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urn:lsid:zoobank.org:pub:F37943EB-017F-4C0A-802F-892B672DD26B

A new highland species of treefrog of the *Dendropsophus columbianus* group (Anura: Hylidae) from the Andes of Colombia

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Abstract

A new species of tree frog of the genus *Dendropsophus* is described from the highlands of the Cordillera Central of the Andes, departamento de Antioquia, Colombia (06°58'50"N, 75°08'07"W, 1700 m a.s.l.). *Dendropsophus norandinus* **sp. nov.** differs from other Andean *Dendropsophus* previously described by the following combination of traits: dorsal skin smooth with minute scattered tubercles; axillary membrane developed; distal subarticular tubercle of fourth finger bifid; ventral surfaces cream with variable brown markings on gula, throat, and outer region of belly; medial area of the belly immaculate; in life axilla and groin pale yellow in males and bright orange in females; toe webbing extensive [I (1–1⁺)–(1^{1/2}–1^{3/4}) II 1–(2–2⁺) III 1–(2–2⁺) IV (2–2⁺)–1 V], and tadpoles with tooth row formula of 0/2. On the basis of morphological similarities, principally between tadpoles, we tentatively assign this new species to the *Dendropsophus columbianus* group.

Key words: Andes, external morphology, tadpole, taxonomy

Resumen

Describimos una nueva especie de rana arbórea del género *Dendropsophus* de las tierras altas de la Cordillera Central de los Andes en el departamento de Antioquia, Colombia (06°58'50"N, 75°08'07"W, 1700 m s.n.m.). *Dendropsophus norandinus* **sp. nov.** se diferencia de otros *Dendropsophus* andinos previamente descritos por la siguiente combinación de características: piel dorsal lisa con tubérculos diminutos; membrana axilar desarrollada, tubérculo subarticular distal en el cuarto dedo bífido; superficie ventral crema con pequeñas manchas irregulares en la gula, garganta y en la región lateral del abdomen; región medial del vientre immaculado; en vida axila e ingle amarillo pálido en machos y naranja brillante en hembras; membranas interdigitales de los pies más desarrolladas [I (–1⁺)–(1^{1/2}–1^{3/4}) II 1–(2–2⁺) III 1–(2–2⁺) IV (2–2⁺)–1 V] y renacuajos con una fórmula de hileras de dientes 0/2. Basándonos en la similitud morfológica, principalmente entre los renacuajos, asignamos la nueva especie de forma tentativa al grupo *Dendropsophus columbianus*.

Palabras clave: Andes, morfología externa, renacuajo, taxonomía

Introduction

The genus *Dendropsophus* Fitzinger, 1843 currently contains 95 species (Amphibiaweb 2012) distributed in tropical America from southern Mexico across Central and South America south to northern Argentina and Uruguay (Frost 2011). The monophyly of *Dendropsophus* is supported by molecular data. Other suggested synapomorphies are the occurrence of 30 chromosomes in all species with known karyotypes, the extreme

reduction in the quadratojugal, and tadpoles with a 1/2 labial tooth row formula with subsequent reduction in some species (Duellman & Trueb 1983; Duellman *et al.* 1997; Faivovich *et al.* 2005 and references therein). Faivovich *et al.* (2005) recognized nine species groups for *Dendropsophus*, of which the *D. columbianus*, *D. garagoensis*, and the *D. labialis* species groups are endemic to the highlands of the northern Andes of Colombia, Ecuador and Venezuela.

While conducting biodiversity amphibian's surveys in the northern mountains of the Cordillera Central of Colombia, we collected a series of individuals of a species that was relatively abundant in puddles of pasturelands. Through comparisons with museum specimens and original descriptions of other *Dendropsophus* inhabiting the highlands of the Andes, we considered that the specimens collected belong to an undescribed species. Thus, the goals of this paper are to (1) name and describe this new species, using adult and tadpole morphology and (2) briefly discuss the composition of the *Dendropsophus columbianus* group.

Material and methods

Adults and juveniles were captured manually and tadpoles were collected with dip nets. All individuals were sacrificed in 0.25% chloroform solution and fixed in 10% formaldehyde solution. Adults were transferred to and kept in 70% ethanol within five days of fixation. Prior to fixation, tissue samples from some specimens were collected and preserved in 96% ethanol. Measurements of adults (n = 24) follow Duellman (1970) and Heyer *et al.* (1990). Webbing formulae follow Savage and Heyer (1967) as modified by Myers and Duellman (1982). Measurements (all in mm) were taken with digital calipers to the nearest 0.1 mm under a dissecting stereomicroscope, abbreviations used throughout the text are: SVL (snout-vent length), TBL (tibia length), HW (head weight), HL (head length), IOD (inter-orbital distance), IND (inter-nostril distance), END (nostril-eye distance), NSD (nostril-tip of snout distance), ED (eye diameter), TD (tympanic diameter), TFD (third finger diameter), FTD (fourth toe diameter), THL (thigh length), and FL (foot length).

Tadpoles were staged according to Gosner (1960) and larval morphological terminology follows Altig and McDiarmid (1999). Lateral line system nomenclature follows Lannoo (1999). Measurements (all in mm) of tadpoles (n = 22) correspond to values obtained from individuals at stages 30 to 39, abbreviations used throughout the text are: TL (total length), BL (body length), BH (body height), OD (eye diameter), ND (nostril diameter), BW (body weight), IO (inter-orbital distance), IN (inter-nostril distance), NS (nostril–snout distance), ES (eye–snout distance), SS (spiracle–snout distance), ODL (oral disc length), TMH (tail muscle height), and MTH (maximum tail height). To confirm the association of tadpoles with adults of the new species we sequenced a fragment (585 bp) of the mitochondrial ribosomal gene 16S rRNA from one adult (MHUA-A 4092) and one tadpole (MHUA-L 0153); DNA isolation and sequencing followed Faivovich *et al.* (2005). Genetic divergence between adults and tadpole was minimal (= 0.17%; Victor Orrico and MRC, unpublished data). The sequence of the new species was compared with the most similar sequences available in GenBank by BLAST (*Dendropsophus carnifex*: AY843616.1 and *D. labialis*: AY843635.1). Coloration was based field notes and life photographs. Drawings were made using a Zeiss stereomicroscope with attached drawing tube. Field numbers correspond to Marco Rada and Mauricio Rivera (MAR and MRC respectively). Institutional acronyms are ICN (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia), and MHUA-A (amphibian collection to Museo de Herpetología Universidad de Antioquia, Medellín, Colombia), MHUA-L (tadpole collection to MHUA).

Results

Dendropsophus norandinus sp. nov.

(Fig. 2)

Holotype. MHUA-A 3781, adult female, Colombia, departamento de Antioquia, municipio de Anorí, vereda El Roble, Bosque La Forzosa, 06°58'50"N, 75°08'07"W, ca. 1700 m a.s.l., November 14, 2003, collected by Mauricio Rivera and Paula Mejía.

Paratypes. 15 adult males (MHUA-A 3768-3777, 3786-3790) and seven adult females (MHUA-A 3778-80, 3782-85), collected with the holotype; MHUA-A 4092, adult female, Colombia, departamento de Antioquia,

municipio de Anorí, vereda el Retiro, finca El Chaquiral, 6°58.8' N, 75°7.83'W, ca. 1732 m a.s.l., November 26, 2005, collected by Taran Grant and Paul D. Gutiérrez. MHUA-A 5274, adult male, Colombia, departamento de Antioquia, municipio de Amalfi, vereda Salazar, Finca Bodega Vieja, ca. 1440 m a.s.l., July 6–7, 2006, collected by Marco Rada. MHUA-L 0152, (13 tadpoles), Colombia, departamento de Antioquia, municipio de Anorí, vereda El Roble, Bosque La Forzosa, 06°58'50"N, 75°08'07"W, ca. 1700 m a.s.l., November 2005, collected by Paul D. Gutiérrez. MHUA-L 0153, (9 tadpoles), Colombia, departamento de Antioquia, municipio de Amalfi, vereda Salazar, Finca Bodega Vieja, ca. 1440 m a.s.l., July 6–7, 2006, collected by Marco Rada.

Diagnosis. We assigned the new species to the genus *Dendropsophus* because of the reduced labial tooth row formula in tadpoles (Duellman & Trueb 1983), overall similarity with other species of the genus (Fig. 1) and DNA sequences similarity. A blast of a fragment (585 bp) of the 16S rRNA to sequences deposited in Genbank retrieved *D. carnifex* as the most similar sequence (Max ident = 94.88%). *Dendropsophus norandinus* is distinguished from other species of *Dendropsophus* by the following combination of traits: 1) SVL in adult females (Fig. 2) 30.4–35.8 (n = 9), in adult males 24.8–27.8 (n = 15); 2) snout short, rounded in dorsal view and slightly rounded in lateral view, head wider than long; 3) *canthus rostralis* rounded in cross-section, loreal region slightly concave; 4) tympanum rounded, tympanic annulus distinct, upper edge covered by a supratympanic fold; 5) vomerine teeth prominent, left and right odontophores separated medially, between choanae; 6) skin on dorsal surfaces smooth, with some minute scattered tubercles; 7) axillary membrane present and developed; 8) discs relatively wide, webbing formulae of fingers I (2–2^{1/2})–2 II 1^{1/2}–(2–2^{1/2}) III (2–2^{1/2})–2 IV, webbing formulae of toes I (1–1⁺)–(1^{1/2}–1^{3/4}) II 1–(2–2) III 1–(2–2) IV (2–2)–1 V; 9) bifid distal subarticular tubercle in the fourth finger; 10) in life, ventral surfaces cream with brown marks on the gula, throat, and the lateral areas of the belly in females; 11) medial area of the belly immaculate; 12) in life, dorsum reddish brown in females and cream or silver grey in males 13) in life, axilla and groin bright orange in females and pale yellow in males; 14) light gray iris with gold and copper chromatophores and purple dark blotches; 15) pupil horizontal, palpebral membrane translucent.

Comparisons with similar species. *Dendropsophus norandinus* is most similar to the species of the *D. columbianus* and *D. garagoensis* groups than to species of the *D. labialis* group, and is distinguished from these by the following characteristics (those of *D. norandinus* in parenthesis). *Dendropsophus bogerti* (Cochran & Goin) and *D. columbianus* (Boettger) have head longer than wide (wider than long); finger webbing absent (present between fingers III and IV) and toe webbing never starting of the base of the disc (starting in the base of the disc of toes I, II, and III). Additionally, the females of *Dendropsophus bogerti* and *D. columbianus* in life have belly yellow or orange with brown blotches and reticulated pattern in the medial area, being more conspicuous in *D. columbianus* (cream belly with a spotted pattern and markings only in the flanks and never in medial area of belly; Fig. 3B, C); tadpole with labial tooth row formula 1/2 and anterior region of caudal musculature less than 40% of body height (0/2 and musculature more wide, 60% of body height). *Dendropsophus carnifex* (Duellman) have head longer than wide (wider than long); yellow belly in life (cream belly); absence of axillary membrane (axillary membrane present); tadpole with labial tooth row formula 1/2 and anterior region of caudal musculature less than 50% of body height (0/2 and musculature more wide, 60% of body height) and a genetic distance of 5.12% in a fragment 585 pb of mitochondrial DNA sequences between *D. carnifex* and *D. norandinus*. *Dendropsophus garagoensis* (Kaplan) possesses a dorsolateral narrow light green stripe with brown borders from the tip of the snout to the groin (stripe absent); without dark flecks or marks in the gula (dark brown marks present; Fig. 3D); toe webbing less extensive, I 2–2^{1/2} II 1^{1/2}–3⁻ III 1^{1/2}–3⁻ IV 3⁻–1⁺ V [more extensive, I (1–1⁺)–(1^{1/2}–1^{3/4}) II 1–(2–2) III 1–(2–2) IV (2–2)–1 V]. *Dendropsophus labialis* (Peters) with snout short somewhat triangular in dorsal view (short and rounded); *canthus rostralis* moderately defined (rounded); loreal region nearly flat and slightly oblique (slightly concave); a black line extending from the *canthus rostralis* back over the tympanum to widen and fade out the body (absent); axillary membrane well developed bright blue (axillary membrane developed bright orange or pale yellow); axilla and groin blue (bright orange in females and pale yellow in males); vomerine teeth small, odontophores close together between choanae (vomerine teeth prominent, odontophores separated medially) and a genetic distance of 6.90% in a fragment 585 pb of mitochondrial DNA sequences between *D. labialis* and *D. norandinus*. *Dendropsophus meridensis* (Rivero) with black and yellow mottling or marbling on flanks, axilla, groin, ventral parts of the hind limbs, and posterior parts of thighs (absent); ventral surfaces yellowish orange (cream); tadpole with labial tooth row formula 2(2)/2 and oral disc with multiple rows of papillae (0/2 and a single row of papillae present) (Rivero 1961; Mijares-Urrutia 1990). *Dendropsophus padreluna* (Kaplan & Ruiz) have black spots on anteroventral and posterodorsal surfaces of thighs (thighs without spots; Fig. 3E); finger II > IV

(finger II < IV); a dorsolateral stripe extending from the *canthus rostralis* to the end of body (absent). *Dendropsophus pelidna* (Duellman) with snout long (short); head as wide as long (wider than long); webbing absent between fingers I and II (more extensive, I 2–2 II); relative length of toes 1<2<3<5<4 (1<2<3=5<4); venter white with bluish gray suffusion (cream with brown marks in females); flanks areolate (smooth); throat coarsely granular (smooth); ventral surfaces of thighs coarsely granular (finely granular); axilla, groin and hidden surfaces of limbs mottled black and blue (bright orange in females and pale yellow in males); iris deep bronze (light gray) (Duellman 1989). *Dendropsophus praestans* (Duellman & Trueb) possesses bluish gray groin with black spots (orange groin in females and pale or light yellow in males); lacks ulnar tubercles (always with ulnar tubercles); abundant spots in the medial area of the belly and thighs present (medial area of the belly and thighs immaculate; Fig. 3F); *Dendropsophus virolinensis* (Kaplan & Ruiz) has dorsolateral stripe narrow of uniform widths and bordered by black pigment (stripe absent); an indistinct tympanic annulus (tympanic annulus distinct and conspicuous); absence of axillary membrane (axillary membrane present).

Description of holotype. Adult female; SVL 35.8; head slightly narrower than the body, wider than long (HW/HL = 1.17%; Table 1); snout short, rounded in dorsal view (Fig. 4A), slightly rounded in lateral view (Fig. 4B); distance from nostril to eye less than diameter of eye (END/ED = 0.76%); *canthus rostralis* indistinct, rounded; loreal region slightly concave, slightly sloping to upper lip; internarial area depressed; nostrils barely protuberant, openings directed laterally; eye large, its diameter about three times depth of lip below eye; tympanic membrane round, distinct, its diameter about one third of eye length, separated from eye by a distance equal to its diameter; tympanic annulus distinct ventrally, barely hidden dorsally; supratympanic fold evident conspicuous, inclined posteroventrally.

Forelimbs not hypertrophied; axillary membrane present, extending along proximal two fifths of upper arm; minute ulnar tubercles present along the ventrolateral edge of the forearm; fingers short, bearing round discs, wider than digit; relative length of fingers I<II<IV<III (Fig. 4C); distal subarticular tubercle in fourth finger bifid; supernumerary tubercles very small, barely detectable; palmar tubercle flat, elliptical; thenar tubercle large, flat, elliptical; nuptial excrescences absent; finger webbing formula I 2–2 II 1^{1/2}–2 III 2–2 IV (Fig. 4C). Hind limbs long, slender, lacking calcar tubercles, tarsal fold absent, but some tarsal tubercles presents; toes moderately long, bearing round discs, slightly smaller than finger discs; relative length of toes 1<2<3=5<4 (Fig. 4D); outer metatarsal tubercle small, round, inconspicuous; inner metatarsal tubercle large, flat, elliptical; subarticular tubercles small, subconical; supernumerary tubercles minute, subconical, numerous on proximal segments of each digit; toe webbing formula I 1–1^{1/2} II 1–2 III 1–2 IV 2–1 V (Fig. 4D).

Skin on head, dorsum, and dorsal surfaces of limbs smooth with few scattered minute tubercles; skin on flanks, throat and neck smooth; skin on belly coarsely granular; skin on another ventral surfaces and proximal area of thighs finely granular. Cloacal opening directed posteriorly at upper level of thighs; cloacal sheath short, covering upper edge of cloacal opening; cloacal folds absent; minutes scattered cloacal tubercles present. Vomerine odontophores prominent, posteromedially inclined, moderately separated medially, between posterior border of choanae, bearing each, five vomerine teeth; tongue approximately round, barely notched and free posteriorly; pectoral fold absent.

Coloration of holotype in life. Coloration between night and daylight was not observed to vary. Dorsal surfaces of head, body, and limbs reddish brown with numerous small and scattered dark brown spots and markings. Region around nostrils dark brown; supratympanic fold dark brown, tympanic annulus pale brown, tympanic region dark brown; upper lip slightly pale brown, with scattered melanophores and distinct cream spots below the eye; light gray iris with gold and copper chromatophores and purple dark blotches; eyelid without pigmentation. Axilla, groin, anterior and posterior surfaces of thigh, and anterior surface of shank bright orange; flanks whitish with few dark brown blotches; gula, throat and lateral region of belly cream with brown scattered spots, medial area of belly immaculate; ventral surfaces of hands, feet, and webbing yellowish.

Coloration of holotype in preservative. Dorsum reddish brown with a similar pattern of dark brown markings and spots as in the life specimen; head dark reddish brown laterally; flanks posteriorly whitish with spots and blotches brown; supratympanic fold and tympanic region reddish; upper lip slightly pale, with scattered melanophores and distinct white spots below the eye; axilla, groin, anterior and posterior surfaces of thigh, and anterior surface of shank pink; flanks whitish with irregular brown blotches; gula, throat and lateral region of belly cream with brown scattered spots, center of belly without spots; ventral surfaces of hands, feet, and webbing cream.



FIGURE 1. Living specimens of some high Andean species of genus *Dendropsophus*. A) *D. bogerti*, Medellín, Antioquia, Colombia (MRC 999, SVL = 32.6 mm, female); B) *D. carnifex*, Maquipucuna, Pichincha, Ecuador (QCAZ 42387, SVL = 32.6 mm, female); C) *D. columbianus*, Calima, Valle del Cauca, Colombia (MRC 920, SVL = 33.2 mm, female); D) *D. garagoensis*, Garagoa, Boyacá, Colombia (MRC 730, SVL = 28.3 mm, female); E) *D. labialis*, San Juanito, Meta, Colombia (MRC 644, SVL = 42.6 mm, male); F) *D. meridensis*, Merida, Venezuela (voucher number unknown); G) *D. padreluna*, Fusagasuga, Cundinamarca, Colombia (specimen not collected); H) *D. virolinensis*, Virolín, Santander, Colombia (MAR 2298, SVL = 25.4 mm, male). The specimens are not to scale. Photos: M. Rivera-Correa (A, C-D) S. Ron (B); M. Rada (E, H); F. Rojas-Runjaic (F); H. Bernal (G).



FIGURE 2. *Dendropsophus norandinus* sp. nov. (MHUA-A 4092, paratype, adult female in life, SVL = 35.6 mm). Photo: T. Grant.

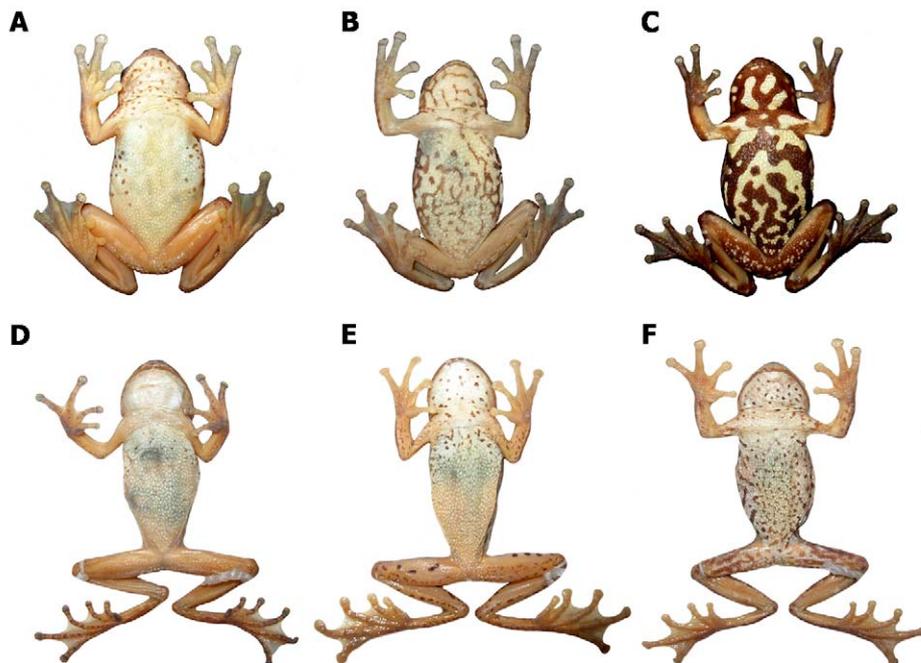


FIGURE 3. Ventral color patterns of females of some *Dendropsophus* species from the highlands of the Andes of Colombia. (A) *Dendropsophus norandinus* sp. nov. MHUA-A 3781 (holotype); (B) *D. bogerti* MHUA-A 4599; (C) *D. columbianus* MHUA-A 3583; (D) *D. garagoensis* ICN 17803; (E) *D. padreluna* ICN 22021 (paratype); (F) *D. praestans* ICN 7559. The specimens are not to scale. Photos: M. Rivera-Correa.

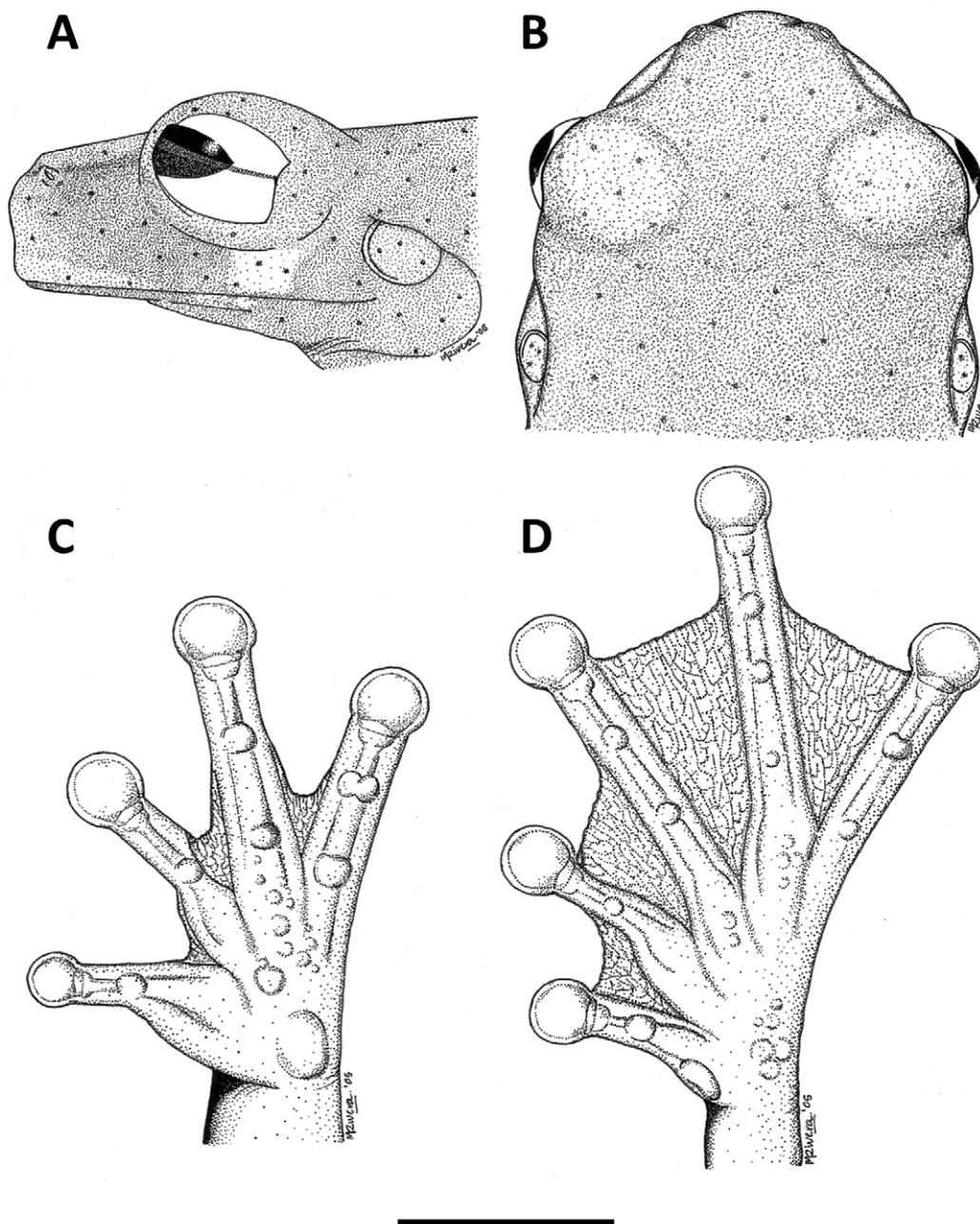


FIGURE 4. Drawings of holotype of *Dendropsophus norandinus* sp. nov. (MHUA-A 3781). (A) Lateral, and (B) dorsal views of the head; (C) palmar, (D) plantar views of left hand and foot. Scale bar = 5 mm. Drawings: M. Rivera-Correa.

Measurements of holotype (in mm). SVL 35.8; TBL 16.9; HW 11.9; HL 10.2; IOD 4.4; IND 2.8; END 2.6; NSD 1.3; ED 3.4; TD 1.7; TFD 1.9; FTD 1.8; THL 16.9; FL 23.7.

Variation and sexual dimorphism. Variation of measurements and body proportions is given in Table 1. The variation on finger webbing formulae is I ($2 - 2^{1/2}$) - 2 II $1^{1/2} - (2 - 2^{1/2})$ III ($2 - 2^{1/2}$) - 2 IV, and the variation on toe webbing formulae is I ($1 - 1^+$) - ($1^{1/2} - 1^{3/4}$) II $1 - (2 - 2)$ III $1 - (2 - 2)$ IV ($2 - 2$) - 1 V. The adults males have vocal slits extending from mid lateral base of tongue to posterior level of it; vocal sac single, median, subgular. This new species has an evident sexual dimorphism in the color pattern in life. The female dorsum is reddish brown or cream (cream and silver grey with blotches and brown and yellow spots in males); in males, axilla, groin, anterior and posterior surfaces of thigh, and anterior surface of shank are pale yellow. Some individuals, mainly females, possess an X-shaped pattern brown dark, which extends from the posteromedial edge of the orbit along

the dorsum. Most juveniles with dark brown dorsal transverse bands and on entire hind limbs, additionally, *canthus rostralis* and region around nares brown dark, lips speckled; most individuals have white spots below the eye, in some cases these spots extend toward inferior postocular region.

TABLE 1. Variation of measurements (in mm) of the type series of *Dendropsophus norandinus* sp. nov. See text for abbreviations. Range (average \pm standard deviation).

Measurement	Males (n = 15)	Females (n = 9)
SVL	24.8–27.8 (26.5 \pm 0.9)	30.4–35.8 (32.9 \pm 1.7)
TBL	11.9–13.7 (13.0 \pm 0.6)	15.0–16.9 (15.8 \pm 0.9)
HW	8.2–10.2 (9.4 \pm 0.5)	10.7–11.8 (11.3 \pm 0.3)
HL	7.1–8.9 (8.1 \pm 0.4)	9.0–10.2 (9.8 \pm 0.4)
IOD	3.7–4.1 (3.1 \pm 0.2)	3.6–4.8 (4.1 \pm 0.4)
IND	1.8–2.4 (2.1 \pm 0.1)	2.3–2.7 (2.5 \pm 0.1)
END	1.7–2.5 (2.1 \pm 0.2)	2.3–2.7 (2.5 \pm 0.1)
NSD	0.8–1.2 (1.0 \pm 0.1)	1.1–1.3 (1.3 \pm 0.1)
ED	2.6–3.2 (2.8 \pm 0.2)	2.9–3.5 (3.2 \pm 0.2)
TD	0.9–1.5 (1.3 \pm 0.1)	1.3–1.6 (1.5 \pm 0.1)
TFD	0.9–1.5 (1.3 \pm 0.2)	1.5–1.9 (1.8 \pm 0.1)
FTD	1.1–1.6 (1.2 \pm 0.2)	1.2–1.8 (1.7 \pm 0.2)
THL	11.5–13.4 12.6 \pm 0.6)	14.8–16.6 15.6 \pm 0.7)
FL	16.3–19.5 18.2 \pm 1.0)	20.4–23.9 22.2 (\pm 1.2)

Tadpole. MHUA-L 0153-1 (stage 39, Fig. 5, Table 2). Body ovoid, wider than deep, body length approximately 38% of total length (Fig. 5A); snout rounded in dorsal and profile view; eyes large approximately 30% of body height, directed laterally; nostrils moderately large, elliptical, located frontally, directed anteroventrally, midway between eye and tip of snout; spiracle sinistral, short, directed posterodorsally, distance from opening to snout 66% of body length; neuromasts of the lateral line system evident mainly of supraorbital, infraorbital, ventral body and dorsal body lines; intestines located approximately at the center of abdominal region, intestines ventrally visible and coiled clockwise; cloacal tube very short, dextral. Caudal musculature robust, in the anterior region correspond to 60% of body height, tapering to a point posteriorly; dorsal fin beginning at posterior edge of body, slightly more arched than ventral fin; fins deepest at about midlength of tail; tail acute. Oral disc very small 25% of body width, anteroventral, directed frontally upper jaw sheath wide, arch-shaped, with no lateral processes; marginal papillae single laterally and ventrally, marginal papillae interrupted dorsomedially in the anterior labium forming a wide gap (Fig. 5D); lower jaw sheath broadly U-shaped; labial tooth row formula 0/2; P-1 larger than P-2; teeth of P-1 larger than P-2; one toothless ridge present on anterior (upper) labium, broadly arched.

In life, dorsal and lateral view body brown; anterior region ventrally dark brown, with very small spots black, turning translucent posteriorly just in the joint with the tail. Intestines reddish brown; iris reddish copper; tail musculature pale brown, fins light orange or light yellow, both with irregular brown blotches forming reticulations in some specimens; posterior region of tail musculature dark brown while the fin is translucent. In preservative, colors on the fins become creamy or light gray.

Etymology. The specific epithet *norandinus* is composed by the prefix *nor* from “norte” (Spanish word for “north”), and the New Latin noun *andinus* meaning “Andes”. The specific name in reference to the septentrional distribution of this species in South America, and a tribute to Andean mountains of Colombia.

Geographic distribution and natural history. *Dendropsophus norandinus* is known from only three localities in the northeastern part of the Cordillera Central: in the vereda El Roble (type locality) and vereda El Retiro, both at municipio de Anorí and in the vereda Salazar, municipio de Amalfí (06°57'N, 75°03'W, 1420 m a.s.l.), both municipalities in the departamento de Antioquia, Colombia (Fig. 6). Altitudinal range is between 1420–1950 m a.s.l. The type locality and the locality from municipio de Amalfí are distanced approximately to

each other 10 km, separated by the Porce river valley. Individuals of *D. norandinus* inhabit semi-permanent swamps, with abundant grasses, in pasturelands. Most males called from the emerging vegetation, near the water surface during or immediately after light rains, while females remain hidden in the aquatic vegetation. Some males called during the day, but their activity peak is between 19:00 and 02:00 h. Amplexus is axillar and clutches are laid under water attached to the submerged vegetation. Some individuals were found in secondary forest, along the creeks. In the shallow swamps, *D. norandinus* is syntopic with *Leptodactylus colombiensis* (Heyer) and an undescribed species of *Scinax*. An adult female of *D. norandinus* was found in the stomach of *Leptodeira septentrionalis* Kennicott (MHUA 14315).

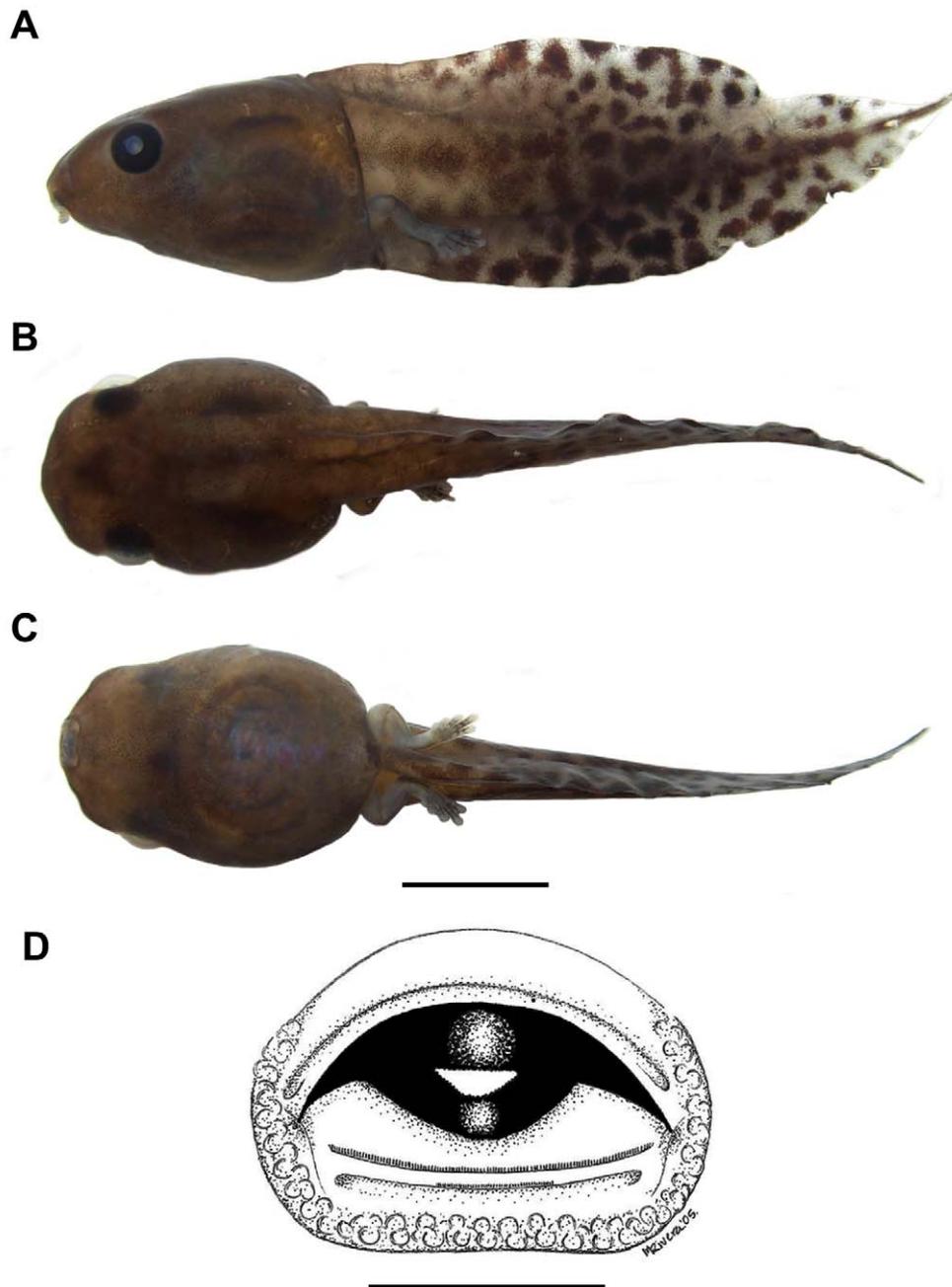


FIGURE 5. Tadpole of *Dendropsophus norandinus* **sp. nov.** from the type locality (MHUA-L 0153-1). (A) lateral, (B) dorsal, (C) ventral views; scale bar = 5 mm; (D) Oral disc, scale bar = 1 mm. Photos and drawing: M. Rivera-Correa.

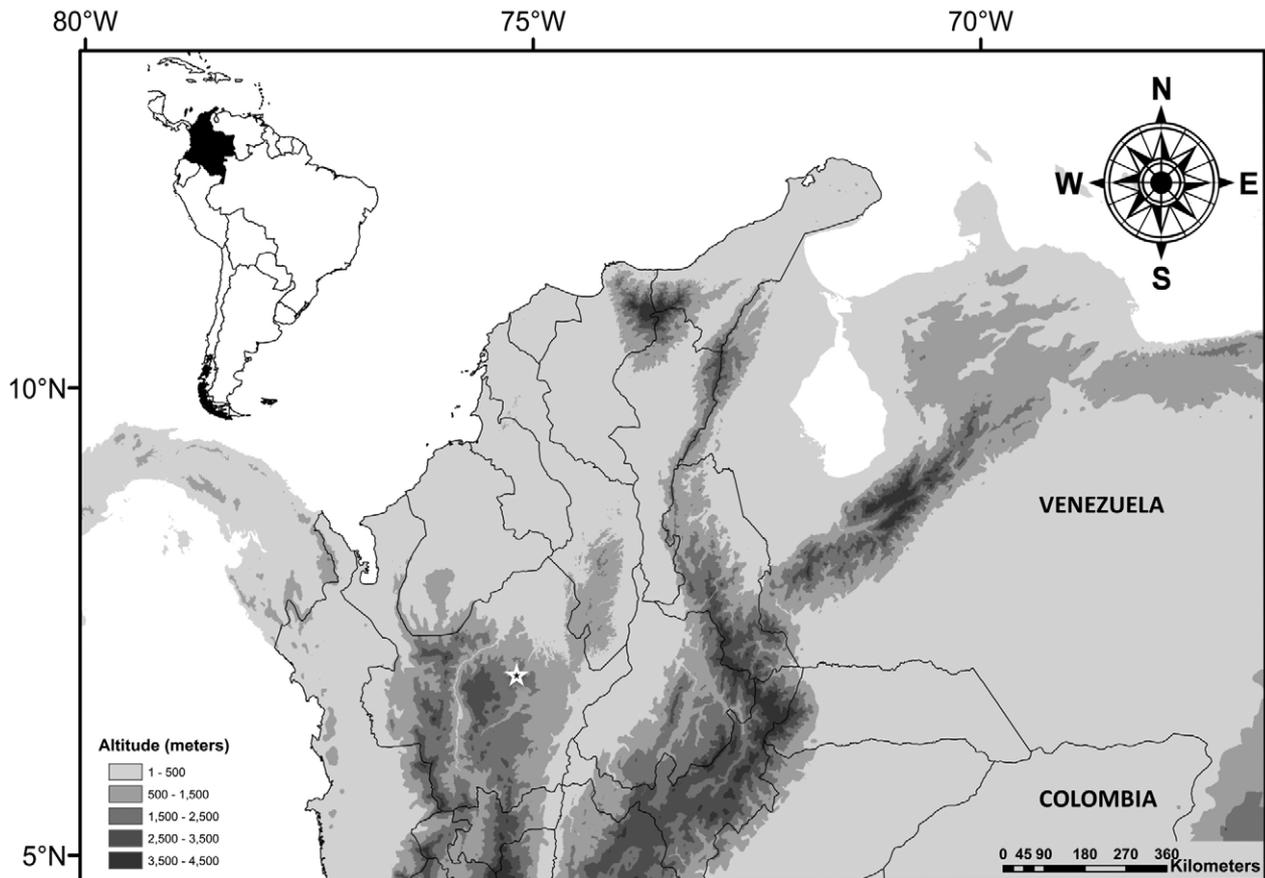


FIGURE 6. Map showing the known distribution of *Dendropsophus norandinus* **sp. nov.** The star indicates the only two known localities, which are separated by 10 Km.

TABLE 2. Measurements of selected characters of tadpoles of *Dendropsophus norandinus* **sp. nov.** from the type locality; in stage 30–39 (Gosner, 1960). See text for abbreviations. Range (average \pm standard deviation).

Measurement	(n = 22)
TL	28.1–32.0 (30.2 \pm 1.1)
BL	10.9–11.9 (11.3 \pm 0.3)
BH	6.3–7.2 (6.7 \pm 0.2)
OD	1.8–2.1 (2.0 \pm 0.1)
ND	0.3–0.4 (0.3 \pm 0.0)
BW	6.6–7.8 (7.2 \pm 0.3)
IO	5.2–5.7 (5.4 \pm 0.2)
IN	3.2–3.9 (3.6 \pm 0.1)
NS	1.9–2.1 (2.0 \pm 0.1)
ES	3.5–4.0 (3.8 \pm 0.1)
SS	6.8–7.4 (7.1 \pm 0.2)
ODL	1.7–1.9 (1.8 \pm 0.0)
TMH	3.1–4.3 (3.8 \pm 0.3)
MTH	6.2–7.8 (7.1 \pm 0.3)

Discussion

The high mountain species of the genus *Dendropsophus* constitute a difficult taxonomic problem among Neotropical anurans. The complexity is due to: (1) difficulties in species delimitation (e.g. extensive intraspecific variation and weakly defined species boundaries, small sample sizes and few characters studied in the original descriptions of some species) and (2) absence of a deep understanding of phylogenetic relationships among species, in spite of various systematic proposals both within and among species-groups (e.g. Duellman & Trueb 1983; Duellman *et al.* 1997; Kaplan & Ruíz 1997; Kaplan 1999; Faivovich *et al.* 2005; Motta *et al.* 2012).

Duellman and Trueb (1983) hypothesized that *Dendropsophus carnifex* (which at that time included *D. bogerti* as a synonym), *D. columbianus* and *D. praestans* formed the *D. columbianus* group, but they did not provide any synapomorphies. Subsequently, Kaplan (1999) suggested a single morphological synapomorphy for this group: “the presence of two close, triangular lateral spaces between the cricoid and arytenoids at the posterior part of the larynx”, which supported a monophyletic *D. columbianus* species group that included *D. bogerti* (resurrected by Kaplan 1997) but excluded *D. praestans*. While *D. garagoensis*, *D. padreluna*, and *D. virolinensis* form a putative clade supported by dark longitudinal stripes on the hind limbs in tadpoles (Kaplan & Ruiz 1997) and a small medial depression on the internal surface of the arytenoid cartilage (Kaplan 1999). Although the tadpole of *D. praestans* is unknown, Faivovich *et al.* (2005) included this species in the *D. garagoensis* group based on the state of the character of the larynx reported by Kaplan (1999).

On the other side, the oral disc of the tadpoles in *Dendropsophus columbianus* group has tooth row formulae 1/2, while in *D. norandinus* upper tooth row is absent (LRTF 0/2), an unusual combination for *Dendropsophus* species with highland distribution, but reported for an Amazonian species (i.e. *D. minutus* [Duellman 1978; Lynch and Suárez-Mayorga 2011]). The rows of teeth can be acquired during ontogeny (e.g. Sánchez 2010) and may be partially or completely lost by the effects of disease (i.e. chytridiomycosis, e.g. Berger *et al.* 1998; Drake *et al.* 2007) or mechanical damage (MRC, pers. obs.). However, the tooth row formulae 0/2 in *D. norandinus* in different Gosner’s stages (assessed in 30 tadpoles between 25 to 39 of two populations), suggests that the absence of teeth in anterior labium is because never has been acquired during development.

Tadpoles of *Dendropsophus norandinus* have morphological attributes that are present in *D. columbianus* group (i.e. body shape, color and pigmentation of fins, shape of nostrils, spiracle extension, and anteroventral oral disc position; see Duellman 1969; Duellman & Trueb 1983; Kaplan 1997). While the tadpoles of the *Dendropsophus garagoensis* group are characterized by having a dark longitudinal line on the limbs, terminal oral disc and tooth row formula of 0/0, characters states absent in the tadpoles of *D. norandinus* and *D. columbianus* group (Duellman 1969; Duellman & Trueb 1983; Kaplan 1997; Kaplan & Ruiz 1997). Given the above, we tentatively assign *D. norandinus* to the *D. columbianus* group and advocate that this assignment is tested with subsequent evidence. Assumed this, the current composition of the *D. columbianus* group is expanded to four species (i.e. *D. bogerti*, *D. carnifex*, *D. columbianus* and *D. norandinus*) and its distribution is restricted to the Cordillera Central and Occidental of Colombia and the Pacific foothills of the Andes of Ecuador (Frost 2011; Ron & Read 2012).

Current knowledge of the geographic distribution of hyline frogs (Duellman 1999; Faivovich *et al.* 2005), suggest a limited impact of the Andean uplift in the speciation of this anuran subfamily compared with other groups (Faivovich *et al.* 2005). However, the accelerated rate of deforestation in the Colombian mountains reduces the eventual discovery of species and knowledge of their geographic distribution patterns. This can hinder our understanding of the real impact of the Andean orogeny in the diversity and distribution of tree frogs. *Dendropsophus norandinus* is known only from the northern part of the Cordillera Central, in the type locality and surroundings (in an area of ca. 10 km²), where several hydroelectric megaprojects are flooding large tracts of forests and pasturelands (i.e. Porce III Hydroelectric Project). The implications of such extensive habitat modification are unknown and the effect for this and other anuran species from region demand urgent study (Finer & Jenkins 2012).

Acknowledgments

We are grateful to P. Mejía, J. Arredondo, and C. Molina for field assistance. For the loan of specimens or access to collections we are indebted to V. Páez (MHUA), J. Lynch (ICN), and S. Ron (QCAZ). For the valuable comments

to the preliminary version of manuscript, we thank to J. Faivovich, T. Grant, V. Orrico, S. Castroviejo and D. Cisneros-Heredia. For providing some scientific articles we thank to J. Köhler. To T. Grant, M. Rada, S. Ron, F. Rojas-Runjaic and H. Bernal for allowing us to use their photos. To E. Alzate and M. Rada for edited some digital pictures and J.P. Hurtado for provided detailed locality data for some specimens. We are especially grateful to H. Castaño, J. Zapata and L. Ramírez for their kind help and hospitality in the field. Financial support was provided by the Universidad de Antioquia (grant CODI-IN517CE); Universidad Nacional de Colombia, sede Medellín (grant DIME-030803682) and, The Organization for Tropical Studies (grant post-course OTS 2004-13). Scholarship grant support of MRC is provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and PDAGC receive Ph.D. grant from CAPES (bolsista da CAPES/CNPq – IEL Nacional - Brasil). MRC is grateful to the Rivera Correa family for their constant support; this work is especially dedicated to the memory of my father Alvaro Fabio Rivera.

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APPENDIX I. Additional specimens examined

- Dendropsophus bogerti*: Colombia: ICN 41652–60, Antioquia, Betania, vereda Piedra Alta, hacienda Agua Linda, 1960–2000 m; MHUA-A 3879–90, 4599, 4600, Antioquia, Itagüí, barrio Loma Linda, 1550 m; MHUA-A 4242–44, Antioquia, Guatapé, finca Villa de Bermeo; MHUA-A 3870–3878, Antioquia, San Pedro, vereda La Lana, 2615 m.
- Dendropsophus carnifex*: Ecuador: MCZ A-75064 (paratype), Pichincha, Tandapi 1460 m; QCAZ 23130-40, Pichincha, canton Quito, parroquia Chillogallo, 1680 m.; QCAZ 24338–24349, Esmeraldas, Reserva La Perla; QCAZ 32927–49, Cotopaxi, Naranjito; finca de don Tomas Granja.
- Dendropsophus columbianus*: Colombia: ICN 30381–96, Risaralda, Mistrató, corregimiento de San Antonio de Chamí, vereda Arcacay, quebrada La Cementera. 1130 m; MHUA-A 3849–3863, Valle del Cauca, Cali, Universidad del Valle - ciudadela universitaria sede Meléndez, 1000 m.
- Dendropsophus garagoensis*: Colombia: ICN 12950, 17781, 17784–94, 17796-97, 17800–17806, 17814–15, Boyacá, Miraflores, vereda Tunjito, finca El Vergel, 2000 m.
- Dendropsophus labialis*: Colombia: MHUA-A 1618-25, 1781-82, 2062, Norte de Santander, Cucutilla, Sisavita, 1400 m.
- Dendropsophus padreluna*: Colombia: ICN 22231–59, Cundinamarca, Albán, Las Marias, Granjas infantiles el Gran Ciudadano Padre Luna, 4°45'N - 74°50'W, 2060 m; ICN 8631–46, Cundinamarca, Tena, Laguna Pedro Palo, 2000 m.
- Dendropsophus praestans*: Colombia: ICN 07558–61, Huila, Isnos, vereda Hornitas a 7.4 km NW de Isnos, 1940 m.
- Dendropsophus virolinensis*: Colombia: ICN 12512–37, Santander, Charalá, Inspección de Policía de Virolín, Cañaverales km 70 Duitáma–Charalá, 1830 m; ICN 12538–62, Santander, Charalá, Inspección de Policía de Virolín, confluencia Rio Guillermo y Rio Cañaverales.