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A name for the nurse-frog (*Allobates*, Aromobatidae) of Floresta Nacional de Carajás, Eastern Brazilian Amazonia

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Abstract

We describe a new species of nurse-frog (Aromobatidae, *Allobates*) from Floresta Nacional de Carajás, southeastern Brazilian Amazonia. *Allobates carajas* **sp. nov.** is distinguished from similar congeneric species by the combination of the following characters: body-size range (snout-to-vent length 16.5–19.1 mm), dorsal color pattern with a dark brown hourglass-shaped mark, by the absence of a pale dorsolateral stripe and presence of a pale ventrolateral stripe, absence of a pale paracloacal mark, by overall bright yellow ventral colors of live male and female specimens, and by the posterior labium of tadpoles, with a single row of pyramidal papillae medially. The advertisement call of the new species is highly variable, with four possible temporal arrangements of notes (continuous emission of notes separated by regular silent intervals, continuous emission of notes separated by irregular silent intervals, emission of discrete note trills, and sporadic emission of single notes). Duration of notes range between 0.020–0.060 s, and the dominant frequency of notes range from 4.75 to 5.38 kHz. The new species is currently known only from forested habitats within Floresta Nacional de Carajás.

Key words: Advertisement calls, conservation unit, Dendrobatoidea, mitochondrial DNA, Pará

Resumo

Descrevemos uma nova espécie de rã-cuidadora (Aromobatidae, *Allobates*) da Floresta Nacional de Carajás, no sudeste da Amazônia Brasileira. *Allobates carajas* **sp. nov.** se distingue de espécies similares congenéricas pela combinação dos seguintes caracteres: amplitude de variação em tamanho do corpo (comprimento rostro-uróstilo 16.5–19.1 mm), padrão de coloração dorsal com uma marca marrom escura em forma de ampulheta, linha dorsolateral clara ausente, linha clara ventrolateral presente, marca paracloacal clara ausente, coloração ventral em vida predominantemente amarelo brilhante em machos e fêmeas, e presença de uma fileira única de papilas piramidais medialmente no lábio posterior dos girinos. O canto de anúncio da espécie é altamente variável, com quatro arranjos possíveis para a emissão de notas (emissão contínua de notas separadas por intervalos silenciosos regulares, emissão contínua de notas separadas por intervalos silenciosos irregulares, emissão de notas em grupos discretos e emissão esporádica de notas isoladas). A duração das notas varia entre 0.020–0.060 s e a frequência dominante varia entre 4.75 to 5.38 kHz. A nova espécie é atualmente conhecida apenas de habitat florestais dentro da Floresta Nacional de Carajás.

Palavras-chave: Vocalizações de anúncio, unidade de conservação, Dendrobatoidea, DNA mitocondrial, Pará

Introduction

Nurse-frogs (*Allobates* Zimmermann & Zimmermann, 1988) are an important part of the diurnal amphibian community in the leaf litter of Amazonian rainforests (Menin *et al.* 2008; Dias-Terceiro *et al.* 2015). Despite their

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frequently high abundance at the local scale, the alpha taxonomy of nurse-frogs and species determination in the field remain contentious, as evidenced by the steady pace of new species discoveries (*e.g.*, Lima *et al.* 2015; Simões 2016; Simões *et al.* 2018; Melo-Sampaio *et al.* 2018).

Floresta Nacional de Carajás (Carajás, hereafter) is a conservation unit located in the southeastern portion of state of Pará, in Brazilian Amazonia. This forest preserve was delimited in 1998 and covers an area of 4119.5 km^2 in the municipalities of Parauapebas, Canaã dos Carajás and Água Azul do Norte. All areas surrounding Carajás have been extremely impacted by changes in land use and deforestation in the last decades, which originated mostly from conversion of natural habitats into pasture or mining fields (Martins *et al*. 2012). Despite being a conservation unit, mining is allowed inside the boundaries of Carajás and it currently harbors the largest iron mine in the world, with additional mining of manganese, gold and granite. Natural landscapes protected within the reserve are characterized by a mosaic of vegetation types, in great part determined by edaphic characteristics. Those include dense and open Amazon rainforests, deciduous forests and xerophytic open vegetation (*canga*) typical of rocky outcrops (Martins *et al*. 2012).

Sixty-eight amphibian species are currently registered in Carajás, 74% of which are Amazonian endemics. The remaining 26% are widespread species distributed in eastern Amazonia, but also reaching other Brazilian dry biomes (*Cerrado* and *Caatinga*). This mixed species composition is unique of Carajás and possibly explained by its geographic location at the southeastern boundary of the Amazon forest with the Brazilian Cerrado (Neckel-Oliveira *et al.* 2012).

Earlier surveys reported two species of *Allobates* as occurring in Carajás: the brightly colored *Allobates femoralis* (Boulenger, 1884) and a cryptically colored species, which was tentatively associated to *Allobates marchesianus* (Melin, 1941) (Neckel-Oliveira *et al.* 2012). Recent work on taxonomy and phylogenetics of *Allobates* at the family and genus level (Grant *et al.* 2017; Simões *et al.* 2018) uncovered samples of the second species as phylogenetically and phenetically distinct in relation to all other species of *Allobates*. Herein, we describe this new species based on quantitative and qualitative morphological, acoustic, reproductive and larval traits, with further evidence from analyses of mtDNA genetic distances.

Material and methods

Study area. From15 to 24 February 2014 we sampled three sites for diurnal frogs in Carajás (Fig. 1). The first site, Serra Sul (06°23'34.7" S, 50°19'09.8" W, elevation 660 m a.s.l.), consisted of a gallery rainforest strip alongside a water stream running on sloping rocky terrain, on the ecotone between the uphill open *canga* environment and the downhill Amazon rainforest, on the southernmost region of Carajás. This forest strip was limited by rocky walls, punctuated by several dens and small caves, and leaf litter accumulated in flat surfaces between these and the fast-flowing stream.

The second site, Trilha do Lago (06°02'41.1" S, 50°05'29.7" W, elevation 688 m a.s.l.) consisted of a trail along well-preserved, closed canopy *terra-firme* rainforest on the northeastern edge of Carajás. The trail was located near Carajás' main access road and was open to public visitation during the day. The third sampling site, N1 Trail (06°03'06.3" S, 50°15'39.9" W, elevation 711 m a.s.l.), was located on the northeastern section of the reserve, 7.0 km west of Carajás' largest iron mine (Fig. 1). The trail was used for environmental monitoring and access was restricted to researchers and staff of the conservation unit. Vegetation consisted of transition between closed canopy and open forest. Tadpoles were found and collected at an additional site, in a shallow valley that crossed the access road to Serra Sul (06°13'00.9" S, 50°20'14.4" W, elevation 671 m a.s.l.), in dense forest habitat.

Data collection. In the three sites described above we made acoustic and visual searches for diurnal anurans along the available trails, from 07:30 to 17:00h. The new species was generally found among the leaf litter on the forest floor or perched on rocks or on the lower undergrowth vegetation, no higher than 0.5 m from the ground.

Calls of ten males were recorded with a Marantz PMD 660 and a Sennheiser ME 66 directional microphone positioned approximately 1 m from each calling male. Recordings used a sample rate of 44.1 kHz and were stored in .WAV format. Four recordings were made in the morning, from 07:50 to 11:40h, and six recordings were made in the afternoon, from 14:00 to 17:45h. Air temperature at time of recordings ranged between 21.3–25.0 °C (average 22.4 °C, n = 10).

From the recordings of each male, we sampled 25 notes for temporal and spectral call measurements. Note samples were evenly distributed along the recording's length, by dividing the total number of notes in that

recording by 25 and using the resulting ratio as the sampling interval. From each note, we measured note duration, lower frequency (LF), upper frequency (UF) and dominant (i.e., peak) frequency (DF). We also measured duration of the silent interval between notes. Duration of notes and silent intervals were measured from waveforms. Measurements of spectral properties (LF, UF, DF) were conducted on power spectra, applying a Blackman window type and a frequency resolution of 82 Hz and 2048 points. Lower and upper frequencies were measured 20 dB below the peak of the dominant frequency, in order to avoid overlap with background noise. Acoustic analyses were conducted in Raven PRO 1.4 (Bioacoustics Research Program 2011).

Five recorded males were captured manually after recording procedures. Additionally, eight males and five females were collected during surveys along the access trails. Specimens were transported to an improvised lab in a nearby lodge, anesthetized and killed with topical benzocaine solution (50 mg/g), fixed in 10% formalin solution and preserved in 70% ethanol. A sample of muscular tissue was dissected from a hind limb of each specimen prior to fixation (or a piece of the upper tail fin, in the case of tadpoles) and preserved in 95% ethanol for molecular analyses.

Preserved specimens were examined and measured under a stereomicroscope with graduated lenses (to the nearest 0.1 mm). Morphometric measurements followed Lima *et al*. (2007) and Barrio-Amorós & Santos (2009). Additional morphological terminology and characters followed Grant *et al.* (2006). Measurements were taken as follows: snout to-vent length (SVL); head length from tip of snout to posterior edge of maxilla articulation (HL); head width at the level of maxilla articulation (HW); snout length from tip of snout to the center of nostril (SL); eye-to-nostril distance from anterior corner of the eye to the center of nostril (EN); internarial distance (IN); eye diameter from anterior to posterior corner (ED); interorbital distance (IO); maximum diameter of tympanum (TYM); forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow (FAL); upper arm length from anterior corner of arm insertion to the outer edge of flexed elbow (UAL); lengths from proximal edge of palmar tubercle to tips of fingers I, II, III, and IV (respectively HAND I, HAND II, HAND III, HAND IV); width of disc on Finger III (WFD); width of Finger III's third phalanx (WPF); diameter of palmar tubercle (DPT); diameter of thenar tubercle (DTT); leg length from the posterior extremity of the urostyle region to the outer edge of flexed knee (LL); tibia length from outer edge of flexed knee to heel (TL); foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV (FL); width of disc on Toe IV (WTD).Voucher specimens were deposited in the collection of amphibians and reptiles of Instituto Nacional de Pesquisas da Amazônia, in Manaus, Brazil (INPA-H 38624, 38632–38650).

Description of color in life was based on field observations and photographs of specimens forming the type series.

Thirteen tadpoles were found in a single pool in forested environment (see *Natural history notes* below). All tadpoles were transported to the lodge, anesthetized and killed in a solution of benzocaine diluted in water. Ten tadpoles were preserved in 10% formalin and used for the description of external morphology of the larvae. The remaining three tadpoles had their tails dissected for the preservation of muscle tissue in 95% ethanol and were not included in the morphological description. Developmental stages of tadpoles were determined according to Gosner (1960). Diagnostic characters, terminology and measurements followed Altig and McDiarmid (1999) and Sánchez (2013). We recorded the following measurements from individual tadpoles: total length from tip of tail to tip of snout (TL); body length from tip of snout to body-tail insertion (BL); tail length from tip of tail to body-tail insertion (TAL); body width at the level of spiracle (BW); body height at the level of spiracle (BH); width of head at the level of the eyes (HWLE); maximum width of tail muscle (TMW); maximum tail height (MTH); maximum height of tail muscle (TMH); interorbital distance (IOD); internarial distance (IND); eye-naris distance (END); naris-snout distance (NSD); eye diameter (ED); vent tube length (VTL), spiracle tube length (STL); and width of oral disc (ODW).

As sampling sites covered different habitats and considerable variation in advertisement calls was uncovered by bioacoustical analyses (see Results), we used a DNA-barcoding approach (Vences *et al.* 2005) in order confirm that all collected specimens, including tadpoles, belonged to the same species. Total genomic DNA was extracted from preserved tissue samples of 17 adults and one juvenile specimen (INPA-H 38624, INPA-H 38633–38650) and one tadpole (INPA-H 38632) using the Wizard Genomic DNA Purification Kit (Promega, Madison-WI, USA) following instructions indicated by the manufacturer. Polymerase chain reactions (PCR) were performed in 15 µL volumes with 1.0 µL of genomic DNA and the universal primers 16Sar (5′-CGCCTGTTTATCAAAAACAT-3′) and 16Sbr (5′-CCGGTCTGAACTCAGATCACGT-3′) (Palumbi 1996) in order to amplify ~ 566 bp fragment of

the 16S rRNA mitochondrial gene. PCR and DNA sequencing protocols were identical to those described in previous studies (Simões *et al.* 2010; 2013a). Resulting sequences were checked by eye against their original chromatograms using Sequencher 4.1.4 (Gene Codes Corporation, Ann Arbor, MI, USA).

We used a neighbor-joining phenetic tree and average 16S rDNA genetic distances among nominal taxa in order to estimate genetic divergence between the new species and other *Allobates*. First, we obtained additional 16S rDNA sequences from the National Center for Biotechnology Information's GenBank. Sequence selection was restricted to *Allobates* species collected in cis-Andean South America, most of which were from topotypic voucher specimens (Appendix I). When sequences from topotypic specimens were not available, we selected sequences from specimens collected as near as possible to type localities. We did not include sequences referred as *Allobates marchesianus* or *Allobates brunneus* because these names have been erroneously assigned to sequences belonging to several species, none of which correspond to these taxa (Lima *et al.* 2014; 2015).

New sequences and sequences obtained from GenBank were aligned in MAFFT v7.309 (Katoh *et al*. 2013), using the Q-INS-I alignment strategy. Because many sequences from GenBank were shorter, we trimmed our initial alignment so that the final dataset does not include missing data (final alignment of 466 positions). We generated a neighbor-joining tree in MEGA 7.0.14 (Kumar *et al.* 2015) considering a Kimura-2-parameter model (K2P; Kimura 1980) and gamma distributed rates among sites. Cluster support was inferred from 5000 bootstrap replicates. We used the same program to estimate average interspecific genetic distances using nominal taxa as a criterion to group sequences. We calculated two genetic distances commonly used in *Allobates* taxonomy: uncorrected-pairwise and Kimura-2-parameter (K2P).

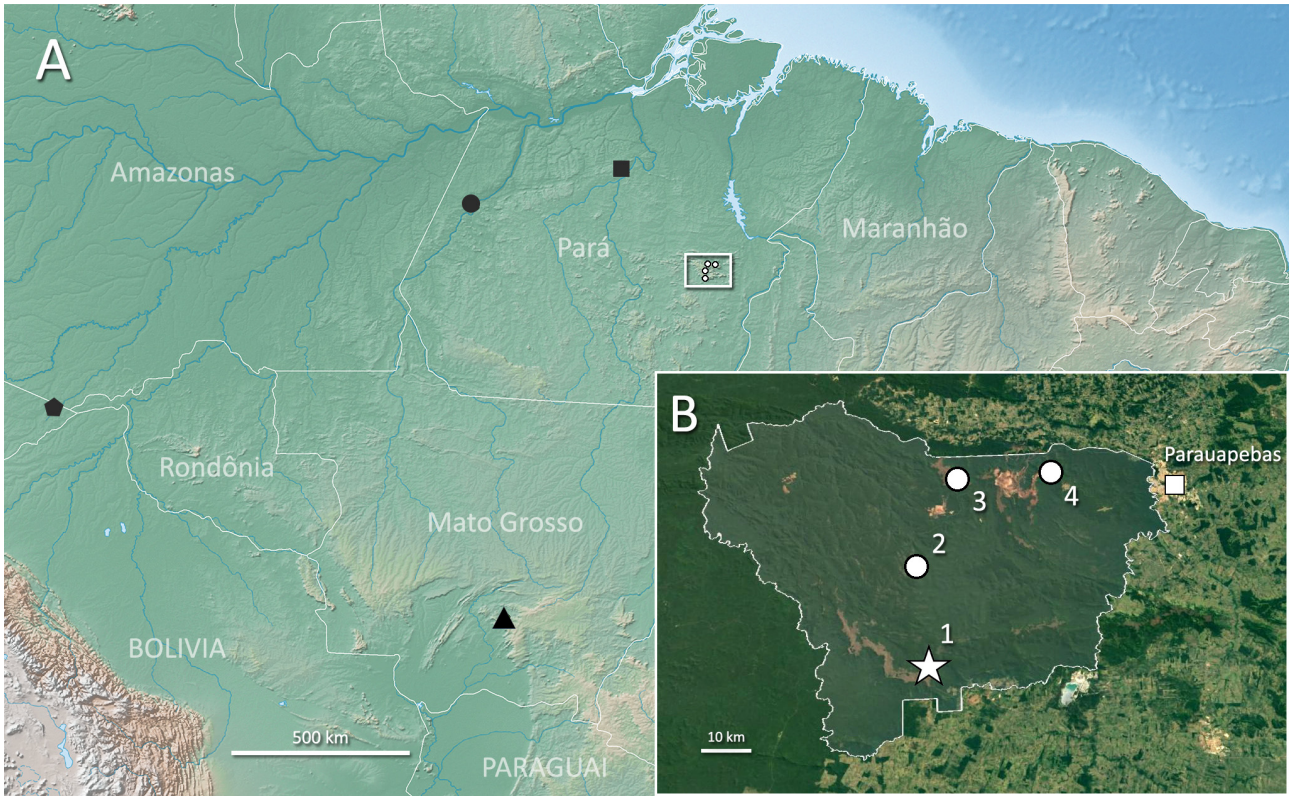

FIGURE 1. (A) Relative position of Floresta Nacional de Carajás in northern Brazil (area delimited by white square) and type localities of large species of Brazilian *Allobates* with hourglass-shaped marks on dorsum: *Allobates brunneus* (triangle), *A. crombiei* (square), *A. flaviventris* (pentagon), *A. magnussoni* (circle). (B) Detailed view of Floresta Nacional de Carajás and relative position of sampling sites of *Allobates carajas* **sp. nov.:** 1—Serra Sul, the type locality of the new species; 2—access road to Serra Sul; 3—N1 Trail; 4—Trilha do Lago.

***Allobates carajas* sp. nov.**
Figures 2–10, 14

Allobates gr. *marchesianus* Neckel-Oliveira *et al.* 2012 p. 79.
Allobates sp. Carajas Grant *et al.* 2017 p. S29, Fig. 21.
Allobates sp. (Carajás BR) Simões *et al.* 2018 p. 125, Fig. 9.

Holotype. INPA-H 38643 (field code APL 20621). An adult male collected by P.I. Simões and D. Rojas, on 18 February 2014, in an area of streamside dense canopy forest in the Serra Sul region of Floresta Nacional de Carajás, in the municipality of Parauapebas, state of Pará, Brazil (06°23'34.7" S, 50°19'09.8" W).

Paratopotypes. Eight adult specimens (two females, six males). Females: INPA-H 38635, 38642 (field codes APL 20620, 20622, respectively). Males: INPA-H 38633, 38637, 38640, 38641, 38646, 38649 (field codes APL 20617, 20625, 20624, 20623, 20618, 20626). One juvenile specimen: INPA-H 38647 (field code APL 20619). All collected by P.I. Simões and D. Rojas between 18–20 February 2014 at the same locality as the holotype.

Paratypes. Nine adult specimens (three females, six males). All collected by P.I. Simões and D. Rojas, within Floresta Nacional de Carajás, Parauapebas, state of Pará, Brazil. **Trilha do Lago:** Female: INPA-H 38638 (field code APL 21110). Males: INPA-H 38639, 38644, 38645, 38648, 38650 (field codes APL 20629, 21109, 20627, 21108, 20628, respectively). Collected between 22–24 February 2014 (coordinates 06°02'41.1" S, 50°05'29.7" W). **N1 Trail:** Female: INPA-H 38634 (field code APL 21105). Male: INPA-H 38636 (field code APL 21106). Collected on 23 February 2014 (coordinates 06°03'06.3" S, 50°15'39.9" W). **Road to Águas Claras:** Female: INPA-H 38624 (field code APL 20608). Thirteen tadpoles: INPA-H 38632 (field code APL 20610). Collected on 16 February 2018 (coordinates 06°13'00.9" S, 50°20'14.4" W).

Etymology. The specific epithet is a noun in singular nominative and refers to the species type locality at Floresta Nacional de Carajás.

Generic placement. The new species was assigned to *Allobates* based on overall similarity with other species of the genus and presence of the following diagnostic phenotypic characters proposed by Grant *et al*. (2006, 2017): (1) Finger IV reaching distal half of distal subarticular tubercle of Finger III, (2) webbing absent on postaxial side of Toe I, (3) webbing absent on preaxial side of Toe II, (4) webbing absent on postaxial side of Toe II, (5) webbing absent on preaxial side of Toe III, (6) webbing present on preaxial side of Toe IV, (7) oblique lateral line absent or diffuse, and (8) pale ventrolateral stripe present.

Definition. *Allobates carajas* is characterized by: (1) skin texture of dorsum smooth, weakly granular posteriorly, small granules more prominent from mid to posterior dorsum; (2) paired dorsal digital scutes present; (3) distal tubercle present on Finger IV; (4) discs on fingers I–IV moderately expanded; (5) dermal lateral fringes and basal webbing absent on fingers; (6) metacarpal ridge absent; (7) Finger III not swollen in male or female specimens; (8) carpal pad absent; (9) excrescences on thumbs of males absent; (10) thenar tubercle conspicuous; (11) black gland absent on arm; (12) tarsal keel present, tubercle-like, strongly curved; (13) discs on toes I-V moderately expanded; (14) basal webbing present between toes III and IV; (15) metartarsal fold absent; (16) cryptic, predominantly brown dorsal and lateral coloration; one to four transverse dark brown bars or blotches may be present on dorsal surface of thigh; pale dorsolateral stripe absent; a dark brown lateral stripe surrounds the whole body; pale oblique lateral stripe absent; pale ventrolateral stripe present, with a diffuse lower margin from behind the eyes to groin, iridescent white in live specimens, indistinct from background color of abdomen in preserved specimens; pale paracloacal mark absent; (17) dark throat-collar absent; (18) throat cream to white in preserved male specimens, with a variable number of melanophores; uniformly cream to white in preserved female specimens; (19) ventral surfaces uniformly yellow in life in male and female specimens; throat and vocal sac pinkish to translucent or peppered with a variable number of melanophores in live male specimens, uniformly yellow in female specimens; (20) iris dark with metallic gold flecks and a golden pupil ring; (21) large intestine unpigmented; (22) testis unpigmented; (23) mature oocytes not pigmented; (24) median lingual process absent; (25) tympanum inconspicuous to the naked eye; (26) vocal sac single; (27) maxillary teeth present; (28) advertisement calls characterized by the emission of notes in at least four different temporal arrangements: continuous calls with notes separated either by (i) regular or (ii) irregular silent intervals, (iii) emission of notes arranged in trills, and (iv) emission of isolated notes between long silent intervals. Temporal and spectral properties of notes are similar among call arrangements, note duration ranging between 0.02–0.06 s, dominant frequency between 4.75–5.38 kHz) and frequency bandwidth of notes between 0.53–0.92 kHz.

Description of the holotype. Adult male of SVL = 17.3 mm, in good state of preservation, with a piece of muscle ventrally cut from left thigh, preserved as tissue sample. Measurements of the holotype are presented in Table 1. Body robust, head wider than long (HL/HW = 0.94), head length 0.30 times the SVL (Fig. 2). Eye

diameter larger than distance from anterior corner of the eye to nostril (EN/ED = 0.64) (Fig. 3). Nares located posterolaterally to tip of snout, directed laterally, visible in lateral, ventral and anterior views. Distance between nostrils 0.43 times the HW. Snout truncate in dorsal view. *Canthus rostralis* straight from nostril to anterior corner of the eye in dorsal view, rounded in cross section. Loreal region vertical. Tympanum round, 0.32 times ED. Margins of tympanum indistinct to the naked eye (visible under magnification) (Fig. 3). Maxillary teeth present, concealed by inner surface of upper lip, detectable under 20X magnification or by moving a wire probe along the maxillary surface. Tongue longer than wide, anterior third attached to the mouth floor. Median lingual process absent. Choanae round, positioned anteriorly to eye bulge. Vocal sac single, covering most of the medial and posterior portions of the subgular region. Lateral vocal slits conspicuous.

FIGURE 2. Left: Dorsal and ventral views of the holotype of *Allobates carajas* **sp. nov.** (INPA-H 38643). Right: Dorsal and ventral views of a female paratype (INPA-H 38642).

FIGURE 3. Profile of the holotype of *Allobates carajas* **sp. nov.** (INPA-H 38643).

FIGURE 4. Left: hand of the holotype of *Allobates carajas* **sp. nov.** (INPA-H 38643). Right: hand of the female paratype INPA-H 38642.

TABLE 1. Morphometric measurements (in mm) and morphometric ratios of *Allobates carajas* **sp. nov.** holotype (INPA-H 38643) and male and female specimens in type series. Values in type-series columns correspond to mean ± one standard deviation (range). See text for a description of measurements.

	Holotype	Males (n = 12)	Females (n = 5)
SVL	17.3	17.4 ± 0.6 (16.5–18.5)	18.6 ± 0.5 (18.0–19.1)
HL	5.2	5.4 ± 0.4 (4.8–6.0)	5.6 ± 0.2 (5.3–5.7)
HW	5.5	5.6 ± 0.3 (5.1–6.0)	5.9 ± 0.1 (5.8–6.1)
SL	2.2	2.4 ± 0.2 (2.2–2.7)	2.7 ± 0.2 (2.4–3.0)
EN	1.6	1.6 ± 0.1 (1.5–1.7)	1.8 ± 0.2 (1.5–2.1)
IN	2.4	2.3 ± 0.1 (2.0–2.5)	2.5 ± 0.2 (2.2–2.6)
ED	2.5	2.3 ± 0.1 (2.1–2.4)	2.3 ± 0.1 (2.2–2.4)
IO	4.5	4.9 ± 0.3 (4.4–5.4)	5.2 ± 0.2 (4.9–5.4)
TYM	0.8	1.1 ± 0.1 (0.9–1.4)	1.2 ± 0.1 (1.0–1.3)
FAL	3.5	3.6 ± 0.3 (3.1–4.0)	3.7 ± 0.2 (3.4–3.8)
UAL	4.2	4.5 ± 0.2 (4.2–5.0)	4.8 ± 0.3 (4.4–5.2)
HAND I	3.0	3.2 ± 0.3 (2.7–3.6)	3.6 ± 0.3 (3.2–4.0)
HAND II	3.4	3.1 ± 0.2 (2.7–3.4)	3.3 ± 0.2 (3.0–3.5)
HAND III	4.4	4.3 ± 0.2 (3.8–4.6)	4.5 ± 0.2 (4.2–4.8)
HAND IV	3.1	2.9 ± 0.1 (2.6–3.1)	3.1 ± 0.3 (2.7–3.5)
WFD	0.5	0.5 ± 0.05 (0.5–0.6)	0.5 ± 0.1 (0.4–0.6)
WPF	0.7	0.8 ± 0.05 (0.7–0.8)	0.8 ± 0.1 (0.6–0.9)
DPT	1.0	1.1 ± 0.1 (0.9–1.3)	1.1 ± 0.2 (1.0–1.3)
DTT	0.7	0.7 ± 0.1 (0.6–0.9)	0.8 ± 0.1 (0.7–0.9)
LL	7.6	7.9 ± 0.3 (7.4–8.4)	8.1 ± 0.4 (7.5–8.5)
TL	8.0	8.5 ± 0.4 (8.0–9.3)	8.7 ± 0.5 (8.1–9.3)
FL	7.8	7.8 ± 0.6 (6.8–8.5)	7.9 ± 0.8 (6.8–8.7)
HL/SVL	0.3	0.3 ± 0.02 (0.3–0.3)	0.3 ± 0.0 (0.3–0.3)
HW/SVL	0.3	0.3 ± 0.01 (0.3–0.3)	0.3 ± 0.0 (0.3–0.3)
HL/HW	0.9	1.0 ± 0.04 (0.9–1.0)	0.9 ± 0.0 (0.9–0.9)
FAL/SVL	0.2	0.2 ± 0.01 (0.2–0.2)	0.2 ± 0.0 (0.2–0.2)
TL/SVL	0.5	0.5 ± 0.02 (0.5–0.5)	0.5 ± 0.02 (0.4–0.5)

Palmar tubercle round to slightly elliptical. Thenar tubercle present, elliptical, evident in ventral view, less conspicuous in profile. Maximum diameter of thenar tubercle 58% of maximum diameter of palmar tubercle (Fig. 4). Subarticular tubercles of fingers III and IV round, small, not exceeding the width of phalanges. Subarticular tubercle on Finger II round, protuberant, 1.3 times larger than thenar tubercle in maximum diameter. Subarticular tubercle on Finger I very protuberant, elliptical, 1.4 times wider than thenar tubercle in maximum diameter. Distal subarticular tubercle present on Finger IV. Supernumerary tubercles absent. Metacarpal ridge absent. Finger fringes and hand webbings absent. Length of Finger II equivalent to approximately 96% of Finger I's length. Tip of Finger IV reaching mid length of distal subarticular tubercle of Finger III when fingers are juxtaposed. Relative lengths of fingers: IV < II < I < III. Finger III not swollen. Discs of fingers I–IV moderately expanded, width of discs corresponding to 1.5, 1.5, 1.6 and 1.5 times the width of their respective adjacent phalanges (Fig. 4).

Tibia length approximately half the SVL (TL/SVL = 0.46). Tarsal keel present, tubercle-like, strongly curved at its proximal end, flattening and straightening towards metatarsal tubercle, but not reaching it (Fig. 5). Preaxial edge of tarsus smooth, not fringed. Metatarsal fold absent. Basal webbing present between toes III and IV. Basal webbing absent between other toes. Relative lengths of toes: I < II < V < III < IV. Discs of toes I–V moderately expanded, width of discs corresponding to 1.4, 1.5, 1.7, 1.7 and 1.6 times the width of adjacent phalanges, respectively.

FIGURE 5. Top: foot of the holotype of *Allobates carajas* **sp. nov.** (INPA-H 38643). Bottom: foot of the female paratype INPA-H 38642.

Skin on dorsum smooth, weakly granular only posteriorly, from urostyle region to about mid body. Skin smooth laterally and ventrally. Dermal flap absent above cloaca (Fig. 2).

Color in alcohol of holotype. Dorsal surface of body tan to light brown, conspicuously lighter from tip of snout to the level of the anterior corner of the eye and dorsolaterally, from the level of posterior corner of the eye to the urostyle region (Fig. 2). Skin dark gray above orbits. Distinct longitudinal brown mark on dorsum, hourglass-shaped, extending centrally from the level of anterior corner of the eye (where it forms a triangle-shaped interorbital blotch) to the urostyle region. Longitudinal tan brown mark with diffuse outer edges, merging with the light brown background of dorsum. Pale dorsolateral stripe absent. Lateral surface of body characterized by a solid dark brown stripe, extending from tip of snout to groin, surrounding the body (Fig. 3). Solid dark brown stripe broadening only slightly from posterior margin of the eye towards groin. Solid dark brown stripe faded posteriorly, on the inguinal region, but not forming a vertical bar or oblique line. Pale ventrolateral stripe indistinct from cream to white background of ventrolateral surfaces of body (Fig. 3). Ventral surfaces cream to white, with a few dark brown melanophores scattered only on chin and throat. Tongue is cream-colored.

Background color of upper arm, forearm and hand cream to pale in dorsal view, with evenly scattered brown melanophores, more densely grouped on wrist and fingers. Tips of fingers brown. Paired scutes on discs of fingers I, II and III cream to gray, brown on Finger IV. Upper arm cream in ventral view, continuous with color pattern of abdomen. Outer lateral edge of upper arm with a thin brown line. Forearm cream, solid brown only along its outer edge in ventral view. Carpal and metarcarpal regions ventrally brown, densely pigmented (Fig. 4).

FIGURE 6. Variation in dorsal color pattern among specimens in three male (upper line) and three female (lower line) paratypes of *Allobates carajas* **sp. nov.** Clockwise from upper left: INPA-H 38636, 38650, 38640, 38635, 38634, 38624. Scale bar = 10.0 mm.

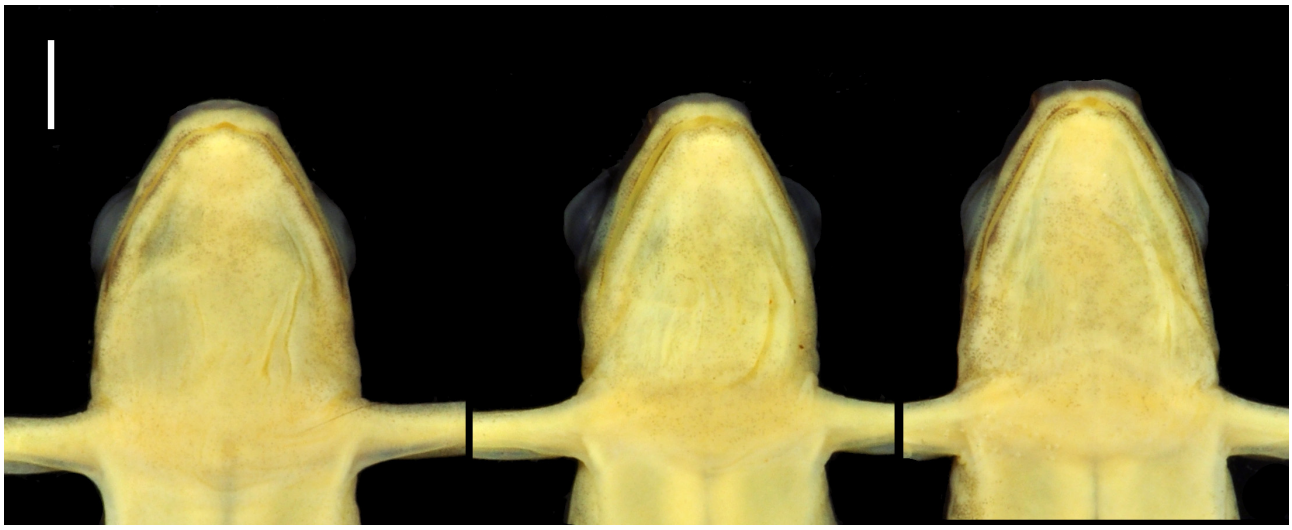

FIGURE 7. Variation in throat pigmentation in three male paratypes of *Allobates carajas* **sp. nov**. From left: INPA-H 38636, 38650, 38640. Scale bar = 2.0 mm.

Area immediately around vent brown. Pale paracloacal mark indistinct. Instead, a pale transversal bar crosses the proximal portion of thigh dorsally, continuous with dorsolateral light brown color of dorsum (Fig. 2). Background color of thigh light brown. Thigh crossed proximally by two transverse dark brown bars in dorsal view (see *Variation in type series* below). Inner and outer dorsolateral surfaces of thigh brown. Dorsal surface of shank

same color as thigh, with three dark brown blotches present medially (the distal one forming a transverse dark brown bar). Dorsal surface of tarsal region lighter than overall color of legs, with irregular dark brown blotches. Toes brown, with irregularly distributed melanophores. Paired scutes on toes dark brown to gray. Ventral surfaces of thigh and shank cream to translucent, free of melanophores. Ventral surfaces of tarsal and metatarsal regions uniformly dark brown. Toes brown, densely pigmented in ventral view (Fig. 5).

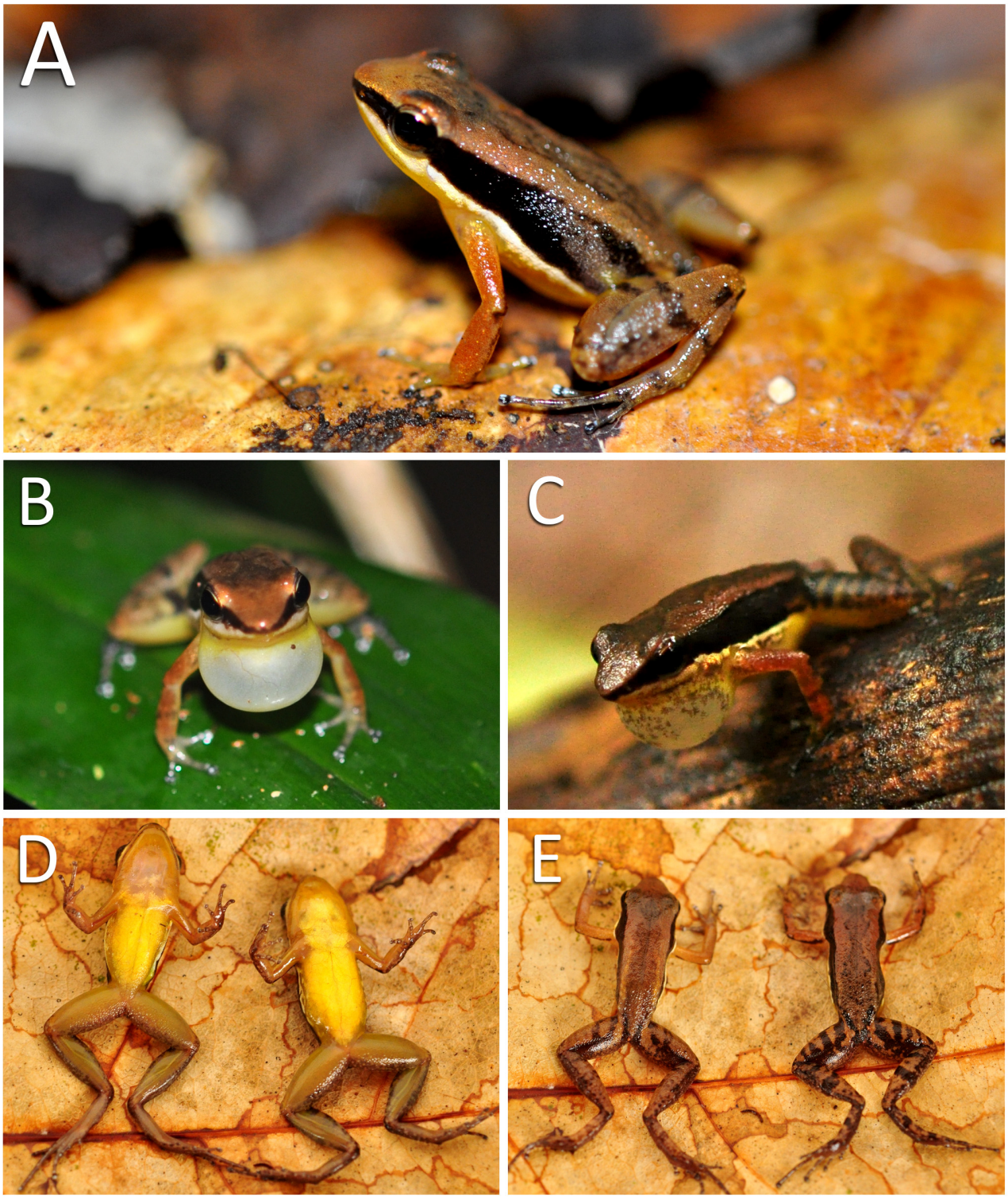

FIGURE 8. Color in life of *Allobates carajas* **sp. nov.** (A) Dorsolateral view of a male specimen at the Serra Sul sampling site within Floresta Nacional de Carajás. Note iridescent white ventrolateral line extending from upper lip to groin. (B) and (C): Males in calling activity at the sampling site in Trilha do Lago. Note difference in pigmentation of vocal sacs. (D) and (E): Ventral and dorsal views of a male (left) and a female (right) specimen collected at the Serra Sul sampling site. Note difference in coloration of throat and variation in number of dark transverse bars on dorsal surface of thighs.

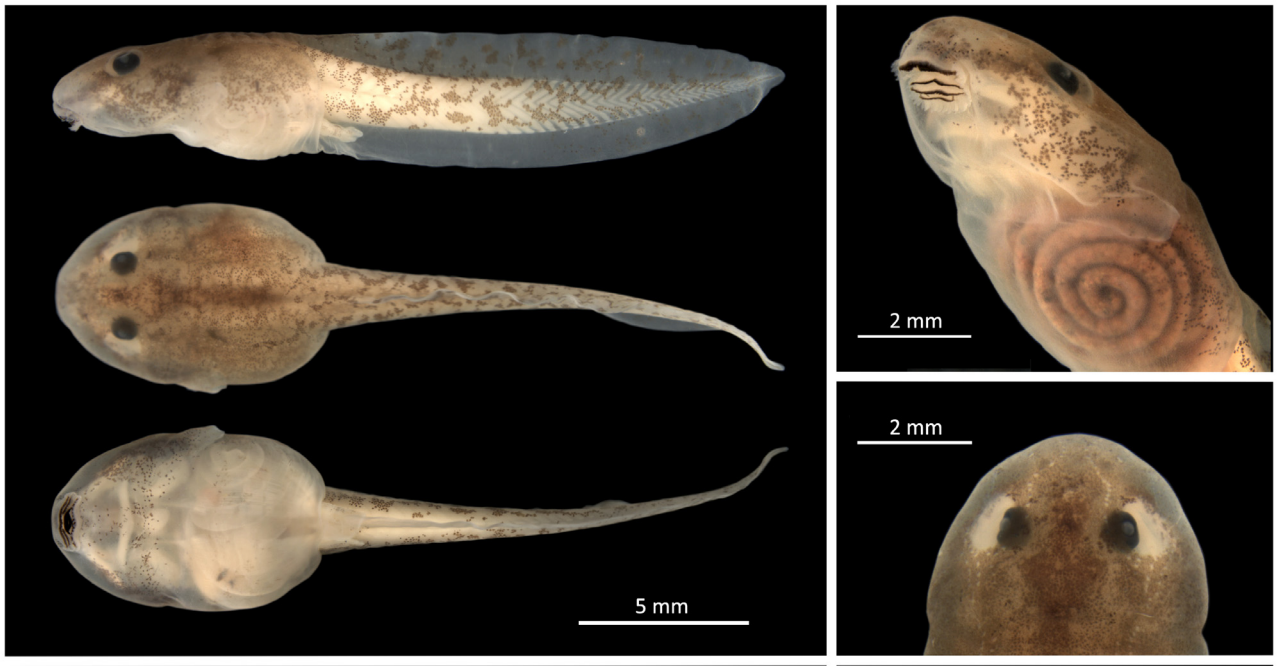

FIGURE 9. External morphology and coloration of tadpoles of *Allobates carajas* **sp. nov.** (lot INPA-H 38632). Clockwise from left: lateral, dorsal and ventral view of a tadpole in developmental stage 34. A second tadpole of *A. carajas*. Note position of spiracular tube and axis of gut coil. Dorsal view of the head of a third tadpole; note unpigmented round patch below the eyes.

Variation in type series. Measurements of specimens in the type series pare presented in Table 1. In average, females are larger than males, but all measurements overlap in range between male and female paratypes. Longitudinal hourglass-shaped brown mark on dorsum variable in width, lightness and conspicuousness among specimens in the type series (Fig. 6). A faint dark brown transverse bar may be present medially on forearm of some specimens (Fig. 6; Fig. 8C). Dorsal surface of thigh medially and distally crossed by 1–4 dark brown transverse bars. Transverse bars on dorsal surface on shank varying between 0–3 (Fig. 6). Throat pigmentation variable on males, dark brown melanophores varying from a few and sparsely scattered (INPA-H 38645 and the holotype), to moderately to densely scattered from chin to pectoral region (Fig. 7; Fig. 8B, C). Females with a few brown melanophores sparsely scattered only on chin and along the upper lip.

Testes cream colored. Smaller oocytes uniformly pigmented, reddish-brown. Mature oocytes uniformly cream to white. Large intestine unpigmented.

Color in life. Dorsum dark brown centrally, forming hourglass or rhomboid patterns on a tan brown background. Head dorsally tan brown from tip of snout to the level of the eye. Area between the eyes dark brown forming a triangular shape which connects with a rhomboid shape posteriorly. Iris golden, with dark brown reticulation. Dorsum laterally tan brown, darker on the urostyle region, where it is flanked by a thin black stripe. Pale dorsolateral stripe absent (Fig. 8A). Lateral surface of body surrounded by a uniformly dark brown stripe from tip of snout to groin. Faint areas may be present posterolaterally on the dark brown stripe on the inguinal region, but never forming a solid pale oblique lateral line. Ventrolateral stripe iridescent white, unbroken, extending along the lower border of dark brown stripe from upper lip to groin (Fig. 8). Ventrolateral surface of body with iridescent white blotches, same color as ventrolateral stripe, on brown background, merging ventrally with the yellow color of chest and abdomen. Throat uniformly yellow in females. Throat and vocal sac pinkish to translucent in live male specimens (Fig. 8D); when inflated vocal sac of males uniformly white to translucent (Fig. 8B) or peppered with a variable number of melanophores (Fig. 8C). Remaining ventral surfaces of body uniformly yellow, paler medially on the abdomen, where underlain by peritoneum.

Dorsal surface of upper and forearm uniformly tan brown, yellowish only around arm-body insertion. A faint dark brown transverse bar may be present medially on forearm (Fig. 8B, C). Upper arm yellow to translucent, darker than chest in ventral view, blood vessels visible through skin. Forearm, carpal and metacarpal regions dark

brown in ventral view. Fingers dark brown in ventral view, light gray brown in dorsal view. Paired scutes on finger discs iridescent white.

Surfaces immediately adjacent to vent uniformly dark brown. Light paracloacal marks absent. Instead, dorsal surface of thigh is proximally crossed by alternating tan brown and dark brown transverse bars. Dorsal surface of thigh medially and distally crossed by a variable number of dark brown transverse bars (Fig 8E). Dorsal surface of shank same color as thigh, with a medial transverse dark brown bar. Smaller dark brown blotches may be present on shank, beside the transverse bar. Ventral surface of thigh and shank solid greenish-yellow, darker than yellow shades of abdomen (Fig. 8D). Dorsal surface of tarsal region tan brown, with one or two transverse dark brown stripes. Tarsal and plantar regions brown in ventral view. Toes with tan brown and dark brown patterning. Paired scutes on toe discs iridescent white.

Color in life of juveniles same as that of adults, except for the lack of yellow colors on ventral surfaces, which are gray to translucent (Fig. 14C, D).

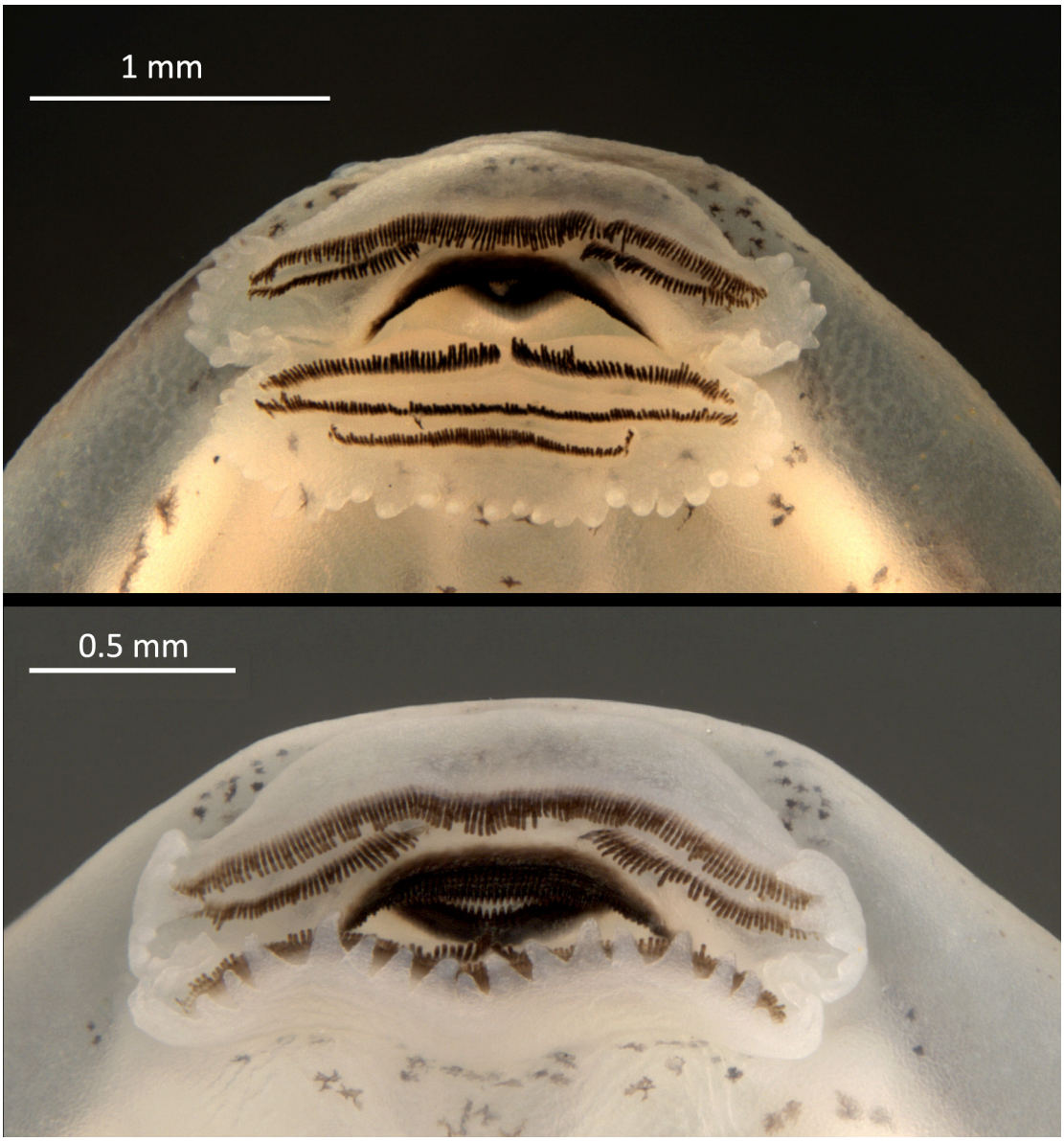

FIGURE 10. Oral discs of two tadpoles of *Allobates carajas* **sp. nov.** (lot INPA-H 38632) in developmental stage 34 emphasizing relative lengths among tooth rows (top) and the shape of labial papillae (bottom).

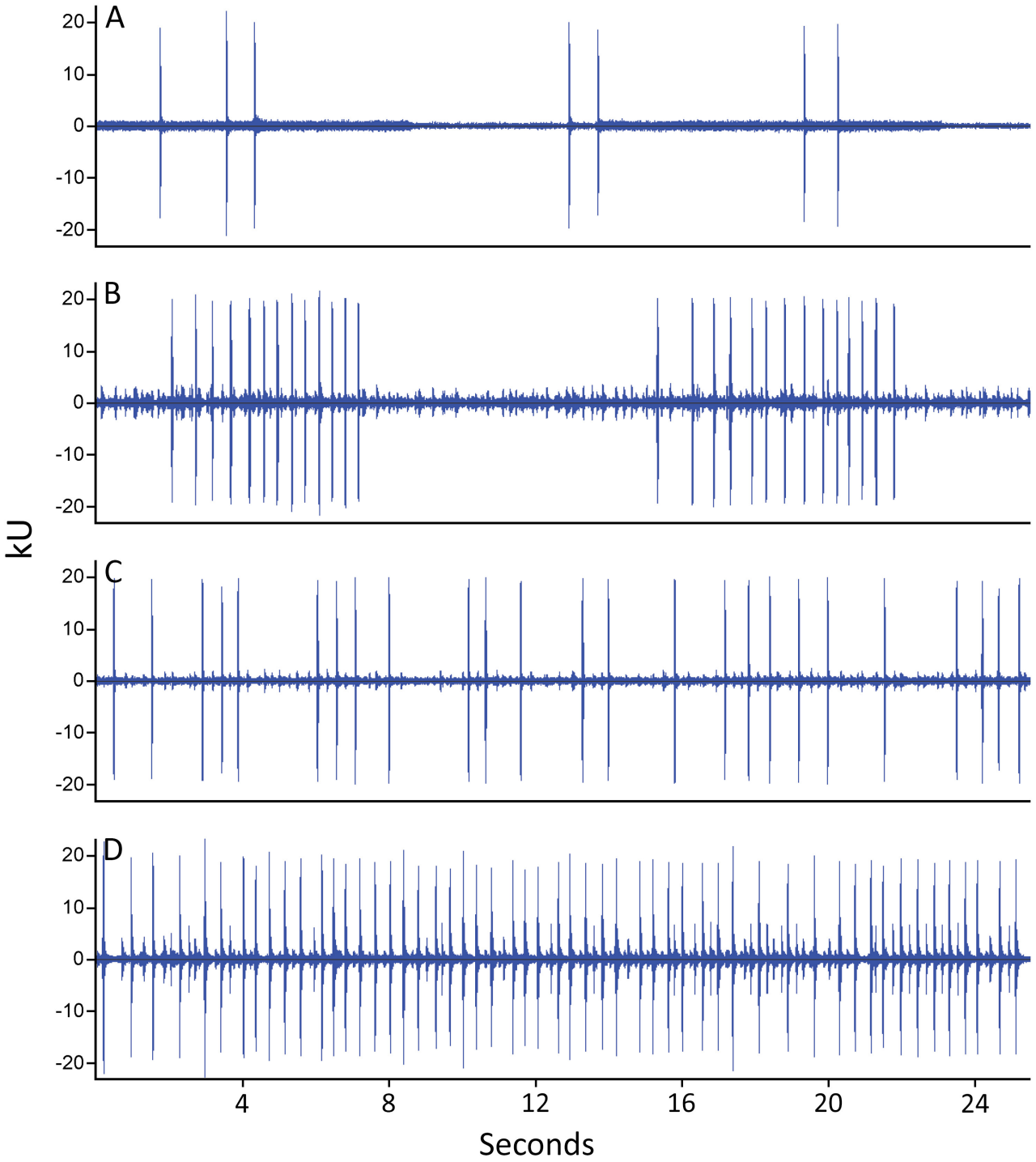

FIGURE 11. Different temporal arrangements of advertisement calls in *Allobates carajas* **sp. nov.** (A) Emission of isolated notes by a male on N1 Trail, recorded on 23 February 2014, at 11:40h and 25.0 °C. (B) Emission of notes arranged in trills by a male in Trilha do Lago, recorded on 22 February 2014, at 17:45h and 21.3 °C. (C) Continuous emission of notes separated by irregular time intervals by a male in Trilha do Lago, recorded on 22 February 2014, at 17:35h and 21.3 °C. (D) Continuous emission of notes separated by regular time intervals by a male in Serra Sul on 20 February 2014, at 08:12h and 22.0 °C.

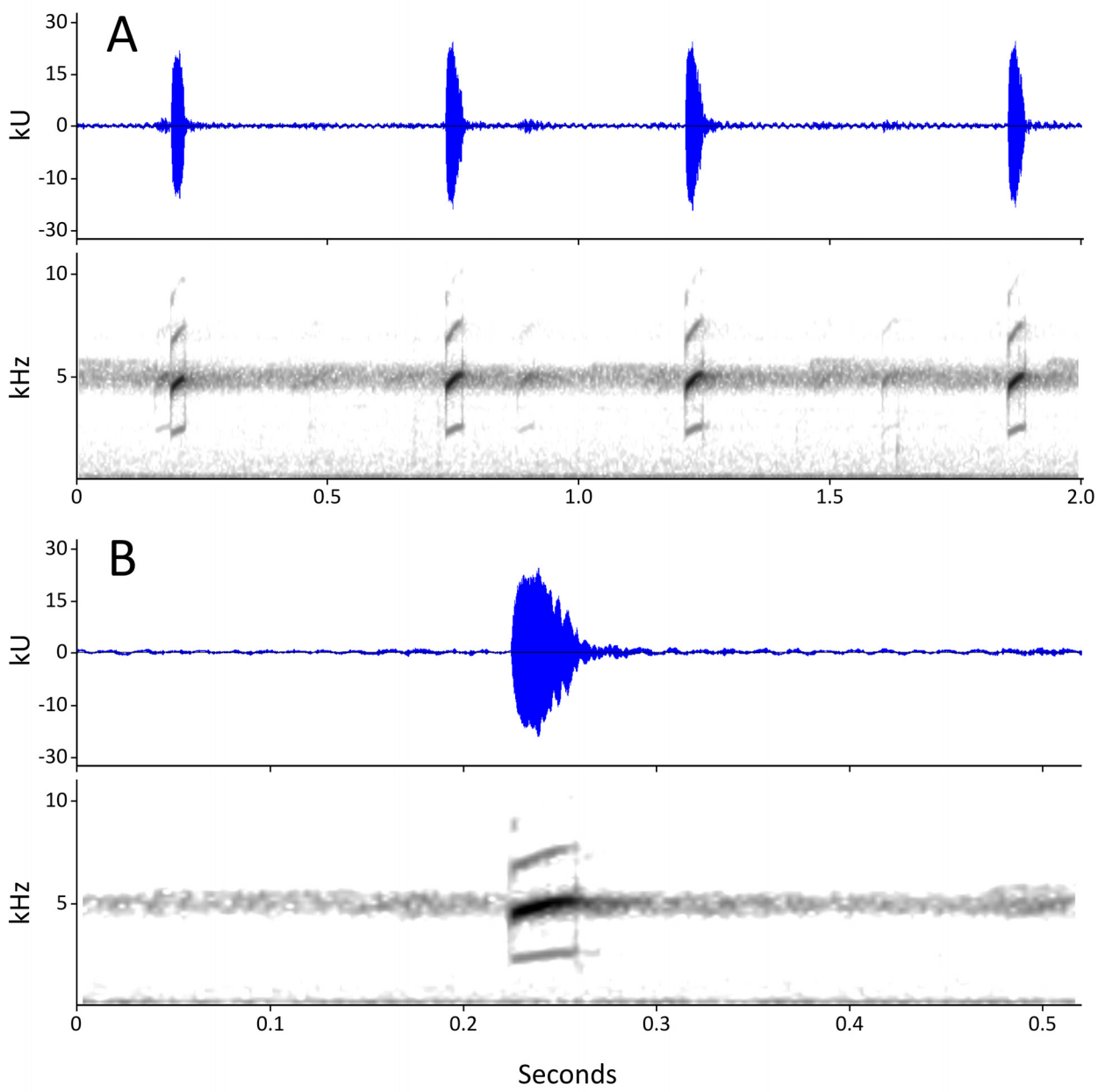

FIGURE 12. (A) Waveform (upper graph) and audiospectrogram (lower graph) of a 2.0 s segment of the advertisement call of a male *Allobates carajas* **sp. nov.** recorded in Trilha do Lago on 22 February 2014, at 17:35h and 21.3 °C. (B) Detailed view of a single note of the same specimen. Note ascending frequency modulation.

Description of larvae. Morphometric measurements of tadpoles are presented in Table 2. A tadpole at developmental stage 34 is shown in Fig. 9. The following description is based on nine tadpoles at developmental stages 31–34: Body ellipsoid, slightly round anteriorly and posteriorly in dorsal view, slightly flattened in lateral view (Fig. 9). Body length 36–40% and tail length 59–64% of TL; body wider than deep, BH 70–77% of BW; HWLE 72–90% of BW; snout truncate to round in dorsal view, round in lateral view; END approximately same length as ED (END/ED = 0.8–1.2); eyes dorsal and directed laterally; IOD 26–31% of HWLE. Small nares located dorsolaterally and directed anterolaterally, visible in dorsal and lateral views; internarial distance 18–23% of HWLE. Fleshy ring present on the inner margin of nostrils, round, straight, not ornamented. Spiracle sinistral, free from the body, tubular, 1.0–1.4 mm in length, attaching to body ventrolaterally at mid-body length (Fig. 9). Gut coiled, with its axis directed to the left side of body and located near the spiracular tube, visible through skin. Vent tube fused to ventral fin, 1.1–1.8 mm in length, dextral. Dorsal fin begins at body-tail insertion, dorsal edge shallow and straight anteriorly (along approximately 10% of its length), deeper posteriorly, reaching maximum depth after

approximately two thirds of tail's length. Dorsal fin slightly deeper than lower fin. Tail tip slightly acuminate. Caudal musculature dorsally reaching up to two thirds of body length from body-tail insertion to the level of spiracle (Fig. 9).

Oral disc located anteroventrally, emarginate laterally, transversely elliptical, 1.7–2.3 mm wide, corresponding to approximately 35% of body width at the level of spiracle (Fig. 10). Anterior labium with a group of 5–8 short, pyramidal papillae distributed in a single row on each side of labium's lateral margins. Groups of marginal papillae on each side of the upper labium split by a medial gap 1.1–1.6 mm long, corresponding to approximately 70% of oral disc's width. Posterior labium with a single row of marginal papillae variable in length, pointing at the same direction. Papillae short and round to pyramidal on the outer lateral folds of labium (4–7 papillae on each side). Longer pyramidal papillae (6–9 papillae on each side) distributed medially on posterior labium, in a single line (Fig. 10). Submarginal papillae, absent.

Upper jaw sheath arch-shaped, longer than lower jaw sheath, with no medial notch. Lower jaw sheath U-shaped, deeper than upper jaw sheath. Cutting edge of upper and lower jaw sheaths serrated; serrations extending along the entire length of both sheaths. Length of tooth rows A-1=A-2=P-1=P-2, 1.2–1.7 mm. Tooth rows A-1, P-2, P-3 complete; tooth row A-2 interrupted by a medial gap, 0.3–0.8 mm (Fig. 10). Tooth row P-1 with a narrow medial gap (< 0.1 mm), evidenced by a break between the underlying tooth ridges. Row P-3 shorter than other rows, 1.0–1.4 mm.

Background color of lateral, dorsal and anteroventral surfaces of body cream, with large darker areas formed by the aggregation of brown melanophores, more densely grouped on dorsum and flanks (Fig. 9). Darker brown color appears on dorsum between the diverging sections of caudal musculature. A pale, unpigmented patch, is present below the eye, slightly larger in area than the eyeball. Ventral surface of body posteriorly transparent and immaculate; intestines visible through skin. Tail muscle cream; tail fins transparent with scattered irregular blotches of brown melanophores distributed more densely over tail muscle and upper fin (Fig. 9).

TABLE 2. Morphometric measurements of ten tadpoles of *Allobates carajas* **sp. nov.** collected from a single pool in Floresta Nacional de Carajás, in State of Pará, Brazil. D.S. = Developmental stage (according to Gosner 1960). Measurements of one tadpole in developmental stage 25 (bottom line) was not accounted in the descriptive statistics. See main text for a detailed description of measurements.

D.S.	TL	BL	TAL	BW	BH	HWLE	TMW	MTH	TMH	IOD	IND	END	NSD	ED	VTL	STL	ODW
31	20.5	8.0	12.5	5.0	4.0	4.2	1.6	3.3	1.3	0.9	0.8	0.8	1.0	0.7	1.2	1.0	1.6
32	22.8	8.5	14.3	5.9	4.5	5.0	2.0	4.5	2.0	1.4	1.2	1.0	1.1	0.9	1.2	1.2	2.1
32	21.7	8.7	13.0	5.5	3.9	5.0	2.0	4.3	1.7	1.3	1.0	0.9	1.2	0.8	1.5	1.2	2.2
32	23.6	8.5	15.1	6.2	4.5	4.8	2.0	3.8	1.8	1.3	1.0	0.9	0.8	0.9	1.2	1.1	2.0
33	21.2	8.3	12.9	5.8	4.5	4.2	2.0	4.0	1.7	1.2	1.0	0.9	1.0	0.8	1.2	1.2	2.0
33	22.7	8.3	14.4	5.6	4.3	4.9	2.2	4.4	2.0	1.3	1.0	0.9	1.0	0.9	1.3	1.5	2.0
33	22.5	8.4	14.1	5.4	4.0	4.5	2.1	4.6	1.5	1.4	1.0	1.0	1.0	0.8	1.4	0.9	1.8
34	23.5	8.5	15.0	6.0	4.2	5.0	2.0	4.1	2.0	1.3	0.9	0.8	1.1	0.9	1.5	1.4	2.1
34	23.0	8.3	14.7	5.7	4.4	4.7	2.2	3.9	2.0	1.2	0.9	0.9	1.1	0.9	1.5	1.3	1.8
Mean	22.4	8.4	14.0	5.7	4.3	4.7	2.0	4.1	1.8	1.3	1.0	0.9	1.0	0.8	1.3	1.2	2.0
s.d.	1.0	0.2	1.0	0.4	0.2	0.3	0.2	0.4	0.3	0.2	0.1	0.1	0.1	0.1	0.1	0.2	0.2
min.	20.5	8.0	12.5	5.0	3.9	4.2	1.6	3.3	1.3	0.9	0.8	0.8	0.8	0.7	1.2	0.9	1.6
max.	23.6	8.7	15.1	6.2	4.5	5.0	2.2	4.6	2.0	1.4	1.2	1.0	1.2	0.9	1.5	1.5	2.2
25	18.3	7.2	11.1	5.0	3.9	4.0	1.8	3.0	1.0	1.0	0.9	0.6	0.7	0.7	0.7	1.1	1.5

Comparison with tadpoles of other species. Tadpoles of *Allobates caeruleodactylus* (Lima & Caldwell, 2001), *A. grillisimilis* Simões, Sturaro, Peloso & Lima, 2013, *A. marchesianus* (Melin, 1941), *A. subfolionidificans* (Lima, Sanchez & Souza, 2007) and *A. tapajos* Lima, Simões & Kaefer, 2015, differ from those of *A. carajas* in having distinctively elongate papillae on posterior labium (papillae round to pyramidal in *A. carajas*). Additionally, *A. caeruleodactylus* and *A. marchesianus* have distinct dark transversal bars on tail (absent in *A. carajas*) (Caldwell *et*

al. 2002a; Simões *et al.* 2013b; Lima *et al.* 2007; 2015). Labial tooth rows P-1, P-2 and P-3 are sub-equal in tadpoles of *A. sumtuosus* (Morales, 2002) (Simões & Lima 2012); row P-3 is lacking in tadpoles of *A. granti* (Kok *et al.* 2006) (all rows present in *A. carajas*, with P-3 distinctively shorter than P-1 and P-2). Row A-2 shorter than A-1 in tadpoles of *A. brunneus* (Cope, 1887) (Lima *et al.* 2009); row A-2 longer than A-1 in *A. magnussoni* Lima, Simões & Kaefer, 2014 (rows A-1 and A-2 with the same length in A. *carajas*). Tadpoles of *A. goianus* (Bokermann, 1975) have large dark blotches distally on tail and short and round papillae medially on posterior labium (pigments distributed over tail muscle and upper fin along the whole length of tail, papillae on medial posterior labium pyramidal). Tadpoles of *A. hodli* Simões, Lima & Farias, 2010, have short and round papillae medially on posterior labium (papillae on medial posterior labium pyramidal). Tadpoles of *A. paleovarzensis* (Lima, Caldwell, Biavati & Montanarin, 2010) have a distinct dark brown longitudinal bar extending from the snout to the eye, and towards mid-body (longitudinal dark brown bar absent in *A. carajas*). Tadpoles of *A. nidicola* (Caldwell & Lima, 2003) and *A. masniger* (Morales, 2002) are endotrophic and develop entirely in a terrestrial nest, and lack oral discs (and associated mouthparts) and spiracles (Caldwell & Lima, 2003; Albertina P. Lima, pers. observation).

Advertisement calls. SVL of captured recorded males ranged between 17.6–18.5 mm (average 17.7 mm, n = 5). By inspecting the waveforms and spectrograms of calls of ten males recorded in Carajás, we identified four types of temporal arrangement of notes (Fig. 11). In Serra Sul, notes were emitted either grouped in discrete trills (n = 2 males) or continuously, separated by regular silent intervals (n = 1 male). At Trilha do Lago, most recorded males (n = 3) emitted isolated notes, separated by long, irregular silent intervals. In this location, two other males emitted notes continuously, but notes were separated by short, irregular silent intervals. A sixth male emitted notes grouped in trills, but turned to a continuous regular call at the end of the recording. A single male was recorded at N1 Trail while emitting notes arranged in trills.

Considering all recordings, notes had an average duration of 0.04 ± 0.01 s (range 0.02–0.06 s) and were emitted at an average dominant frequency of 5101.9 ± 236.1 Hz (range 4752.8–5384.9 Hz). Notes had an ascending frequency modulation (Fig. 12). Average lower frequency of notes was 4655.1 ± 199.9 Hz (range 4402.3–4937.9 Hz) and average upper frequency of notes was 5418.8 ± 232.6 Hz (range 5107.3–5742.0 Hz). In average, notes occupied a frequency bandwidth of 763.7 ± 1129 Hz (range 533.1–920.0 Hz).

When notes were emitted continuously (n = 5 males), silent intervals between notes was extremely variable, ranging between 0.22–3.40 s (mean 0.76 ± 0.62 s; n = 100 silent intervals). When arranged in discrete trills (n = 4 males / 23 trills), trills were formed by 4–22 notes (mode = 8 notes) and their duration ranged between 1.49–7.05 s (mean = 4.38 ± 1.61 s). Trills were emitted between irregular, generally long silent intervals, ranging between 3.03–17.95 s (mean 7.22 ± 3.60 s). Silent interval between notes within a trill ranged between 0.24–0.91 s (mean 0.40 ± 0.14 s; n = 69 silent intervals).

Comparison with advertisement calls of other species. Advertisement calls of *A. caeruleodactylus*, *A. magnussoni*, *A. masniger*, *A. nidicola,* and *A. subfolionidificans* are formed by a single note, emitted continuously between irregular (*A. caeruleodactylus*, *A. subfolionidificans*) or regular (*A. magnussoni*, *A. masniger*, *A. nidicola*) inter-note silent intervals, not arranged in discrete note trills. Dominant frequency of notes in *A. carajas* is lower than that of notes in calls of *A. caeruleodactylus* (dominant frequency 5.54–6.64 kHz) (Lima & Caldwell 2001). Note duration in calls of *A. carajas* is generally longer than that in calls of *A. magnussoni* (note duration 0.047–0.104 s). Additionally, *A. magnussoni* frequently emits calls formed by note-pairs (Lima *et al.* 2014). Silent interval between notes in the continuous calls of *A. nidicola* and *A. masniger* are always regular, ranging between 0.206–0.315 s and 0.253–0.425 s, respectively (Caldwell & Lima 2003; Kaefer *et al.* 2012). Continuous calls of *A. carajas* can not be distinguished from those of *A. subfolionidificans* by their spectral or temporal parameters, overlapping in all measurements (Lima *et al.* 2007).

Some *Allobates* species alternate between two types of advertisement calls, emitting notes continuously or arranged in bouts or trills. When emitting trills of notes, silent interval between notes of *A. carajas* is longer than that in trills of *A. marchesianus* (0.12–0.21 s) (Caldwell *et al.* 2002b).

Continuous calls and note trills of *A. carajas* overlap in temporal parameters with those of *A. olfersioides*, however, notes in calls of *A. olfersioides* occupy a narrower frequency bandwidth (frequency bandwidth range 0.08–0.41 kHz) (Forti *et al.* 2017). Dominant frequency of notes in calls of *A. carajas* is lower than that of notes in calls of *A. sumtuosus* (dominant frequency 5.60–6.48 kHz) (Simões *et al.* 2013a).

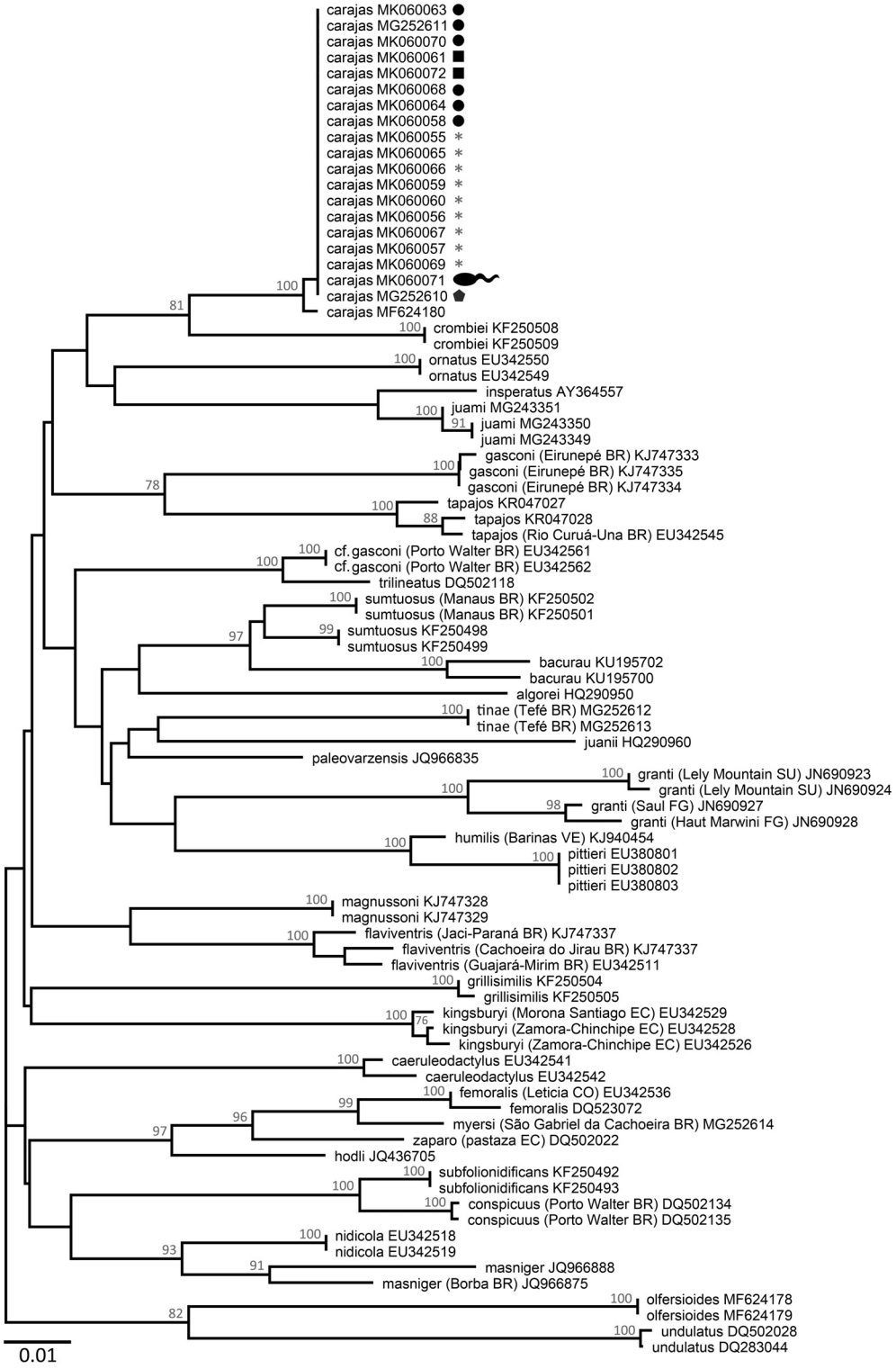

FIGURE 13. Unrooted neighbor-joining tree inferred from a fragment of the mitochondrial 16S rDNA sampled from 19 type specimens of *Allobates carajas* **sp. nov.** and other cis-Andean *Allobates* species. Cluster labels indicate bootstrap support values (in percentage) estimated from 5,000 bootstrap replicates (only support values > 75% are shown). Locations in parentheses are provided for sequences obtained from non-topotypic voucher specimens. Codes following taxon names correspond to GenBank accession numbers. Symbols following *A. carajas* terminals stand for sampling localities in Floresta Nacional de Carajás (asterisks: Serra-Sul, the species type locality; dots: Trilha do Lago; squares: N-1 Trail; pentagon: access road to Serra Sul; tadpole: tadpole collected from a pool on the access road to Serra Sul).

Advertisement calls of some *Allobates* species are constituted exclusively by note trills. However, in comparison to *A. carajas*, note trills are generally longer and formed by a larger number of notes in calls of *A. bacurau* (call duration 6.92–11.07 s, 60–81 notes) (Simões 2016). Trills of *A. crombiei* (Morales, 2002) are formed by a larger number of notes, emitted between much shorter silent intervals (25–59 notes, interval between notes 0.045–0.069 s) (Lima *et al.* 2012). Note trills and silent interval between notes within a trill are shorter in calls of *A. grillissimilis* (trill duration 0.12–0.30 s, interval between notes 0.010–0.043) (Simões *et al.* 2013b). Minimum trill duration in *A. carajas* (1.49 s) only slightly overlapping with maximum trill duration in *A. trilineatus* (trill duration 0.97–1.55 s). Minimum interval between notes in trills of *A. carajas* (0.24 s) much longer than maximum interval between notes in *A. trilineatus* (0.07–0.09 s) (Grant & Rodríguez 2001).

Advertisement calls of *A. flaviventris* Melo-Sampaio, Souza & Peloso, 2013, and *A. hodli* are emitted as trills of note-pairs or couplets, not as trills of single notes (Simões *et al.* 2010; Melo-Sampaio *et al.* 2013; Lima *et al.* 2014). Advertisement calls of *A. femoralis* (Boulenger, 1884) and *A. myersi* (Pyburn, 1981) are emitted as trills of three, four, six or eight notes (Amézquita *et al.* 2006; Simões & Lima 2011).

Note trills of *A. carajas* more closely resemble those of *A. brunneus*, *A. goianus*, *A. paleovarzensis*, and *A. tinae*, overlapping in all call parameters. However, in general, notes in trills of *A. goianus* are shorter and emitted between shorter silent intervals (note duration 0.030–0.051s, interval between notes 0.020–0.048 s) (Carvalho *et al.* 2016). Notes in trills of *A. paleovarzensis* are split by generally shorter silent intervals and emitted with a lower dominant frequency (interval between notes 0.065–0.266 s, dominant frequency 4.05–4.93 kHz) (Lima *et al.* 2010). Note trills of *A. tinae* are generally formed by a small number of notes (2–9 notes) (Melo-Sampaio *et al.* 2018). Additionally, the ability to emit continuous calls is not reported for *A goianus*, *A. paleovarzensis* or *A. tinae*. Continuous calls or note trills of *A. brunneus* can not be distinguished from those of *A. carajas*. However, notes emitted in continuous calls of *A. brunneus* are always regularly spaced, with silent intervals between notes varying between 0.35–0.42 s (Lima *et al.* 2014).

DNA barcoding. All adult specimens (n = 19) and the single tadpole sequenced shared the same mitochondrial 16S rRNA haplotype (Fig. 13) and formed a well-supported group with a second haplotype found in an earlier study that sampled this species in Carajás (Grant *et al.* 2017). This group is nested within *Allobates* inhabiting cis-Andean South America for which 16S rDNA sequences were available (Fig. 13). Two sequences of *A. crombiei* from Cachoeira do Espelho, Pará, Brazil, are the most similar to those of *A. carajas*, with high bootstrap support (Fig. 13). Average uncorrected pairwise and Kimura-2-parameter (K2P) genetic distances between *A. crombiei* and *A. carajas* are 5 and 6%, respectively (Table 3).

Average genetic distances between *A. carajas* and the remaining samples analyzed is ≥ 7 or 8% (uncorrected pairwise and K2P distances, respectively). Average uncorrected pairwise genetic distances estimated between *A. carajas* and other cryptically colored *Allobates* with hourglass-shaped marks on dorsum (*A. flaviventris*, *A. gasconi*, *A. magnussoni*, *A. undulatus*) are ≥ 8% (≥9 % considering K2P genetic distances) (Table 3).

Diagnosis. *Allobates carajas* is distributed in eastern Brazilian Amazonia, south of the Amazon River. Hence, we compare the new species with all *Allobates* species occurring in Brazil and with one additional species from Venezuela, *Allobates undulatus* (Myers & Donnelly, 2001), which is morphologically similar to *A. carajas*. Character states of the new species are in parentheses throughout the diagnosis.

Live specimens of *Allobates femoralis*, *A. hodli* and *A. myersi* have bright yellow, orange or red flash marks on dorsal surface of thigh, and black and white marbling on the surface chest and abdomen (bright colored marks absent on dorsal surface of thigh, abdominal surfaces solid yellow or pale in live and preserved specimens of *A. carajas*). Minimum SVL reported for individuals of these species 22.2 mm in a male of *A. hodli* (largest *A. carajas* male = 18.5 mm).

Allobates bacurau Simões, 2016, *A. caeruleodactylus*, *A. conspicuus* (Morales, 2002); *A. fuscellus* (Morales, 2002), *A. grillisimilis*, *A. juami* Simões, Gagliardi-Urrutia, Rojas-Runjaic & Castroviejo-Fisher 2018, *A. marchesianus*, *A. masniger*, *A. nidicola*, *A. paleovarzensis*, *A. subfolionidificans*, *A. sumtuosus*, *A. tapajos*, *A. tinae* Melo-Sampaio, De Oliveira & Prates, 2018, *A. vanzolinius* (Morales, 2002) lack rhomboid or hourglass-shaped brown marks centrally on dorsum (dorsum with distinct longitudinal brown mark, hourglass-shaped, extending centrally from the level of anterior corner of the eye to the urostyle region in *A. carajas*).

TABLE 3. Average percentage of uncorrected pairwise and Kimura-2-parameter (below and above the diagonal, respectively) genetic distances between *Allobates carajas* **sp. nov.** and other *Allobates* species distributed in *cis*-Andean South America. Distances were based in a 466 bp fragment of the mitochondrial 16S rDNA. Sample size of each taxon is in Appendix I.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**
1.*carajas* sp. nov.		12	12	11	12	6	12	10	14	11	8	12	10	11	10	9	14	11	9	12	12	11	14	9	8	12	11	12	9	10	9	15	11
2.*algorei*	10		12	11	11	12	14	13	14	13	10	14	12	11	10	10	14	14	12	12	14	12	18	12	10	14	12	12	9	12	10	18	13
3.*bacurau*	10	10		14	14	12	16	14	15	15	11	14	13	12	14	14	15	15	12	13	15	11	18	13	9	15	13	14	6	12	11	18	13
4.*caeruleodactylus*	10	10	12		13	12	12	10	15	12	11	13	10	12	13	12	12	13	11	12	12	11	17	12	9	14	11	12	12	13	12	16	12
5.*conspicuus*	10	10	12	11		13	13	13	15	14	13	14	12	13	11	10	13	14	13	12	13	10	15	10	11	14	14	3	11	15	12	18	12
6.*crombiei*	5	10	10	10	11		13	10	13	11	10	10	10	11	12	11	12	11	9	11	11	9	13	11	9	12	11	13	9	13	11	13	11
7.*femoralis*	10	11	13	10	11	11		14	18	18	11	15	6	14	13	13	14	12	13	14	3	11	16	13	10	16	13	12	11	16	11	17	6
8.*flaviventris*	9	11	12	9	11	9	11		15	12	10	11	12	11	13	13	12	12	7	10	12	9	16	11	10	14	12	12	11	12	10	16	12
9.*gasconi*	9	11	12	10	12	10	14	10		13	14	17	13	12	15	15	14	14	12	18	16	14	18	14	11	12	13	16	11	16	14	18	14
10.cf. *gasconi*	7	9	9	10	11	9	10	9	10		12	14	13	12	14	14	13	13	11	13	14	11	19	11	12	15	12	14	12	9	13	15	14
11.*granti*	11	12	12	12	12	11	14	13	11	12		12	11	10	10	10	12	12	10	12	12	10	16	10	7	13	10	12	8	10	2	16	11
12.*grillisimilis*	10	12	12	11	12	9	12	10	12	10	14		14	12	15	15	13	13	13	13	15	12	19	14	12	15	13	15	11	14	11	16	16
13.*hodli*	9	10	11	9	10	9	5	10	11	9	11	11		12	10	11	11	12	10	11	7	9	13	11	9	14	12	11	10	14	10	14	6
14.*humilis*	9	9	10	10	11	9	12	10	10	9	10	10	10		13	14	13	12	11	13	13	10	15	11	9	3	10	13	10	12	10	16	13
15.*insperatus*	8	9	12	11	10	10	11	11	12	9	12	12	9	11		3	14	13	11	11	13	10	17	11	9	15	13	11	12	13	11	16	13
16.*juami*	8	9	12	11	9	9	11	11	11	9	12	12	10	12	3		13	13	12	12	13	11	16	10	10	16	13	10	12	13	11	16	12
17.*juani*	11	11	12	10	11	10	12	10	11	11	12	11	10	11	11	11		13	11	13	14	11	19	15	10	17	11	12	13	14	12	15	13
18.*kingsburyi*	9	12	12	11	12	10	10	10	11	10	11	11	10	10	11	11	11		12	14	13	13	18	14	11	14	12	14	11	14	11	15	11
19.*magnussoni*	8	10	10	9	11	8	11	6	10	9	10	11	9	9	9	10	9	10		10	12	8	15	12	9	13	11	13	10	11	10	14	13
20.*masniger*	10	10	11	10	10	9	12	8	11	10	14	11	10	11	10	10	11	11	8		14	6	17	12	12	15	13	11	11	13	12	16	12
21.*myersi*	10	11	12	10	11	10	3	10	12	10	13	12	6	11	11	11	12	11	11	12		10	16	12	10	15	14	13	12	16	11	16	5
22.*nidicola*	9	10	9	9	8	8	9	8	10	9	11	10	8	9	9	9	10	11	7	5	9		15	10	9	12	13	9	8	10	10	13	9
23.*olfersioides*	12	14	14	13	13	11	13	13	15	13	14	15	11	12	13	13	15	14	13	14	13	12		16	16	15	16	15	16	19	18	14	15
24.*ornatus*	8	10	11	10	9	10	11	10	10	9	12	11	9	9	9	9	12	11	10	10	10	8	13		10	12	13	10	10	13	11	19	14
25.*paleovarzensis*	7	8	8	8	9	8	9	9	10	7	9	10	8	8	8	8	9	9	8	10	9	8	13	9		10	8	9	6	10	8	14	10
26.*pittieri*	10	11	12	11	12	10	12	12	12	11	10	12	11	3	13	13	13	11	11	12	12	10	12	10	9		13	14	12	15	13	17	14
27.*tinae*	9	10	11	10	12	9	11	10	11	8	11	11	10	9	11	11	10	10	9	11	12	11	13	11	7	11		13	9	13	10	17	14
28.*subfolionidificans*	10	10	12	10	2	11	10	10	12	10	13	12	10	11	9	9	10	12	11	9	11	8	12	9	8	11	11		11	14	11	18	11
29.*sumtuosus*	8	8	5	10	10	8	10	9	10	8	10	10	9	9	10	10	11	10	9	9	10	7	13	8	6	10	8	9		10	9	16	9
30.*tapajos*	9	10	10	11	12	11	13	10	8	9	13	11	11	10	11	11	12	12	9	11	13	8	15	10	9	12	11	11	9		11	17	13
31.*trilineatus*	8	9	10	10	10	9	10	9	11	2	12	10	9	9	9	10	10	10	9	10	10	9	14	10	7	11	9	10	8	9		15	11
32.*undulatus*	13	15	14	13	14	11	14	13	13	13	14	13	12	13	13	13	12	12	12	13	13	11	12	14	12	13	13	14	13	13	12		16
33.*zaparo*	10	11	11	10	10	10	5	10	12	9	11	13	6	11	11	10	11	10	11	10	5	8	13	11	9	12	11	10	8	11	9	13	

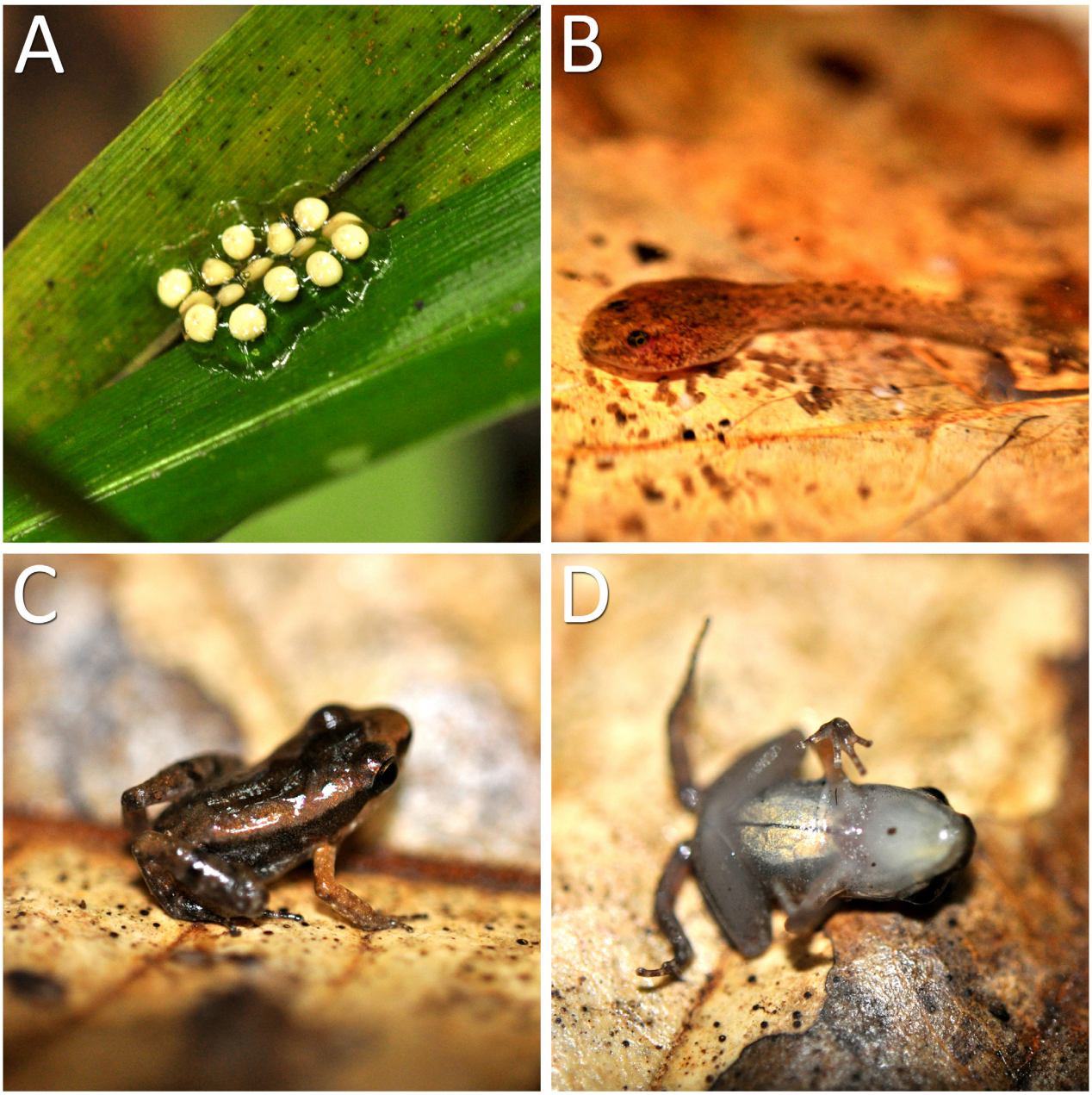

FIGURE 14. (A) Egg clutch of *Allobates carajas* **sp. nov.** photographed at Trilha do Lago sampling site in Floresta Nacional de Carajás, state of Pará, Brazil. (B) Color in life of a tadpole of *A. carajas*. (C) Dorsolateral and (C) ventral views of a juvenile *A. carajas* found at Serra Sul sampling site, in Carajás. Note absence of yellow shades on ventral surfaces.

Allobates bacurau and *A. grillisimilis* are also distinguished from *A. carajas* by their smaller size, reaching a maximum SVL = 16.0 mm, in a female *A. grillisimilis* (minimum SVL of *A. carajas* = 16.5 mm) and by the predominantly white to translucent ventral surfaces, with no shades of yellow in life (ventral surfaces yellow in live *A. carajas*). Fingers sky-blue in live males of *A. caeruleodactylus* (fingers brown in male *A. carajas*). *Allobates caeruleodactylus* also has a diffuse dark brown lateral stripe (solid dark brown lateral stripe). *Allobates conspicuus* has a well-defined pale dorsolateral stripe and pale paracloacal mark (dorsolateral stripe absent, pale paraclacal mark indistinct). Ventral surfaces of male *A. fuscellus* dark gray, transverse dark bars absent on dorsal surfaces of thigh (ventral surfaces yellow in life, white to translucent in preserved specimens, transverse bars present on dorsal surface of thigh). Dark pigments absent on ventral surfaces of male *A. juami* (dark melanophores present on throat, or at least on chin in male *A. carajas*). Pale dorsolateral stripe present and well-defined, pale ventrolateral line

absent in *A. marchesianus* (pale dorsolateral stripe absent, pale ventrolateral stripe present in *A. carajas*). Ventral surfaces of male *A. marchesianus* dark to light gray (Caldwell *et al.* 2002b) (yellow in life, white to translucent in preserved *A. carajas*). Throat black or dark brown in male *A. masniger* and *A. nidicola* (throat pinkish to translucent in life, white in preserved specimens, with scattered melanophores in male *A. carajas*). Throat pinkish gray in life, gray in preserved males of *A. paleovarzensis* (throat pinkish to translucent in life, white in preserved specimens). *Allobates paleovarzensis* also lacks transverse dark bars on dorsal surface of thigh (dorsal surface of thigh with a variable number of transverse dark bars). Ventral surfaces solid white in live males of *A. subfolionidificans* (ventral surfaces predominantly yellow in live males of *A. carajas*). Dorsal color of thighs bluish gray in live *A. sumtuosus*, with no transverse dark bars (dorsal surface of thigh tan brown with a variable number of transverse dark bars). Some specimens of *A. tapajos* may have brown dorsal markings forming approximately rhomboid patterns, but throat and vocal sac are golden yellow in live males (pinkish to translucent) and dark brown lateral stripe is diffuse posteriorly (dark brown lateral stripe solid, not diffuse). Throat and vocal sac golden yellow in live males of *A. tinae* (pinkish to translucent) and no transverse dark bars on dorsal surface of thighs of males or females (dorsal surface of thigh with a variable number of transverse dark bars). Minimum SVL of male *A. vanzolinius* (19.6 mm) larger than maximum SVL of A. *carajas* (18.5 mm). *Allobates vanzolinius* also lacks transverse dark bars on dorsal surface of thigh (dorsal surface of thigh with a variable number of transverse dark bars).

X-shaped dark brown mark present on dorsum and C-shaped pale paracloacal mark present adjacent to vent of *Allobates olfersioides* (Lutz, 1925) (Verdade & Rodrigues 2007) (hourglass-shaped mark present on dorsum, pale paracloacal mark absent in *A. carajas*).

Allobates brunneus, *A. crombiei*, *A. flaviventris*, *A. gasconi* (Morales 2002), *A. goianus*, *A. magnussoni* and *A. undulatus* (Myers & Donnelly, 2001) have distinct diamond-shaped or hourglass patterns on dorsum and could be potentially mistaken for *A. carajas*. However, lateral brown stripe surrounding body and pale ventrolateral line are diffuse posteriorly in *A. brunneus* (Lima *et al*. 2009) (lateral stripe dark brown and solid, pale ventrolateral stripe continuous). *Allobates crombiei* lacks a distal subarticular tubercle on Finger IV, and male specimens lack dark pigments on throat (Morales 2002; Lima *et al.* 2012) (distal subarticular tubercle present on Finger IV, males with throat conspicuously peppered by dark melanophores in *A. carajas*). Live specimens of *A. flaviventris* and *A. magnussoni* with an interrupted or diffuse pale ventrolateral stripe, formed by iridescent-white dots and blotches, males with pinkish-white chest and silvery-white anterior abdomen, yellow colors projecting only marginally from posterior to anterior abdomen (pale ventrolateral stripe unbroken, abdomen uniformly yellow in live male specimens of *A. carajas*). Maximum SVL of male *A. gasconi* (16.3 mm) shorter than minimum SVL of *A. carajas* (16.5 mm). Pale dorsolateral stripe present in *A. gasconi* (absent in *A. carajas*). *Allobates goianus* with a conspicuous pale paracloacal mark, evident in live and preserved specimens and basal webbing present between toes II-III (Carvalho *et al*. 2016) (pale paracloacal mark absent, basal webbing absent between toes II-III). Minimum SVL of *A. undulatus* (20.0 mm) larger than maximum SVL of *A. carajas* (19.1 mm). Additionally, lateral stripe surrounding body black and broad, covering whole flank posterior to arm in *A. undulatus* (lateral stripe dark brown, limited inferiorly by pale ventrolateral stripe)

Geographic distribution. The current distribution of *Allobates carajas* encompasses forested areas of Floresta Nacional de Carajás, where the species was detected in at least four locations on its southern, northern and central regions (Fig. 1). During fieldwork in Carajás, we did not observe any specimens of *A. carajas* in *canga* (open xerophytic vegetation growing on exposed rocky terrain) or swampy environments. Given the increasing isolation of the forested environments of Carajás due to mining and cattle ranching along its borders, and the paucity of anuran surveys in neighboring forest remnants, the presence of the new species outside of Carajás is uncertain.

Natural history notes. In Carajás, *Allobates carajas* was found exclusively in well-preserved dense-canopy forest habitat. At Serra Sul, males called atop rocks, in areas where the leaf litter layer on the forest floor was deeper, or near the entrance of dens alongside rocky walls. Calling sites were better characterized at Trilha do Lago. Average calling site height was 23.5 cm (range 1.0–41.0 cm, $n = 11$). Males called while perched on green leaves ($n = 3$) or twigs ($n = 3$) in the lower understory vegetation, perched on the blades of leaves of stemless palms ($n = 2$), on the leaf litter of the forest floor ($n = 2$) or atop termite nests ($n = 1$). Also at Trilha do Lago, a single jelly nest was found on the upper surface of a broadleaf herb, less than 20 cm from the calling site of a male (Fig. 14). The jelly was transparent and contained 17 white-yolked eggs, ranging from 1.9 to 3.0 mm in maximum diameter (average = 2.2 mm).

Juvenile specimens were common in the leaf litter of Serra Sul, and shared the same color pattern of the adult specimens, except for the lack of yellow shades on ventral surfaces of body and limbs (Fig. 14). Water accumulated in holes and on the concave surfaces of rocks, providing isolated water bodies adequate for tadpole deposition, but no *Allobates* tadpoles were found. Tadpoles were also absent in phytotelmata or rain puddles in all sampling sites. These facts suggest that the peak of the reproductive season must have occurred earlier than February in that year.

Tadpoles were only found at the bottom of a shallow valley that crossed the access road to Serra Sul (50°20'14.4" W, 06°13'00.9" S), where water accumulated in a single pool in a forested habitat. A female specimen (INPA-H 38624) was captured near the pool, while males were heard calling at least 20 m far from the site. DNA barcoding analyses confirmed these tadpoles as belonging to *A. carajas* (see *DNA barcoding* above). In life, tadpoles had yellow and pinkish brown coloration, merging with the background color of the leaf litter at the bottom of the pool (Fig. 14).

Discussion

Allobates carajas is the 26th species of nurse-frog recorded in Brazil, and the 18th to be described from specimens collected in Brazilian Amazonia. It is morphologically more similar to *Allobates brunneus* and *A. crombiei*. *Allobates brunneus* was described from Chapada dos Guimarães, a rocky plateau area nested within the dry Brazilian Cerrado biome, approximately 1.200 km southwest of Carajás (Cope 1887; Lima *et al*. 2009). *Allobates crombiei* was described from Cachoeira do Espelho, a locality on the right bank of the Xingu River, 350 km northwest of Carajás (Morales 2002; Lima *et al.* 2012). Genetic distance data suggest that *A. carajas* is closely related to *A. crombiei*, and their distinction as separate species is supported by morphological (presence of distal subarticular tubercle on Finger IV in *A. carajas*), color (presence of dark pigmentation on the throat and chin of males in *A. carajas*) and acoustic traits (call arrangement and duration of silent intervals between trills). No DNA sequence data is currently available for *A. brunneus*, but it can be also distinguished from *A. carajas* by color traits, such as posteriorly diffuse lateral and ventrolateral stripes.

Large tributaries of the Amazon such as the Xingu river are important biogeographic barriers to *Allobates* nurse-frogs and are often implicated in the geographic distribution of genetic and phenotypic intraspecific variability (*e.g.*, Kaefer *et al.* 2013; Simões *et al.* 2014; Maia *et al.* 2017). *Allobates crombiei* and *A. carajas* are distributed in the same interfluve (Xingu-Tocantins). Large rivers do not bisect this interfluve and could not be implicated as vicariant barriers associated with the evolutionary divergence between these two species. However, *A. crombiei* was recorded in lowland environments along the banks of the Xingu River (ca. 100 m a.s.l.), whereas the known distribution of *A. carajas* comprises closed canopy forests covering the Carajás rocky plateau at altitudes above 650 m a.s.l.. Revisionary work suggests that Andean anuran species with narrow altitudinal ranges (< 100 to 600 m) outnumber those with wide altitudinal ranges, implicating in speciation related to local adaptation as an evolutionary process more frequent than altitudinal range expansion of generalist phenotypes (Navas 2006). The system formed by *A. carajas* and *A. combiei* may provide an interesting model in order to test the role of altitude differences in the divergence of morphological, behavioral and genetic traits at the scale of a single Amazonian interfluve.

Previous studies had reported the emission of more than one advertisement call arrangement in other cryptically-colored nurse-frogs. Most species with alternative call arrangements shift between continuous call and note trills (*e.g.*, *A. brunneus*—Lima *et al.* 2009; *A. sumtuosus*—Simões *et al.* 2013a; *A. tapajos*—Lima *et al.* 2015), whereas *Allobates magnussoni* alternates between the continuous emission of note-pairs and single notes (Lima *et al.* 2014). We were able to identify four different call arrangements from recordings of ten males of *A. carajas* at different sampling localities not far from each other (distances between sampling sites were always < 50 km). Call arrangements varied among individuals in the same sampling site, indicating that call arrangements are not fixed geographically and reinforcing earlier statements that a reliable characterization of the acoustic repertoire of nurse-frog species should consider recordings of a large number of males. To date, different call arrangements were only identified in studies that encompassed recordings of eight or more individuals (Amézquita *et al.* 2006; Simões & Lima 2011; Simões *et al.* 2013a; Lima *et al.* 2014; 2015).

Allobates carajas' known distribution is restricted to Floresta Nacional de Carajás, Pará, Brazil. Although a national conservation unit, the natural landscape of Carajás is heavily and consistently impacted by governmentally

authorized large-scale mining within the reserve (Martins *et al.* 2012). This fact makes it difficult to assess the conservation status (*sensu* IUCN guidelines) of the new species based on trends of habitat loss or fragmentation. On the other hand, based on current data, we have no reason to believe that intraspecific genetic or phenotypic diversity in *A. carajas* is geographically structured within the reserve. Hence, the species should not be vulnerable to localized interventions to the reserve's native landscape, as long as most of its forested habitat remains unaltered.

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APPENDIX I. Origin and accession numbers of 16S rDNA sequences of *Allobates* species occurring in Brazil and of other species similar to *Allobates carajas* **sp. nov** distributed in northern South America used in this study.

Species	Locality	Coordinates	16S	Reference
carajas sp. nov.	Serra Sul, Floresta Nacional de Carajás, Pará, Brazil	06°23'34.7" S, 50°19'09.8" W	MK060055	*This study*
carajas sp. nov.	Serra Sul, Floresta Nacional de Carajás, Pará, Brazil	06°23'34.7" S, 50°19'09.8" W	MK060056	*This study*
carajas sp. nov.	Serra Sul, Floresta Nacional de Carajás, Pará, Brazil	06°23'34.7" S, 50°19'09.8" W	MK060057	*This study*
carajas sp. nov.	Serra Sul, Floresta Nacional de Carajás, Pará, Brazil	06°23'34.7" S, 50°19'09.8" W	MK060058	*This study*
carajas sp. nov.	Serra Sul, Floresta Nacional de Carajás, Pará, Brazil	06°23'34.7" S, 50°19'09.8" W	MK060059	*This study*
carajas sp. nov.	Serra Sul, Floresta Nacional de Carajás, Pará, Brazil	06°23'34.7" S, 50°19'09.8" W	MK060060	*This study*
carajas sp. nov.	Serra Sul, Floresta Nacional de Carajás, Pará, Brazil	06°23'34.7" S, 50°19'09.8" W	MK060062	*This study*
carajas sp. nov.	Serra Sul, Floresta Nacional de Carajás, Pará, Brazil	06°23'34.7" S, 50°19'09.8" W	MK060065	*This study*
carajas sp. nov.	Serra Sul, Floresta Nacional de Carajás, Pará, Brazil	06°23'34.7" S, 50°19'09.8" W	MK060066	*This study*
carajas sp. nov.	Trilha do Lago, Floresta Nacional de Carajás, Pará, Brazil	06°02'41.1" S, 50°05'29.7" W	MK060067	*This study*
carajas sp. nov.	Trilha do Lago, Floresta Nacional de Carajás, Pará, Brazil	06°02'41.1" S, 50°05'29.7" W	MK060063	*This study*
carajas sp. nov.	Trilha do Lago, Floresta Nacional de Carajás, Pará, Brazil	06°02'41.1" S, 50°05'29.7" W	MK060064	*This study*
carajas sp. nov.	Trilha do Lago, Floresta Nacional de Carajás, Pará, Brazil	06°02'41.1" S, 50°05'29.7" W	MK060068	*This study*
carajas sp. nov.	Trilha do Lago, Floresta Nacional de Carajás, Pará, Brazil	06°02'41.1" S, 50°05'29.7" W	MK060070	*This study*
carajas sp. nov.	Trilha do Lago, Floresta Nacional de Carajás, Pará, Brazil	06°02'41.1" S, 50°05'29.7" W	MG252611	Simões *et al.* 2018
carajas sp. nov.	N1-Trail, Floresta Nacional de Carajás, Pará, Brazil	06°03'06.3" S, 50°15'39.9" W	MK060061	*This study*
carajas sp. nov.	N1-Trail, Floresta Nacional de Carajás, Pará, Brazil	06°03'06.3" S, 50°15'39.9" W	MK060072	*This study*
carajas sp. nov.	Road to Serra Sul, Floresta Nacional de Carajás, Pará, Brazil	06°13'00.9" S, 50°20'14.4" W	MK060071	*This study*
carajas sp. nov.	Road to Serra Sul, Floresta Nacional de Carajás, Pará, Brazil	06°13'00.9" S, 50°20'14.4" W	MG252610	Simões *et al.* 2018
carajas sp. nov.	Igarapé Bahia, Floresta Nacional de Carajás, Pará, Brazil		MF624180	Grant *et al.* 2017
algorei	Road to Rio Negro, Tachira, Venezuela	10°19'17" S, 64°33'47" W	HQ290950	Santos & Cannatella 2011
bacurau	Manicoré, Amazonas, Brazil	05°52'05" S, 61°17'13" W	KU195700	Simões 2016
bacurau	Manicoré, Amazonas, Brazil	05°52'05" S, 61°17'13" W	KU195702	Simões 2016
caeruleodactylus	Castanho, Amazonas, Brazil	03°37'10" S, 59°86'78" W	EU342541	Santos *et al*. 2009
caeruleodactylus	Castanho, Amazonas, Brazil	03°37'10" S, 59°86'78" W	EU342542	Santos *et al*. 2009
conspicuus	Porto Walter, Rio Juruá, Acre, Brazil	08°15'31" S, 72°46'37" W	DQ502135	Grant *et al.* 2006
conspicuus	Porto Walter, Rio Juruá, Acre, Brazil	08°15'31" S, 72°46'37" W	DQ502134	Grant *et al.* 2006
crombiei	Cachoeira do Espelho, Altamira, Pará, Brazil	03°39'00" S, 52°22'33" W	KF250508	Simões *et al.* 2013a

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APPENDIX 1. (Continued)

Species	Locality	Coordinates	16S	Reference
crombiei	Cachoeira do Espelho, Altamira, Pará, Brazil	03°39'00" S, 52°22'33" W	KF250509	Simões *et al.* 2013a
femoralis	Letícia, Amazonas, Colômbia		EU342536	Santos *et al.* 2009
femoralis	Yurimaguas, Loreto, Peru		DQ523072	Roberts *et al.* 2006
flaviventris	Jaci-Paraná, Rondônia, Brazil	09°12'16" S, 64°21'43" W	KJ747337	Lima *et al.* 2014
flaviventris	Cachoeira do Jirau, Rondônia, Brazil	09°19'27" S, 64°42'39" W	KJ747336	Lima *et al.* 2014
flaviventris	Guajará-Mirim, Rondônia, Brazil	10°19'17" S, 64°33'47" W	EU342521	Santos *et al.* 2009
cf. *gasconi*	Porto Walter, Rio Juruá, Acre, Brazil	08°15'31" S, 72°46'37" W	EU342561	Santos *et al.* 2009
cf. *gasconi*	Porto Walter, Rio Juruá, Acre, Brazil	08°15'31" S, 72°46'37" W	EU342562	Santos *et al.* 2009
gasconi	Eirunepé, Rio Juruá, Amazonas, Brazil	06°45'50" S 70°09'49" W	KJ747333	Lima *et al.* 2014
gasconi	Eirunepé, Rio Juruá, Amazonas, Brazil	06°45'50" S 70°09'49" W	KJ747334	Lima *et al.* 2014
gasconi	Eirunepé, Rio Juruá, Amazonas, Brazil	06°45'50" S 70°09'49" W	KJ747335	Lima *et al.* 2014
granti	Lely Mountain, Suriname		JN690923	Fouquet *et al.* 2012
granti	Lely Mountain, Suriname		JN690924	Fouquet *et al.* 2012
granti	Saul, French Guiana		JN690927	Fouquet *et al.* 2012
granti	Haut Marwini, French Guiana		JN690928	Fouquet *et al.* 2012
grillisimilis	Borba, Amazonas, Brazil	04°26'03" S, 59°37'25" W	KF250504	Simões *et al.* 2013a
grillisimilis	Borba, Amazonas, Brazil	04°26'03" S, 59°37'25" W	KF250505	Simões *et al.* 2013a
hodli	Cachoeira do Jirau, Rondônia, Brazil	09°19'27" S, 64°42'39" W	JQ436705	Simões *et al.* 2010
humilis	Road to San Ramón, Barinas, Venezuela	08°52'04" N, 70°29'09" W	KJ940454	Santos *et al.* 2014
insperatus	Yasuní, Ecuador		AY364557	Santos *et al.* 2003
juami	Estação Ecológica Juami-Japurá, Amazonas, Brazil	01°57'52" S, 67°56'08" W	MG243349	Simões *et al.* 2018
juami	Estação Ecológica Juami-Japurá, Amazonas, Brazil	01°57'52" S, 67°56'08" W	MG243350	Simões *et al.* 2018
juami	Estação Ecológica Juami-Japurá, Amazonas, Brazil	01°57'52" S, 67°56'08" W	MG243351	Simões *et al.* 2018
juanii	Villavicencio, Meta, Colômbia		HQ290960	Santos & Cannatella 2011
kingsburyi	Near Panguitza, Zamora Chinchipe, Ecuador		EU342526	Santos *et al.* 2009
kingsburyi	Near Arenas, Zamora Chinchipe, Ecuador		EU342528	Santos *et al.* 2009
kingsburyi	10 km South of Gualaquiza, Morona Santiago, Ecuador		EU342529	Santos *et al.* 2009
magnussoni	Parque Nacional da Amazônia, Itaituba, Pará, Brazil.	04°33'12" S; 56°18'00" W	KJ747328	Lima *et al.* 2014
magnussoni	Parque Nacional da Amazônia, Itaituba, Pará, Brazil.	04°33'12" S; 56°18'00" W	KJ747329	Lima *et al.* 2014
masniger	Borba, Amazonas, Brazil	04°26'03" S, 59°37'25" W	JQ966875	Kaefer *et al.* 2013

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APPENDIX 1. (Continued)

Species	Locality	Coordinates	16S	Reference
masniger	Parque Nacional da Amazônia, Pará, Brazil	04°32'51" S, 56°18'13" W	JQ966888	Kaefer *et al.* 2013
mysersi	São Gabriel da Cachoeira, Amazonas, Brazil	00°09'21" S, 67°05'10" W	MG252614	Simões *et al.* 2018
nidicola	Autazes Road Km 12, Amazonas, Brazil	03°28'02" S, 59°49'09" W	EU342518	Santos *et al.* 2009
nidicola	Autazes Road Km 12, Amazonas, Brazil	03°28'02" S, 59°49'09" W	EU342519	Santos *et al.* 2009
olfersioides	São José da Vitória, Bahia, Brazil	15°28' S, 39°18' W	DQ502120	Grant *et al.* 2006
ornatus	Tarapoto, San Martin, Peru		EU342549	Santos *et al.* 2009
ornatus	Tarapoto, San Martin, Peru		EU342550	Santos *et al.* 2009
paleovarzensis	Careiro, Amazonas, Brazil	03°22'26" S, 59°52'06" W	JQ966835	Kaefer *et al.* 2013
pittieri	La Trilla, Estado Aragua, Venezuela		EU380801	Manzanilla *et al.* 2009
pittieri	La Trilla, Estado Aragua, Venezuela		EU380802	Manzanilla *et al.* 2009
pittieri	La Trilla, Estado Aragua, Venezuela		EU380803	Manzanilla *et al.* 2009
subfolionidificans	Rio Branco, Acre, Brazil	09°57' S, 67°57' W	KF250492	Simões *et al.* 2013a
subfolionidificans	Rio Branco, Acre, Brazil	09°57' S, 67°57' W	KF250493	Simões *et al.* 2013a
sumtuosus	REBio Trombetas, Pará, Brazil	01°22'12" S, 56°51'08" W	KF250499	Simões *et al.* 2013a
sumtuosus	REBio Trombetas, Pará, Brazil	01°22'12" S, 56°51'08" W	KF250498	Simões *et al.* 2013a
sumtuosus	Reserva Ducke, Manaus, Amazonas, Brazil	02°55'–03°01'S, 59°53'–59°59'W	KF250501	Simões *et al.* 2013a
sumtuosus	Reserva Ducke, Manaus, Amazonas, Brazil	02°55'–03°01'S, 59°53'–59°59'W	KF250502	Simões *et al.* 2013a
tapajos	Fazenda Treviso, near river Curuá-Una, Pará, Brazil	03°08'44" S, 54°50'33" W	EU342545	Santos *et al.* 2009
tapajos	Parque Nacional da Amazônia, Itaituba, Pará, Brazil.	04°33'12" S; 56°18'00" W	KR047027	Lima *et al.* 2015
tapajos	Parque Nacional da Amazônia, Itaituba, Pará, Brazil.	04°33'12" S; 56°18'00" W	KR047028	Lima *et al.* 2015
tinae	Tefé, Amazonas, Brazil	03°25'52" S, 64°44'49" W	MG252612	Simões *et al.* 2018
tinae	Tefé, Amazonas, Brazil	03°25'52" S, 64°44'49" W	MG252613	Simões *et al.* 2018
trilineatus	Panguana, Rio Llullapichis, Huanuco, Peru		DQ502118	Grant *et al.* 2006
undulatus	Cerro Yutaje, Amazonas, Venezuela	05°46' N, 66°08' W	DQ502028	Grant *et al.* 2006
undulatus	Cerro Yutajé, Amazonas, Venezuela	05°46' N, 66°08' W	DQ502029	Grant *et al.* 2006
undulatus	Cerro Yutajé, Amazonas, Venezuela	05°46' N, 66°08' W	DQ283044	Grant *et al.* 2006
zaparo	Coca, Pastaza, Ecuador		DQ502022	Grant *et al.* 2006

APPENDIX II. Examined material

*Allobates alessandroi**—PERU: Depto. de Cuzco: Paucartambo, Cosñipata. AMNH 157004. *Allobates bacurau*—BRAZIL: Amazonas: Manicoré. INPA-H 35397–35409. *Allobates gasconi*—Brazil: Amazonas: Rio Juruá, Jainu. INPA-H 3082, 3085, 3087, 3090, 3150, 3151, 3172, 3249, 3406, 3415, 3483, 3484, 3491, 3494, 3496, 3512, 3513. *Allobates grillisimilis*—BRAZIL: Amazonas: Borba: INPA-H 30779–30808; Amazonas: Nova Olinda do Norte. INPA-H 30809–30823. *Allobates hodli*—BRAZIL: Rondônia: Cachoeira do Jirau. INPA-H 16541–16569. *Allobates juami*—BRAZIL: Amazonas: Japurá. MCP 13287–13293. *Allobates magnussoni*—BRAZIL: Pará: Itaituba, Parque Nacional da Amazônia. INPA-H 32960–32976; Pará: Belterra, Fazenda Treviso. INPA-H 10105–10109, 33930–33934. *Allobates masniger**—BRAZIL: Pará: Itaituba, Parque Nacional da Amazônia. USNM 303584, 303585, 303587, 303589, 303590. *Allobates mcdiarmidi**—BOLIVIA: Depto. de Cochabamba: Cochabamba. USNM 257804–257806. *Allobates myersi*—BRAZIL: Amazonas: São Gabriel da Cachoeira: INPA-H 26396–26372, 26374, 26376, 26377, 26379. *Allobates nidicola*—BRAZIL: Rondônia: Porto Velho. INPA-H 28602–28612. *Allobates sumtuosus*—BRAZIL: Pará: Reserva Biológica do Rio Trombetas: INPA-H 31952–31956, INPA-H 31958–31960. *Allobates tapajos*—BRAZIL: Pará: Itaituba, Parque Nacional da Amazônia. INPA-H 34402–34406, 34410–34412, 34414–34416, 34418, 34423, 34407–34409, 34413, 34417, 34419–34422, 34424–34425.

*Specimens examined via high-quality photographs, courtesy of Pedro. L. V. Peloso.