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Source: South American Journal of Herpetology, 11(1):66-80.

Published By: Brazilian Society of Herpetology

DOI: <http://dx.doi.org/10.2994/SAJH-D-16-00003.1>

URL: <http://www.bioone.org/doi/full/10.2994/SAJH-D-16-00003.1>

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A New Species of Clown Tree Frog, *Dendropsophus leucophyllatus* Species Group, from Amazonia (Anura, Hylidae)

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Abstract. We describe a new species of *Dendropsophus* (Anura: Hylidae: Hylinae: Dendropsophini) from the Amazon river (= Rio Amazonas) basin, state of Amazonas, northern Brazil. The new taxon is included in the *D. leucophyllatus* group based on its phylogenetic position and on the presence of a pair of pectoral glands (a likely synapomorphy of the group). The species is distinguished from other species in the group by its color pattern and the morphology of hand and feet tubercles. In order to assess the phylogenetic relationships of the new taxon, we compiled a dataset including mitochondrial and nuclear DNA sequence data for all but one species in the *D. leucophyllatus* group, plus a series of hylid outgroups. A tree-alignment (direct optimization) parsimony analysis firmly support the new species as the sister taxon of *D. sarayacuensis*. The monophyly of the *D. leucophyllatus* species group is not recovered in our analysis and the issue is discussed further.

Keywords. Amazon; Amphibia; Biodiversity; Hylinae; Phylogeny; Systematics; Taxonomy.

INTRODUCTION

Dendropsophus Fitzinger, 1843 was resurrected in Faivovich et al. (2005) to include species formerly referred to as “the 30-chromosomes *Hyla*”. Faivovich et al. (2005) also represented a major step for the sorting out of the dozens of *Dendropsophus* species into species-groups assumed to represent natural lineages (i.e., monophyletic groups). Since then, minor rearrangements were necessary, many species were allocated in one group or another, and many new taxa were named (e.g., Moravec et al., 2006; 2008; Jungfer et al., 2010; Fouquet et al., 2011; Guarnizo et al., 2012; Motta et al., 2012; Rivera-Correa and Orrico, 2013; Orrico et al., 2014). One of the arrangements that remains largely unchanged since Faivovich et al. (2005) is the *D. leucophyllatus* species group (clown tree frogs).

Faivovich et al. (2005) suggested the existence of a monophyletic *Dendropsophus leucophyllatus* species group based on several molecular synapomorphies. The authors further suggested that, with the exception of *D. anceps*, all species of the group share the presence of a pair of pectoral glands. Faivovich et al. (2005) considered this gland to be absent in *D. anceps*, but Rivera-Correa and Orrico (2013) reported its presence in that species, albeit in a slightly different arrangement.

The contents of this species group have been largely corroborated, except for the inclusion/exclusion of *D. anceps*. Originally referred to the *D. leucophyllatus* group by

Faivovich et al. (2005), Jungfer et al. (2010) suggested *D. anceps* should be removed from the group based on its phylogenetic position. The exclusion of *D. anceps* from the *D. leucophyllatus* group received ambiguous support by additional phylogenetic work. The exclusion was supported (by implication) by Wiens et al. (2010) and Pyron and Wiens (2011), whereas it was not supported by Moen and Wiens (2009) and Rivera-Correa and Orrico (2013). In addition to the *D. anceps* problem, other long standing problems in the phylogeny of *D. leucophyllatus* groups are the paraphyly of *D. leucophyllatus* and *D. triangulum* with respect to each other (Chek et al., 2001; Loughheed et al., 2006) and the existence of several putative unnamed species in the group (personal observations).

Aside from the ambiguous inclusion of *Dendropsophus anceps*, the monophyly of the *D. leucophyllatus* group has not been seriously questioned, and the group currently includes 10 species: *D. anceps* (Lutz, 1929), *D. bifurcus* (Andersson, 1945), *D. ebraccatus* (Cope, 1874), *D. elegans* (Wied-Neuwied, 1824), *D. leucophyllatus* (Beireis, 1783), *D. manonegra* Rivera-Correa and Orrico, 2013, *D. rossaleni* (Goin, 1959), *D. salli* Jungfer, Reichle, and Piskurek, 2010, *D. sarayacuensis* (Shreve, 1935), and *D. triangulum* (Günther, 1869).

During an ongoing systematic study on Amazonian hylid frogs, we came across (in the field and in zoological collections) an unnamed species that we suspected to be part of the *Dendropsophus leucophyllatus* group (based on color pattern and the presence of pectoral glands). The

new species is found in a few localities in northern Brazil, and is described herein.

MATERIALS AND METHODS

Preliminary analysis of morphological features (color pattern, presence of pectoral glands, morphology of hand, and feet tubercles) revealed that a series of specimens deposited in the herpetological collections Oswaldo Rodrigues da Cunha, housed at the Museu Paraense Emilio Goeldi, Belém, Brazil (MPEG), and Museu Nacional, Rio de Janeiro, Brazil (MNRJ), represent an unnamed species of the *Dendropsophus leucophyllatus* group. However, given the polymorphism of some taxa in the group (Duellman, 1974; Titus et al., 1989), a phylogenetic analysis was needed to assess the actual taxonomic status and historical relationships of these populations. The use of phylogenies is a well-supported and powerful tool to aid in species delimitation of taxonomically challenging groups. Therefore, we include the description within a phylogenetic framework. The phylogeny was also needed to confirm our initial suspicion that this new species is not a member of the *D. leucophyllatus*/*D. triangulum* complex, which would certainly delay its description until a better taxonomic resolution is available for that clade (see Discussion).

Taxon and character sampling

In order to assess the phylogenetic position of the new species within *Dendropsophus*, we compiled a molecular dataset including several representatives of the genus. To that end, a single terminal was included for several nominal species of *Dendropsophus*. The dataset is more densely sampled within the *D. leucophyllatus* species group, including multiple terminals per species. Outgroup selection is based on the phylogenies of Faivovich et al. (2005) and Wiens et al. (2010) and includes members of clades close to *Dendropsophus*: *Lysapsus*, *Phyllodytes*, *Pseudis*, *Scarthyla*, *Scinax*, *Sphaenorhynchus*, and *Xenohyla*. The tree is rooted with *Hyposiboas albomarginatus*.

We sequenced up to two mitochondrial genes (12S and 16S) and one nuclear locus (Recombination Activation Gene I–RAG1) for three specimens of the new taxon from two localities. In addition, we sequenced a fragment of 16S from a sample of *Dendropsophus triangulum*, sympatric with the new taxon, to test if they are morphs of the same taxon. New sequences were generated following the protocols and using the same primers used in Faivovich et al. (2005). We combined these data with sequences from GenBank as follows: we downloaded the *Dendropsophus* sequences from Faivovich et al. (2005), including additional genes not sequenced by us (e.g., the

mitochondrial Cytochrome B, and the nuclear Rhodopsin, Seven in Absentia Homolog 1, Tyrosinase, and 28S). In addition, we included several 12S and 16S sequences of species of the *D. leucophyllatus* group for which sequences were available in GenBank.

Novel sequences were deposited in GenBank with accession numbers KX018314–KX018318. The complete taxon and character sets (including all GenBank accession numbers) included in the analyses are given as online supplementary information (Appendix S1).

Tree search

For the phylogenetic inference, we used direct optimization parsimony (Wheeler, 1996; Wheeler et al., 2006) as the preferred optimality criterion. All transformations (substitutions and insertion/deletion events) were considered to have equal costs (= 1). Sequence optimization in the tree-alignment framework was performed in POY 5 (Wheeler et al., 2014). All POY analyses were performed using 1–32 Intel Xeon 3.0 Ghz processors in one of the American Museum of Natural History cluster computers (Enyo). Contiguous sequences were preliminarily delimited in fragments of putative homology (using the pound [#] sign) to allow incorporation of partial sequences following (Wheeler et al., 2006). Sequences of protein coding genes with the exact same length (Cytochrome B, Rhodopsin, Seven in Absentia Homolog 1, Tyrosinase) were treated as pre-aligned in the POY analyses to speed up the analysis with the underlying assumption that they represent homologous fragments. Initial tree searches were conducted with the command search, which implements time-constrained searches with as many replicates of RAS (Random Addition Sequences) + TBR (Tree Bisection and Reconnection) as possible, followed by Parsimony Ratchet (Nixon, 1999) and Tree Fusing (Goloboff, 1999). Several runs can be initiated in parallel and the command (search) stores the shortest trees of each independent run and implements a final round of Tree Fusing using the pooled trees as a source of topological diversity. We performed two consecutive searches of 6 h (to create an initial pool of trees) followed by four consecutive searches of 72 hours using 16 parallel processors. For a more thorough search, the best trees from the initial searches were submitted to additional rounds of TBR under an iterative pass (IP) optimization (Wheeler, 2003a).

Nodal support for the optimal tree was assessed with the Goodman-Bremer metric (Goodman et al., 1982; Bremer, 1988; Grant and Kluge, 2008) by calculating the difference in length between the optimal tree and the length of each of the trees visited during a complete TBR swap of the optimal topology.

Morphology

Specimens used in the description, examined for comparisons, or discussed below are deposited in the following institutions: AMNH (American Museum of Natural History, New York, USA), CFBH (Coleção de Anfíbios Célio F.B. Haddad, Rio Claro, Brazil); FSM (Florida State Museum, University of Florida, Gainesville, USA); MNCN: (Museo Nacional de Ciencias Naturales, Madrid, Spain); MNRJ: (Museu Nacional, Rio de Janeiro, Brazil); MPEG (Coleção Herpetológica Oswaldo Rodrigues da Cunha, Museu Paraense Emílio Goeldi, Belém, Brazil); MZUSP (Museu de Zoologia, Universidade de São Paulo, Brazil); NHRM (Naturhistoriska Riksmuseet, Stockholm, Sweden); QCAZ (Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador); USNM (Smithsonian Institution, National Museum of Natural History, Washington, D.C., USA). A complete list of specimens examined is given in Appendix 1.

In order to help diagnose the new taxon, 12 measurements were taken under a stereomicroscope, using a digital caliper (to the nearest 0.1 mm), following the method and landmarks described in Peloso et al. (2014): SVL (snout–vent length); HL (head length; from snout to angle of the jaw); HW (head width; between the angle of jaws); ED (eye diameter; between anterior and posterior corner of the eye); ELW (eyelid width); IOD (interorbital distance; distance between anterior corner of the eyes); IND (internarial distance); END (eye–nostril distance; from the anterior corner of the eye to the posterior margin of nostril); THL (thigh length; from the middle of the cloacal opening to the outer edge of the flexed knee); TBL (tibia length; from the outer edge of the flexed knee to the heel); FL (foot length; from tibio-tarsal articulation to tip of fourth toe). An additional measurement TD (tympanum diameter; measured at the widest portion) was taken. Fingers and toes are numbered and abbreviated as follows: Fingers II–V = FII–V, Toes I–V = TI–V.

The description of color pattern and variation of live individuals is based on photographs and notes taken from the three specimens from the type locality (MPEG 28681–28683: day phase, taken one day after collection). Color in preservative is based on all specimens of the type series.

RESULTS

Phylogenetic analyses

Tree search in POY performed a total of 1,235 replicates of RAS + TBR, 657,706 rounds of Tree Fuse, and 6,513 rounds of Parsimony Ratchet. The direct optimization analysis found 49 equally parsimonious trees of 9,668 equally weighted steps—the best score was hit

89,174 times (strict consensus shown in Figure 1). The implied alignment (Wheeler, 2003b) of the optimal tree contains 5,771 columns.

Our results recover *Dendropsophus* as the monophyletic sister taxon of *Xenohyla truncata*. Because of limited taxon sampling outside of *Dendropsophus*, we refrain from commenting on the relationships among outgroup taxa. The monophyly of the *D. leucophyllatus* group (sensu Rivera-Correa and Orrico, 2013) is not corroborated by our dataset. The strict consensus depicts a paraphyletic *D. leucophyllatus* group, with *D. minutus* + *D. miyatai* nested within the group if *D. anceps* is considered part of the group. We recovered *D. minutus* and *D. miyatai* as the sister of *D. salli* + *D. elegans* and, by implication, inside the *D. leucophyllatus* group, as currently defined.

Regarding the new taxon, our phylogenetic analyses firmly places it within the *Dendropsophus leucophyllatus* group as the sister species of *D. sarayacuensis*. Together, those species form the sister clade of (*D. bifurcus* + *D. manonegra*), and these four taxa are the sister clade to another large clade containing all specimens identified as *D. leucophyllatus* or *D. triangulum* (which are not reciprocally monophyletic but, collectively, form a well-supported monophyletic group).

The phylogenetic and morphological analyses support the recognition of a new species of *Dendropsophus*. The new taxon is a member of the *Dendropsophus leucophyllatus* group based on the phylogenetic analyses (Fig. 1) and on the presence of a glandular patch on each side of the chest (only visible after dissection).

Dendropsophus mapinguari sp. nov. (Figs. 2–6, 7A, 8A, 9C)

Holotype (Figs. 2A, 3, 4, 5, 7A, 9C)

MPEG 28682 (field number FPR 295), an adult male, from Brazil: state of Amazonas: Municipality of Maués: Floresta Nacional de Pau-Rosa, Comunidade Santa Teresa, Rio Paraconi (03°53'18"S, 58°20'42"W), collected by M.J. Sturaro and P.L.V. Peloso, on 03 March 2009.

Paratypes (Figs. 2B, 6, 8B)

MPEG 28681 (field number FPR 294) and MPEG 28683 (field number FPR296), both adult males, collected by M.J.S. and P.L.V.P. together with the holotype. MPEG 33905 (field number M3A42), adult male, collected 05 February 2009, by E.G. Pereira; R.A.K. Ribeiro; R.W. Ávila; J.A. Scolzo, in Brazil: Amazonas: Uruará (02°24'49"S, 58°38'20"W). MPEG 33964–33967 (field numbers respectively M4A63, M4A67–M4A69), MNRJ 56732–56735 (field numbers respectively M4A64, M4A70, M4A71, M4A76), all adult males, collected 31

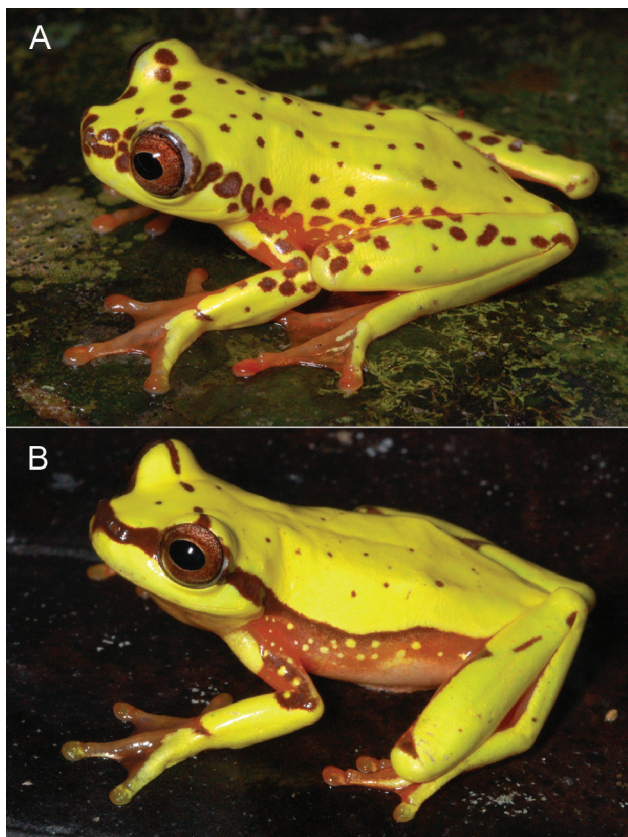


Figure 2. *Dendropsophus mapinguari* sp. nov. in life. Both specimens are males from Floresta Nacional de Pau-Rosa, Amazonas, Brazil. **(A)** Holotype, MPEG 28682 (22.2 mm SVL); **(B)** paratype MPEG 28683 (24.1 mm SVL).

January 2009, by E.G. Pereira; R.A.K. Ribeiro; R.W. Ávila; J.A. Scolzo, in Brazil: Amazonas: Itacoatiara, Lindóia (02°58'06"S, 58°59'45"W).

Etymology

The *mapinguari* (also spelled as *mapinguary*) is a mythological creature inhabiting the imagination of residents of the Amazonian region, especially in Brazil and Bolivia. This creature has been portrayed in many shapes, but usually a tall and furry beast with a single eye, long claws, and a second mouth in its belly. Although *mapinguari* is the most commonly used name, the creature is also known by the names of *isnashi* or *juma*. It is very likely that the *mapinguari* is another example where mysticism and reality get mixed up. The region where the *mapinguari* is thought to exist was also home to large mammals that are now extinct but were likely to have co-existed with ancient human populations (e.g., the giant ground sloths, *Megatherium*). It has been suggested that these giant sloths were the inspiration for these long-preserved folkloric portraits of the *mapinguari* (Oren, 1993; Oren, 2001). This would be a case similar to the study of Lozier et al. (2009), where the authors suggest that sightings of the Sasquatch are probably observations of black bears (*Ursus americanus*). Nonetheless, the *mapinguari* is an important part of Amazonian folklore, which is here perpetuated as the name of this exquisite frog. The specific name is used as a noun in apposition.

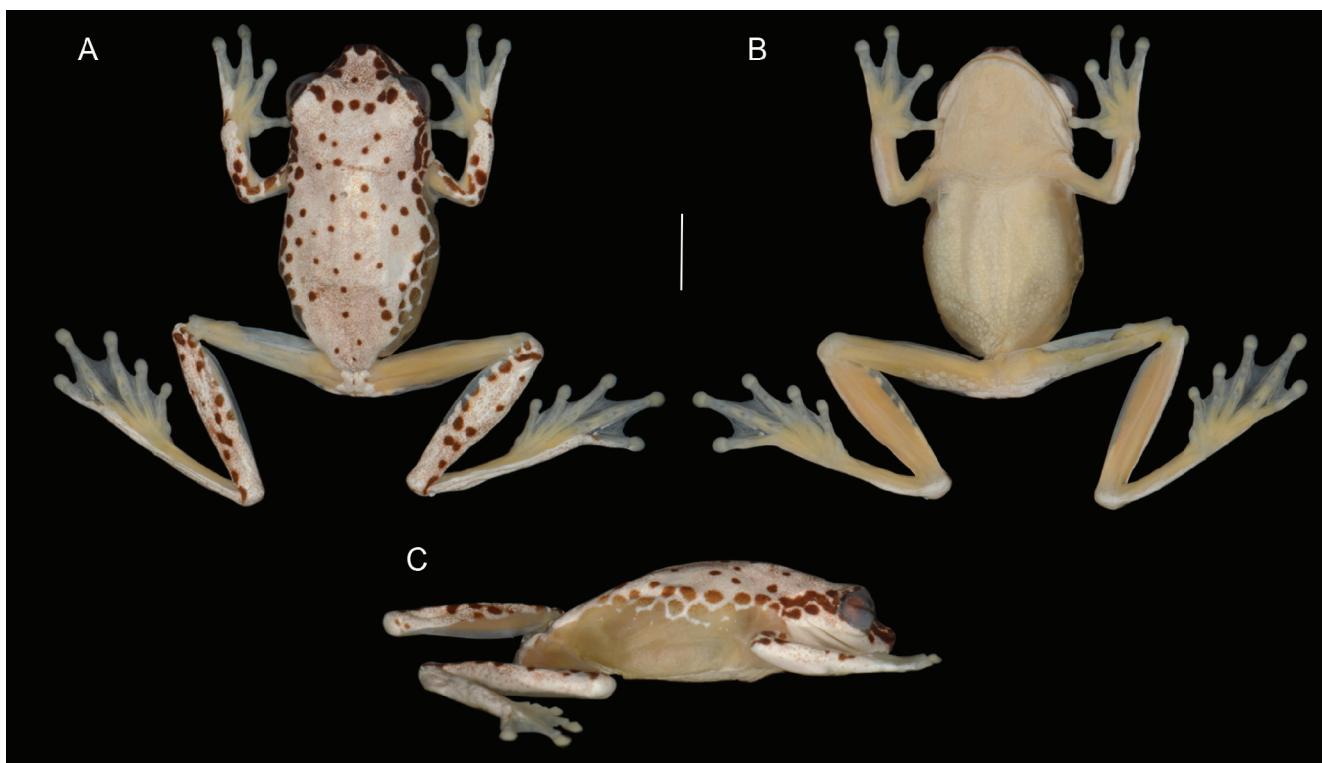


Figure 3. Holotype of *Dendropsophus mapinguari* sp. nov. (MPEG 28682) in **(A)** dorsal, **(B)** ventral, and **(C)** lateral views. Bar = 10 mm.

Diagnosis

The combination of the following character states can be used as a diagnosis for the new taxon: (1) SVL of males 22.2–24.8 mm ($n = 8$; females unknown); (2) head slightly wider than long (1.0–1.2 times wider than long); (3) snout truncate in dorsal and lateral views (Fig. 4); (4) tympanum round, with tympanic membrane not visible (completely covered by skin), and tympanic annulus distinct except for the uppermost part which is not distinct in some specimens (covered by the supratympanic fold); (5) a pair of vomerine odontophores present; (6) skin on dorsal surfaces of body and limbs

smooth; (7) skin on ventral surface of body granular; (8) finger discs present, expanded, round; (9) distal sub-articular tubercle on FV round, may be slightly notched in some specimens; (10) axillary membrane present; (11) dorsum ground color bright yellow in life (white in preservative) with small brown dots all over dorsal surface of body and limbs; (12) digits, webbing, groin, and hidden surfaces of the limbs orange or reddish in life (cream in preservative); (13) absence of pigmentation on chin and throat; (14) absence of pigmentation in the dorsal surface of the thigh; (15) dorsum bright yellow in life (white in preservative) with brown spots and stains.

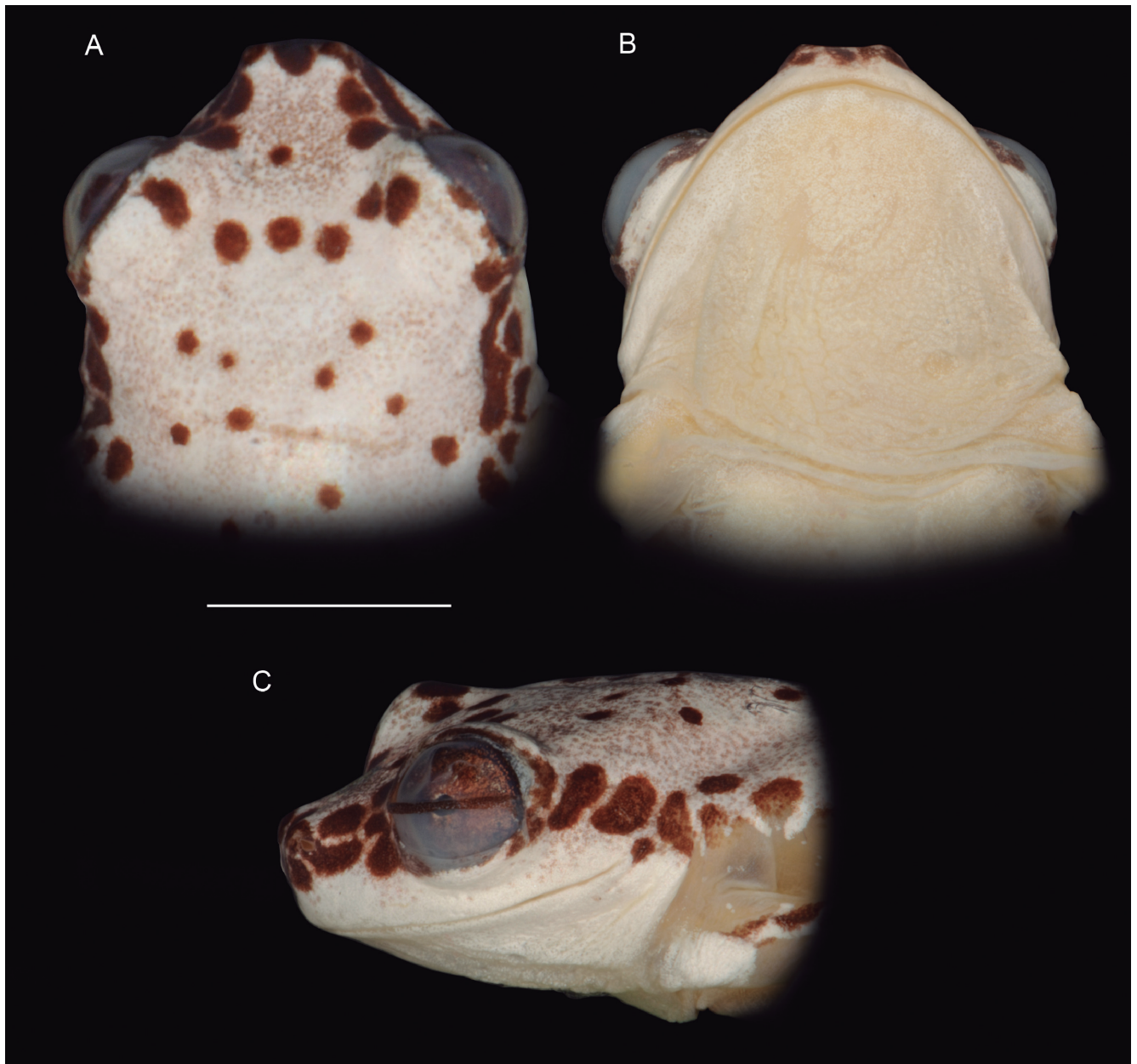


Figure 4. *Dendropsophus mapinguari* sp. nov. (A) Dorsal, (B) ventral, and (C) lateral views of the head of holotype (MPEG 28682). Bar = 5 mm.

Comparison with other species in the *Dendropsophus leucophyllatus* group

Given the phylogenetic position of *Dendropsophus mapinguari* we limit the comparisons of the new taxa with species in the *D. leucophyllatus* group. Comparisons are more detailed and extensive with *D. sarayacuensis* (its sister taxon) and *D. rossalleni* (a member of the *D. leucophyllatus* group, but for which phylogenetic position is unknown). For the pairwise comparison given below the

character state given in parenthesis represents that of the species being compared to the new taxon, whereas the character states of *D. mapinguari* are those in the descriptions of the taxon (above).

The new species differs from all species in the group by its color pattern. Although there is some degree of variation and distinct color morphs among some of the taxa in the group (especially in the *Dendropsophus leucophyllatus/triangulum* species complex, see below), at least *D. bifurcus*, *D. ebraccatus*, *D. elegans*, *D. leucophyllatus* (part), *D. salli*, and *D. manonegra* share the pattern Duellman (1974) describe as a “broad U-shaped pale cream mark covers the top of the snout edges of the eyelids and extends posteriorly as a pair of broad dorsolateral stripes to the sacral region.” Additionally, *D. mapinguari* differs from *D. rossalleni* by its larger size (SVL in males 17.5–22.8; mean 20.8 mm; $n = 16$); color pattern (dark dorsum usually with light markings on the snout region, extending from the nostrils to the anterior portion of the eyes—pattern never light with dark spots or marks); absence of pigmentation on the anterior portion of the chin (Fig. 7A; pigmentation present in *D. rossalleni*; Fig. 7B); less developed hand and foot tubercles (much more prominent in *D. rossalleni*); and round subarticular tubercle on FV, usually not notched or just slightly notched anteriorly (tubercles more developed, elongated and heavily notched—bifid, in *D. rossalleni*). *Dendropsophus mapinguari* differs from *D. sarayacuensis* by its smaller size (SVL in males 24.9–28.2; mean 28.2 mm; $n = 11$); color pattern (dark dorsum with a light mark on the snout region, extending from nostrils to anterior portion of eyes, delimited by *canthus rostralis*; light dorsolateral blotched area extending from tympanic region to midbody; light markings also present on arms and legs, usually two on arms and three on legs, being one invariably on elbow, one invariably on knee and one on heel); in having a round subarticular tubercle on FV, usually not notched or just slightly notched anteriorly (tubercles more developed, elongated and heavily notched—bifid, in *D. sarayacuensis*).

It is clear that both nominal taxa *Dendropsophus triangulum* and *D. leucophyllatus* require redefinition and that specimens currently assignable to these two names might in fact represent a complex of several species (Chek et al., 2001; Loughheed et al., 2006; Fig. 1). Inasmuch as the actual diversity within this species complex deserves a study of its own (see Discussion) it is possible to easily diagnose *D. mapinguari* from specimens assignable to *D. leucophyllatus* and *D. triangulum*. Collectively, all specimens assigned to the *D. leucophyllatus/triangulum* species complex (including those taxa currently considered synonyms of *D. leucophyllatus* and *D. triangulum*) present some characters that will distinguish *D. mapinguari* from them. *Dendropsophus mapinguari* differs from specimens in the *D. leucophyllatus/triangulum* complex by the absence of pigmentation on the dorsal surface of the thigh

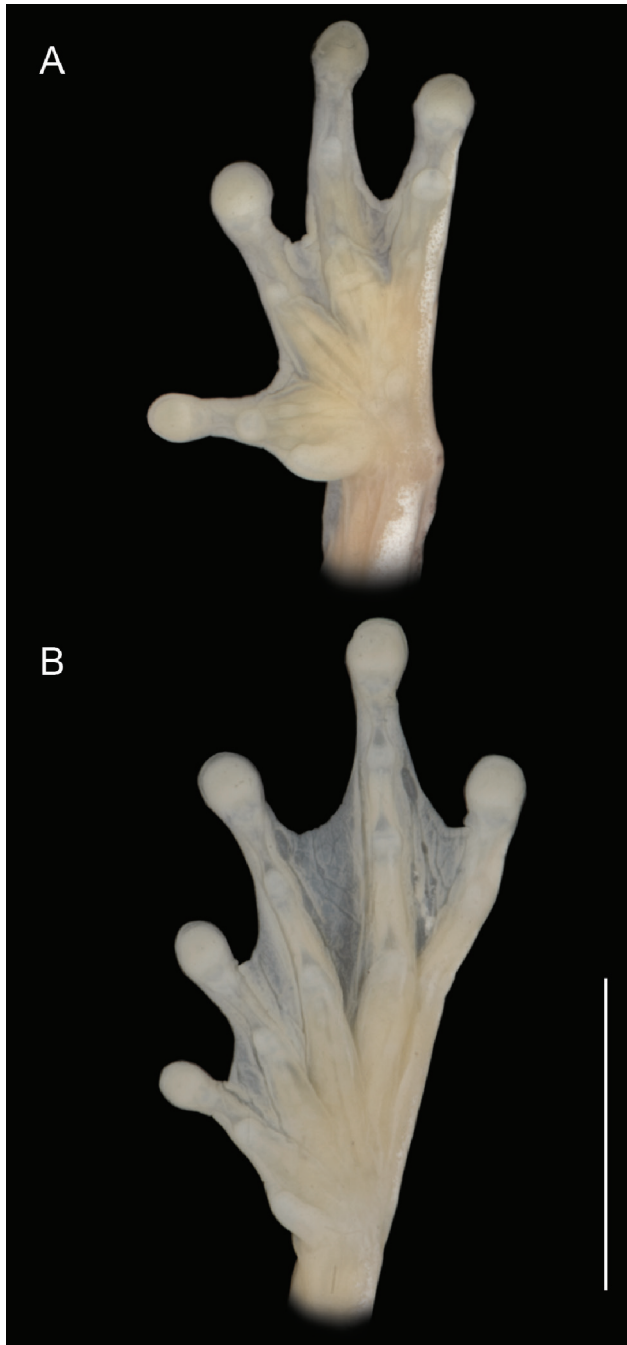


Figure 5. *Dendropsophus mapinguari* sp. nov. (A) Left hand and (B) left foot of the holotype (MPEG 28682). Bar = 5 mm.

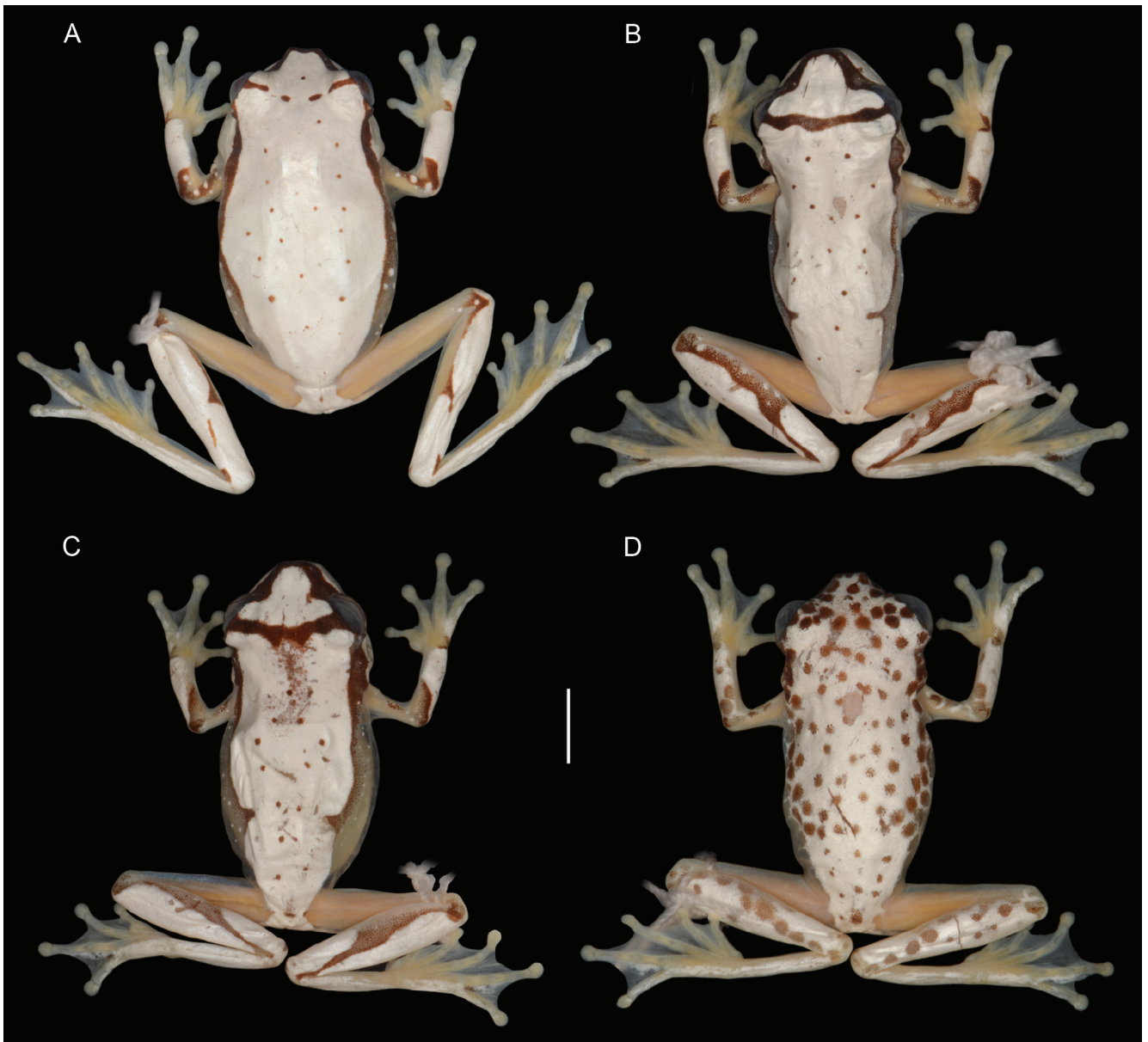


Figure 6. Dorsal variation in color pattern in the type series of *Dendropsophus mapinguari* sp. nov. (paratypes). Specimen from (A) the type locality, Santa Teresa, Maués, Amazonas, Brazil: MPEG 28683 and (B–D) Lindóia, Itacoatiara, Amazonas, Brazil, (B) MPEG 33964, (C) MPEG 33966 and (D) MPEG 33967. Bar = 5 mm.

(examined specimens of *D. leucophyllatus/triangulum* always have some pigmentation along the dorsal surface of the thigh; Fig. 8); absence of black dots on anterior margins of mandible (black dots present in *D. leucophyllatus/triangulum*); less developed tubercles on hands and feet (much more prominent in *D. leucophyllatus/triangulum*; Fig. 9); tubercles round or only slightly notched anteriorly (tubercles deeply notched, clearly bifurcated in *D. leucophyllatus/triangulum*; Fig. 9).

Dendropsophus mapinguari differs further from *D. leucophyllatus* and *D. triangulum* in its color patterns. *D. leucophyllatus* is polymorphic with the two most common patterns being “U”-shaped mark or dorsum dark brown with

a fine cream reticulation, the latter popularly known as the “giraffe pattern”. The most common pattern in *D. triangulum* is white dorsum with a large brown spot or triangle between the eyes. Other patterns in *D. triangulum* vary from dorsum completely white or white with large dark brown spots or, rarely, dorsum brown with cream reticulation. Both *D. leucophyllatus* and *D. triangulum* are polymorphic in color (Duellman, 1974; Titus et al., 1989; Rodriguez and Duellman, 1994), which can make the assignment of some specimens to one or the other species difficult. Nonetheless, all color patterns known to occur within the *D. leucophyllatus/D. triangulum* species complex differ from the two patterns known for *D. mapinguari*.

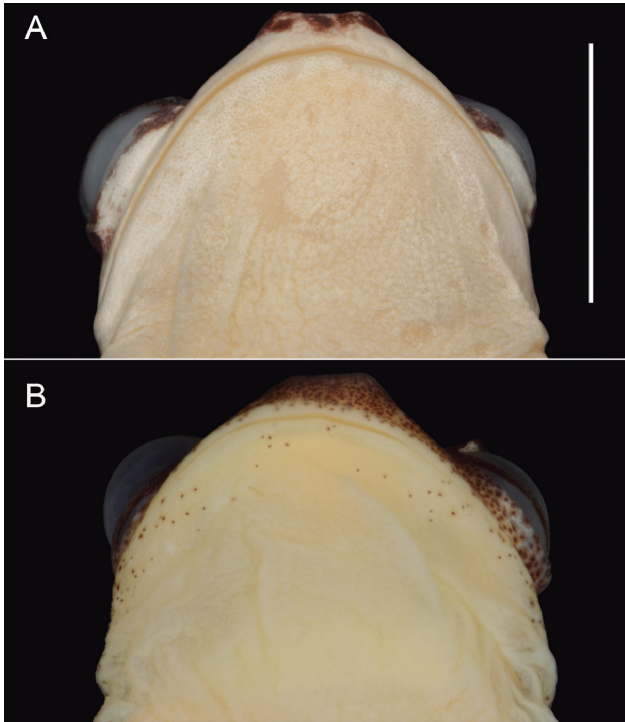


Figure 7. Throat of (A) *Dendropsophus mapinguari* sp. nov., holotype, MPEG 28682; and (B) *D. rossalleni*, MPEG 20051. Note the lack of black dots in *D. mapinguari*. Bar = 5 mm.

Description of the holotype (MPEG 28682)

Adult male, SVL 22.2 mm. Head wider than long (HW/HL 1.08), widest at corner of the mouth; snout truncate in both dorsal and lateral views; inter-orbital distance more than twice distance between the nostrils (IOD/IND 2.55); eye diameter greater than eye–nostril distance (ED/END 1.32); *canthus rostralis* indistinct; nostrils protuberant, nearly elliptical, directed dorsolaterally; internarial area slightly convex, interorbital region flat, loreal area slightly concave. Eyes large and protuberant, directed laterally, larger than tympanum diameter (ED/TD 2.90); pupil horizontally elliptical; nictitating membrane mostly transparent, its border brown. Supratympanic fold barely evident; tympanum small (diameter almost three times smaller than eye, TD/ED 0.34), round, completely covered by skin but tympanic annulus barely evident. Vocal sac subgular, single, extending slightly over the forearms. Choanae small, round, not concealed by palatal shelf, larger than vomerine odontophores; a pair of vomerine odontophores present; tongue ovoid, nearly one third of posterior end free; vocal slits present, extending diagonally from lateral base of tongue (anterior third) almost to angle of jaw.

Arms slender, not hypertrophied; axillary membrane reaching midway along upper arm. Lateral margins of arm and forearm free of tubercles, fringes, or membranes; finger tips round; finger disks present on all fingers, disk on FII smallest; relative lengths of fingers

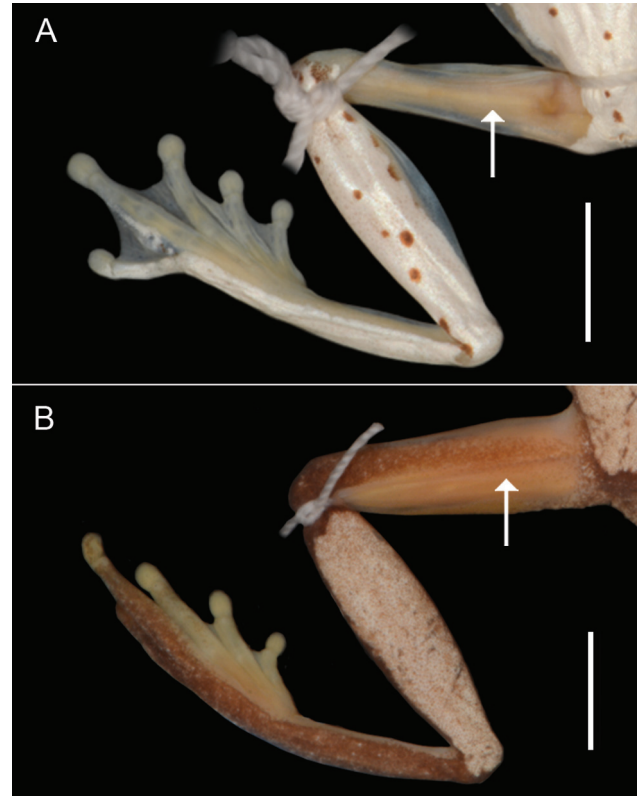


Figure 8. Dorsal view of the left legs of (A) *Dendropsophus mapinguari* sp. nov. (MPEG 28681, paratype) and (B) *D. triangulum* (MPEG 15976). Arrows point to area of leg where pigmentation is lacking in the new species and present in several others (e.g., *D. leucophyllatus*, and *D. triangulum*). Bar = 5 mm.

II < III < V < IV; subarticular tubercles round, narrower than finger width; subarticular tubercles on FII and FV larger than those of FIII and FIV; distal subarticular tubercle on FV not bifid on both sides; supernumerary tubercles present; inner metacarpal tubercle flat, elliptical, larger than outer metacarpal tubercle; weak glandular nuptial pad covering area corresponding to prepollex; outer metacarpal tubercle small, almost round, barely distinguishable. Webbing between FII and FIII basal, more extensive between FIII–FIV and IV–V. Webbing formula II 2⁺–2⁺ III 1⁺–2⁺ IV 2⁺–2⁺ V on both sides. Legs long and slender, lacking appendages (e.g., fringes, folds, or tubercles). Calcar free of appendices or tubercles. All toes well developed, bearing expanded round, medium sized disks; relative lengths of toes I < II < V < III < IV. Subarticular tubercles round; inner metatarsal tubercle flat, slightly elliptical; outer metatarsal tubercle not visible. Webbing formula I 1–1 ½ II 1⁺–2– III 1⁺–2 IV 2–1⁺ V on left foot and I 1–1 ½ II 1–2– III 1⁺–2 IV 2–1⁺ V on right foot.

Skin on dorsum, head, dorsal surfaces of limbs, flanks and groin smooth; skin on chest, belly and undersurfaces of thigh areolate; skin on vocal sac granular; skin on ventral parts of fore limb and tibia smooth. Cloacal opening directed posteriorly; cloacal region lacking tubercles.



Figure 9. Variation in hand morphology of species in the *Dendropsophus leucophyllatus* species group. **(A)** *Dendropsophus leucophyllatus*, from Caxiuanã, Pará, Brazil, MPEG 8808, **(B)** *D. sarayacuensis*, Careiro da Várzea, Amazonas, Brazil, MPEG 13878, and **(C)** *D. mapinguari* sp. nov., holotype, MPEG 28682. All specimens are adult males. Bar = 5 mm.

Color pattern and variation

Variation in measurements among specimens in the type-series are given in Table 1. In life, dorsum and dorsal areas of limbs yellow (white or pinkish white in preservative) with variable number of small brown or reddish spots (brown or cream in preservative; Figs. 2–3, 6). In some specimens a continuous stripe, instead of several spots, runs along the snout (MPEG 28683, holotype; MPEG 33905; MPEG 33964–33966; MNRJ 56733–35) and

between the eyes (MPEG 33905; MPEG 33964–33966; MNRJ 56733–35, line incomplete in MNRJ 56735; Fig. 6); in the specimens with a stripe along the snout, the line ends at the anterior corner of the eye but is continuous with another stripe starting on the posterior corner of the eye and extending towards the inguinal region, forming a clear demarcation between dorsal and lateral patterns (Fig. 2B); in those specimens without a stripe, a series of spots is present on the dorsolateral region, but dorsal and lateral patterns are not clearly demarcated (Fig. 2A).

Table 1. Measurement (in mm) of specimens in the type series of *Dendropsophus mapinguari* sp. nov. The holotype is marked in **bold**. Abbreviations are listed in Materials and Methods.

| Collection Number | SVL | HL | HW | ED | TD | IOD | IND | END | ELW | THL | TBL | FL |
|-------------------|-------------|------------|------------|------------|------------|------------|------------|------------|------------|-------------|-------------|-------------|
| MPEG 28681 | 23.7 | 7.4 | 8.4 | 2.5 | 1.0 | 4.7 | 1.8 | 2.3 | 2.1 | 12.4 | 12.7 | 16.8 |
| MPEG 28682 | 22.2 | 7.8 | 8.5 | 2.9 | 1.0 | 4.6 | 2.0 | 2.2 | 1.8 | 12.1 | 12.3 | 17.3 |
| MPEG 28683 | 24.1 | 7.5 | 8.9 | 2.8 | 1.6 | 5.0 | 2.0 | 2.2 | 2.0 | 13.5 | 13.4 | 18.0 |
| MPEG 33964 | 24.8 | 8.0 | 8.9 | 2.9 | 0.9 | 4.8 | 1.9 | 2.0 | 2.2 | 12.5 | 13.4 | 18.0 |
| MPEG 33965 | 23.7 | 7.6 | 8.7 | 2.4 | 0.9 | 4.6 | 1.6 | 1.9 | 2.2 | 11.4 | 11.8 | 16.5 |
| MPEG 33966 | 24.2 | 7.8 | 9.1 | 2.6 | 0.9 | 4.5 | 1.9 | 1.8 | 1.7 | 11.6 | 12.4 | 16.7 |
| MPEG 33967 | 23.3 | 8.3 | 8.8 | 2.8 | 1.1 | 4.9 | 1.9 | 2.2 | 1.8 | 12.6 | 13.4 | 18.3 |
| MPEG 33905 | 24.6 | 8.2 | 8.4 | 2.7 | 1.1 | 4.9 | 1.8 | 2.1 | 2.2 | 12.2 | 12.6 | 18.1 |

Lateral region orange to reddish with yellow spots in life (cream with white spots in preservative).

Snout with either brown spots or a stripe extending from the anterior corner of each eye and along the *canthus rostralis* (Figs. 2–3, 6). Temporal region with brown spots or a continuous stripe extending from posterior corner of eye and past the tympanum. Flanks with several orange spot or completely orange with yellow spots. Hidden parts of thigh, shanks, as well as fingers and toes bright orange.

Distribution

Dendropsophus mapinguari was originally discovered by two of us (PLVP and MJS) during an amphibian survey in Floresta Nacional de Pau-Rosa, Maués, Amazonas, Brazil, in 2009. We later found additional specimens in the collection at MPEG and MNRJ from Itacoatiara and Urucará, Amazonas, Brazil. So far as we are aware, *D. mapinguari* is only known from three localities (Fig. 10).

Natural history

The specimens from the type locality were found at night while calling from the vegetation along the edge of the Paraconi river (*Rio Paraconi*). Frogs were calling perched on branches and leaves immediately above the water, with individuals found from just a few centimeters to > 3 m above the water. Additional frog species found syntopically with *D. mapinguari* were *Hypsiboas cinerascens* (Spix, 1824), *H. boans* (Linnaeus, 1758), and *O. taurinus* Steindachner, 1862.

DISCUSSION

The *Dendropsophus leucophyllatus*/*D. triangulum* species complex

There is a considerable amount of evidence that the populations currently regarded as *D. leucophyllatus* and *D. triangulum* are not reciprocally monophyletic (Chek et al., 2001; Loughheed et al., 2006: fig. 1) and actually form a complex of species; however, in the present study we do not attempt to resolve the taxonomy of the

D. leucophyllatus/triangulum species complex. Nonetheless, we have studied a series of specimens in the MPEG collection (see Appendix 1 for list specimens examined) that can be referred to each nominal based on direct comparison with the original descriptions material (as discussed below: assignment largely based on color pattern of types and examined specimens).

Dendropsophus leucophyllatus was named by Beireis (1783, as *Rana leucophyllata*). No type specimen was designated but an illustration was provided. Duellman (1977) considered NHRM 157 to be the holotype of *R. leucophyllata*, but this designation is controversial. Böhme (1981) disputed Duellman's holotype designation, provided convincing evidence that NHRM 157 is a syntype of *R. boans* Linnaeus, 1758, and further considered that the type of *R. leucophyllata* is actually lost. In addition, the exact type locality of *R. leucophyllata* is unknown but believed to be Suriname (Beireis, 1783). Clearly, the actual identity of *D. leucophyllatus* needs to be clarified, but it deserves a concentrated effort and possibly even the designation of a neotype. This is, however, beyond the scope of this work. Nonetheless, we have examined the drawing of the type of *R. leucophyllata* (Beireis, 1783) and the color pattern it depicts differs greatly from that of *D. mapinguari*. The type of *R. leucophyllata* has a dark dorsum with a broad "U"-shaped pale cream band from the top of the snout and extends posteriorly as a pair of broad dorsolateral stripes to the sacral region. The dorsal region immediately above the sacrum also has a cream band. Several specimens from the MPEG collection fit the description of *D. leucophyllatus* and closely resemble the original drawing of the type, and were, therefore, used for additional comparisons.

Hyla triangulum was described by Günther (1869 "1868"), who provided an illustration of the type specimen. The type was considered to be specimen BMNH 1947.2.23.88 (formerly BMNH 68.11.15.2) by Condit (1964). Even though a type apparently exists for this taxon, the problem of defining what exactly constitutes the nominal species *D. triangulum* is aggravated by the fact that no exact type locality was given for the BMNH specimen. Even the Brazilian provenance of the type specimen is in question, being reported merely as "probably from Brazil" by Günther (1869 "1868"). We were unable to examine

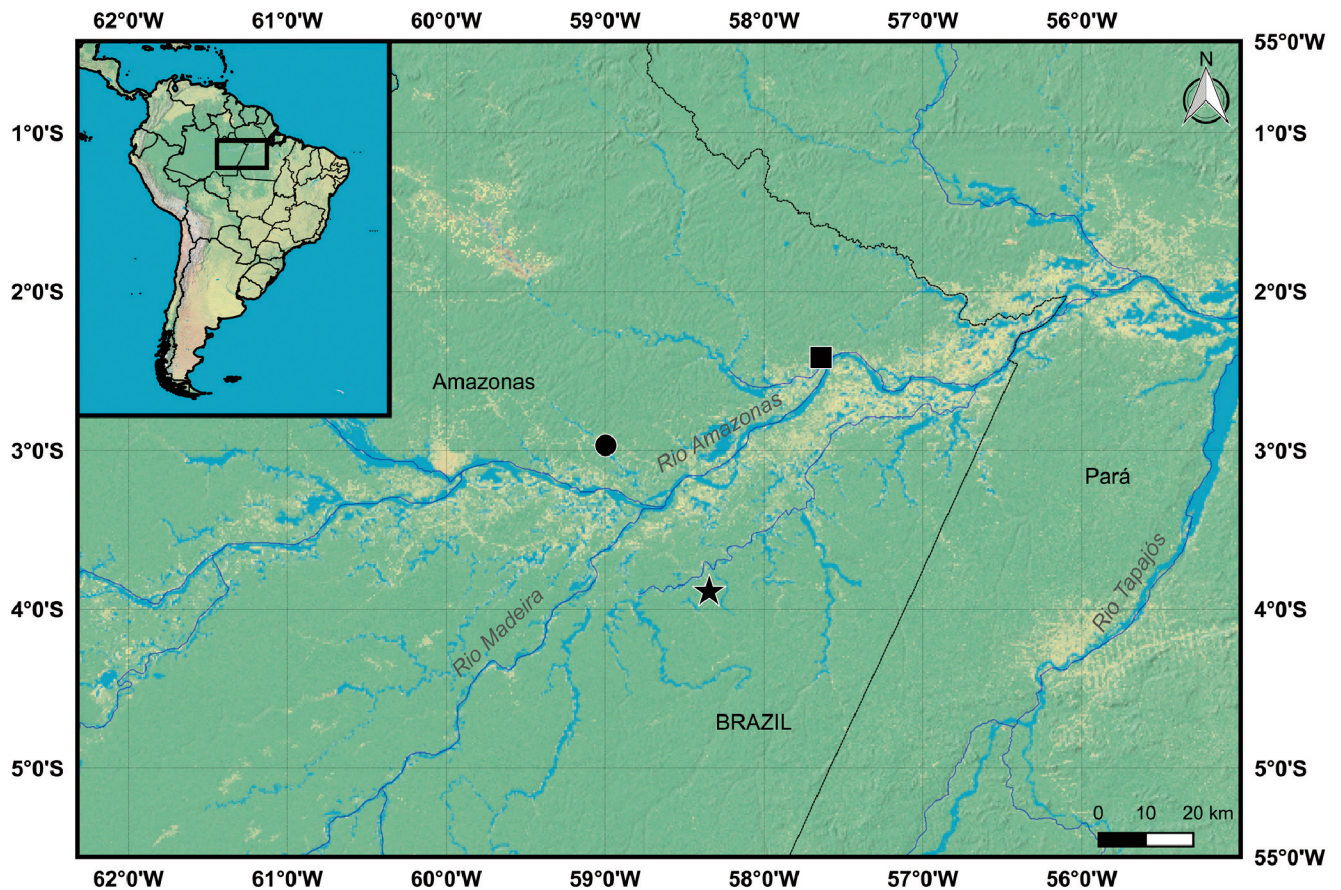


Figure 10. Geographic distribution of *Dendropsophus mapinguari* sp. nov. Star = type locality, Floresta Nacional de Pau-Rosa, Maués, Amazonas. Square = Urucará, Amazonas. Circle = Itacoatiara, Amazonas.

the holotype of *D. triangulum* (BMNH 1947.2.23.88) because it is currently missing, although a full inventory of the amphibian types at the BMNH is currently underway (J. Streicher, personal communication) and we hope the holotype will be found in the near future. Nevertheless, the color pattern of the type is evident from the original illustration: a light dorsum with dark flanks and a dark triangle shaped mark on the dorsum. Several specimens from the MPEG collection fit the description of *Hyla triangulum* and closely resemble the drawing of the holotype and, therefore, were used for additional comparisons.

Perhaps a thorough genetic study with samples from several localities in South America and across all color morphs will be able to better define the limits of *Dendropsophus leucophyllatus* and *D. triangulum*, and address the actual species diversity within this clade. There are some names currently within the synonymies of *D. leucophyllatus* (*Hyla frontalis* Daudin, 1800; *H. favosa* Cope, 1885) and *D. triangulum* (*H. reticulata* Jiménez de la Espada, 1870; *H. membranacea* Andersson, 1945; *H. laynei* Goin, 1957; *H. oliveae* Cochran and Goin, 1970), but all of them represent color morphs of these two taxa (Duellman, 1974; Titus et al., 1989; Rodriguez and Duellman, 1994) and are readily distinguished from *D. mapinguari*.

Amazonian frog diversity

Dendropsophus mapinguari is the fourth species described that includes material collected by P.L.V.P. and M.J.S. during a single, short, scientific expedition to Floresta Nacional de Pau-Rosa, Amazonas, in 2009. In addition to *D. mapinguari*, two other hylid species (*D. ozzyi* Orrico et al., 2014; *Scinax sateremawe* Sturaro and Peloso, 2014) and one arobatid (*Allobates grillisimilis* Simões et al., 2013) were named from that forest. Furthermore, at least two additional hylid species are probably unnamed taxa, one *Scinax* and yet another *Dendropsophus* (personal observation). The discovery of as many as six new frog species in the area—especially given the relatively low sampling effort—highlights how poorly known the region is and reinforces its importance in terms of biodiversity and as an area of high priority for additional biodiversity surveys.

The known populations of *Dendropsophus mapinguari* are distributed narrowly. On the other hand, the populations from Itacoatiara and Urucará are geographically isolated from the type locality by the Amazon river (*Rio Amazonas*), which has been suggested to be a biogeographical barrier for several vertebrate groups, including

frogs (Hayes and Sewal, 2004; Ribas et al., 2012; Fouquet et al., 2014). We emphasize that a concerted effort is necessary to resolve the taxonomic problems involving the nominal taxa *D. leucophyllatus* and *D. triangulum*. These are likely to represent a complex of several species, or (less likely, in our opinion) a single widely polymorphic form widespread across the entire Amazon basin. A more extensive phylogeographic study of the *D. leucophyllatus* group as a whole will undoubtedly provide insights into the geographic history and species diversity of these frogs.

The species groups of *Dendropsophus* and the allocation of *D. anceps*

The inclusion of *Dendropsophus anceps* in the *D. leucophyllatus* group is a matter of ongoing discussion (Moen and Wiens, 2009; Wiens et al., 2010; Pyron and Wiens, 2011; Rivera-Correa and Orrico, 2013) and is not supported in our analysis. *Dendropsophus anceps* is the sister taxon of a clade comprising all other species of the *D. leucophyllatus* group plus *D. minutus* and *D. miyatai*, neither of which was referred to this group previously. As such, in order to remedy the paraphyly of the *D. leucophyllatus* group, *D. anceps*, *D. salli*, and *D. elegans* must either be excluded or *D. minutus* + *D. miyatai* must be included in the group. However, given our limited taxon sampling outside of the *D. leucophyllatus* group and the fact that the placement of these species has varied in recent studies (e.g., Moen and Wiens, 2009; Wiens et al., 2010; Pyron and Wiens, 2011; Rivera-Correa and Orrico, 2013), we refrain from changing group composition. Moreover, as stated before (Fouquet et al., 2011; Motta et al., 2012), the entire genus *Dendropsophus* is in need of a comprehensive analysis and a systematic review. Before a more extensive analysis, including more extensive taxon sampling and combined analyses of phenotypic and genotypic data, any further changes in the content of species groups would be premature.

ACKNOWLEDGMENTS

We thank the curators and staff at AMNH (especially David Kizirian and Lauren Vonnahme), MNCN (Marta Calvo), MPEG (Ana Prudente and Fabricio Sarmiento), MNRJ (José Pombal Jr and Manoela Cardoso), MZUSP (Taran Grant), QCAZ (Santiago Ron) and USNM (Ron Heyer and Kevin de Quigeroz) for access to specimens housed at those institutions. For photographs of types for which examination would be impossible otherwise, we are extremely grateful to Kenneth L. Krysko (Florida Museum of Natural History, University of Florida) and Marta Calvo (Museu Nacional de Ciencias Naturales). Jeff Streicher kindly looked for the type of *D. triangulum* in the Natural History Museum collection (BMNH). P.L.V.P. and

M.J.S. are thankful to Conservation International Brazil (especially Thais P. Kasecker), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) and Fundação Djalma Batista for logistic and financial support for fieldwork at FNPR. The authors also thank the boat crew and fellow researchers aboard the “Cometa Halley” for companionship and help during the fieldwork. P.L.V.P., G.R.L.F., and M.J.S. are supported by grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; grant numbers 313680/2014-0, 400252/2014-7, and 400770/2014-8). V.G.D.O. thanks Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP; grant #2012/12500-5). C.F.B.H. also thanks FAPESP (grant #2013/50741-7) and a research fellowship from CNPq. G.R.L.F., thank CNPq (PCI-DC) for a fellowship. José Pombal Jr and an anonymous reviewer provided valuable comments that improved the manuscript.

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ONLINE SUPPORTING INFORMATION

The following Supporting Information is available for this article online:

Appendix S1. Taxon sampling employed in phylogenetic analysis, including GenBank accession numbers for all sequences use herein. Institutional abbreviations are listed in Materials and Methods.

APPENDIX 1

Specimens examined for comparisons:

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

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

Dendropsophus ebraccatus. HONDURAS: **Gracias a Dios** (USNM 559102, 559105, 559107, 550109–550113, 550115, 550116).

Dendropsophus elegans. BRAZIL: **Bahia**: Guandú (CFBH 27974); BRAZIL: **Bahia**: Caravelas (AMNH 784 [holotype]); BRAZIL: **Espírito Santo**: Linhares (CFBH 22663–22667).

Dendropsophus leucophyllatus. BRAZIL: **Amazonas**: Auari, Estação Ecológica Mamirauá (MPEG 7215–7216, 7220, 7232–7235, 7247–7253, 7262–7264, 7272, 7298, 7323, 7327, 7382, 7405–7409, 7484, 7510, 7515–7516, 8255); BRAZIL: **Pará**: Itaituba, Parque Nacional da Amazônia (MPEG 19008–19023). ECUADOR: **Orellana**: Río Napo (QCAZ 44293, 44455, 44539, 44552, examined from photographs); Orillas del Napo (MNCN 529, [holotype of *Hyla reticulata*], examined from photographs). SURINAM: Zanderij: MPEG 8255.

Dendropsophus rhodopeplus. ECUADOR: “Andes de Ecuador” (BMNH 1947.2.23.53 [holotype], examined from photographs).

Dendropsophus rossalleni. BRAZIL: **Amazonas**: Maraã: Lago Amanã (MPEG 17658–17659); BRAZIL: **Amazonas**: Uarini, Estação Ecológica Mamirauá (MPEG 7229–7231, 7410, 7487, 7518); BRAZIL: **Pará**: Oriximiná, Porto Trombetas, Lago Caramã (MPEG 20050–20052); BRAZIL: **Pará**: Terra Santa, Vila Maracanã (MPEG 33269–33270).

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

Dendropsophus sarayacuensis. BRAZIL: **Amazonas**: Jutai, R.D.S. Cujubim, Rio Curuena (MPEG 32748–32749); BRAZIL: **Amazonas**: Manaus, Careiro da Várzea (MPEG 13876–13881); BRAZIL: **Rondônia**: Guajará-Mirim, Parque Estadual Guajará Mirim (13479–13481); ECUADOR: **Pastaza**: Sarayacu (MCZ 19729 [holotype], examined from photographs); **Napo**: Sector Churuyacu (QCAZ 47173, examined from photographs); ECUADOR: **Pastaza**: Palta (QCAZ 52774, examined from photographs).

Dendropsophus triangulum. BRAZIL: **Acre**: Tarauacá: BR 364 (MPEG 36507–36509). BRAZIL: **Amazonas**: Juruti (MPEG 15976). COLOMBIA: **Amazonas**: Leticia (FSM 8555 [holotype of *Hyla oliveae*], examined from photographs). COLOMBIA: **Amazonas**: “near Leticia” (FSM 8503 [holotype], FSM 8504–8505 [paratypes])—types of *Hyla laynei*, examined from photographs). ECUADOR: **Pastaza**, Palta (QCAZ 52774, examined from photographs); ECUADOR: **Pastaza**, Lorocachi, Río Curaray (QCAZ 55854, examined from photographs); ECUADOR: **Orellana**: Rio Napo (QCAZ 44293, 44455, 44539, 44552, examined from photographs); ECUADOR: **Napo**: Rio Napo (MNCN 3474, examined from photographs—holotype of *Hyla reticulata*).