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Description and phylogenetic relationships of a new species of treefrog of the *Dendropsophus leucophyllatus* group (Anura: Hylidae) from the Amazon basin of Colombia and with an exceptional color pattern

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Abstract

We describe *Dendropsophus manonegra* **sp. nov.** from the upper Amazon basin in the eastern foothills of the Andes in Colombia (1° 47' 42.2" N, 75° 38' 48.7" W; 1040 m a.s.l.). Phylogenetic analysis of DNA sequences of 2582 aligned base pairs of the 12S and 16S rRNA genes recovered the new species as a member of the *D. leucophyllatus* species group and sister to *D. bifurcus*. Morphological traits, such as the presence of pectoral glands in males and females, support this hypothesis. The new species is readily distinguished from all other members of the species group by having bluish-black coloration on fingers, toes, webbing, axillary membranes, groin and hidden surfaces of arms and legs. Some aspects on the composition and systematics of the *D. leucophyllatus* group are discussed.

Key words: Amphibia, Amazonia, morphology, species description, taxonomy

Resumen

Describimos *Dendropsophus manonegra* **sp. nov.** de la cuenca alta del Amazonas en las estribaciones orientales de los Andes en Colombia (1° 47' 42.2" N, 75° 38' 48.7" W; 1040 m s.n.m.). Un análisis filogenético de secuencias de DNA de 2582 pares de bases de los genes 12S rRNA y 16S rRNA recuperan la nueva especie como miembro del grupo *D. leucophyllatus* y especie hermana de *D. bifurcus.* Atributos morfológicos como la presencia de glándulas pectorales en machos y hembras apoyan esta hipótesis. La nueva especie es fácilmente distinguible de todos los miembros del grupo por tener coloración negra azulada en dedos, membranas interdigitales, ingle y en las superficies ocultas de brazos y piernas. Adicionalmente, discutimos algunos aspectos acerca de la composición y sistemática del grupo *D. leucophyllatus*.

Palabras clave: Amphibia, Amazonia, morfología, descripción de especie, taxonomía

Introduction

With 97 described species, *Dendropsophus* is currently the second most specious genus in Hylinae (Amphibiaweb 2013, Frost 2013). The genus was resurrected by Faivovich *et al.* (2005) from its synonymy with *Hyla*, where it had been placed by Kellogg (1932), to accommodate species known or suspected to have a karyotype of 2N = 30. Although the genus maintained most of the traditional species groups, the monophyly and relationships among members within these groups are, in many cases, either unknown or weakly supported (Fouquet *et al.* 2011; Pyron & Wiens 2011; Motta *et al.* 2012). One of these groups is the charismatic *Dendropsophus leucophyllatus* species group (or leaf-gluing frogs) currently composed of nine species (according to Faivovich *et al.* 2005; Frost 2013):

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Dendropsophus anceps (Lutz), *D. bifurcus* (Andersson), *D. ebraccatus* (Cope), *D. elegans* (Wied-Neuwied), *D. leucophyllatus* (Beireis), *D. rossalleni* (Goin), *D. salli* Jungfer, Reichle and Piskurek, *D. sarayacuensis* (Shreve) and *D. triangulum* (Günther).

The group is widespread through the Neotropics. All species are cis-Andean except for *Dendropsophus ebraccatus*, which is trans-Andean. *Dendropsophus anceps* and *D. elegans* occur in the Brazilian Atlantic forest; while the remaining species are distributed through the Amazon basin (Frost 2013). Putative morphological synapomorphies for this group are the presence of paired oval pectoral glands in both males and females, with the exception of *D. anceps* (Cochran & Goin 1970; Duellman 1970; Faivovich *et al.* 2005), vivid flash colors (Lutz 1973) and violin-shaped tadpole bodies (Duellman 1970; Gomes & Peixoto 1991; Duellman 2001).

Dendropsophus anceps, *D. ebraccatus* and *D. sarayacuensis* are distinctive and easily recognizable by their descriptions in the pertinent literature. However, the high morphological variability of some species (e.g. *D. leucophyllatus* and *D. triangulum*), misidentifications in the literature and in museum specimens (e.g. *D. rossalleni*) and high morphological similarity among some species (i.e. *D. elegans* vs. *D. leucophyllatus* vs. *D. triangulum*; *D. bifurcus* vs. *D. salli*) leave the taxonomy of the remaining species a hard task (see Duellman 1966; Cochran & Goin 1970; Caramaschi & Jim 1982; De la Riva & Duellman 1997; Chek *et al.* 2001; Jungfer *et al.* 2010).

All species of the *Dendropsophus leucophyllatus* group have flash colors on the hidden surfaces of thighs, groin, and webbings. These flash colors vary from bright yellow to orange, pink, and/or red (Cochran 1955; Lutz 1973; Duellman 1978; Jungfer *et al.* 2010). An exception is a taxon found in the Colombian Amazon basin, which exhibits bluish-black colors; evidence that suggests that it is an undescribed species. Using morphological and genetic data we herein describe these Colombian populations as a new species of *Dendropsophus* and infer its phylogenetic relationships. On the basis of our results, we discuss the composition of the *Dendropsophus leucophyllatus* group.

Materials and methods

All individuals were collected in the field and euthanized in a 0.25% chloretone solution, fixed in a 10% formaldehyde solution and stored in 70% ethanol within five days of fixation. Tissues for molecular analyses (muscle) were previously removed from some specimens and preserved in 98% ethanol. Webbing formula follows that of Savage and Heyer (1967) as modified by Myers and Duellman (1982). Measurements (in millimeters) follow Duellman (1970) as adjusted by Rivera-Correa and Gutiérrez-Cárdenas (2012), and were taken with a digital caliper to the nearest 0.1 mm under a stereomicroscope. Acronyms for morphological measurements are as follows: SVL (snout–vent length), HL (head length), HW (head width), ED (eye diameter), END (eye to nostril distance), NSD (nostril to tip of snout distance), IND (internarial distance), AMD (distance between the anterior margins of eyes), TD (tympanum diameter), IOD (interorbital distance), FAL (forearm length), FAB (forearm breadth), HAL (hand length), THL (thigh length), TL (tibia length), TAL (tarsal length), FL (foot length), TFD (third finger disk diameter) and FFD (fourth toe disk diameter).

Geographic coordinates were taken with a global positioning system (GPS) device (Datum WGS84). Sex and maturity were determined by examination of secondary sexual characters (presence of vocal slits and expansion of the vocal sac in males) and by behavior (amplexus) observed in the field. Illustrations were made with a drawing tube attached to a Zeiss Stemi SV-11 stereomicroscope. Color and pattern descriptions are based on photographs taken in the field and field notes. Institutional acronyms are: CFBH (Célio F. B. Haddad collection, Universidade Estadual Paulista, Brazil); ICN (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Colombia); MCNAM (Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais, Brazil); MHUA-A (Museo de Herpetología Universidad de Antioquia, Colombia); QCAZ (Museo de Zoología, Pontificia Universidad Católica del Ecuador); USNM (National Museum of Natural History, Smithsonian Institution, USA). TG correspond to Taran Grant field numbers. Information on other species was taken from preserved specimens (listed in Appendix I) and data from the literature.

Molecular procedures (including primers) follow Motta *et al.* (2012). Sequencing was performed at Macrogen Inc. (Korea). We sequenced the complete 12S rRNA gene and a fragment of the 16S rRNA gene (and the intervening valine-tRNA) in five concatenated fragments for two specimens of the new species (MHUA-A 7337 and TG 1850; GenBank accession numbers: KF009942 and KF009943 respectively) resulting in 2422 bp. Data from complementary strands were compared to generate a consensus sequence for each DNA fragment using Sequencher 4.1 (Gene Code Corp, Ann Arbor, USA).

In order to assess the relationships of the new species within *Dendropsophus*, we downloaded homologous sequences of all species of the genus available in GenBank (Appendix I). According to Faivovich *et al.* (2005), we used *Phyllodytes luteolus* (Wied-Neuwied 1824) to root the trees and *Xenohyla truncata* (Izecksohn 1959), *Lysapsus limellum* Cope 1862, *Pseudis minuta* Günther 1858, *P. paradoxa* (Linnaeus 1758), *Scarthyla goinorum* (Bokermann 1962), *Scinax berthae* (Barrio 1962), *S. fuscovarius* (Lutz 1925), *Sphaenorhynchus dorisae* (Goin 1957), *S. lacteus* (Daudin 1800) and *S. orophilus* (Lutz & Lutz 1938) as outgroups.

Static alignments were obtained using the web version of the software Mafft version 6.903 (Katoh *et al.* 2005) under the Q-INS-I strategy. Individual gene alignments were later concatenated into a single matrix of up to 2582 bp for 50 terminals using Sequence Matrix (Vaidya *et al.* 2011). Maximum parsimony analyses were conducted in TNT (Goloboff *et al*. 2008). Searches were conducted at level 100, including sectorial searches, ratchet, drift, and tree fusing. All characters were equally weighted and gaps were treated as missing data. Jackknife support values were evaluated with 1000 pseudoreplicates. We calculated uncorrected pairwise genetic distances of 862 bp of the 16S rRNA fragment because this gene is widely used as a genetic barcode for amphibians (Vences *et al*. 2005) and because this was the maximum number of homologous positions for all sequences.

Results

Dendropsophus manonegra sp. nov.

(Figs. 1–3)

Holotype. MHUA-A 7336; an adult male from kilometer 60 road Florencia — Altamira, 1° 47' 42.2" N, 75° 38' 48.7" W, 1040 m a.s.l., vereda Sucre, municipio de Florencia, departamento de Caqueta, Colombia, collected on November 14, 2010 by Marco Rada.

Paratypes. All adults. MHUA-A 7337, female; MHUA-A 7668, male; both with same data as the holotype. ICN 23973–24000; 28 males from kilometer 19 of the road Florencia —El Paraíso, 740 m a.s.l., vereda El Paraíso, municipio de Florencia, departamento de Caquetá, Colombia, collected by Pedro Ruiz, John Lynch and Ricardo Sánchez on May 28, 1990. ICN 39875, 39877–80; five males from Serranía de los Churumbelos, mouth of the Rio Intiyaco on the Rio Caquetá, 1º 5' 57.7" N, 76º 34' 5.8" W, 400 m a.s.l., municipio de Mocoa, departamento de Putumayo, Colombia, collected by José V. Rueda (unknown date).

FIGURE 1. Dorsal and ventral view of the preserved holotype of *Dendropsophus manonegra* **sp. nov.** (MHUA-A 7336, SVL 23.7 mm).

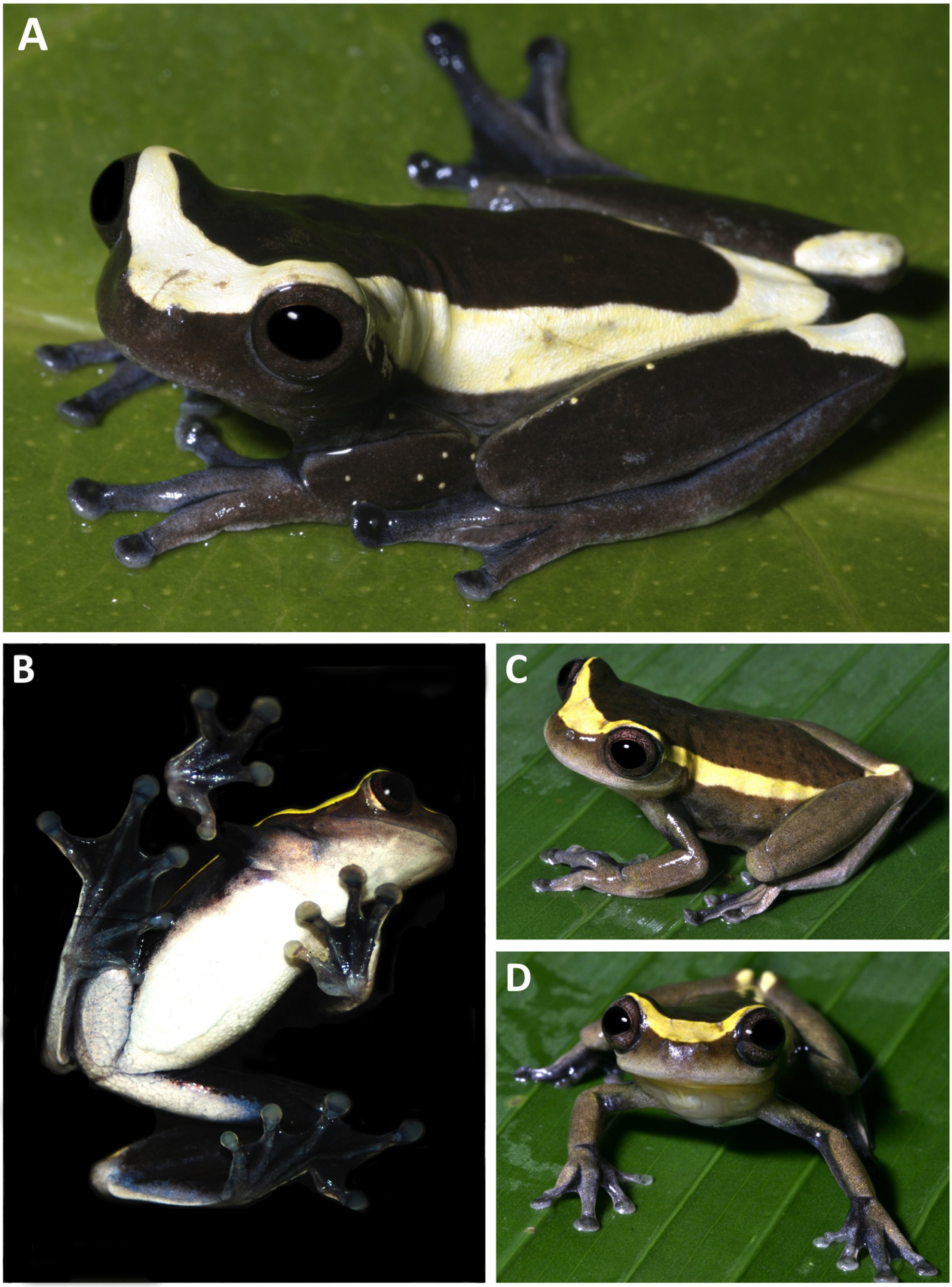

FIGURE 2. *Dendropsophus manonegra* **sp. nov.** in life. (A) Lateral view (TG 1850, adult male, SVL 25.1 mm); (B) ventral view (MHUA-A 7337, paratype, adult female, SVL 32.5); (C) lateral view (TG1815, adult male, SVL 23.0 mm); (D) frontal view (TG 1815, adult male, SVL 23.0 mm). Photos: T. Grant (A, C, D); M. Rada (B).

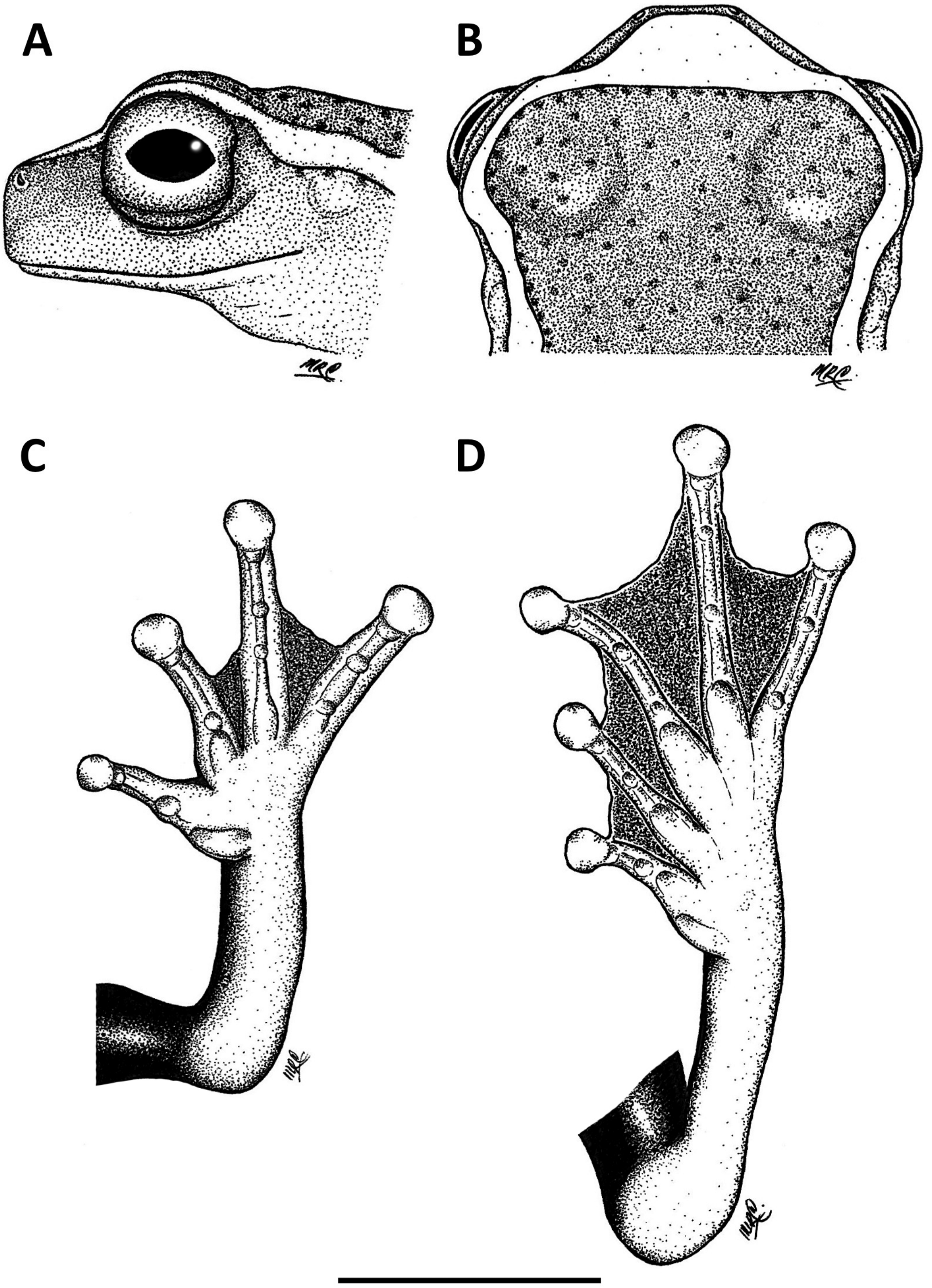

FIGURE 3. Drawings of the holotype of *Dendropsophus manonegra* **sp. nov.**, MHUA-A 7336. (A) Head in lateral view, (B) head in dorsal view, (C) palmar surface of left hand, (D) plantar surface of left foot. Scale bar = 5 mm. Drawings: M. Rivera-Correa.

Referred specimens. TG 1815; an adult male from kilometer 28 of the road Florencia — Suaza, municipio de Florencia, departamento de Caquetá, Colombia, 800 m a.s.l.; TG 1850; an adult male from kilometer 20 of the road Florencia — Suaza, municipio San José de la Fragua, departamento de Caquetá, Colombia, 720 m a.s.l.; both vouchers deposited at ICN but not yet catalogued.

Diagnosis. We assigned the new species to the genus *Dendropsophus* on the basis of our phylogenetic results (see below). Furthermore, we assigned it to the *Dendropsophus leucophyllatus* species group based on the close phylogenetic relationship with *D. bifurcus* and its relatives. Males and females of the new species exhibit a pair of oval pectoral glands, a character that is considered a putative morphological synapomorphy of the *D. leucophyllatus* species group (Cochran & Goin 1970; Duellman, 1970; Faivovich *et al.* 2005).

Dendropsophus manonegra **sp. nov.** (Figs. 1–3), can be distinguished from all its congeners by the following combination of traits: (1) SVL in males 22.7–25.1 mm (N = 12), female (N = 1) SVL of 32.5 mm; (2) very short snout, approximately 28% of head length, truncate in dorsal and lateral views; (3) head wider than long; (4) *canthus rostralis* straight and indistinct, loreal region flat; (5) tympanum rounded, tympanic annulus distinct except for its uppermost part, tympanic membrane indistinct; (6) vomerine teeth absent; (7) skin on dorsal surfaces smooth; (8) axillary membrane present, reaching the first proximal third of the arm; (9) finger discs round, about five thirds of the width of the finger; (10) webbing formulae of fingers I – II (1^{-}–$1^{1/2}$) – ($2^{1/3}$–$2^{1/2}$) III (2^{-}–2) – ($1^{1/2}$–2) IV, webbing formulae of toes I (1^{-}–1) – (1–$1^{3/4}$) II (1–1^{+}) – ($1^{1/2}$–2) III (1^{-}–1) – ($1^{1/2}$–$1^{3/4}$) IV 2 – (1^{-}–1^{+}) V; (11) oval pectoral glands present; (12) inner tarsal fold present; (13) tarsal, heel, and calcar tubercles absent; (14) dorsum ground color brown with black spots and with dorsal yellow light markings consisting of a triangular head blotch connected to narrow or broad dorsolateral bands along the anterior two thirds of body (composing an inverted U-shape), often connected posteriorly at the groin, producing a pattern resembling a frame; (15) one yellow light blotch on heel present; (16) ventral surfaces white, being the mental region smoky gray; (17) digits, webbing, axillary membranes, groin, and hidden surfaces of arms and legs bluish-black; (18) iris coppery brown with fine brown reticulations and a narrow homogeneous, non reticulated copper ring around the pupil.

Comparison with other species of the *D. leucophyllatus* species group. The new species is distinguishable from all species of the *Dendropsophus leucophyllatus* group by having, in life, bluish-black coloration on digits, webbing, axillary membranes, groin and hidden surfaces of arms and legs (Figs. 1, 2). This color pattern fades to grayish black in preservative. All other species of the *D. leucophyllatus* group have yellow, orange, pink or red surfaces in life, fading to cream in preservative.

Dendropsophus manonegra **sp. nov.** is distinguishable from all other species of the group by the absence of vomerine teeth (present in other species of the *D. leucophyllatus* group, except in *D. bifurcus*) and a single blotch over the heel (*D. elegans* and *D. leucophyllatus* having a pair of blotches, reticulated blotches, or a blotch that covers the dorsal surface of the shank completely). From *D. sarayacuensis* and *D. rossalleni*, *D. manonegra* **sp. nov.** can be distinguished by the presence of a triangular interorbital blotch ("T-shaped" in *D. sarayacuensis*; two small, not connected, transversal bars in *D. rossalleni*). The dorsolateral bands of *D. manonegra* **sp. nov.** are regular, homogeneously filled, with straight borders while *D. ebraccatus* have irregular dorsolateral bands that can be interrupted by brown blotches. Many specimens of *D. triangulum* have and uniform dorsal color pattern, sometimes punctuated by one or two small brown blotches or even, reticulated—the *favosa* pattern (*D. manonegra* **sp. nov.** exhibit the frame pattern), the pectoral glands of *D. triangulum* are large and in contact or nearly so (pectoral glands are more inconspicuous and distinctly apart in *D. manonegra* **sp. nov.**).

Dendropsophus manonegra **sp. nov.** males (22.7–25.1 mm) are smaller than males of *D. anceps* (31.0–40.0 mm, Lutz 1973), *D. leucophyllatus* (30.4–36.0 mm, Duellman 1978; Caldwell & Araújo 2005), and *D. salli* (25.4–30.1 mm, Jungfer et al. 2010) and are larger than males of *D. rossalleni* (19.0–22.3 mm, De la Riva & Duellman 1997). The single known female of *D. manonegra* **sp. nov.** (32.5 mm) is smaller than females of *D. anceps* (39.0–42.0 mm, Lutz 1973), *D. leucophyllatus* (37.7–50.0 mm, Caldwell & Araújo 2005; Lescure & Marty 2000), *D. sarayacuensis* (34.0–37.0 mm, Rodriguez & Duellman 1994), and *D. triangulum* (36.0–42.0 mm, Rodriguez & Duellman 1994). The female of *D. manonegra* **sp. nov.** is larger than females of *D. rossalleni* (28.2–28.7 mm, De la Riva & Duellman 1997).

Description of the holotype. An adult male of 23.7 mm SVL. Head as wide as body, slightly wider than long, head lenght representing 33% of SVL. Snout very short, approximately 28% of head length, truncate in both dorsal and lateral views. Internarial region subtly depressed. Nostril openings directed anterolaterally, not protuberant. Loreal region flat. *Canthus rostralis* indistinct. Lips thin and barely flared. Eye large, ED 1.6 times the distance between the eye and nostril, palpebral membrane translucent, with brown pigmentation at its border. A faint supratympanic fold, extending posteriorly from the posterior corner of the eye to an area above the anterior part of the arm insertion. Tympanum round, slightly wider than high, directed laterally. Tympanic annulus distinct, except for the uppermost part (about 1/4 of its diameter) that is obscured by the supratympanic fold; its diameter equals the diameter of the digital disc of finger III and is only slightly smaller (84%) than the distance between the eye and the tympanum. Digital discs round. Digital disc of finger III about 1.6 to 1.8 times the width of the finger. Relative length of fingers I < II < IV < III. Subarticular tubercles round, distal tubercle on finger IV bifid. Supernumerary tubercles on the proximal segments of digits present. Palmar tubercle flat, divided, inconspicuous. A flap-like fold extends from the palmar tubercle to the base of the digital disc of finger IV. Inner metacarpal tubercle flat, elongate. Prepollex lacking nuptial excrescences. Webbing formula of the hand: I – II $1^{¼}$–$2^{1/3}$ III 2^{-}–$1^{1/2}$ IV. Vocal sac single, median, subgular, externally evident by the loose skin on the sides of the jaw and immediately below the mental region. Axillary membrane reaches the first proximal third of the arm. Two glandular patches visible on the chest, separated from each other by about half their width. Hind limbs long, TL equaling 54% of SVL. Toes bearing round digital discs, slightly smaller than those on fingers. Inner metatarsal tubercle large, ovoid. Outer metatarsal tubercle indistinct. Subarticular tubercles round, subconical. Few supernumerary tubercles on proximal segments of digits, indistinct. Relative lengths of toes I < II < III <V < IV. Webbing formula of the foot: I 1–1 II 1^{+}–$1^{1/2}$ III 1–$1^{3/4}$ IV 2–1^{+} V. External tarsal fold and tubercles absent. Internal flap-like tarsal fold present, extending from the inner metatarsal tubercle to the tibiotarsal articulation. Calcar and heel tubercles absent. Cloacal opening directed posteriorly, situated at the level of the upper edges of thighs. Small cloacal sheat present, dorsal to the cloaca, not covering it completely. Skin smooth, except for the oval pectoral patches, which are finely granular, and the belly that is coarsely granular. Tongue oval, free laterally and posteriorly, shallowly notched behind. Vocal slits present, longitudinal, and long, originating below the rim of the central part of the tongue and running towards the corner of the mouth. Choanae small, rounded, separated by a distance almost five times its diameter. Process and vomerine teeth absent.

In life, dorsal ground color of the body, flanks and limbs dark brown with black, small, regularly disposed, well defined spots. Interocular blotch on head, dorsolateral bands, blotches on the heel and the rump are light yellow. Upper lips gray. Belly and pectoral glands are white. Digits, webbing, axillary membranes, groin, and hidden surfaces of the arms and legs are bluish-black. Chin, throat, and ventral areas of arms and legs are smoky gray. Ventrally, the pads of the digits are blue-gray. Iris coppery brown with tiny dark brown reticulations and a narrow non-reticulated copper ring around the pupil.

In preservative the dorsum is dark brown. Interocular and dorsolateral bands are creamy white, axillary membranes, groin, thigh, webbings, and digits are grayish black. Venter is creamy white and iris dark gray.

Measurements of holotype (in mm). SVL 23.7, HL 7.6, HW 8.4, ED 3.3, END 2.1NSD 1.2, IND 2.1, AMD 5.7, TD 1.4, FAL 5.7, FAB 1.7, HAL 8.7, THL 12.9, TL 12.7, TAL 6.9, FL 11.1, TFD 1.2, FFD 1.0.

Variation. Measurements of the type series are summarized in Table 1. The body is slightly wider than the head in some specimens. In some specimens the dorsolateral bands are connected posteriorly to the spot in the rump forming a frame, the color varies from light yellow to bright yellow; the dorsum may be light brown to dark brown. The bluish-black color is more intense and more exposed on the flanks in the only known female (MHUA-A 7337, Fig. 3B). Variation exists with respect to the amount of black spots on the dorsum, more abundant at ICN 39877–39980 then on ICN 23973–24000. Few scattered yellow dots are present in some specimens (TG 1850, Fig. 3A). Webbing on the hand varies slightly among specimens II (1^{-}–$1^{1/2}$) – ($2^{1/3}$–$2^{1/2}$) III (2^{-}–2) – ($1^{1/2}$–2) IV and variation of webbing between toes is I (1^{-}–1) – (1–$1^{3/4}$) II (1–1^{+}) – ($1^{1/2}$–2) III (1^{-}-1) – ($1^{1/2}$–$1^{3/4}$) IV 2 – (1^{-}–1^{+}) V. The pectoral glands are more elliptical in the female when compared to the glands of males, which are oval. Subarticular tubercles of finger IV may be simple, bifid or divided.

Geographic distribution and natural history. *Dendropsophus manonegra* **sp. nov.** is known from three localities of the upper Amazon basin at the eastern foothills of the Andes in southern Colombia (Fig. 4), departamentos de Caquetá, Cauca and Putumayo, approximately between 400 and 1200 m a.s.l. The type locality is a temporary pond in a pasture without forest cover in the immediate vicinity. Males were calling perched on vegetation on the edge of the pond or on floating or emergent vegetation. One amplectant pair was observed (MHUA-A 7336–37). Tadpoles and advertisement calls are currently unknown. The only sympatric anuran species found at the site was *Hypsiboas lanciformis.*

Phylogenetic relationships. Tree search retrieved 10 equally most parsimonious trees with 6833 steps. The consensus tree is shown in Fig. 5. Most of the conflict among the shortest trees occurs at the species group-level relationships. Of the species groups retrieved by Faivovich *et al.* (2005) only the *Dendropsophus leucophyllatus* and the *D. marmoratus* groups were recovered as monophyletic. Overall Jackknife values are low except in some internal nodes such as the least inclusive clade containing the new species. All tree topologies depict *D. manonegra* **sp. nov.** as sister species to *D. bifurcus*. See Table 2 for genetic distances between species of the *D. leucophyllatus* species group.

TABLE 1. Measurements (mm) of adults of *Dendropsophus manonegra* **sp. nov.** (S.D. = standard deviation).

	Males (n=12)				Female (n=1)
Measurements	Min	Max	Average	S.D.	
SVL	22.7	25.1	23.4	0.7	32.5
HL	7.3	8.7	7.8	0.41	9.9
HW	8.0	9.5	8.6	0.45	11.5
ED	2.8	3.5	3.2	0.21	3.7
END	1.7	2.5	2.1	0.23	2.0
NSD	1.1	1.4	1.2	0.1	2.8
IND	2.0	2.5	2.2	0.15	2.6
AMD	5.1	6.2	5.5	0.31	1.3
TD	1.1	1.5	1.3	0.13	2.0
FAL	4.6	5.7	5.1	0.37	7.3
FAB	1.6	2.4	1.8	0.2	2.2
HAL	6.9	8.7	7.8	0.55	10.8
THL	11.8	13.9	12.7	0.63	17.0
TL	12.4	14.3	13	0.59	18.7
TAL	6.7	8.0	7.2	0.43	9.6
FL	10.8	12	11.3	0.38	16.5
TFD	1.1	1.6	1.3	0.16	1.8
FFD	1.0	1.5	1.2	0.15	1.7

TABLE 2. Genetic distance (%) among species of the *Dendropsophus leucophyllatus* species group. Values are estimated from 862 aligned bp of the 16S rRNA gene.

	Specie	GenBank	1	2	3	4	5	6	7	8	9	10
1	*D. anceps*	AY843597	–									
2	*D. bifurcus*	AY362975	13.5	–								
3	*D. ebraccatus*	AY843624	12.4	13.5	–							
4	*D. elegans*	AF308103	12.2	13.8	13.3	–						
5	*D. leucophyllatus*	AF308096	12.4	11.9	11.7	14.1	–					
6	*D. manonegra*	KF009942	13.5	2.5	12.4	13.5	11.8	–				
7	*D. manonegra*	KF009943	13.5	2.5	12.4	13.5	11.8	0	–			
8	*D. salli*	AY362976	13.5	12.4	13.6	11.2	13.9	13.1	13.1	–		
9	*D. sarayacuensis*	AY843664	12.7	10.4	12.6	13.8	11.0	10.6	10.6	13.5	–	
10	*D. triangulum*	AY326053	12.3	11.9	11.3	14.2	9.3	11.8	11.8	14.1	11.0	–

Etymology. The specific name *manonegra* is used as a noun in apposition and is Spanish for “black hand” making reference to the unusual black flash colors of the species, especially in the webbing. It is concurrently a tribute to Mano Negra, a rock band of the 80’s and 90’s. The band was in contact with the nature, culture and society of Colombia through their project “El Expreso del Hielo” (The Train of Ice), a fantastic train ride that crossed Colombia.

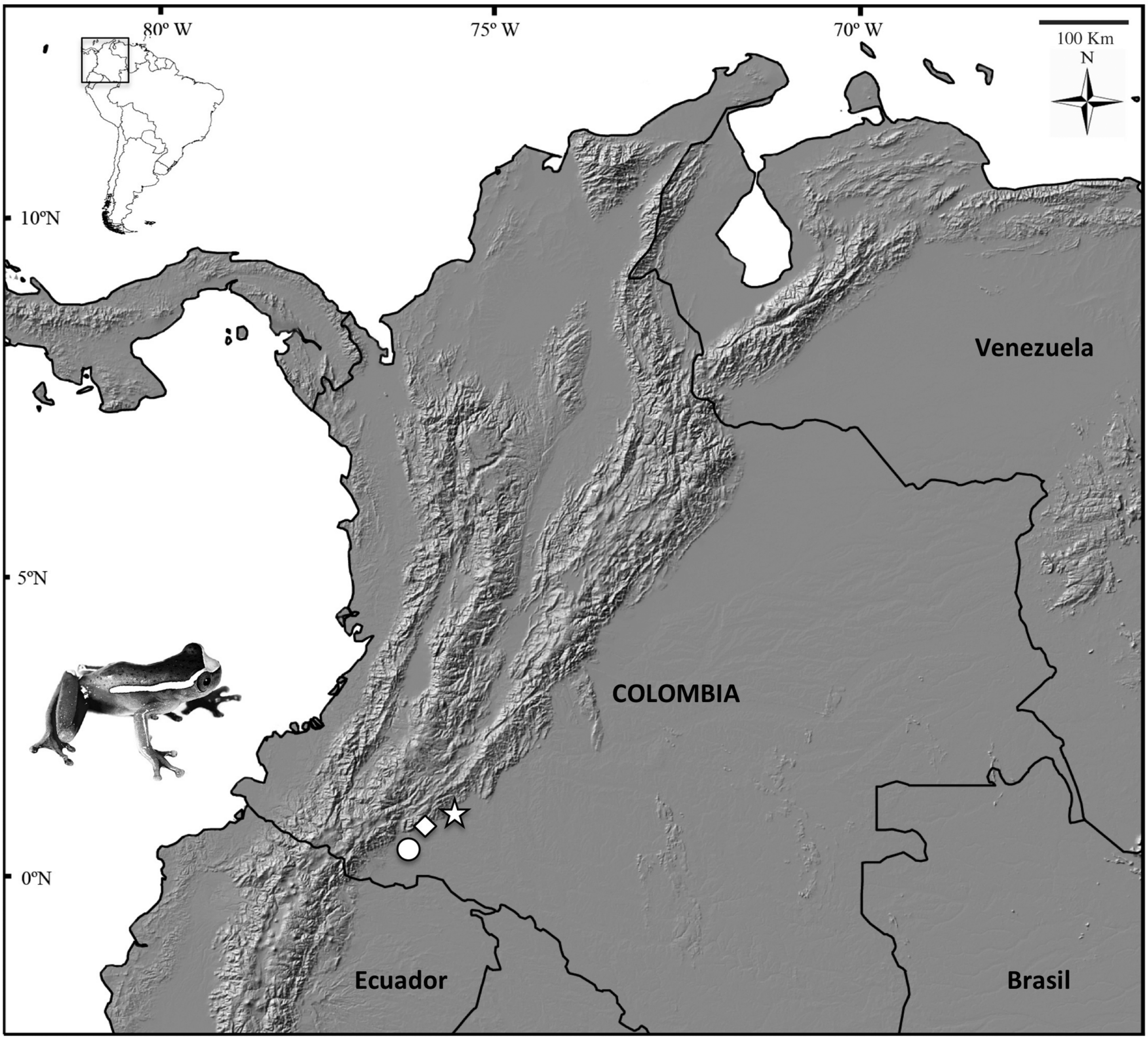

FIGURE 4. Map showing the geographic distribution of *Dendropsophus manonegra* **sp. nov.** in Colombia. San José de la Fragua and Florencia, departamento de Caquetá (star); Bota Caucana, departamento de Cauca (diamond); Serranía de los Churumbelos, departamento de Putumayo (circle).

Discussion

Currently, the *Dendropsophus leucophyllatus* species group is relatively well-known in terms of its species composition (see Duellman 1974; Titus *et al.* 1989; De la Riva & Duellman 1997; Chek *et al.* 2001; Jungfer *et al.* 2010). Although Salducci *et al.* (2002) retrieved this group as paraphyletic, most recent and comprehensive studies have recovered it as a monophyletic group with strong support (e.g. Faivovich *et al.* 2005; Salducci *et al.* 2005; Wiens *et al.* 2005; Moen & Wiens 2009). The only species missing from previous phylogenetic analyses is *D. rossalleni*, although De la Riva and Duellman (1997) suggested its relationship to this group based on their similar morphology. Despite these contributions, there are two aspects of the systematics of the *Dendropsophus leucophyllatus* species group that require special attention.

The first is the placement of *Dendropsophus anceps* as the basal species of the *D. leucophyllatus* group, as first determined by Faivovich *et al.* (2005) and later by Moen and Wiens (2009). This result was not recovered by other recent studies (e.g. Jungfer *et al.* 2010; Wiens *et al.* 2010; Pyron & Wiens 2011). Jungfer *et al.* (2010) excluded *D. anceps* from the *D. leucophyllatus* group because some of their phylogenetic results placed this species nested within their outgroup taxa and because it lacks almost all of the common morphological characters shared by the other members of the group. Unfortunately, their consensus tree (see Jungfer *et al*. 2010: Fig. 7) omits the placement of *D. anceps*, preventing us from establishing the outgroup species to which *D. anceps* clustered with and its corresponding branch support. Our phylogenetic results place *D. anceps* as the sister taxon to all other species of the *Dendropsophus leucophyllatus* group, although with low support (Fig. 5). The presence of pectoral glands, a putative morphological synapomorphy of the *Dendropsophus leucophyllatus* group (Cochran & Goin 1970; Duellman 1970; Faivovich *et al*. 2005), also supports this relationship. Albeit *D. anceps* males do not have pectoral glands divided into two patches, as do females (VGDO pers. obs.), characters operate within the semaphoront logic (Hennig 1966). Given the evidences presented above, we include *D. anceps* in the *D. leucophyllathus* group.

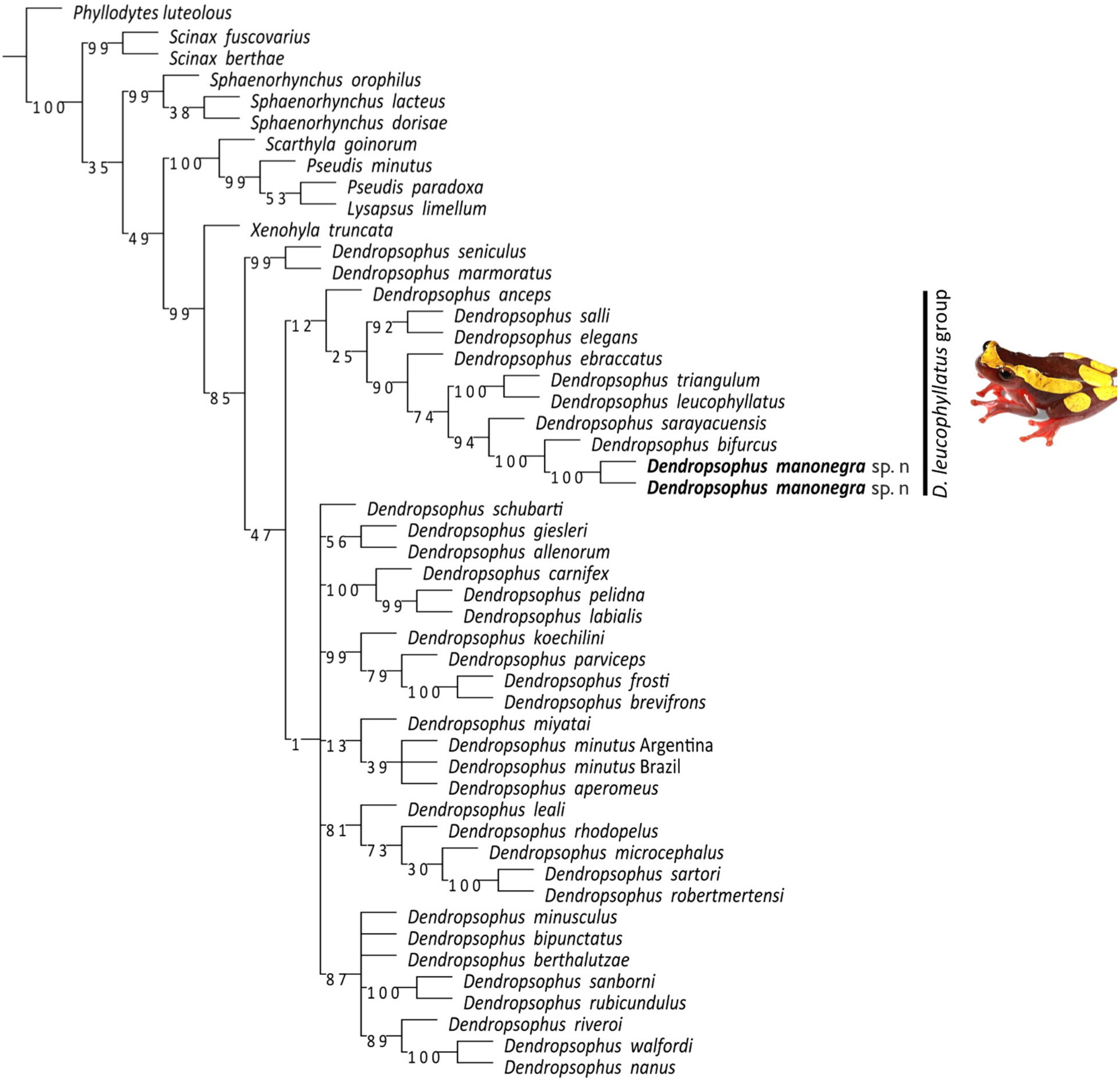

FIGURE 5. Strict consensus topology of the 10 shortest trees (6833 steps) obtained from maximum parsimony analysis of DNA sequences of the 12S and 16S rRNA genes and the interveining tRNA Valine (see text for analysis details). Numbers below nodes are Jackknife values based on 1000 pseudoreplicates. *Dendropsophus manonegra* **sp. nov.** samples are highlighted in bold. Asterisks indicate 100% Jackknife support values.

The second issue pertains to the relationships of *Dendropsophus elegans*. Duellman (1982) proposed, based on dorsal coloration pattern, that *D. elegans* could be the sister species of *D. leucophyllatus*. All subsequent molecular studies were unable to retrieve a close relationship between these two species (e.g. Check *et al.* 2001; Lougheed *et al.* 2006). This was corroborated by Jungfer *et al.* (2010), who retrieved *D. elegans* as the sister species of the southwestern Amazonian species *D. salli*; a clade basal to the other species of the group (except for *D. anceps*, see above). Our analysis also recovers *D. elegans* as sister to *D. salli*, supporting Jungfer *et al.* (2010).

The presence, shape, and number of odontophores and vomerine teeth have been considered to be important taxonomic characters in the history of *Dendropsophus* taxonomy (e.g. Reinhardt & Lütken 1862). Examination of 11 specimens of *D. bifurcus* revealed that only one specimen (MZUSP 116704) has a structure that resembles a vomerine tooth on the right odontophore. It is also remarkable that none of the type specimens of *D. manonegra* **sp. nov.** for which the character was checked (N = 30) have vomerine teeth and/or odontophores. An assessment of specimens from various *Dendropsophus* species revealed that the presence and shape of vomerine teeth is polymorphic in some species (e.g. *D. sanborni*). These observations indicate that the phylogenetic information of presence, shape, and number of odontophores and vomerine teeth need to be carefully reevaluated.

A genetic distance of 3% in the mitochondrial 16S rRNA gene has been proposed as an operational threshold to establish independent evolutionary lineages in Amazonian amphibians (Fouquet *et al.* 2007). However, using a threshold value is arbitrary because it violates predictions under the evolutionary species concept (Padial *et al.* 2009). The magnitude of differences in intraspecific genetic divergences varies strongly between lineages because of the different factors involved in the divergences at the population level (Whitlock 2003). Thus, restricting the limits of species to a percentage value is inappropriate. Furthermore, morphological distinction between species is not always proportional to their genetic differentiation (e.g. Chek *et al.* 2001; Vences *et al.* 2011).

Incongruence among lines of evidence can be due to faster divergence in some characters than in others, promoted by different evolutionary processes (Orr & Smith 1998; Padial *et al.* 2009) or different factors operating such as phenotypic plasticity. Rapid adaptive radiations can result in morphologically divergent species with low levels of genetic differentiation (Cunha *et al.* 2005; Padial *et al.* 2009). This seems to be the case of *Dendropsophus manonegra* **sp. nov.**; while it is clearly morphologically distinguishable from *D. bifurcus*, the genetic distance between these species is relatively low when compared to other species of the group (Table 2). In the Neotropics, this phenomenon has been previously reported for other genera such as *Atelopus* and *Hyloscirtus* (Guayasamin *et al.* 2010; Coloma *et al.* 2012). Further molecular analysis incorporating more sequence data will help assess whether other mitochondrial markers have the same level of variation or not.

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APPENDIX I. Additional specimens examined.

Dendropsophus anceps**:** BRAZIL: Espírito Santo: Linhares: CFBH 5795–5804; São Paulo: Caçapava: CFBH 13208–13210.

Dendropsophus bifurcus**:** ECUADOR: Morona: Santiago: Sevilla Don Bosco: MZUSP 55637; Napo: Santa Cecilia: MZUSP 116703–116706, 116695, 116696; Loreto: MZUSP 116720–116724; Orellana: Estación Científica Yasuní PUCE: QCAZ 24396–24406; Pastaza: Rio Villano: MZUSP 117915; Rio Solís: MZUSP 76478.

Dendropsophus ebraccatus**:** COLOMBIA: Antioquia: Maceo: Las Brisas: 500m. MHUA-A 2159, 2590-2591, 4063, 4807–4810; HONDURAS: Gracias a Dios: USNM 559102, 559105, 559107, 550109–550113, 550115, 550116.

Dendropsophus elegans**:** BRAZIL: Bahia: Guandú: CFBH 27974; Espírito Santo: Linhares: CFBH 22663-22667.

Dendropsophus leucophyllatus**:** ECUADOR: Orellana: Río Napo: Chiroisla: Banco norte: QCAZ 44455–44458.

Dendropsophus rossalleni**:** BRAZIL: Amazonas: CFBH 4988, 4990; Pará: Oriximiná: MCNAM 8671, 8672.

Dendropsophus salli: BRAZIL: Acre: Tarauacá: MZUSP 116707–116719; Rondônia: Porto Velho: MZUSP 117916- 117917, 116697–11702.

Dendropsophus sarayacuensis**:** BRAZIL: Mato Grosso: Aripuanã: MZUSP 80632–80634; Rondônia: Porto Velho: MZUSP 146192, 148388; ECUADOR: Napo: Río Salado: QCAZ 36699-36700, 36801, 36802.

Dendropsophus triangulum**:** ECUADOR: Orellana: Río Napo: Santa Teresita: Nuevo Rocafuerte: Banco norte del Río Napo: QCAZ 44667–44672.

APPENDIX II. GenBank accession numbers for hylid frog sequences (12S and 16S rRNA) used for this study.

Species	12S	16S	Species	12S	16S
Dendropsophus allenorum	DQ380348	–	*D. parviceps*	AY843652	AY843652
D. anceps	AY843597	AY843597	*D. pelidna*	AY819434	–
D. aperomeus	AY819450	–	*D. rhodopeplus*	AY843658	AY843658
D. berthalutzae	AY843607	AY843607	*D. riveroi*	DQ380372	–
D. bifurcus	AY362975	AY362975	*D. robertmertensi*	AY819452	–
D. bipunctatus	AY843608	AY843608	*D. rubicundulus*	AY843661	AY843661
D. brevifrons	AY843611	AY843611	*D. salli*	AY362976	AY362976
D. carnifex	AY843616	AY843616	*D. sanborni*	AY843663	AY843663
D. ebraccatus	AY843624	AY843624	*D. sarayacuensis*	AY843664	AY843664
D. elegans	DQ380355	AF308103	*D. sartori*	AY819453	–
D. frosti	JQ088283	JQ088283	*D. schubarti*	DQ380374	–
D. giesleri	AY843629	AY843629	*D. seniculus*	AY843666	AY843666
D. koechlini	AY819369	–	*D. triangulum*	AY843680	AY843680
D. labialis	AY843635	AY843635	*D. walfordi*	AY843683	AY843683
D. leali	AY819451	–	*Lysapsus limellum*	AY843697	AY843697
D. leucophyllatus	DQ380360	AF308096	*Phyllodytes luteolous*	AY843721	AY843721
D. manonegra	KF009942	KF009942	*P. minutus*	AY843739	AY843739
D. manonegra	KF009943	KF009943	*P. paradoxa*	AY843740	AY843740
D. marmoratus	AY843640	AY843640	*Scarthyla goinorum*	AY843752	AY843752
D. microcephalus	AY843643	AY843643	*Scinax fuscovarius*	AY843758	AY843758
D. minusculus	DQ380362	–	*S. berthae*	AY843754	AY843754
D. minutus	–	AY843647	*Sphaenorhynchus dorisae*	AY843766	AY843766
D. minutus	AF308081	AF308113	*S. lacteus*	AY549367	AY549367
D. miyatai	AY843647	AY843647	*S. orophilus*	DQ380388	–
D. nanus	AY819373	–	*Xenohyla truncata*	AY843775	AY843775