nov. in life: (A, B) The holotype, CVULA 7165. (C, D) The paratype, CVULA 7166. (E, F) A referred specimen, CVULA 7232.

1192 m, collected by César L. Barrio-Amorós and Juan Carlos Santos on 08 June 2007.

Paratopotypes.—Six adult males, CVULA 7159–64, and an adult female, CVULA 7166, with the same data as the holotype.

Referred specimens.—CVULA 7231–35, from Río Negro, Estado Táchira, Venezuela (73°4.7' N, 72°10.7' W), elevation 482 m, collected by César L. Barrio-Amorós and Juan Carlos Santos on 10 June 2007.

Definition.—(1) Dorsal skin smooth to shagreen, with or without granules on posterior trunk and hind limbs. (2) Paired dorsal scutes

present on digits, barely distinct. (3) Distinct distal tubercle on Finger IV. (4) Length of Finger IV reaching or extending beyond distal subarticular tubercle on Finger III. (5) Finger I equal to, or slightly longer than, Finger II. (6) Digital discs present. (7) Finger discs moderately expanded. (8) Narrow finger fringes present. (9) Low metacarpal ridge present. (10) Finger III not swollen in adult males. (11) Carpal pad absent. (12) Excrescences on thumb absent in males. (13) Small thenar tubercle present. (14) Males lacking black arm gland. (15) Tarsal keel straight, flaplike as a continuation of fringe on external side of Toe I to mid-tarsus, slightly

curved at end. (16) Toe discs moderately expanded. (17) Toe webbing fully developed, formula of the holotype $\text{II}-2\text{III}-3\text{III}2-3\frac{1}{2}\text{IV}3-2\text{V}$. (18) Metatarsal fold weakly developed. (19) Dorsal coloration black in males, brown in females; hind limbs barred; dorsolateral stripes absent; ventrolateral stripe absent; oblique lateral stripe partial, solid to almost solid, narrow to wide, to the mid-level of body to posterior arm. (20) Gular chest markings absent. (21) Dermal collar present, solid and wide in males, slightly narrower in females. (22) Male throat coloration evenly stippled gray; female throat coloration light gray in preservative, posterior half yellow in life, stippled anteriorly with dark brown melanophores. (23) Male abdomen color pattern evenly stippled gray; light gray in living males in reproductive condition. (24) Female abdomen nearly devoid of melanophores; color white in living females. (25) Iris light orange with golden to orange pupil ring. (26) Large intestine unpigmented. (27) Testis white, unpigmented. (28) Median lingual process absent on tongue. (29) Tympanum inconspicuous and tympanic annulus indistinct. (30) Vocal sac indistinct. (31) Teeth present on maxillary arcade. (32) Size moderate, males ($n = 7$) 25.4–27.3 mm, mean = 26.5 ± 0.7 ; females ($n = 4$) 29.5–32.9 mm, mean = 31.0 ± 1.6 mm.

Species comparisons.—We compare *Mannophryne orellana* (characteristics noted in parentheses) with other species of the Andean Clade of Manzanilla *et al.* (2009); particular emphasis is placed on comparison with *M. cordilleriana*, of which the new species is vicariant (unpubl. data).

Mannophryne collaris resembles *M. orellana*; there are only subtle morphological differences. In *M. collaris*, the snout is dorsally subovoid (nearly truncated). The canthus rostralis is not well defined (straight, angular) and the loreal region is flat (slightly concave). The round (oval) distal subarticular tubercles on Fingers I and II are smaller than the thenar tubercle (equal). *Mannophryne collaris* lacks metacarpal and

metatarsal ridges (present) and paracloacal marks (present).

Mannophryne cordilleriana differs from *M. orellana* in having less extensive webbing: $\text{II}\frac{1}{2}-2+\text{III}2\frac{1}{3}-3+\text{III}2\frac{1}{2}-3\frac{3}{4}\text{IV}3\frac{3}{4}-2\text{V}$ ($\text{II}-2\text{III}-3\text{III}2-3\frac{1}{2}\text{IV}3-2\text{V}$). The disc on Finger III is $1.7\times$ wider than distal end of adjacent phalanx (1.4). There is a short, oblique lateral stripe that usually is composed of spots (solid color). The distal subarticular tubercles on Fingers I and II are smaller than thenar tubercle (equal). Paracloacal marks are absent (present; contra La Marca 1994).

The disc on Finger III in *Mannophryne yustizi* is $1.8\times$ wider than distal end of adjacent phalanx (1.4) and the disc on Toe IV disc is twice as wide as the distal end of adjacent phalanx (1.6). Toe webbing in *M. yustizi* is less extensive: $\text{II}\frac{1}{2}-2\frac{1}{2}\text{III}2-3+\text{III}2+4\text{IV}4-2\frac{1}{2}\text{V}$ ($\text{II}-2\text{III}-3\text{III}2-3\frac{1}{2}\text{IV}3-2\text{V}$), and the collar is spotted (solid). *Mannophryne larandina* probably is a synonym of *M. yustizi*; the same characters distinguish this species from *M. orellana*.

Mannophryne speeri has short, pale dorsolateral bands (absent) and less toe webbing: $\text{II}^+-2+\text{III}2-3+\text{III}2^+-4\text{IV}4^+-2\frac{1}{2}\text{V}$ ($\text{II}-2\text{III}-3\text{III}2-3\frac{1}{2}\text{IV}3-2\text{V}$); the collar is spotted (solid). *Mannophryne caquetio* is a smaller species; males reach 22.4 mm (27.3 mm) and females 26.3 mm (32.9). There is much less toe webbing; although the webbing formula is unavailable, the foot is illustrated in Mijares-Urrutia and Arends (1999a:fig. 1). The disc of Finger III is $2.2\times$ as wide as the distal end of the adjacent phalanx (1.4) and that of Toe IV is $2.2\times$ as wide as the distal end of the adjacent phalanx (1.6).

Mannophryne lamarcai is a smaller species; males reach 24.6 mm (27.3) and females 28.8 mm (32.9). The disc of Finger III is $2.3\times$ as wide as the distal end of the adjacent phalanx (1.4) and that of Toe IV is $2.4\times$ as wide as the distal end of adjacent phalanx (1.6). There is a short oblique lateral stripe (long) and a dorsolateral dark stripe (absent).

Mannophryne herminae is small: the average snout–vent length of males is 21.4 mm (La

Marca 1994; 26.5) and that of females is 25.2 mm (31 mm). There is a spotted collar (solid). The toe webbing formula is $\text{I1-2II1}\frac{1}{3}\text{-3III2}\frac{1}{2}\text{-4IV4}\text{-2}\frac{2}{3}\text{V}$ ($\text{I1-2II1-3III2-3}\frac{1}{2}\text{IV3-2V}$). The skin on throat, chest, and venter is shagreen (smooth). Pale paracloacal bands are present (absent), and a shorter, not flap like tarsal keel (longer and flaplike).

Description of the holotype.—Adult male, 27.0 mm SVL. Body slender, round in cross section. Dorsal skin, including dorsal surfaces of hind limbs, shagreen in life and in preservative, lacking tubercles (Figure 1A); ventral skin smooth (Figure 1B). Head slightly wider than long, head length 35.1% SVL; greatest head width between angles of jaws 35.9% SVL. Snout rounded in lateral profile (Figure 1C), nearly truncate in dorsal profile (Figure 1D). Nares situated lateral to the tip of snout; nares barely visible when head viewed from anterior and ventral aspects, not visible in dorsal view. Canthus rostralis straight, angular; loreal region slightly concave. Interorbital distance slightly greater than width of upper eyelid; snout longer than eye diameter. Eye diameter 31.5% HL. Tympanum small, TD 33.3% ED, quite indistinct, without elevated margin, two thirds of the tympanum concealed posterodorsally by straight, distinct supratympanic bulge formed by superficial slip of *m. depressor mandibulae*; tympanum located near eye, and low, with ventral margin narrowly separated from angle of jaw. Teeth present on maxillary arcade. Vocal slits strongly curved, located under the tongue, laterally, and with posterior end of each lying close to mandible. Tongue triangular, half-free posteriorly.

Hand (Figure 1E) moderate in size (27.0% SVL). Relative lengths of adpressed fingers: $\text{III} > \text{IV} > \text{I} > \text{II}$; finger discs slightly expanded, round; F-III disc 1.4× as wide as distal end of adjacent phalanx. Base of palm with large, rounded palmar tubercle; small (~20% of palmar tubercle), oval thenar tubercle on base of FI, same size as F-I subarticular tubercle; each of FI and FII with one or two subarticular tubercles—

one large, oval tubercle on both FI and FII, and two smaller, round tubercles on each of FIII and FIV; supernumerary tubercles absent. Fringes on fingers distinct on FII and FIII, indistinct on FIV and absent on FI. Metacarpal ridge present, low, indistinct.

Hind limbs moderately long, SL 48.1% SVL. Relative lengths of adpressed toes: $\text{IV} > \text{III} > \text{V} > \text{II} > \text{I}$; TI short, with toe tip reaching the mid-point of T-II subarticular tubercle. Toe discs expanded, TIV about 1.6× as wide as distal end of adjacent phalanx; all horizontally oval. Feet (Figure 1F) long, 45.9% SVL; fringes on toes extensive, flaplike, folding around toes; webbing formula: $\text{I1-2II1-3III2-3}\frac{1}{2}\text{IV3-2V}$. One to three flat, moderate, oval subarticular tubercles present (1 on TI and TII, 2 on TIII and TV, 3 on TIV). One outer and one inner metatarsal tubercle present, both oval and about equal in size. Straight, flaplike tarsal keel continuing from flaplike fringe on external side of TI to mid-tarsus (broken at level of the right side), keel slightly curved at the end. Anal opening at upper level of thighs, with a short flap above vent; two small paracloacal tubercles.

Color.—In life (Figure 2A), the dorsal ground color is dark brown; there are irregular black marks that do not form any definite dorsal pattern. A lateral black band extends from tip of the snout to the groin, and covers the upper half of the tympanum and flanks. An oblique, pale gray lateral stripe runs anteriorly from the groin to more than the midlength of the body. There is a pair of small, light gray spots above the oblique lateral stripe and another pair on the shoulder. The dorsal surfaces of arms are dark brown with some irregular black spots. Fingers I and II are pale brown with white tips; Fingers III and IV are dark brown and bear black cross bars. Dorsal surfaces of hind limbs are dark brown, and bear black cross bars. The toes are dark brown with black cross bars. Paracloacal marks are missing or poorly defined.

Ventrally (Figure 2B), the throat is pale gray anteriorly and dark gray posteriorly. A wide black collar is evident. The chest and anterior

part of the belly are dark gray and the belly is pale gray. The ventral surfaces of the fore- and hind limbs are dark gray and the palmar and plantar surfaces are darker gray.

In preservative, the dorsum is dark gray, and the black dorsal marks are indistinct; arms and legs are pale gray with black marks (Figure 1A); the ventral side is pale gray except the chin and thighs, which are dirty white, and the dark gray collar (Figure 1B).

Variation.—In males, a solid, wide collar always is present and the dorsum is black, with CVULA 7163 having the most evident pattern. Ventral coloration varies little from that of the holotype. CVULA 7159 has two abnormalities associated with the limbs. On the right hand, Finger III is shorter than Fingers IV and II, and it bears only one subarticular tubercle; the digital disc is small, suggesting that it may be regenerated. Toe IV of the right foot is shorter than its counterpart on the left foot; in addition, Toe III reaches the intercalary cartilage, whereas in the normally developed left foot, Toe III does not reach the distal subarticular tubercle. CVULA 7164 has a reduced disc on Finger III of the right hand. CVULA 7166 (Figure 2C) is a female with a more contrasting dorsal pattern, consisting of irregular black marks on a dark brown ground color; the fore- and hind limbs are pale brown with dark brown to black cross bars. The oblique lateral band is solid and long, and almost reaches the upper arm on the right side; on the left side it is a little shorter. Ventrally the throat, chest, belly and undersides of limbs are white. The collar is narrower than on males, but solid. The palmar and plantar surfaces are gray (Figure 2D). This individual has low, narrow, extensive fringes on all fingers and flaplike, folding fringes on the toes. The metacarpal ridge is also present on the female, almost indistinct. There is a weakly developed medial tarsal tubercle on the right foot of the female. The three females from Río Negro (CVULA 7231–32, 7234) are larger than CVULA 7166. The oblique lateral stripe is long and solid in CVULA 7234, long and narrower on CVULA 7231, and short and composed

of a series of spots on CVULA 7232 (Figure 2E). Each of these individuals has a solid collar that is narrower than that typical of males (Figure 2F). Morphometric data describing the type series are presented in Table 1.

Natural history.—We found two populations. The topotypic population was associated with a small creek (<1 m wide) along the dirt road from La Trampa to Pregonero. The specimens were collected from an inundated culvert beneath the road. Males were calling from a shallow pool and jumped into the water and swam to escape. The population at Río Negro was found along a high-gradient creek flowing into the Río Negro; individuals were found in a shallow pool under a 4 m high waterfall. They moved quickly to escape under rocks and into crevices.

Vocalization.—A single call was analyzed; it was recorded at the type locality on the afternoon of 06 June 2007 and at an ambient temperature of 20.6°C. The complete call consists of 73 pulsed notes (Figure 3A) and lasts 6.8 sec, with 10–13 notes being emitted per second. The dominant frequency is 3423 Hz and the fundamental frequency is 3036 Hz. Six consecutive notes were chosen at random on the spectrogram to determine note duration and inter-note interval (Figure 3B). Note duration and inter-note interval are (mean \pm SD and range, respectively): 0.038 \pm 0.004; 0.03–0.04 sec, and 0.048 \pm 0.004; 0.004–0.005 sec.

Distribution.—*Mannophryne orellana* occurs at the southwestern edge of the Cordillera de Mérida in the Uribante Valley, and the northeastern side of the Cordillera Oriental de Colombia, which enters Venezuela (Figure 4). The species also might occur in Departamento Norte de Santander in Colombia. Figure 5 shows the general area of the type locality.

Etymology.—We dedicate this species to Andrés Orellana, an excellent lepidopterologist and better friend, for his dedication to the understanding of butterfly taxonomy and his interest in amphibians. The specific epithet is used as a substantive in apposition.

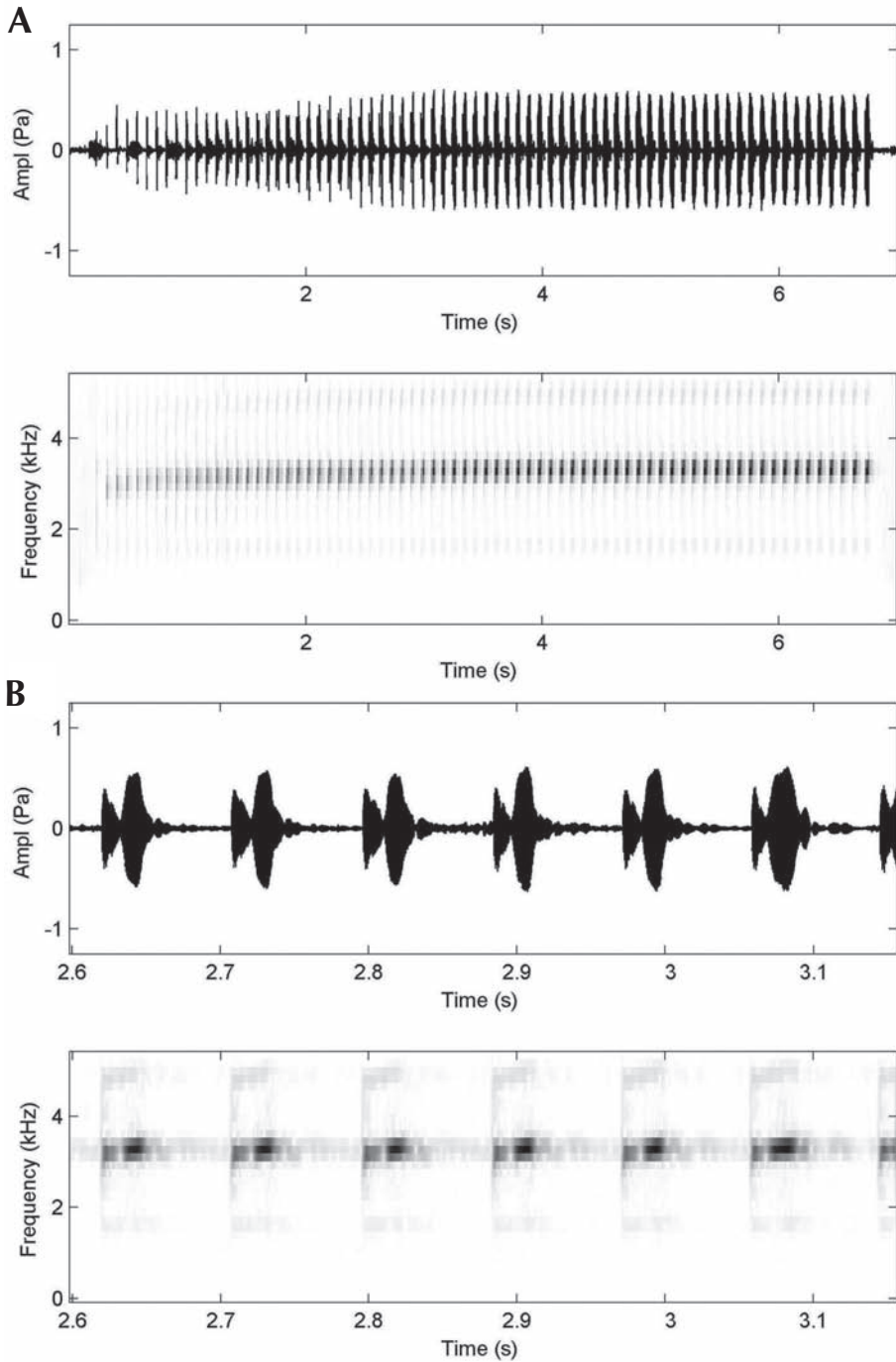


Figure 3. (A) Waveform and spectrogram of a 7-sec trill call of *Mannophryne orellana* sp. nov. (B) Waveform and spectrogram of six notes chosen at random.

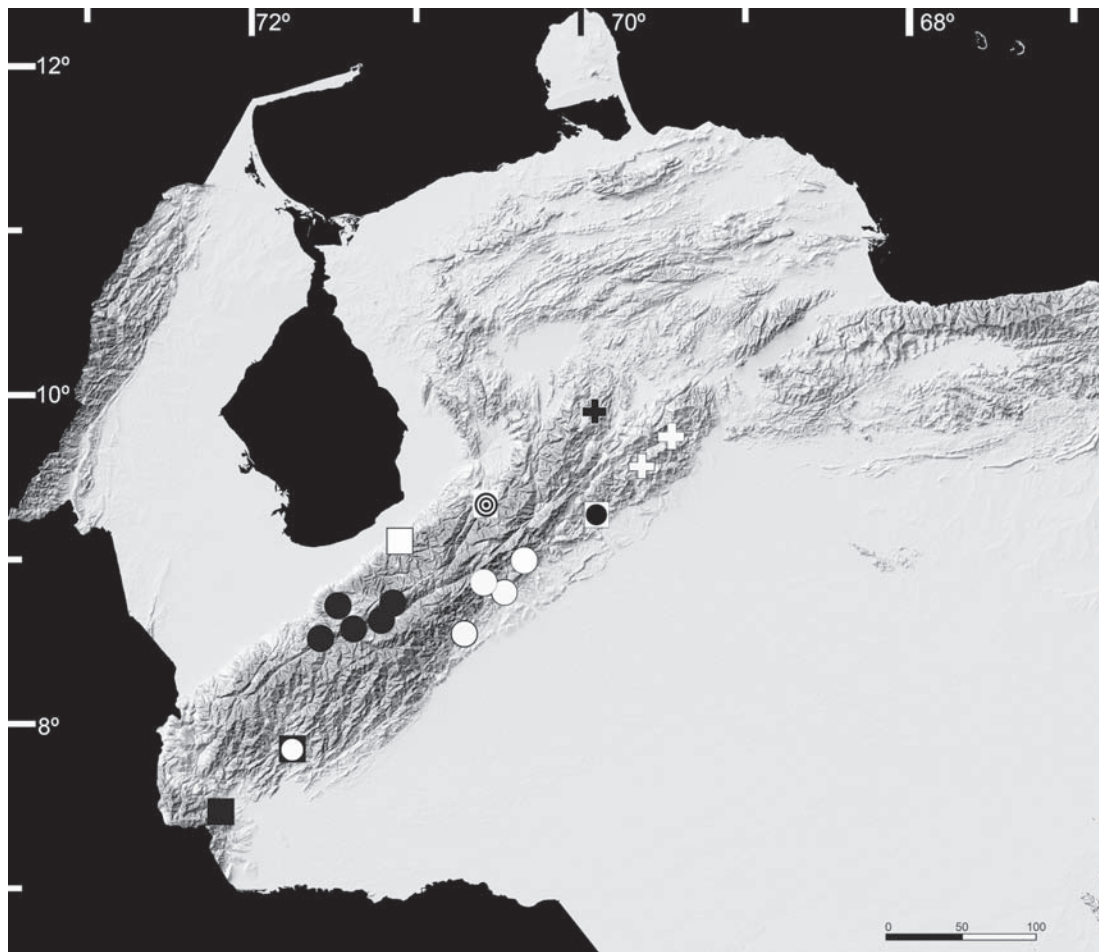


Figure 4. Distribution of the Andean species of collared frogs in western Venezuela. *Mannophryne orellana* sp. nov.: black squares; square with a white circle inside indicates the type locality. *M. collaris*: black dots. *M. cordilleriana*: white circles. *M. urticans* sp. nov.: white square. *M. speeri*: white square with black circle inside. *M. yustizi*: white crosses. *M. larandina*: black cross. *M. trujillensis*: diana symbol.

***Mannophryne urticans* sp. nov.**

(Figures 6, 7)

Spanish name: Ranita acollarada urticante

English name: Urticant collared frog

Holotype.—CVULA 7224, an adult male from Río Frío, northwestern slope of the Cordillera de Mérida, Estado Mérida, Venezuela (08°51' N, 71°17' W), elevation 676 m, collected by César L. Barrio-Amorós and Alan Highton on 24 November, 2006.

Paratopotypes.—An adult female, CVULA 7230, with same data as holotype. Two adult females, CVULA 7223 and 7226, and one subadult female, CVULA 7225, collected at the type locality by Erik Arrieta and César L. Barrio-Amorós on 10 March 2007. CVULA 7227 and 7229, subadult females, and CVULA 7228, a juvenile, collected by César L. Barrio-Amorós and Juan Carlos Santos at the type locality on 29 May 2007.



Figure 5. General view of the type locality of *Mannophryne orellana* sp. nov., the Pregonero–La Trampa Road, Estado Táchira.

Definition.—(1) Dorsal skin completely smooth on males and females in preservative; a few granules on the posterior parts of the body and hind limbs in living males. (2) Paired dorsal scutes present on digits, distinct in males, barely distinct in females. (3) Distal tubercle on Finger IV present but indistinct. (4) Length of Finger IV extending beyond distal subarticular tubercle of Finger III. (5) Finger I slightly longer than II. (6) Digital discs present. (7) Finger discs moderately expanded. (8) Finger fringes narrow and slightly distinct on FII and FIII, and absent on FI and FIV. (9) Metacarpal ridge absent. (10) Finger III not swollen in adult males. (11) Carpal pad absent. (12) Excrescences on thumb absent in

males. (13) Small thenar tubercle present. (14) Males lacking black arm gland. (15) Tarsal keel straight from preaxial edge of inner metatarsal tubercle to mid-tarsus. (16) Toe discs moderately expanded. (17) Toe webbing moderately developed, formula of the holotype $\text{I}1\frac{2}{3}\text{--}2\frac{2}{3}\text{II}2\text{--}3\text{III}2\frac{2}{3}\text{--}4\text{IV}4\text{--}2\frac{1}{2}\text{V}$. (18) Metatarsal fold weakly developed. (19) In preservative, dorsal coloration black in males (orange brown with irregular, dark brown marks in life) and brown to gray with dark brown marks on females; hind limbs barred; dorsolateral stripes absent; ventrolateral stripe absent; short oblique lateral stripe may extend to midbody, wide or narrow, solid and or composed of a series of white spots. (20) Gular

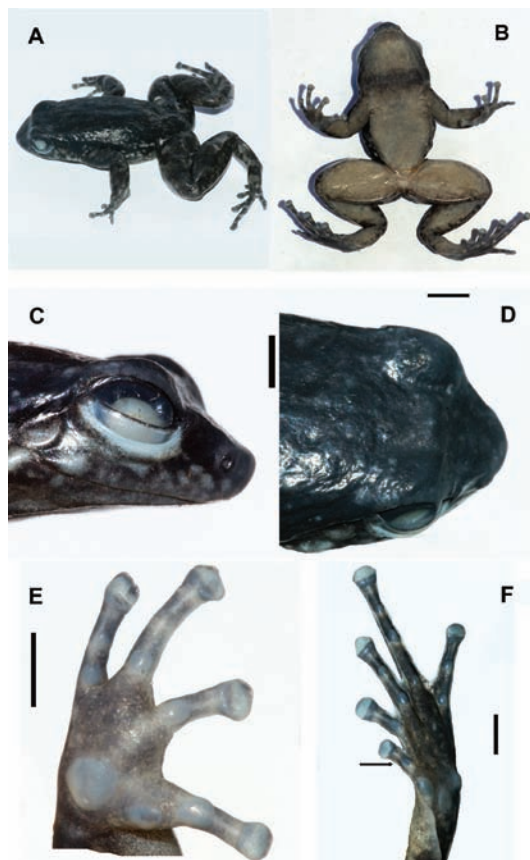


Figure 6. Holotype of *Mannophryne urticans* sp. nov. Dorsolateral (A), ventral (B), and lateral (C) view of the head; scale equal 2 mm. (D) Dorsal view of the head; scale bar = 2.5 mm. (E) Ventral view of left hand; scale bar = 2.5 mm. (F) Ventral view of right foot; scale bar = 2 mm. The arrow indicates the subarticular tubercle on Toe I, which bears a superficial longitudinal division.

chest markings absent. (21) Dermal collar present, very dark gray, barely visible on males; dark gray and narrow on females. (22) Male throat coloration evenly stippled gray; female throat coloration gray-white in preservative, yellow in life except for the chin and peripheral areas, stippled anteriorly with melanophores. (23) Male abdomen color pattern evenly stippled gray. (24) Female abdomen color pattern nearly

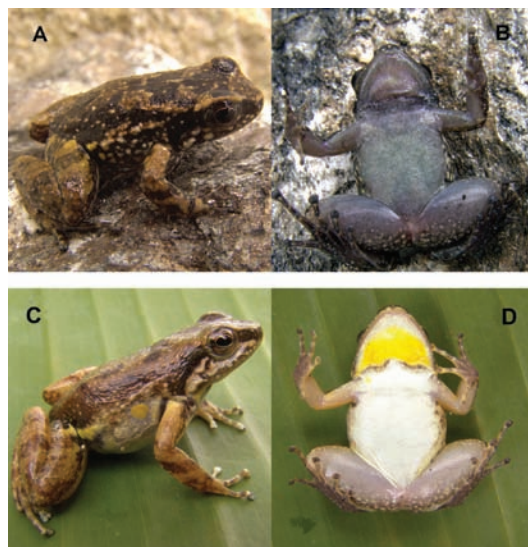


Figure 7. *Mannophryne urticans* sp. nov. in life. (A, B) Lateral and ventral views of the holotype, CVULA 7224. (C, D) Lateral and ventral views of the paratype, CVULA 7230.

devoid of melanophores; color white in preserved and living females. (25) Iris pale to dark brown with golden pupil ring. (26) Large intestine unpigmented. (27) Testis white, unpigmented. (28) Median lingual process absent. (29) Tympanum distinct posteroventrally, tympanic annulus barely distinct. (30) Vocal sac indistinct. (31) Teeth present on the maxillary arcade. (32) Size moderate, male 26.9 mm; females ($n = 6$) 22.2–30.8 mm, mean = 24.3 ± 3.7 mm.

Species comparisons.—*Mannophryne urticans* (characteristics in parentheses) differs morphologically and genetically from its congeners (J. C. Santos *et al.* in prep.). Here, it is compared to other species from the Andean Clade of Manzanilla *et al.* (2009), in addition to *M. speeri*, which is presumed to belong to the same clade based on shared characteristics with *M. yustizi*.

Mannophryne collaris is the vicariant species of *M. urticans* (unpubl. data) and closely resembles *M. urticans*, from which it differs only subtly in morphological characters. *Mannophryne*

collaris has a subovoid (rounded) snout in dorsal profile and a poorly defined canthus rostralis (straight, angular); males have a moderately long snout, 112.4% of ED (short snout, 107.9% of ED) and moderately large eyes, 33% of HL and 88.9% of ETS (large eyes, 38% of HL; 92.6% of ETS), and more extensive toe webbing: $\text{II}1\frac{1}{2}-2\frac{1}{2}\text{III}1-2\frac{1}{2}\text{III}2-3\frac{1}{2}\text{IV}4-2\frac{1}{2}\text{V}(\text{II}1\frac{2}{3}-2\frac{2}{3}\text{III}2-3\text{III}2\frac{2}{3}-4\text{IV}4+-2\frac{1}{2}\text{V})$. The tympanum is inconspicuous (distinct posteroventrally), and lacks raised margins (present). Finger I is equal in length to FII (slightly longer). The collar is solid or spotted and wide (narrow, usually non spotted). The flanks usually are solid black with a long, narrow oblique lateral stripe (flanks without definite dark band, spotted with white and yellow round spots).

Mannophryne cordilleriana has slightly more extensive webbing: $\text{II}1\frac{1}{2}-2\text{III}1\frac{2}{3}-3\text{III}2\frac{1}{2}-3\frac{3}{4}\text{IV}3\frac{3}{4}-2\text{V}(\text{II}1\frac{2}{3}-2\frac{2}{3}\text{III}2-3\text{III}2\frac{2}{3}-4\text{IV}4-2\frac{1}{2}\text{V})$. The length of Finger I equals that of II (slightly longer), and males have a moderately long snout, 103.8% of ED (short snout, 135% of ED) and moderately large eyes, 31.4% of HL and 71.6% of ETS (large eyes, 38% of HL; 92.6% of ETS).

Mannophryne yustizi has pale dorsolateral bands (absent) and less extensive toe webbing: $\text{II}1\frac{1}{2}-2\frac{1}{2}\text{III}2-3\text{III}2-4\text{IV}4-2\frac{1}{2}\text{V}(\text{II}1\frac{2}{3}-2\frac{2}{3}\text{III}2-3\text{III}2\frac{2}{3}-4\text{IV}4-2\frac{1}{2}\text{V})$, its collar is wide and spotted collar (narrow).

Mannophryne larandina probably is a synonym of *M. yustizi*; the same characters differentiate this species from *M. urticans*.

Mannophryne speeri is smaller, females reach 24.1 mm (females up to 30.8 mm), has short pale dorsolateral bands (absent), and less toe webbing: $\text{II}1-2\text{III}2-3\text{III}2-4\text{IV}4-2\frac{1}{2}\text{V}(\text{II}1\frac{2}{3}-2\frac{2}{3}\text{III}2-3\text{III}2\frac{2}{3}-4\text{IV}4-2\frac{1}{2}\text{V})$. In addition, it has a wide, spotted collar (narrow).

Mannophryne caquetio is smaller, with males reaching 22.4 mm (26.9 mm), and females 26.3 mm (30.8). It has much less toe webbing; the webbing formula is unavailable, but see Figure 1 in Mijares-Urrutia and Arends 1999a). In addition, the disc of Finger III is $2.2\times(1.8\times)$ wider than the distal end of the adjacent phalanx

and the disc of Toe IV is $2.2\times(1.8\times)$ wider than distal end of the adjacent phalanx (1.8).

Mannophryne lamarcai is small, with males reaching 24.6 mm (26.9) and females 28.8 mm (30.8). The disc of Finger III disc is $2.3\times(1.8\times)$ the width of the distal end of the adjacent phalanx, that of Toe IV $2.4\times(1.8\times)$ the width of the distal end of the adjacent phalanx. A dorsolateral dark stripe is present (absent).

Mannophryne herminae has a wide, spotted collar (narrow), pale dorsolateral stripes (absent), and shagreen (smooth) skin on throat, chest, and venter. It also has a shorter, unflaplike tarsal keel (longer, flaplike).

Mannophryne orellana lack paracloacal marks (present). The disc on Finger III is $1.4\times(1.8\times)$ the width of the distal end of adjacent phalanx and that of Toe IV $1.6\times(1.8\times)$ the width of the distal end of adjacent phalanx. The sizes of the distal subarticular tubercles on Fingers I and II are equal to that of the thenar tubercle (smaller). The snout nearly truncate in dorsal and ventral profiles (rounded).

Description of the holotype.—Adult male, 26.9 mm (SVL). Body stout, short. Dorsal skin, including dorsal surfaces of hind limbs, smooth in preservative, bearing few, small, non-keratinized granules on the dorsolateral posterior part of the body and thighs (Figure 6A), only apparent in life (Figure 7A); ventral skin smooth (Figure 6B). Head slightly longer than wide, head length 38.2% SVL; greatest head width between angles of jaws 36.8% SVL. Snout subacuminate in dorsal, ventral, and lateral profiles (Figures 6C, D). Nares are situated lateral to the tip of snout; nares visible in anterior and ventral views, not visible dorsally. Canthus rostralis strait, angular; loreal region flat. Interorbital distance less than width of upper eyelid; snout length equal to eye diameter. Eyes large, ED 35% HL. Tympanum moderate in size, TD 47.2% ED, distinct, with tympanic annulus barely distinguishable beneath skin; half of the tympanum concealed posterodorsally by straight, distinct supratympanic bulge formed by superficial slip of m. depressor mandibulae;

tympanum located near eye and low, with ventral margin narrowly separated from angle of jaw. Teeth present on maxillary arcade. Vocal slits curved, located under the tongue, laterally, and with posterior end of each lying close to mandible. Tongue triangular, half-free posteriorly.

Hand (Figure 6E) moderate in size (27.0% SVL). Relative lengths of adpressed fingers: III > IV > I > II; finger discs expanded, horizontally oval; F-III disc 1.8× as wide as distal end of adjacent phalanx. Base of palm with large, rounded palmar tubercle; smaller (~25% of palmar tubercle), oval thenar tubercle on base of FI, slightly larger than F-I subarticular tubercle; each of FI and FII with one or two subarticular tubercles—one large, oval on FI and one round on FII and two smaller, round tubercles on each of FIII and FIV; supernumerary tubercles absent. Fringes on fingers are narrow and slightly distinct on FII and FIII, and absent on FI and FIV. Metacarpal ridge absent.

Hind limbs moderately long, SL 48.6% SVL. Relative lengths of adpressed toes are: IV > III > V > II > I; TI is short, the tip reaching the mid point of the the subarticular tubercle of TII. Toe discs are expanded, that on TIV 1.8 times wider than distal end of adjacent phalanx; all horizontally oval. Feet (Figure 6F) are long, 49.4% of the SVL; fringes on toes are extensive, flap-like; webbing formula is $I1\frac{2}{3}-2\frac{2}{3}II2-3III2\frac{2}{3}-4IV4-2\frac{1}{2}V$. One to three flat, moderate, round to oval subarticular tubercles present (one on TI and TII, two on TIII and TV, three on TIV), that on TI of both feet superficially divided longitudinally (see Remarks). Three metatarsal tubercles are present, one round outer, one oval inner, and an oval medial one, being the largest the medial, then the inner, and the smaller is the outer. The right foot medial metatarsal tubercle is less distinct. There is a flap-like straight tarsal keel as a continuation of the fringe on external side of TI to mid tarsus, slightly curved at the end. Anal opening is at superior level of thighs, with a short flap above vent.

Color.—In life (Figure 7A), the dorsal ground color is brownish orange with irregular dark

brown marks that do not form an obvious pattern. The flanks of the body are black with white spots anterior and some yellow spots posteriorly. The canthal stripe is black with small brown spots, and the upper lip is dark brown with white spots; this coloration extends to the anterior side of the arm. An oblique lateral stripe extends from groin to above shoulder; it is diffuse and composed of a series of yellow and white spots. The dorsal surfaces of the arms are uniform pale brown; the anterior surfaces have a narrow, longitudinal black stripe that is outlined inferiorly by small white spots. The forearms bear dark brown transverse bars. The black fingers bear poorly defined gray-white transverse bars. The finger discs and digital scutes are gray-white. The dorsal surfaces of the hind limbs are pale brown with dark brown cross bars. The toes are pale brown with dark gray cross bars; the toe discs and digital scutes are gray-white.

Ventrally (Figure 7B), the throat, chest, and anterior part of the belly are gray, with a diffuse dark gray collar. The inferior parts of the arms, forelimbs, hands, hind limbs, and feet are gray. The posterior surfaces of the thighs bear small, diffuse whitish spots. The iris is dark brown with a golden pupil ring.

In preservative, the orange-brown and dark brown colors change to dark gray and blackish gray, respectively. There are two vertically elongated paracloacal spots that are grayish white. The dorsum is gray with black markings, and the arms and legs are pale gray with dark gray cross bars (Figure 6A); the ventral surface is pale gray except for the darker, better-defined, wide, solid collar (Figure 6B).

Variation.—In life, the dorsum and dorsal surfaces of the limbs in the female are pale brown with dark brown marks (CVULA 7230; Figure 7C). The canthus and supratympanic bulge are dark gray, and the upper lip is white with gray spots. The lower half of the tympanum is white. The flanks lack a definite dark band; they are grayish white suffusing with pale brown of the dorsum. On the right side, there is a round yellow spot behind the shoulder; the oblique

Table 1. Measurements (in mm) of adult male and female *Mannophryne orellana* sp. nov. from the type and referred localities (in text). Abbreviations are described in the text. Values are range and mean \pm standard deviation.

Character	Males ($n = 7$)		Females ($n = 5$)	
	Range	Mean \pm SD	Range	Mean \pm SD
SVL	26.0–27.3	26.5 \pm 0.7	29.5–32.9	31.0 \pm 1.6
SL	12.1–13.2	12.7 \pm 0.4	13.7–15.3	14.5 \pm 0.7
FL	11.1–12.7	12.3 \pm 0.6	13.5–14.6	13.8 \pm 0.5
HeL	8.4–9.7	9.4 \pm 0.5	9.7–11.5	10.6 \pm 0.8
HW	8.5–9.7	9.3 \pm 0.4	10.0–10.7	10.5 \pm 0.3
ED	2.7–3.7	3.1 \pm 0.4	3.1–4.1	3.7 \pm 0.5
TD	1.0–1.3	1.2 \pm 0.1	1.4–1.7	1.5 \pm 0.2
F3D	0.7–1.1	0.9 \pm 0.1	1.0–1.2	1.1 \pm 0.1
T4D	0.9–1.2	1.0 \pm 0.1	1.2–1.4	1.3 \pm 0.1
1FiL	3.7–4.6	4.2 \pm 0.3	4.6–5.1	5.0 \pm 0.2
2FiL	3.4–4.5	3.9 \pm 0.4	4.3–4.9	4.7 \pm 0.2

Table 2. Measurements (in mm) of adult males and females *Mannophryne urticans* sp. nov. from the type and referred localities (in text). Abbreviations are described in the text.

Character	Male ($n = 1$)	Females ($n = 6$)	
	Value	Range	Mean \pm SD
SVL	26.9	22.2–30.8	24.3 \pm 3.7
SL	13.1	11.0–15.1	12.6 \pm 1.9
FL	13.3	9.6–14.8	12.0 \pm 2.1
HeL	10.3	8.1–11.3	9.4 \pm 1.3
HW	9.9	7.6–10.4	8.8 \pm 1.2
ED	3.6	2.7–3.8	3.1 \pm 0.6
TD	1.7	1.1–1.5	1.3 \pm 0.1
F3D	1.1	0.7–1.1	0.8 \pm 0.2
T4D	1.5	0.7–1.4	0.9 \pm 0.3
1FiL	4.9	3.6–5.3	4.4 \pm 0.8
2FiL	4.6	3.3–4.9	3.9 \pm 0.7

lateral stripe is short and yellow. The iris is pale brown with a golden pupil ring. Ventrally, the chest and belly are immaculate white; the chin and peripheral areas of the throat are grayish white, whereas the rest is yellow. The collar is black, narrow, and spotted with small, gray-white speckles. The ventral surfaces of the arms are pale orange-brown, whereas those of the hind limbs are pale gray; palmar and plantar surfaces are dark gray (Figure 7D).

Females are larger than males (mean \pm Standard Deviation [SD] for females: 31.6 ± 1.4 vs. 26.5 ± 0.7 for males), with bars on the limbs varying from highly contrasting (CVULA 7226–27) to less contrasting (CVULA 7229–30). The oblique lateral stripe can be (1) long, extending to the midbody, solid, and wide (CVULA 7225–26); (2) short, solid, and wide (CVULA 7227, 7230); (3) narrow (CVULA 7229); or (4) composed of a series of white spots (CVULA 7223). Both CVULA 7226 and 7227 have a wide interorbital bar; CVULA 7226 bears a “M” mark behind the head, whereas CVULA 7227 has a “V” mark. Both individuals have two symmetrical, dorsolateral round spots at midbody level and a central lumbar mark that is horizontally oval. The marks are dark brown on a pale brown background, and are less well defined on CVULA 7223. Paracloacal marks on females may be ill defined, vertically elongated (CVULA 7225), or curved from lateral sides of the vent flap to the posteroventral side of the thigh (in the rest of females of the type series). Ventrally, females are immaculate white, except for the collar, which is dark gray, and narrow (all specimens except CVULA 7225) and diffuse in CVULA 7227. Plantar and palmar surfaces are pale gray, with all tubercles well marked in dark gray. None of specimens in the type series has any deformity of the fore- or hind limbs. The paratopotypes lack median tarsal tubercles on the feet. Basic measurements of the type series are presented in Table 2.

Natural history.—The habitat is evergreen forest with many high-gradient creeks and streams. The species is inconspicuous, and only

a few males were heard during many visits. *Mannophryne urticans* is shy and escapes quickly into crevices and under rocks. No males were seen carrying tadpoles.

Vocalization.—A single call was analyzed; it was recorded at the type locality on the afternoon of 02 June 2007 and at an ambient temperature of 23.7°C . The complete call consists of 155 pulsed notes (Figure 8A) and lasts 26.2 sec, with five to seven notes being emitted per second (Figure 8B). The dominant frequency is 3567 Hz and the fundamental frequency is 3189 Hz. Four consecutive notes were chosen randomly on the spectrogram to determine note duration and inter-note interval. Note duration and inter-note interval are (mean \pm SD and range, respectively): 0.02 ± 0.0 ; and 0.076 ± 0.005 ; 0.007 – 0.008 sec.

The advertisement call of *Mannophryne collaris* never has been published (La Marca 1994). The brief description of Edwards (1974) does not correspond with *M. collaris* sensu stricto; it probably is *M. trujillensis* from 3 km NE Boconó, Estado Trujillo. We offer a basic description in order to compare the call of this species with the vicariant *M. urticans* sp. nov. The single call analyzed was recorded at Estanquillo, San Juan de Lagunillas, Estado Mérida ($8^{\circ}31.2'$ N, $71^{\circ}21.4'$ W, 1120 m) during the morning of the 01 of June 2007 when the ambient temperature was 22.4°C . The complete call has 132 pulsed notes (Figure 9A) and lasts 16 sec. Eight or nine notes are produced per second. The dominant frequency is 3547 Hz and the fundamental frequency is 3181 Hz. Five consecutive notes were chosen at random on the spectrogram to determine note duration and inter-note interval (Figure 9B). Note duration and inter-note interval were measured, respectively (mean \pm SD and range, respectively), 0.04 ± 0.005 ; 0.036 – 0.048 ; and 0.074 ± 0.009 ; 0.06 – 0.08 sec.

The calls of both species are nearly identical, with the most striking difference being that *M. urticans* produces 5–7 notes per second (contra 8 or 9 in *M. collaris*). Dominant and fundamental

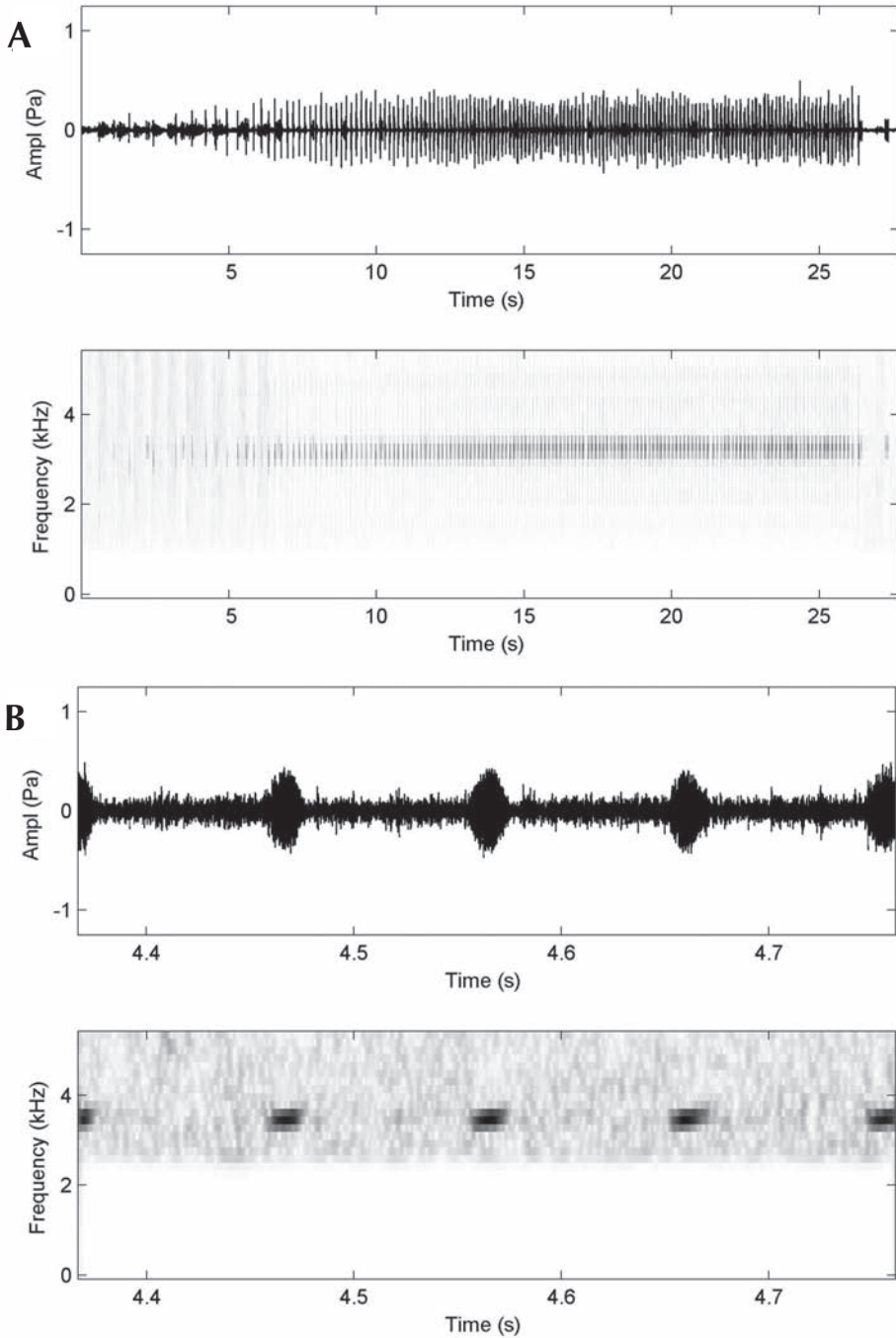


Figure 8. (A) Waveform and spectrogram of a 27-sec trill call of *Mannophryne urticans* sp. nov. (B) Waveform and spectrogram of four notes chosen at random.

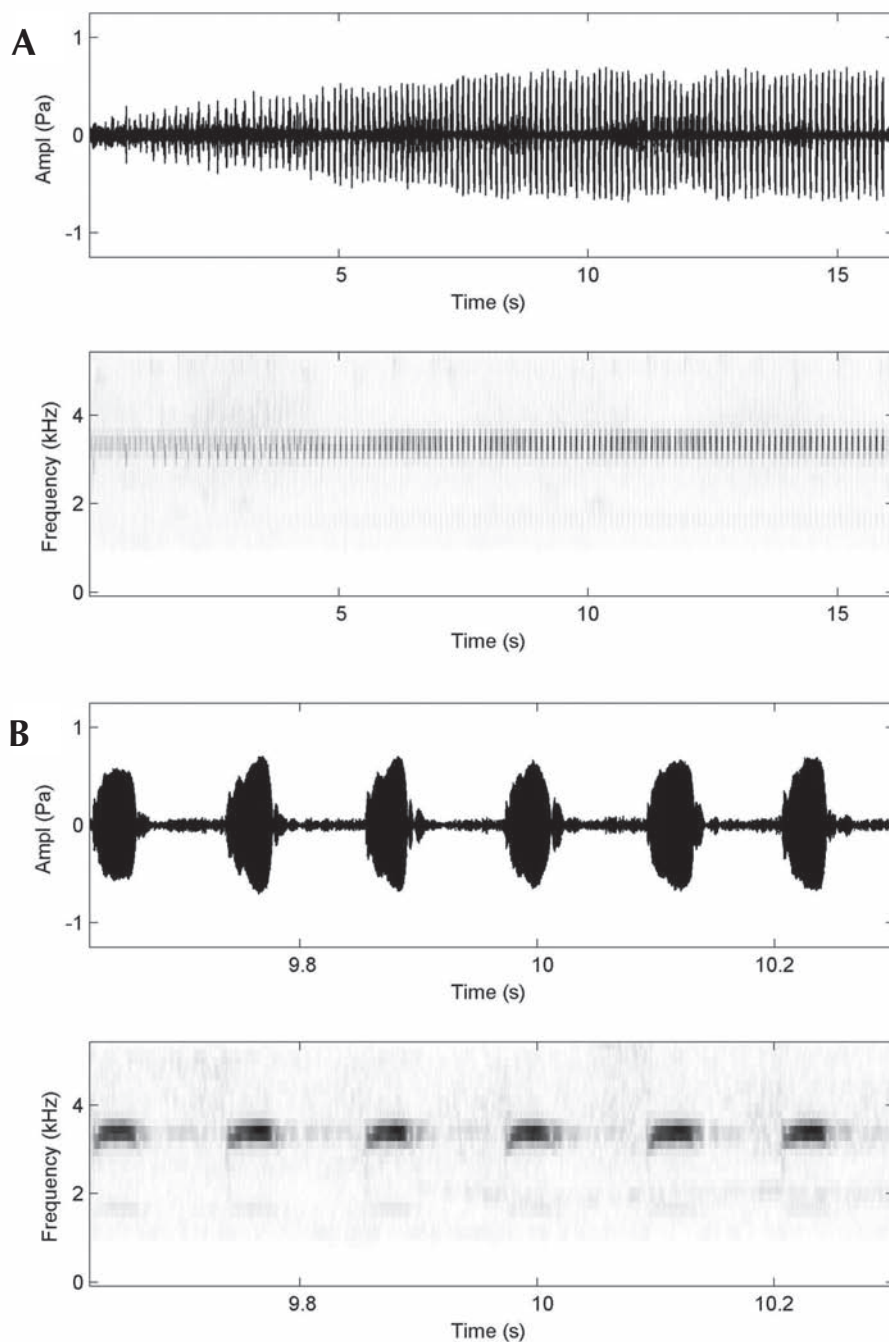


Figure 9. (A) Waveform and spectrogram of a 16-sec trill call of *Mannophryne collaris*. (B) Waveform and spectrogram of six notes chosen at random.

frequencies are almost identical, suggesting a recent speciation event.

Distribution.—To date this species is only known from the type locality, where it occurs in small streams flowing to the Río Frío, a small river coming from the high páramos of the Sierra de la Culata, and flowing to the southeastern side of the Maracaibo Lake Basin. It is possible that *M. urticans* is more widespread in similar habitats in the western piedmont of the Cordillera de Mérida (Figure 4).

Etymology.—The specific name refers to the abundance of urticant plants (Urticaceae: *Urtica* sp.) in the natural habitat of this species; these plants were a major handicap to the collection of these frogs.

Remarks.—The holotype has a character heretofore unknown in dendrobatid frogs; the subarticular tubercle on the first toe of each foot bears a superficial longitudinal division (arrow in Figure 6F). This feature is absent in the rest of the type series (all females); thus, we cannot ascertain if this is a sexually dimorphic feature or is an anomaly.

***Mannophryne vulcano* sp. nov.**

(Figures 10, 11)

Spanish name: Ranita acollarada de Caracas

English name: Caracas collared frog

Holotype.—CVULA 7170, an adult male from the northern slope of Cerro El Volcán, Baruta, Estado Miranda, Venezuela (10°25' N, 66°51' W), elevation 1064 m, collected by Charles Brewer on 30 June, 2007.

Paratopotypes.—CVULA 7168, an adult male, and CVULA 7167, 7169, 7171–73, five adult females, with the same data as the holotype.

Referred specimens.—CVULA 7236–39 from Quebrada Maripérez, Cerro El Ávila, Caracas; CVULA 7312–17 from El Hatillo, Estado Miranda.

Definition.—(1) Dorsal skin completely smooth in females, smooth with a few granules on the posterior parts of the body and hind limbs in males. (2) Paired dorsal scutes present on

digits, barely distinct. (3) Indistinct distal tubercle on Finger IV. (4) Length Finger IV extending beyond distal subarticular tubercle on Finger III. (5) Finger I equal to, or slightly longer than, Finger II. (6) Digital discs present. (7) Finger discs weakly expanded. (8) Finger fringes absent. (9) Metacarpal ridge absent. (10) Finger III not swollen in adult males. (11) Carpal pad absent. (12) Excrescences on thumb absent in males. (13) Small thenar tubercle present. (14) Males lacking black arm gland. (15) Straight tarsal keel extending from preaxial edge of inner metatarsal tubercle to mid-tarsus. (16) Toe discs weakly expanded. (17) Toe webbing present only basally between Toes III and IV. (18) Metatarsal fold weakly developed. (19) Dorsal ground color pale brown with small, irregular dark brown marks; hind limbs barred; with distinct dorsolateral stripes; ventrolateral stripe absent; partial oblique lateral stripe, either solid or composed of a series of spots. (20) Gular chest markings absent. (21) Dermal collar present, subtle to broken medially. (22) Male throat coloration evenly stippled gray; female throat coloration white in preservative, yellow in life, nearly devoid of melanophores except on chin. (23) Male abdomen evenly stippled gray, fainter posteriorly; dark gray in living males in reproductive condition. (24) Female abdomen color pattern lacking, or nearly lacking, melanophores; color white in living females. (25) Iris copper–orange with gold to orange pupil ring. (26) Large intestine mostly unpigmented. (27) Testis white, unpigmented. (28) Median lingual process absent. (29) Tympanum large, conspicuous, with elevated margin. (30) Vocal sac indistinct. (31) Teeth present on the maxillary arcade. (32) Size small, males ($n = 2$) 18.5–19.2 mm, mean = 18.8 ± 0.5 ; females ($n = 5$) 22.3–23.1 mm, mean = 22.6 ± 0.3 .

Species comparisons.—*Mannophryne vulcano* is compared to other species from northern Venezuela belonging to the “*Mannophryne trinitatis* species group” as defined by Manzanilla et al. (2009) (characteristics of *M. vulcano* in parentheses). *Mannophryne leonardo* has a short head that is wider than long (longer than wide).

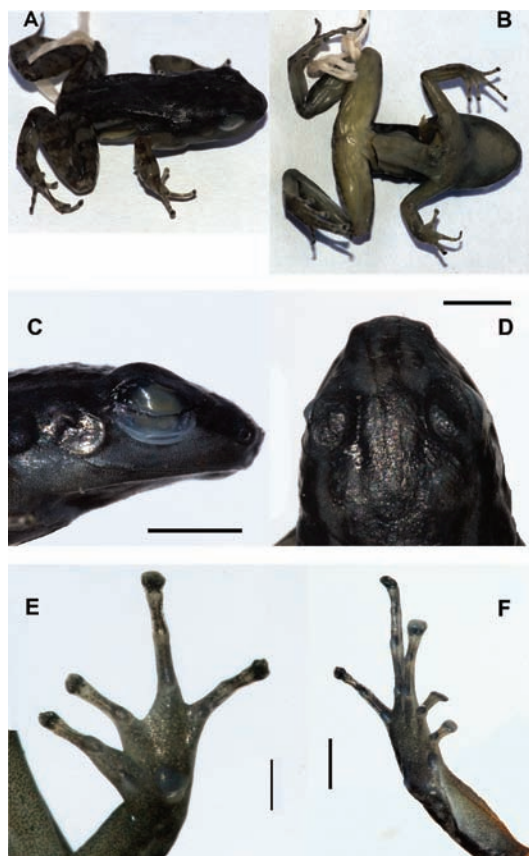


Figure 10. Holotype of *Mannophryne vulcano* sp. nov., CVULA 7170. (A, B) Dorsolateral and ventral views. (C, D) Lateral and dorsal views of the head; scale bars = 2 mm. (E) Palmar view of left hand; scale bar = 1 mm. (F) Plantar view of right foot; scale bar = 2 mm.

Its fingers have lateral keels (absent) and there is a keel present only on Toe V (all toes); basal webbing is present between Toes I, II, and III (only between III and IV). The oblique lateral stripe is long and solid (shorter and inconsistently solid). In females, the belly is pigmented (immaculate), and the collar is wide and well marked (narrower and medially broken).

Mannophryne trinitatis has basal webbing between the toes (absent except between Toes III and IV) and lateral fringes on the fingers (absent)

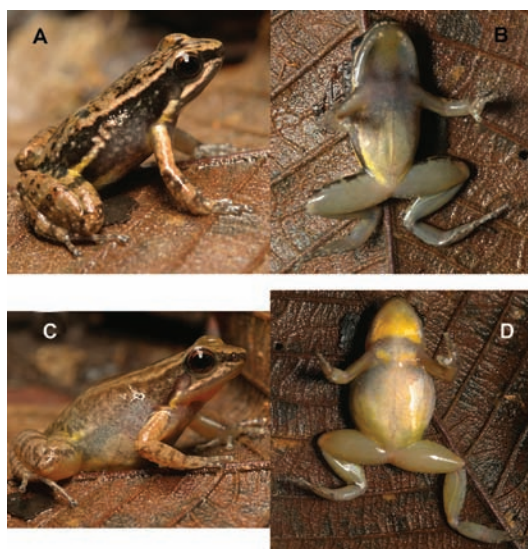


Figure 11. *Mannophryne vulcano* sp. nov. in life. (A, B) Lateral and ventral views of the holotype, CVULA 7170. (C, D) Lateral and ventral views of the paratype, CVULA 5681.

The disc on Finger III is 1.6× as wide as the adjacent phalanx (1.2×) and the disc on Toe IV is 2× (1.4×) as wide as the adjacent phalanx. Pale dorsolateral stripes are absent (present).

Mannophryne venezuelensis has basal webbing between toes (absent except between Toes III and IV). The collar is poorly defined and usually absent in females (present). The fingers bear lateral fringes (absent) and the dorsal digital scutes are distinct (indistinct).

Mannophryne riveroi has extensive webbing (basal) and is much larger, with adults being up to 46.2 mm (23.1) SVL.

Mannophryne olmonae from Tobago has dark dorsolateral stripes (light) and a narrow, solid collar (collar indefinite on males, poorly defined on females).

The new species can be also confused with *Mannophryne herminae* from the western section of the Coastal Cordillera, although it belongs to the Andean clade or Clade B of Manzanilla *et al.* (2009). *Mannophryne herminae* has a reticulated

collar (poorly defined) and more extensive toe webbing (absent except between Toes III and IV).

Mannophryne neblina is larger, with males up to 25.3 mm (19.2 mm), and females up to 27.4 mm (23.1 mm). It has lateral fringes on Fingers II and III (absent). The tympanum is inconspicuous (conspicuous); the head is slightly wider than long (longer than wide), and it bears an immaculate stripe on the upper lip (not immaculate).

Description of the holotype.—Adult male, 18.5 mm SVL). Body slender, rounded in cross section. Dorsal skin, including dorsal surfaces of hind limbs, smooth in preserved specimens, bearing small, non-keratinized tubercles on the posterior part of the body and hind limbs in life (Figure 10A); ventral skin smooth (Figure 10B). Head longer than wide, head length 37.8% SVL; greatest head width between angles of jaws 32.4% SVL (Table 1). Snout subacuminate in lateral profile (Figure 10C), nearly truncate in dorsal and ventral views (Figure 10D). Nares are situated lateral to the tip of snout; nares visible from anterior and ventral aspects, not visible dorsally. Canthus rostralis rounded; loreal region slightly concave. Interorbital distance equal to width of upper eyelid; snout longer than eye diameter. Eyes small, ED 25.7% HL. Tympanum is large (TD 66.6 % ED), distinct, with elevated margins; about one third of tympanum concealed posterodorsally by low supratympanic bulge formed by superficial slip of m. depressor mandibulae; tympanum located near eye and low, with ventral margin narrowly separated from angle of jaw. Teeth present on maxillary arcade. Vocal slits long, extending posterolaterally from midlevel of tongue to the angle of jaws. Tongue long, half-free posteriorly.

Hand (Figure 10E) moderate in size (29.7% SVL). Relative lengths of adpressed fingers: III > IV > I > II; finger discs slightly expanded, round. Finger-III disc 1.2× as wide as distal end of adjacent phalanx. Base of palm with large, rounded palmar tubercle; a small (~25% of palmar tubercle), slightly elliptical thenar

tubercle on base of FI. Each of FI and FII with one subarticular tubercle, and each of FIII and FIV with two subarticular tubercles, all tubercles flat and round; supernumerary tubercles absent. Intercalary cartilage in FIII. Fringes on fingers absent. Dorsal digital scutes present but indistinct.

Hind limbs moderately long, SL 47% SVL. Relative lengths of adpressed toes: IV > III > V > II > I; TI short, with toe tip reaching subarticular tubercle of TIII. Toe discs slightly expanded, about 1.4× as wide as distal end of adjacent phalanx; discs horizontally oval, except for round disc on TI. Feet (Figure 10F) long, 43.7% SVL; fringes on toes narrow. Basal webbing evident between TIII and TIV. One to three non-protuberant, small subarticular tubercles present (1 on TI and TII; 2 on TIII and V; 3 on TIV, distal one indistinct). Two metatarsal tubercles present, including a small, round outer, and an oval inner tarsal tubercle; inner tarsal tubercle double size of outer. Well-defined, straight tarsal keel extending from preaxial edge of inner metatarsal tubercle to mid-tarsus. Anal opening at upper level of thighs, lacking flap above vent.

Color.—In life (Figure 11A), the dorsal ground color is pale brown with small, irregular, dark brown marks. The dorsolateral stripes match the dorsal ground color, and extend posterodorsally from the eye to the mid-body or slightly beyond. A black lateral band extends along the side of the body from the tip of the snout to the groin, covering the tympanum and flanks. On the right side, an oblique lateral stripe extends from the groin to the midbody; it is white anteriorly and yellow posteriorly. On the left side, the oblique lateral stripe is discontinuous (composed of a series of spots) and white. The dorsal surfaces of arms are uniform pale orange; the anterior surface of each arm has a narrow, longitudinal, black stripe. The elbows are dark brown and the forearms bear dark brown transverse bars. The fingers are black, with poorly defined, white transverse bars; the finger discs are black with white digital scutes. The

dorsal surfaces of the hind limbs are pale brown, with dark brown transverse bars. Toes are dark gray, with pale gray transverse bars; the toe discs are black with white digital scutes.

Ventrally (Figure 11B), the throat is dark gray with pale spots lateral to the chin. The chest and anterior part of the belly are dark gray and the black collar is indistinct. The posterior part of the belly is white medially and yellow laterally. The inferior parts of arms, forelimbs, hind limbs and the plantar and palmar surfaces are pale gray.

In preservative, the pale brown and dark brown colors fade to pale gray and dark, blackish gray, respectively. The dorsum is gray with dark gray markings. The arms and legs are pale gray (Figure 10A) and the digital scutes are gray and indistinct. The venter is pale gray except for the thighs, which are yellowish white. After 2 years, the yellow coloration faded to white, and the spots on the chin disappeared (Figure 10B).

Variation.—The male paratopotype, CVULA

7168, is basically identical to the holotype, save for being slightly lighter dorsally and ventrally. It has lost the distal phalanx on Toe II on the right foot. Females are larger than males, with less-defined hind-limb transverse bars (CVULA 7173) or highly contrasting bars (CVULA 7171–72). The dorsolateral stripes are scarcely discernable (CVULA 7171, Figure 11C and 7173) or distinct (CVULA 7167, 7172). CVULA 7173 has lost the distal phalanx of Toe IV of the left foot. CVULA 7172 has median tarsal tubercles on both feet. Ventrally, females are pale gray to gray-white, and the plantar and palmar surfaces are gray. The collar is light gray and not well defined on CVULA 7169, 7171 (Figure 11D), and 7173; however, on CVULA 7167 and 7172, the collar is broad and broken medially. On all specimens, the lateral keels on toes become more noticeable the longer the specimens are out of preservative. Basic measurements of the type series are presented in Table 3.

Table 3. Measurements (mm) of adult male and female *Mannophryne vulcano* sp. nov. from the type locality. Abbreviations are described in the text.

Character	Males (n = 2)		Females (n = 5)	
	Range	Mean ± SD	Range	Mean ± SD
SVL	18.5–19.2	18.8 ± 0.5	22.3–23.1	22.6 ± 0.3
SL	8.7–9.1	8.9 ± 0.3	10.0–10.8	10.6 ± 0.3
FL	8.1–8.8	8.4 ± 0.5	9.8–10.8	10.3 ± 0.4
HeL	6.7–7.0	6.9 ± 0.2	7.9–8.8	8.3 ± 0.3
HW	6.0–6.6	6.3 ± 0.4	7.3–7.8	7.5 ± 0.2
ED	1.8–2.8	2.3 ± 0.7	2.7–3.1	2.8 ± 0.2
TD	1.2–1.6	1.4 ± 0.3	1.3–1.8	1.5 ± 0.2
F3D	0.6–0.6	0.6 ± 0.0	0.6–0.9	0.7 ± 0.1
T4D	0.7–0.8	0.7 ± 0.1	0.7–0.8	0.8 ± 0.1
1Fil	2.9–2.9	2.9 ± 0.0	3.3–3.7	3.6 ± 0.1
2Fil	2.6–2.8	2.7 ± 0.1	3.2–3.6	3.4 ± 0.1

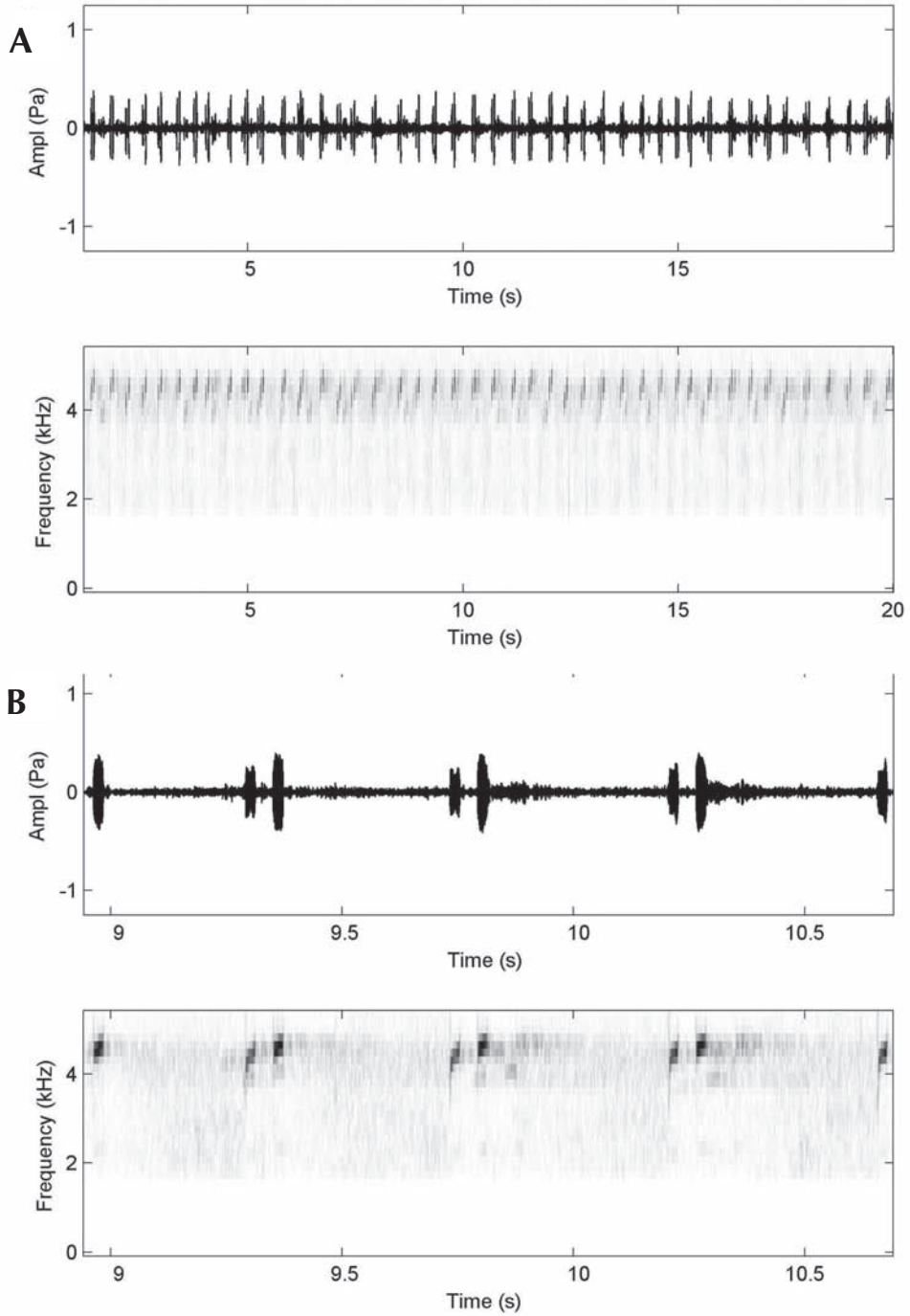


Figure 12. (A) Waveform and spectrogram of a 20-sec sequence of the trill call of *Mannophryne vulcano* sp. nov. (B) Waveform and spectrogram of three couplets of notes chosen at random.

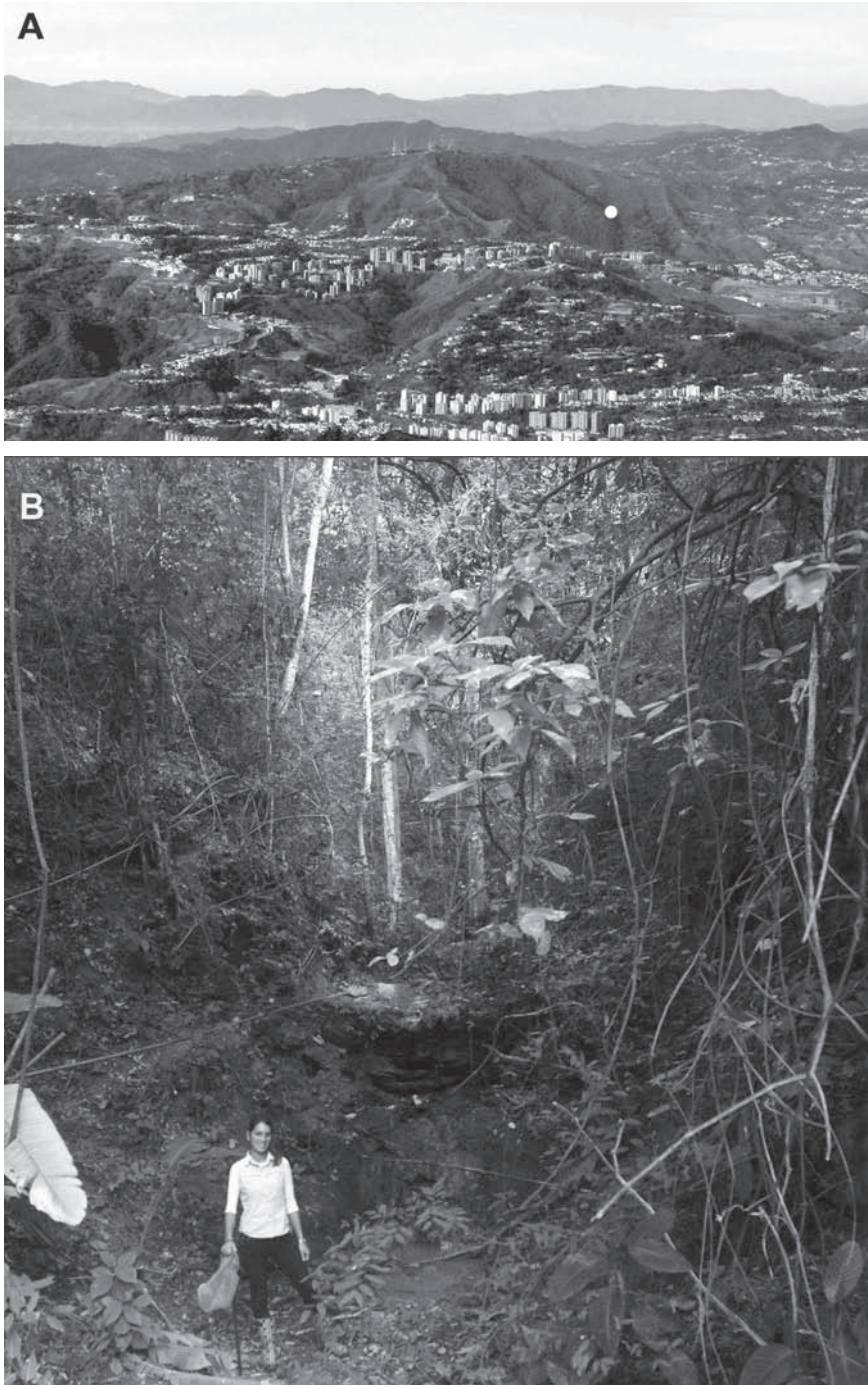


Figure 13. (A) General view of the type locality of *Mannophryne vulcano* sp. nov. The white dot indicates the type locality creek at Cerro El Volcán, Caracas. (B) Habitat at the type locality. Photos by Charles Brewer-Carías.

Table 4. List of endangered *Mannophryne* species mentioned by different selected sources. DD = Data Deficient; LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR = Critically Endangered. Criteria follow the IUCN parameters (Stuart et al. 2008).

Taxon	Data source			
	Young et al. 2004	Rodríguez and Rojas Suárez 2008	Stuart et al. 2008	This study
<i>M. caquetio</i>	CR B1ab(iii,v) + 2ab(ii,v)	VU B1ab(iii)/ CR B1ab(iii,v) + 2ab(iii,v)	CR B1ab(iii,v) + 2ab(iii,v)	CR B1ab(iii,v) + 2ab(ii,v)
<i>M. collaris</i>	EN B1ab(iii,v)+2ab(iii, v)	DD/ EN B1ab(iii,v) + 2ab(iii,v)	EN B1ab(iii,v) + 2ab(iii,v)	VU A3ce
<i>M. cordilleriana</i>	VU D2	DD/ VU D2	VU D2	VU D2
<i>M. herminae</i>	NT	NT/ NT	—	LC
<i>M. lamarcai</i>	CR B1ab(iii)	EN B1ab(iii)/ CR (B1ab(iii)	CR B1ab(iii)	CR B1ab(iii)
<i>M. neblina</i>	CR/A1ab(v) + 2ab(v)	CR B1ab(iv) + 2ab(iv)/ CR B1ab(v) + 2ab(v)	CR B1ab(v) + 2ab(v)	CR A1ab(v) + 2ab(v)
<i>M. orellana</i>	—	—	—	VU D2
<i>M. riveroi</i>	—	—	EN B1ab(iii)	EN B1ab(iii)
<i>M. urticans</i>	—	—	—	EN B1ab(iii)
<i>M. vulcano</i>	—	—	—	EN B1ab(iii)
<i>M. yustizi</i>	EN/B1ab(iii)	DD/ EN B1ab(iii)	EN B1ab(iii)	VU D2

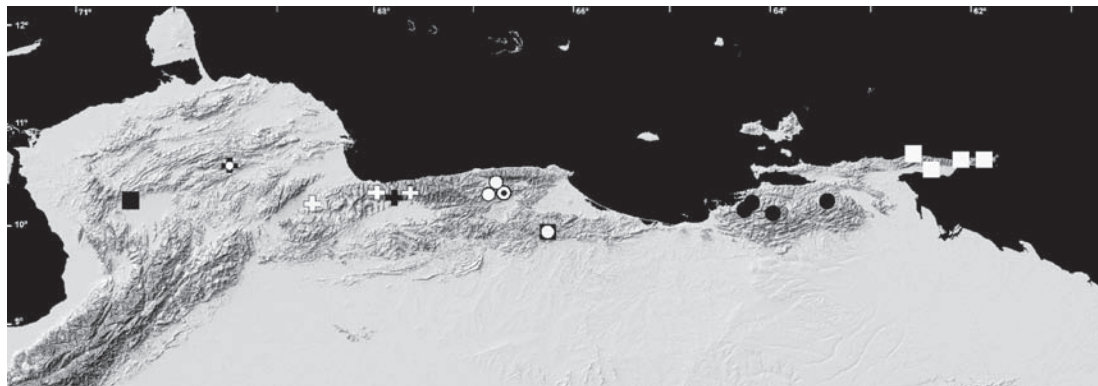


Figure 14. Distribution of *Mannophryne* in the Cordillera de la Costa. *M. lamarcai*: black square. *M. caquetio*: black cross with white circle inside. *M. herminae*: white crosses. *M. neblina*: black cross. *M. vulcano* sp. nov.: white circles; white circle with a black dot inside indicates type locality. *M. oblitterata*: black square with white circle. *M. leonardo*: black dots. *M. venezuelensis*: white squares (easternmost two coincide with the distribution of *M. riveroi*).

Natural history.—Males have been heard frequently at the type locality in the dry season (February–April), as well as in the wet season (June and September–November). No males were seen carrying larvae. Females were more conspicuous than males in the streambed; they used long jumps to escape quickly to debris or even to the water, where they were easily captured. The streams where the species was collected are narrow (Figure 13B) and sometimes deep, located in trenches several meters deep. The apparently conspecific population at Monte Avila, also occurs along streams (Quebrada Maripérez, Quebrada Chacafto); males have been noted to call insistently from leaf-litter debris (exposed or not) as far as several dozen meters from the stream.

Vocalization.—The call that was analyzed call is a section of a trill that lasted several minutes. It was recorded at 21.5 °C the evening of the 19 of June, 2007 at the type locality. The recorded section of the call has 44 duplets of notes (Figure 12A), lasting 20 sec. Two whistle-like notes with ascending frequency modulation form the duplets. Two to three duplets of notes are produced per second (Figure 12B). The dominant frequency of the first pulse is lower

than the second (mean \pm SD and range, respectively) with a dominant frequency of 4550 ± 28.0 , 4502–5599 Hz while the fundamental is 4226 ± 23.4 , 4212–4260 Hz, and the second pulse with a dominant frequency of 4712 ± 39.7 , 4647–4744 Hz and a fundamental frequency of 4437 ± 24.8 , 4405–4453 Hz. Ten consecutive duplets were chosen at random on the spectrogram to determine note duration and inter-note interval. All call parameters include mean \pm SD and range. Duplet duration (0.09 ± 0.011 ; 0.08–0.11 sec), first note duration (0.03 ± 0.004 ; 0.0023–0.0033 sec), second note duration (0.027 ± 0.005 ; 0.0023–0.0034 sec), inter-duplet interval (0.33 ± 0.08 ; 0.02–0.041 sec) and inter-note interval (0.04 ± 0.003 ; 0.0033–0.0043 sec).

Distribution.—*Mannophryne vulcano* is currently known from the type locality at Cerro El Volcán in Baruta, southern Caracas, Estado Miranda (Figure 13A). Other populations of similarly shaped and sized *Mannophryne* are known in Caracas at the Monte Avila National Park (the northern range of the Cordillera de la Costa), el Hatillo (Alemán 1952), and Caricuao (Molina 2003); these could prove to be the same taxon (Figure 14).

Etymology.—The specific name refers to the primary locality where the species was collected—viz., Cerro el Volcán—although the species is more widespread in the Caracas Valley. This *cerro*, or mountain, resembles, but is not, a volcano.

Discussion

Frogs of the genus *Mannophryne* are known from the Andes and the Cordillera de la Costa of Venezuela. In the Andes, only *Mannophryne collaris* (Boulenger, 1912) was known until La Marca (1989) described *M. yustizi*. Most populations of *Mannophryne* from the Mérida Andes were assumed to be *M. collaris*, including all populations from the eastern versant of the Cordillera de Mérida toward Los Llanos. *Mannophryne cordilleriana* was thought to be a restricted endemic from the surroundings of its type locality in Pueblo Llano (La Marca 1994), but Barrio-Amorós and Molina (2010) reported it from three more sites in the eastern versant of the Cordillera de Mérida, and with our data we see that it is more widespread through the eastern versant of the Cordillera de Mérida from 200–1950 m (Figure 4). Therefore, *M. collaris* is restricted to the Chama River Valley and its tributaries (Río Mocotíes) between 195 and 1900 m. *Mannophryne yustizi* also has a wider distribution than previously assumed through the northeastern branch of the Cordillera de Mérida (Figure 4). *Mannophryne larandina*, as recently demonstrated by Manzanilla *et al.* (2009) most probably is a synonym of *M. yustizi*, although no taxonomic change has been made yet. Two recently described species, *M. trujillensis* (Vargas and La Marca 2007) and *M. speeri* (La Marca 2009), apparently have restricted distributions in the Venezuelan Andes.

In the Cordillera de la Costa, members of *Mannophryne* (as *Phyllobates*, *Prostherapis*, and *Colostethus*) have been known from the area of Caracas. The earliest account of collared frogs was provided by Boettger (1896), who

identified them as *Prostherapis trinitatis*. Following him, other authors (e.g., Stejneger 1901, Lutz 1927, Hellmich 1940, Alemán 1952, Rivero 1961, Solano 1968) also mentioned collared frogs from the creeks at the Monte Avila (= Serranía El Ávila at the northern city limit of Caracas). More recently, La Marca (1994) assumed *M. trinitatis* to occur in three states of Venezuela (Guárico, Monagas, and Sucre), and Barrio-Amorós (1998) reported *M. trinitatis* from eight states (Distrito Federal, Guárico, Lara, Miranda, Monagas, Sucre, and Yaracuy). However, Barrio-Amorós *et al.* (2006) restricted the distribution of that species to Trinidad, leaving the Venezuelan populations as putative undescribed species. The population from Península de Paria was described already as *M. venezuelensis* (Manzanilla *et al.* 2007) and the rest of populations remained unnamed. *Mannophryne* in the region of Caracas have been also assumed to be *M. herminae* (*sensu* Molina 2003). Although no taxonomic study has been undertaken to determine the identity of the Caracas frogs, it seemed clear to Barrio-Amorós *et al.* (2006) that they were not *M. trinitatis*, and that their taxonomic status required a careful review of all available and new specimens to be collected. Herein, we provide the first clear taxonomic description of the Caracas Collared Frog, applying the new name *Mannophryne vulcano*. The genus *Mannophryne* seems to be highly speciose in the Cordillera de la Costa; we anticipate that there are many species yet to be described. Similarly, the diversity surveys and careful inventories are required in Venezuelan Andes, which doubtless also will produce many more undescribed species to increase the already rich diversity of Venezuelan dendrobatids.

Almost all species of *Mannophryne* remain abundant in appropriate habitats, with only two species seemingly threatened by restriction to their natural distributions. *Mannophryne neblina*, considered by Stuart *et al.* (2008) as Critically Endangered, was described by Test (1956), and since then, only a few specimens have been

captured and deposited in museums. Its declination parallels that of other formerly abundant species at the same locality—Rancho Grande at Parque Nacional Henri Pittier, Estado Aragua—such as *Hylomantis medinae*, *Atelopus cruciger*, and *Pristimantis anotis*. *Mannophryne neblina* is much rarer than its sympatric congener, *M. herminae*, at Rancho Grande; despite this, we have observed some individuals, as apparently Lotkatz (2007) did at Macizo de Nirgua, Estado Yaracuy. We cannot speculate the cause of the decline of *M. neblina*, because its sympatric congener, *M. herminae*, remains abundant in Rancho Grande and surroundings.

The only other *Mannophryne* that might be endangered by habitat destruction in its restricted distribution is *M. lamarcai* (as already pointed out Mijares Urrutia and Arends 1999b), another species that is considered as Critically Endangered by Stuart *et al.* (2008). *Mannophryne caquetio* also is noted as Critically Endangered, although its distribution is much broader than the previous species. We observed recently abundant populations at Sierra de San Luis, estado Falcón. La Marca (1995) observed a sudden local decline of *M. collaris* in the city of Mérida, which is consistent with urbanization and habitat destruction. The species, endemic from the Río Chama Valley and its tributaries (Figure 4), survives well only in undisturbed areas; in perturbed habitats, its populations clearly vanished or disappeared (e.g., El Vallecito, El Arenal, and other areas where it was formerly known). *Mannophryne riveroi* is considered Endangered by Stuart *et al.* (2008) and Barrio-Amorós *et al.* (2010). Lampo *et al.* (2006) reported infection with *Batrachochytrium dendrobatidis* (*Bd*) in *M. cordilleriana* and Sánchez *et al.* (2008) found *M. collaris* also infected with *Bd*.

The three new species can be quite common in appropriate areas, but in many parts of Caracas, the populations of *Mannophryne vulcano* are threatened by anthropogenic habitat alteration and urban development. We consider this species as Endangered (details in Table 2).

We urge the environmental authorities (Ministerio del Ambiente) to enforce the protection policies for Parque Nacional El Avila, which harbors the only endemic species of *Mannophryne* of Caracas. It is expected, however, that the increase of use of agrochemicals will quickly affect *M. urticans* and *M. orellana* (pers. obs.), although the southern population of the latter species is protected by the Parque Nacional El Tamá. Owing to its apparently wider distribution, we consider *M. orellana* as Vulnerable species under the UICN criteria, and *M. urticans* as Endangered, given its seemingly much restricted distribution. Table 4 shows all endangered species of *Mannophryne* with its respective categories sensu different criteria.

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References

- Alberch, P. and E.A. Gale, 1985. A developmental analysis of an evolutionary trend: digital reduction in amphibians. *Evolution* 39: 8–23.
- Alemán, C. 1952. Apuntes sobre reptiles y anfibios de la región Baruta-El Hatillo. *Memoria Sociedad Ciencias Naturales La Salle* 12: 11–30.
- Barrio-Amorós, C. L. 1998. Sistemática y biogeografía de los anfibios (Amphibia) de Venezuela. *Acta Biologica Venezuelica* 18: 1–93.
- Barrio-Amorós, C. L. 2001. Some aspects of Dendrobatids in Venezuela: declines and nomenclature. *British Dendrobatid Group Newsletter* 44: 1–5. (<http://www.thebdg.org/library/Conservation/venezuela.htm>.)
- Barrio-Amorós, C. L. 2009. Riqueza y Endemismo. Pp. 25–39 in C. Molina, J. C. Señaris, M. Lampo and A. Rial (eds.), *Anfibios de Venezuela – Estado del Conocimiento y Recomendaciones para su Conservación*. Ediciones Grupo TEL, Caracas. 131 pp.
- Barrio-Amorós, C. L. 2010. A suggestion about common nomenclature for dendrobatids. Available online at: http://www.dendrobates.org/common_names.html.
- Barrio-Amorós, C.L. and C. Molina. 2010. Herpetofauna del Ramal de Calderas, Andes de Venezuela. Pp. 74–80 in A. Rial, J. C. Señaris, C. A. Lasso and A. Flores (eds.), *Evaluación Rápida de la Biodiversidad y Aspectos Socioecosistémicos del Ramal de Calderas. Andes de Venezuela. RAP Bulletin of Biological Assessment* 56. Conservation International, Arlington, VA. U.S.A. 183 pp.
- Barrio-Amorós, C. L. and J. C. Santos. 2009. Description of a new *Allobates* (Amphibia: Anura: Dendrobatidae) from the eastern Andean piedmont, Venezuela. *Phyllomedusa* 8: 89–104.
- Barrio-Amorós, C. L., G. Rivas, C. Molina and H. Kaiser. 2006. *Mannophryne trinitatis* (Anura: Dendrobatidae) is a Trinidadian single-island endemic. *Herpetological Review* 37: 298–299.
- Barrio-Amorós, C. L., G. Rivas, C. Molina, J. C. Santos and H. Kaiser. 2010. Intraspecific variation in the endangered frog *Mannophryne riveroi* (Anura, Dendrobatidae, Aromobatinae), with comments on coloration and natural history. *Herpetological Notes* 3: 151–160.
- Boettger, O. 1896. Geschenke und Erwerbungen, Juni 1895 bis Juni 1896, Reptilien und Batrachiersammlung. *Berichte der Senckenbergischen naturforschenden Gesellschaft* 1896: LIV–LV.
- Boulenger, G. A. 1912. Descriptions of new Batrachians from the Andes of South America, preserved in the British Museum. *Annals of the Magazine of Natural History* 10: 185–191.
- Coloma, L. 1995. Ecuadorian frogs of the genus *Colostethus* (Anura: Dendrobatidae). *University of Kansas Natural History Museum Miscellaneous Publications* 87: 1–72.
- Dixon, J. R. and C. Rivero-Blanco. 1985. A new dendrobatid frog (*Colostethus*) from Venezuela with notes on its natural history and that of related species. *Journal of Herpetology* 19: 177–184.
- Donoso-Barros, R., 1964. A new species of dendrobatid frog, *Prostherapis riveroi*, from Venezuela. *Caribbean Journal Science* 4: 485–489.
- Garman, S. 1887. On West Indian reptiles and batrachians in the Museum of Comparative Zoology. *Bulletin Essex Institute* 19: 1–24.
- Grant, T., E. C. Humphrey and C. W. Myers. 1997. The median lingual process of frogs: a bizarre character of old world ranoids discovered in South American dendrobatids. *American Museum Novitates* 3212: 1–40.
- Grant, T., D. R. Frost, J.P. Caldwell, R. Gagliardo, C. F. B. Haddad, P. J. R. Kok, D. B. Means, B. P. Noonan, W. E. Schargel and W. C. Wheeler. 2006. Phylogenetic systematics of dart-poison frogs and their relatives (Amphibia: Athesphatanura: Dendrobatidae). *Bulletin of the American Museum of Natural History* 299: 1–262.
- Hellmich, W. 1940. Contribución al conocimiento de la fauna Venezolana. *Boletín de la Sociedad Venezolana de Ciencias Naturales* 6: 318–327.
- Kaiser, H., L. A. Coloma and H. M. Gray. 1994. A new species of *Colostethus* (Anura: Dendrobatidae) from Martinique, French Antilles. *Herpetologica* 50: 23–32.
- La Marca, E. 1989. A new species of collared frog (Anura: Dendrobatidae: *Colostethus*) from Serranía de Portuguesa, Andes of Estado Lara, Venezuela. *Amphibia-Reptilia* 10: 175–183.
- La Marca, E. 1992. *Catálogo taxonómico, biogeográfico y bibliográfico de las ranas de Venezuela*. Cuadernos Geográficos U.L.A., Mérida 9: 1–197.
- La Marca, E. 1994. Taxonomy of the frogs of the genus *Mannophryne* (Amphibia: Anura: Dendrobatidae). *Publicaciones Asociación Amigos Doñana* 4: 1–75.
- La Marca, E. 1995. Crisis de biodiversidad en anfibios de Venezuela: estudio de casos. Pp. 47–70 in M. Alonso (ed.), *Cuadernos-Química Ecológica 4 “La Biodiversidad Neotropical y la Amenaza de las Extinciones”* Facultad Ciencias ULA, Mérida, Venezuela. 160 pp.

- La Marca, E. 2009. A frog survivor (Amphibia: Anura: Aromobatidae: *Mannophryne*) of the traditional coffee belt in the Venezuelan Andes. *Herpetotropicos* 5: 49–54.
- Lampo, M., A. Rodríguez, E. La Marca and P. Daszak. 2006. A chytridiomycosis epidemic and a severe dry season precede the disappearance of *Atelopus* species from the Venezuelan Andes. *Herpetological Journal* 16: 395–402.
- Lotkatz, S. 2007. Taxonomía y zoogeografía de la herpetofauna del macizo de Nirgua, Venezuela. Unpublished PhD Thesis, Johann Wolfgang Goethe-Universität, Frankfurt am Main, Germany. 160 pp.
- Lutz, A. 1927. Notas sobre batrachios da Venezuela e da Ilha de Trinidad. *Memórias do Instituto Oswaldo Cruz* 20: 35–65.
- Manzanilla, J., E. La Marca and M. García-París. 2009. Phylogenetic patterns of diversification in a clade of neotropical frogs (Anura: Aromobatidae: *Mannophryne*). *Biological Journal of the Linnean Society* 97: 135–199.
- Manzanilla, J., M. Jowers, E. La Marca and M. García-París. 2007. Taxonomic reassessment of *Mannophryne trinitatis* (Anura: Dendrobatidae) with a description of a new species from Venezuela. *Herpetological Journal* 17: 31–42.
- Manzanilla, J., E. La Marca, M. Jowers, D. Sánchez and M. García-París. 2005 “2007”. Un nuevo *Mannophryne* del macizo del Turimiquire, noreste de Venezuela. *Herpetotropicos* 2: 105–113.
- Mijares-Urrútia, A. E. and A. Arends. 1999a. Un nuevo *Mannophryne* (Anura: Dendrobatidae) del estado Falcón, con comentarios sobre la conservación del género en el noroeste de Venezuela. *Caribbean Journal Science* 35: 231–237.
- Mijares-Urrútia, A. E. and A. Arends. 1999b. A new *Mannophryne* (Anura: Dendrobatidae) from western Venezuela, with comments on the generic allocation of *Colostethus larandinus*. *Herpetologica* 55: 106–114.
- Molina, C. 2003. Ecología de *Mannophryne herminae* (Boettger 1893) (Anura: Dendrobatidae) en la Cordillera de la Costa, Venezuela. Unpublished PhD Thesis. Facultad de Ciencias, Universidad Central de Venezuela. 223 pp.
- Myers, C.W. and W.E. Duellman. 1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. *American Museum Novitates* 2752: 1–32.
- Rivero, J. A. 1961. Salientia of Venezuela. *Bulletin Museum Comparative Zoology* 126: 1–267.
- Rivero, J. A. 1984. Una nueva especie de *Colostethus* (Amphibia, Dendrobatidae) de la Cordillera de la Costa, con anotaciones sobre otros *Colostethus* de Venezuela. *Brenesia* 22: 51–56.
- Rodríguez, J. P. and F. Rojas-Suárez (eds.). 2008. *Libro Rojo de la Fauna Venezolana*. Provita y Shell Venezuela S.A., Caracas, Venezuela. 332 pp.
- Sánchez, D., A. Chacón-Ortiz, F. León, B. A. Han and M. Lampo. 2008. Widespread occurrence of an emerging pathogen in amphibian communities of the Venezuelan Andes. *Biological Conservation* 141: 2898–2905.
- Santos J. C., L. A. Coloma, K. Summers, J. P. Caldwell and R. Ree. 2009. Amazonian amphibian diversity is primarily derived from late Miocene Andean lineages. *PLoS Biology* 7, e1000056. doi:10.1371/journal.pbio.1000056: 1–14.
- Solano, H. 1968. Anfibios comunes del Valle de Caracas. Pp. 259–294 in *Estudio de Caracas, Vol I (Ecología Vegetal y Fauna)*. Universidad Central de Venezuela, Caracas. 468 pp.
- Stejneger, L. 1901. An annotated list of Batrachians and Reptiles collected in vicinity of La Guaira, Venezuela, with description of two new species of snakes. *Proceedings of the United States Natural Museum* 24: 172–192.
- Stuart, S. N., M. Hoffman, J. Chanson, N. Cox, R. Berridge, P. Ramani and B. Young (eds.). 2008. *Threatened Amphibians of the World*. Lynx Editions, Barcelona, Spain; IUCN, Gland, Switzerland; Conservation International, Arlington, Virginia, U.S.A. 758 pp.
- Test, F. H. 1956. Two new dendrobatid frogs from northern Venezuela. *Occasional Papers of the Museum of Zoology, University of Michigan* 577: 1–9.
- Vargas, J. and E. La Marca. “2006” 2007. A new species of collared frog (Amphibia: Anura: Dendrobatidae: *Mannophryne*) from the Andes of Trujillo State, Venezuela. *Herpetotropicos* 3: 51–57.
- Vences, M., J. Kosuch, R. Boistel, C. Haddad, E. La Marca, S. Lotters and M. Veith. 2003. Convergent evolution of aposematic coloration in Neotropical poison frogs: a molecular phylogenetic perspective. *Organism Diversity Evolution* 3: 215–226.
- Young, B. E., S. N. Stuart, J. S. Chanson., N. A. Cox. and T. M. Boucher. 2004. *Joyas que Están Desapareciendo: el Estado de los Anfibios en el Nuevo Mundo*. NatureServe, Arlington, Virginia. 54 pp.
- Yústiz, E. 1991. Un nuevo *Colostethus* (Amphibia: Dendrobatidae) en la Sierra de Barbacoas, Estado Lara, Venezuela. *Bioagro* 3: 145–151.

Appendix I. Species diversity of *Mannophryne* from Venezuela.

Several species of *Mannophryne* are illustrated for comparative purposes (Figures 15 to 21). The species name is followed by the sex, museum number, and locality of the specimen. All photographs are by C. Barrio-Amorós, unless otherwise indicated. In the case of each species, the left photo depicts a dorsolateral view, whereas the right illustrates the venter and gular regions, unless otherwise described.



Figure 15. *Mannophryne collaris*: (A, B) Male, CVULA 7260, from vía Santa Cruz de Mora-Los Ranchos, 937 m, Estado Mérida. (C, D) Female, CVULA 7255, from Estanquillo, San Juan de Lagunillas, 1120 m, Estado Mérida. *Mannophryne cordilleriana*: (E, F) Male, not collected, La Mitisús-las Piedras Road, 1690 m, Estado Mérida.

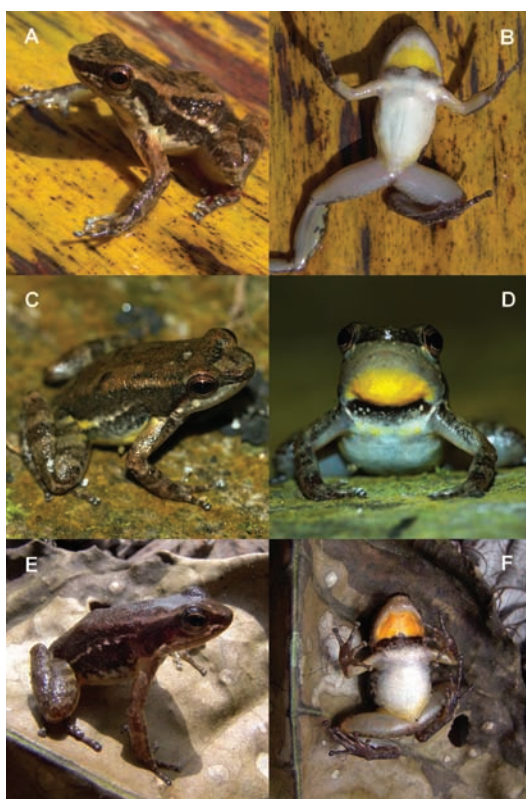


Figure 16. *Mannophryne cordilleriana*: (A, B) Female, CVULA 7218, from La Soledad, 1017 m, Estado Barinas. *Mannophryne herminae*: (C, D) Female, not collected. Rancho Grande, Parque Nacional Henri Pittier, 1100 m. Estado Aragua. (E, F) Female, not collected. Casa María, Bejuma-Canoabo Road, 900 m, Estado Carabobo.



Figure 17. *Mannophryne leonardoi*: (A, B) Male, not collected. Caripe, 1030 m, Estado Monagas. (C, D) Female, CVULA 7243, from Caripe, 1030 m, Estado Monagas. *Mannophryne riveroi*: (E, F) Male, CVULA 7215, from southern slope of Cerro El Humo, Península de Paria, 724 m, Estado Sucre.



Figure 18. *Mannophryne riveroi*: (A, B) Female, MHNLS 17480, From southern slope of Cerro El Humo, Península de Paria, 724 m, Estado Sucre. *Mannophryne speeri*: (C, D) Male, CVULA 7323, from Chavasquén–Guarico Road, 1234 m, Estado Portuguesa; (E, F) Female, CVULA 7322, from same locality as D.



Figure 19. *Mannophryne* cf. *trujillensis*: (A, B) Male, not collected. Monte Carmelo, 1021 m, Estado Trujillo (photos by Juan Pablo Diasparra). *Mannophryne venezuelensis*: (C, D) Male, CVULA 7268, from southern slope Cerro El Humo, Península de Paria, 724 m, Estado Sucre. (E, F) Female, CVULA 7270, from same locality as D.

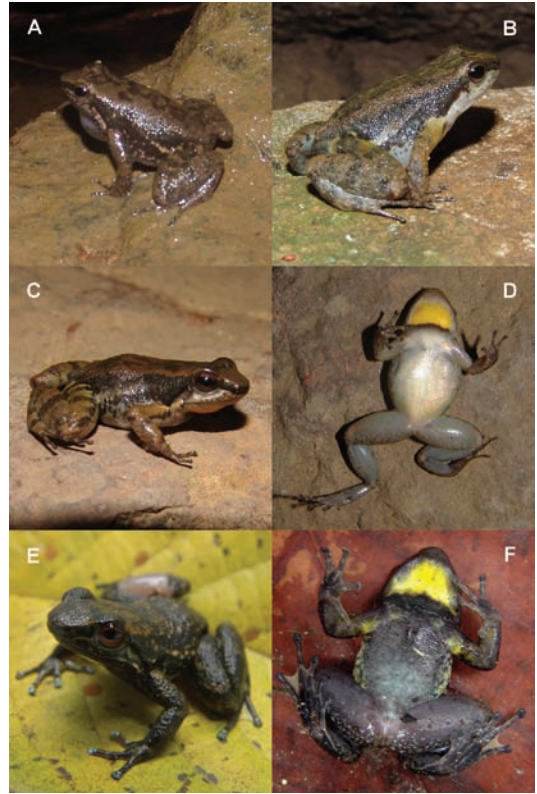


Figure 20. *Mannophryne* cf. *caquetio*: (A) Calling male, not collected. (B) Adult female, not collected. Both from San José, Cabure, Sierra de San Luis, Estado Falcón. (C, D) Female, CVULA 7403, from San José, Cabure, Sierra de San Luis, Estado Falcón. *Mannophryne oblitteratus*: (E, F) Male, CVULA 7240, from Quebrada Macanilla, Guatopo, 569 m, Estado Miranda.



Figure 21. *Mannophryne yustizi*: (A, B) Female, not collected. Sanare–Yacambú Road, 1880 m, Estado Lara.

Appendix II. Specimens Examined (all specimens are from Venezuela).

Mannophryne aff. *caquetio*: ESTADO FALCÓN: Cabure: San José: CVULA 7403.

Mannophryne collaris: ESTADO MÉRIDA: Lagunillas: Estanquillo, 1120 m: CVULA 7251–58; Mérida City: Urbanización Santa María, 1600 m: CVULA 1029, 1464, 1468, 1493, 6232–8; Mérida–Apartaderos Road: El Arenal: MHNLS 6127–33; San Juan de Lagunillas: Jardín Botánico Universidad de los Andes: CVULA 30–35, 55–62, 64–71; Santa Cruz de Mora–Los Ranchos Road, 937 m: CVULA 7259–64; Sector Trujillano: Mérida–El Vigía Road, after the tunnels, 215 m: CVULA 7305–09.

Mannophryne cordilleriana: ESTADO BARINAS: La Soledad, 1017 m: CVULA 7217–22. ESTADO MÉRIDA: La Mitisús–Las Piedras Road, 1690 m: CVULA 7246–50.

Mannophryne cf. *herminae*: ESTADO ARAGUA: Parque Nacional Henri Pittier, Rancho Grande: CVULA 7288.

Mannophryne leonardo: ESTADO MONAGAS: Cueva del Guácharo: CVULA 7242–45.

Mannophryne neblina: ESTADO ARAGUA: Parque Nacional Henri Pittier: Rancho Grande, 1100 m: MBUCV 2091 (ex UMMZ 113022), paratype.

Mannophryne obliterata: ESTADO MIRANDA: Parque Nacional Guatopo: CVULA 7240–41; MBUCV 0858 (two specimens).

Mannophryne rivero: ESTADO SUCRE: Las Melenas–Cerro el Humo Path, 750 m: CVULA 7215–16; MHNLS 17455.

Mannophryne speeri: ESTADO LARA: Biscucuy–Guarico Road, 1459 m: CVULA 7295–304.

Mannophryne trinitatis: TRINIDAD and TOBAGO: Arima Valley: a stream along the Arima–Blanchisseuse Road near Asa Wright Nature Centre, ca. 250 m: CVULA 7275–79; MHNLS 17461.

Mannophryne venezuelensis: ESTADO SUCRE: Península de Paria: southern slope of Cerro El Humo, 10°41' N, 62°37' W, 800 m: CVULA 7265–70; EBRG 299; MHNLS 17449–54, 17499–501.

Mannophryne yustizi: ESTADO LARA: Sanare–Yacambú Road, 1400 m: CVULA 7310–11.

Mannophryne aff. *yustizi*: ESTADO LARA: Barquisimeto: Tarabana: CVULA 7289–94.