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A new diminutive species of *Allobates* Zimmermann and Zimmermann, 1988 (Anura, Aromobatidae) from the northwestern Rio Madeira—Rio Tapajós interfluve, Amazonas, Brazil

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Abstract

We describe *Allobates grillisimilis* from the northwestern region of the Rio Madeira—Rio Tapajós interfluve, state of Amazonas, Brazil. The new taxon is characterized by its small snout-to-vent length (12.8–16.0 mm, the smallest among known *Allobates*), by the color pattern of adults (surfaces of throat, chest and abdomen unpigmented), by morphological traits of larvae (a single row of very elongate papillae on posterior labium), and by its distinctive advertisement call, formed by trills of short pulses emitted in a variable number. We also provide notes on reproductive behavior of the new species.

Key words: Amazonia, *Allobates grillisimilis* **sp. nov.**, Aromobatidae, Brazil, Dendrobatoidea

Introduction

Allobates Zimmermann and Zimmermann, 1988, includes 46 named species of small, diurnal, and generally cryptically colored Neotropical frogs, distributed from northern Central America to the southern reaches of the Amazon river basin in South America (Grant *et al.* 2006; Frost, 2011). Despite the incredible diversity observed in the genus, variation in color and morphological characters between most species is generally subtle, rendering it difficult to identify and diagnose the species based on external morphology.

While several of the original descriptions of *Allobates* relied solely on external morphological characters (*e.g.* Morales, 2000 "2002" [1]; Barrio-Amorós *et al.* 2006; Grant *et al.* 2007), independent authors have called for the importance of a more integrative approach, including data on advertisement calls, reproductive behavior, larval morphology, and, more recently, DNA sequences in the identification of new taxa and in redescriptions of known forms (see examples in Caldwell & Lima 2003; Kok *et al.* 2006; Kok & Ernst 2007; Lima *et al.* 2007; Simões *et al.* 2010; see also Peloso 2010; Padial *et al.* 2010 for the discussion on the importance of integrative taxonomy). Such integrative works have led to the discovery of a plethora of new species and helped to redefine the species boundaries of taxonomically complex nominal taxa (Caldwell *et al.* 2002; Lima *et al* 2009). Some species previously considered widespread in the Amazon basin proved to have relatively narrow distributions. Here, we describe a diminutive new species of litter frog assigned to genus *Allobates*, potentially restricted to the

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1. Although the publication by V. Morales is listed as published in 2000, it was not actually printed until 2002.

northwestern Madeira-Tapajós interfluve, state of Amazonas, Brazil. Reproductive adults of the new species have also the smallest reported body-size among all species within genus *Allobates*.

The Madeira river (= Rio Madeira) is the largest southern tributary of the Amazon river (=Rio Amazonas). At its lower course, it runs through the Amazon plains, characterized by strong sedimentary dynamics and by the presence of floodplains along riverbanks. At some sites, higher plateaus extend from the most central areas of the interfluves reaching areas close to the riverbanks, where *terra-firme* (not seasonally flooded) forests are the predominant (DNPM, 1978). Much of the area adjacent to the river's lower course was remodeled by geologically recent (*i.e.* Cenozoic) tectonic activity. These events gave rise to sedimentary compartments on the right riverbank that are distinct from those on the left riverbank or those adjacent to the middle course of the Madeira river (Costa *et al.*, 2001; Rossetti *et al.*, 2005). Although often considered as a single biogeographic unit or area of endemism (Ron 2000; Silva *et al.* 2005; Morrone 2006), the edaphic variation resulting from the Tertiary and Quaternary sediment deposition of the Madeira-Tapajós interfluve, and its partitioning by smaller tributaries, arguably affects the distribution of local vertebrate species (Roosmalen *et al.* 2002; Geurgas & Rodrigues 2010).

Material and methods

Specimens described here were collected in three sampling areas in the northern Madeira-Tapajós interfluve, State of Amazonas, Central Brazilian Amazonia. Two areas, Borba and Nova Olinda do Norte, are located on the right bank of the Madeira River. The third area corresponds to sites along the Paraconi River, located inside limits of Floresta Nacional do Pau-Rosa, municipality of Maués, approximately 50 km southeast of the mouth of the Madeira River (Fig. 1). Field work was carried out in Borba in February 2007 and January 2008 by P. I. Simões and A. P. Lima; in Nova Olinda do Norte in December 2007, by P. I. Simões and A. P. Lima; and Maués between February and March 2009, by M. Sturaro and P. L. V. Peloso.

Sampling sites in Borba and Nova Olinda do Norte correspond to remnants of primary, old growth *terra-firme* forests located in the outskirts of the respective urban areas. Sampling sites in Maués were located in the vicinities of two riverine communities on the right margin of Paraconi River, Comunidade Bragança and Comunidade São Tomé, also in fragments of primary *terra-firme* forest.

Specimens were collected by hand during the day, brought to improvised labs in camping sites, anesthetized and killed with topic solution of 20% benzocaine, fixed in 10% formaldehyde solution and preserved in 70% ethanol. Specimens were deposited in the herpetology section of the zoological collection of Instituto Nacional de Pesquisas da Amazônia, in Manaus, Brazil (INPA-H), and in the herpetological collection of Museu Paraense Emílio Goeldi, in Belém, Brazil (MPEG). Additional specimens, examined for comparisons are housed at INPA, MPEG, and American Museum of Natural History, New York, USA (AMNH), Sam Noble Oklahoma Museum of Natural History, Norman, USA (OMNH), Smithsonian, National Museum of Natural History, Washington, D.C., USA (USNM).

Preserved specimens were examined and measured under a stereo microscope with graduated lenses or digital caliper (to the nearest 0.1 mm). Terminology follows Grant *et al.* (2006). Morphometric measurements and diagnostic characters follow Lima *et al.* (2007) and Barrio-Amorós & Santos (2009). Measurements taken are 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 (SL), eye-to-nostril distance from anterior corner of the eye to the center of nostril (EN), internarial distance (IN), eye length from anterior to posterior corner (EL), 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 phalange (WPF), diameter of palmar tubercle (DPT), leg length from the posterior extremity of the coccyx 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), width of thenar tubercle (WTT). The existence of statistically significant differences in SVL and body proportions (HL/SVL, HW/SVL, HL/HW, EL/HL, TYM/EL, TL/SVL, HAND II/HAND I, WPF/WFD) between males from distinct sampling sites, and between males and females were evaluated by means of analyses of variance (*ANOVA*), implemented in SYSTAT 8.0 (Wilkinson 1990).
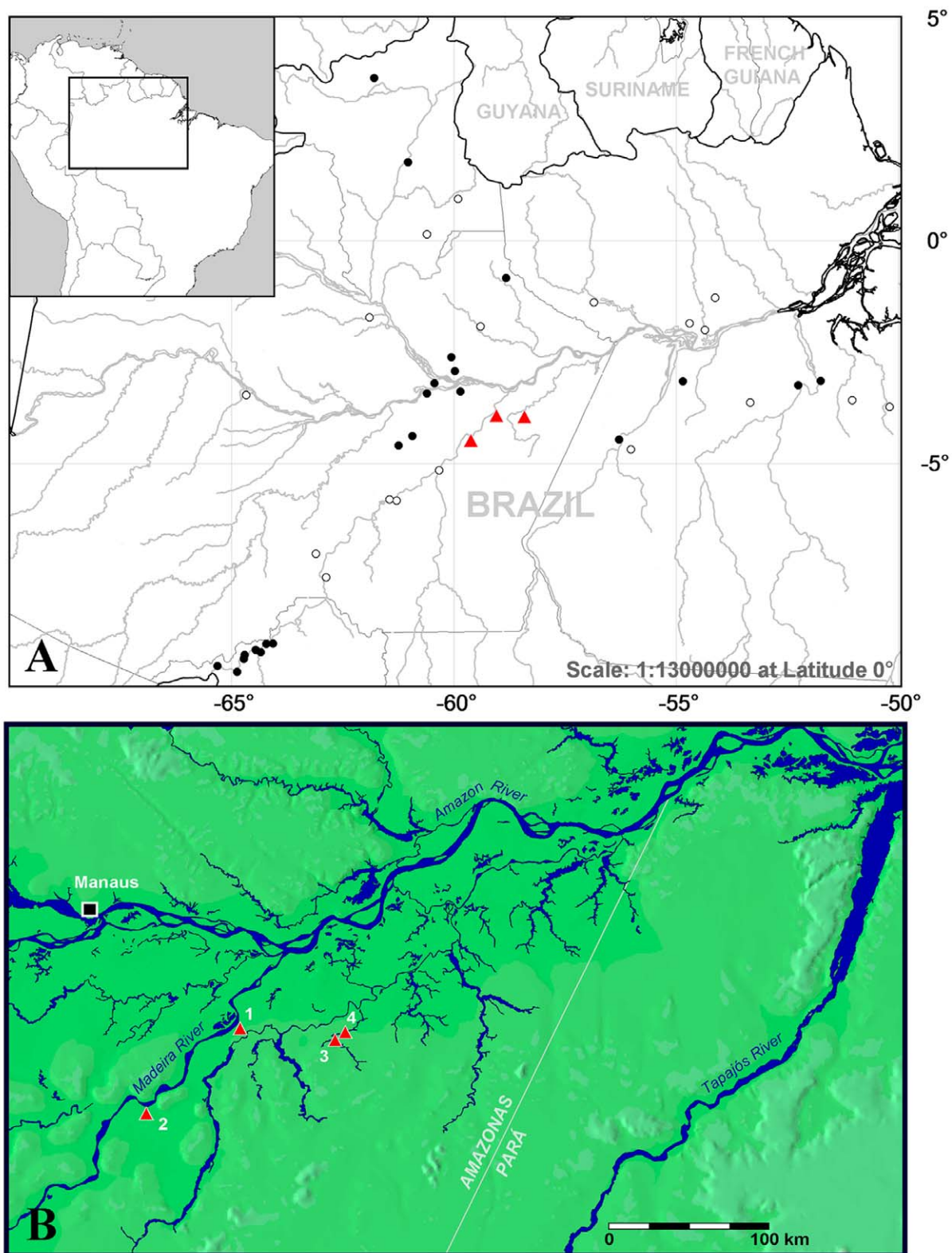
FIGURE 1. Geographic distribution of *Allobates grillisimilis* (A) Inset: relative location of sampling area in northern South America. Red triangles: distribution of *Allobates grillisimilis* in central Brazilian Amazon. Solid dots: location of permanent grids maintained by the Brazilian Program for Biodiversity Research-PPBio (http://ppbio.inpa.gov.br), and sites where intensive studies focusing on diurnal frogs have been conducted at least three times, where the new species was not recorded. Open dots: sites sampled for diurnal frogs in one or two consecutive years by the authors, where the new species was not recorded. (B) Detailed view of sites of occurrence of *Allobates grillisimilis* emphasizing their location in the northwestern Madeira-Tapajós interfluve, State of Amazonas. 1: Nova Olinda do Norte; 2: Type locality in the outskirts of Borba; 3: Rio Paraconi, in Maués; 4: Igarapé Tabacal, a tributary of Rio Paraconi, also in Maués.

Descriptions of adult color in life were based on field notes and photographs by the authors.

Ninety-one larvae were used for tadpole description. Those were obtained from egg clutches (development completed in artificial conditions in the field or in the lab), or were collected while being carried on the backs of males, at the sampling site in Borba. Tadpoles and egg clutches were sorted into distinct lots, and raised in laboratory until developmental stages 25, 26–28, 35–37 or 38–40 of Gosner (1960) (see Results). Tadpoles were anesthetized and killed in benzocaine solution, preserved in 10% formaldehyde solution, and deposited the herpetology section of the zoological collection of Instituto Nacional de Pesquisas da Amazônia, in Manaus, Brazil (voucher numbers INPA-H 30824, 30825, 30826, 30827, 30828). One tadpole at developmental stage 27 was used for a detailed description of external morphology of body, oral disc, and color in formalin. Color in life was described based on photographs by A.P. Lima of live individuals raised in the laboratory. Terminology follows Altig & McDiarmid (1999). Tadpole measurements were obtained separately for each lot of tadpoles belonging to the same developmental stage class (25, 26–28, 35–37, 38–40). Measurements were: total length from tip of snout to tip of tail (TL), body length from tip of snout to body-tail insertion (BL), tail length from body-tail insertion to tip of tail (TAL), body width at spiracle level (BW), body height at spiracle level (BH), head width at the level of the eyes (HWLE), tail muscle maximum width (TMW), maximum tail height (MTH), tail muscle maximum height (TMH), interorbital distance (IOD), internostril distance (IND), distance from eye to nostril (END), distance from nostril to snout (NSD), eye diameter in dorsal view (ED), vent tube length (VTL), and spiracle tube length (STL).

Advertisement calls of 21 males found in the three sampling localities were recorded. In Borba and Nova Olinda do Norte, calls were recorded with a Sony WM-D6C tape recorder and AKG 568 EB directional microphone. In Maués, calls were recorded with a Marantz PMD 620 digital recorder and an internal microphone, at a sample rate of 44.1 kHz. Microphones were positioned approximately 1 m away from each calling individual. All recordings were made between 06:30-18:00 h and air temperature at the moment of recording was registered. Tape recordings were digitized using Raven 1.2 software (Charif *et al*. 2004) at a sample rate of 44.1 kHz and 16 bits sample format.

From the recording of each individual, we sampled eight advertisement calls from which we measured temporal and spectral parameters. Samples were uniformly distributed along the whole length of each recording, intervals between sampled calls being defined by dividing the total number of calls in each recording by eight. As calls were formed by a variable number of short notes slightly different in amplitude, we also measured parameters relative to the first, the last and the most central pulse. Temporal parameters were: duration of silent interval between calls (SIC), silent interval between first and second note (SIF), and silent interval between the most central and the successive note (SIM); duration of call (DC), duration of first note (DFN), duration of most central note (DCN), duration of last note (DLN). Spectral parameters were the peak, lowest and highest frequencies of the whole call (PFC, LFC, HFC), first note (PFFN, LFFN, HFFN), most central note (PFCN, LFCN, HFCN), and last note (PFLN, LFLN, HFLN). Spectral analysis was done by a fast Fourier transform with a frequency resolution of 82 Hz and 2048 points. Lowest and highest frequencies of notes were measured 20 dB below peak frequency.

Descriptions of reproductive behavior were based on field notes, photographs, and video sequences recorded by A.P. Lima in Borba, in January 2008.

Allobates grillisimilis
Figures 2–10.

Holotype. INPA-H 30779 (field number APL 12734). Adult male, collected by A. P. Lima after recording of advertisement calls at 07:28 h, on 12th of January 2008, at Ramal Novo Horizonte, about 5 km southwest of the city of Borba, on the right bank of the Madeira River (04°26'03" S, 59°37'25" W), State of Amazonas, Brazil.

Paratopotypes. INPA-H 30780–30808 (original field numbers APL 12735–12740, APL 12746–12750, 12769–12770, APL 12788–12793, APL 12802), 21 males, 8 females, collected by A. P. Lima and P. I. Simões, during two distinct field expeditions, in February 2007 and January 2008. Female INPA-H 30780 (field number APL 12793) is the designated the species allotype.

Paratypes. All from State of Amazonas, Brazil. **Nova Olinda do Norte:** INPA-H 30809–30823 (field numbers APL 12659–12665, APL 12668, APL 12671–12677), 6 females, 9 males, Ramal do Curupira, Municipality of Nova Olinda do Norte (03°52'28" S, 59°02'46" W), collected in December 2007 by P. I. Simões.

Maués: MPEG 28535, 28536, 28538, 28543, 28545 (field numbers FPR 005, 006, 008, 009, 237, respectively), all males, Floresta Nacional de Pau-Rosa, Municipality of Maués (03°56'50" S, 58°26'36" W); MPEG 28540, 28541, 28543 (field numbers FPR 109, 116, 126), all males, Floresta Nacional de Pau-Rosa, Igarapé Tabacal, Rio Paraconi, Municipality of Maués (03°55'07" S, 58°24'19" W).

Etymology. The specific epithet refers to the species distinctive advertisement call, which resembles (to the human ear) to the sound produced by crickets. The epithet is formed by the conjunction of the appellative substantive *grillus* (cricket, genitive *grilli*) and the adjective *similis* (similar, alike), meaning similar to a cricket.
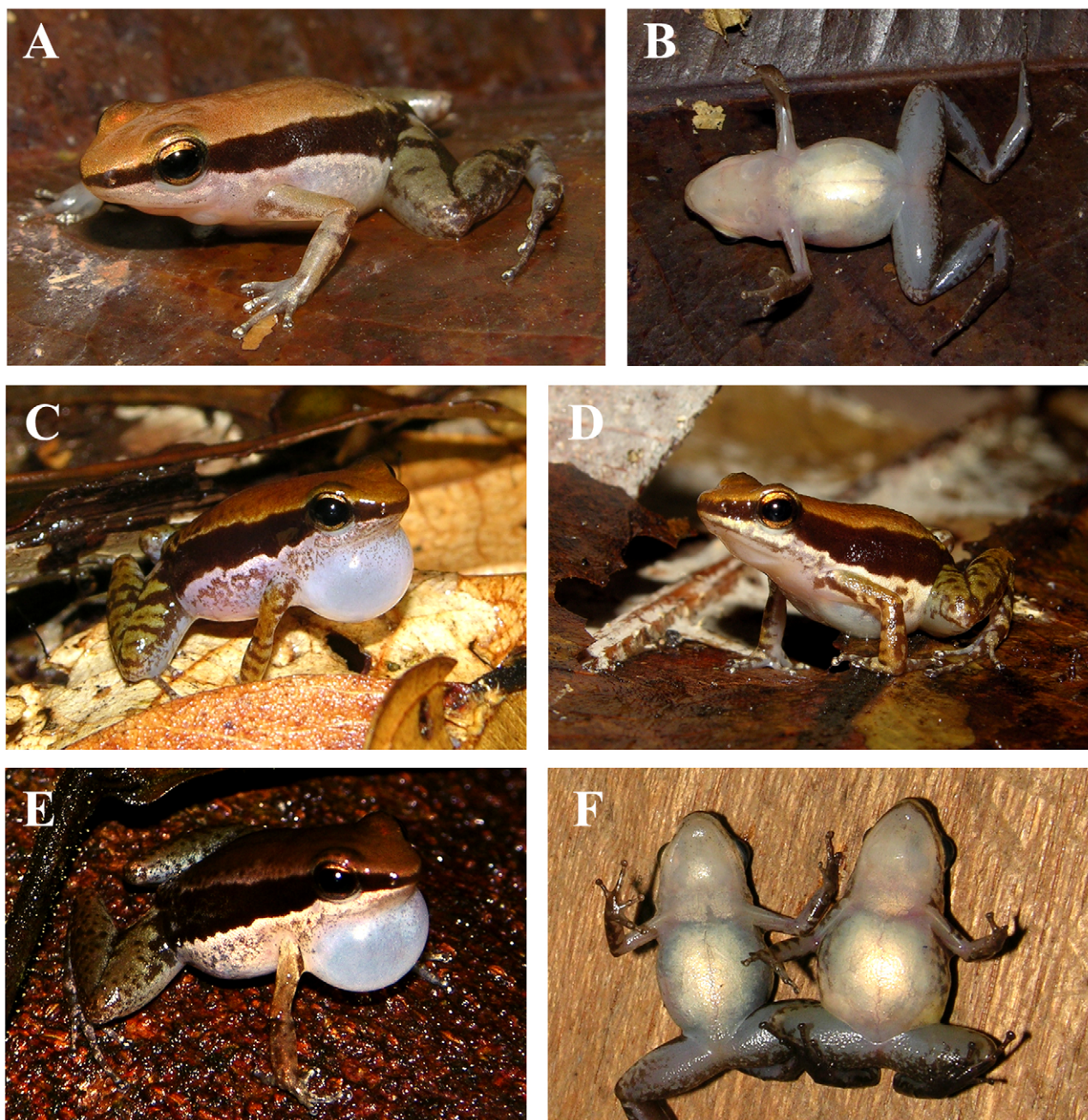
FIGURE 2. Color in life of *Allobates grillisimilis* (A) Dorsolateral and (B) ventral views of holotype (INPA-H 30779), a male collected in Borba, on the right bank of the lower Madeira River, in January 2008. (C) Lateral view of a calling male from type locality (note white vocal sac and multiple dark transverse bars on thighs and shanks). (D) Lateral view of a female photographed at the same locality. (E) Calling male photographed in Nova Olinda do Norte, Amazonas, Brazil. (F) Ventral views of male (left) and female (right) *Allobates grillisimilis*, from the type locality (note the lack of color dimorphism on ventral surfaces of body). Photos by A.P. Lima (A–D, F) and P.I. Simões (E).

Diagnosis. The new species is characterized by: (1) small SVL, adult males 13.9 ± 0.8 mm (range 12.8–15.9 mm), adult females 14.4 ± 0.8 mm (range 12.8–16.0 mm); (2) skin texture of dorsum smooth in most specimens, sometimes granular posteriorly; (3) paired dorsal digital scutes present; (4) median lingual process absent; (5) tympanum inconspicuous, tympanic annulus absent; (6) vocal sac distinct, subgular; (7) maxillary teeth present; (8) distal tubercle absent on Finger IV; (9) tip of finger IV not reaching distal subarticular tubercle of finger III; (10) Finger II about 9% smaller than Finger I; (11) finger discs moderately expanded, middle section of third phalange of Finger III about 35% of finger disc width; (12) lateral fringes absent on fingers; (13) metacarpal ridge absent; (14) Finger III not swollen in males, middle section of the third phalange not measurably wider in males than in females; overall morphology of Finger III similar between males and females; (15) carpal pad absent; (16) thenar tubercle visible, clearly evident on hand profile, but not protuberant; (17) black arm gland absent; (18) tarsal keel present, tubercle-like, strongly curved; (19) disc of Toe IV weakly expanded (20) basal webbing present only between toes III and IV; (21) metatarsal fold absent; (22) fringes absent on toes; (23) external coloration: pattern is cryptic, mostly in shades of brown (Fig. 2); dorsum uniformly tan brown, characterized by evenly distributed reddish-brown dots when seen under stereomicroscope; no distinct larger marks on dorsum; dorsal surfaces of thighs and arms khaki in life, light brown when preserved, with one or more dark brown transverse bars; transverse bars sometimes diffuse; light dorsolateral stripe present or absent; when present, variable in width among individuals; dark brown lateral stripe surrounding the whole body, reaching leg-body insertion; oblique lateral stripe absent; pale ventrolateral stripe present as a diffuse line extending from behind eyes to groin in preserved individuals; small, light-brown irregular blotches or marbling present ventrolaterally from snout to groin; pale paracloacal marks present; (24) throat and abdomen of same color, with no transverse band on chest; (25) dark throat collar absent; (26) throat white to translucent, with a few melanophores only on chin; (27) no sexual dimorphism in ventral coloration, with gular, chest and abdominal regions immaculate in males and females, uniformly white to translucent; (28) iris metallic gold with tiny black flecks and a pupil ring; (29) intestine unpigmented; (30) adult testis unpigmented; (31) mature oocytes pigmented; (32) oral discs of tadpoles emarginate, not umbelliform in shape; (33) papillae on posterior labium of tadpoles pyramidal to very elongate (34) eggs laid on transparent jelly nests, on dead leaves on the forest floor; (35) diurnal habits, males calling during daytime; (36) advertisement calls characterized by trills of 3–15 short notes, repeated between silent intervals.

The new species is unambiguously assigned to the genus *Allobates* by the combination of characters states 4, 10, 20, 23, 25, 30, 32, and 35.

Comparisons with other species. *Allobates grillisimilis* is only known from forests not subject to long-term seasonal flooding (*terra-firme*) in the northwestern Madeira-Tapajós interfluve, in a region limited by the Madeira, Aripuanã and Amazon rivers (Fig. 1). Although surveys were undertaken around this region by the authors and other research groups, the species was not found anywhere else, being probably restricted to this relatively central area of Brazilian Amazonia (see details in the "Distribution" section). For this reason, comparisons with other *Allobates* were limited to species occurring in Brazil, and to three additional species distributed in the Guiana Shield (*Allobates granti*, *Allobates spumaponens*) and Peruvian Amazon (*Allobates trilineatus*) which are morphologically similar to the new species.

Call structure and acoustic parameters set the new species apart from all species of *Allobates* with known advertisement calls, being characterized by the emission of short note trills with peak frequency roughly between 6.0–6.5 kHz, split by irregular silent intervals.

Allobates grillisimilis differs from *Allobates femoralis* (Boulenger 1883), *A. hodli* Simões, Lima & Farias 2010, and *A. myersi* (Pyburn 1981) by the absence of red or yellow flash marks on dorsal surface of thighs, and by the absence of black and white marbling on abdomen.

The new species is readily distinguished from *Allobates brunneus* (Cope 1887), *A. gasconi* (Morales 2000 "2002"), *A. crombiei* (Morales 2000 "2002"), and *A. paleovarzensis* Lima, Caldwell, Biavati & Montanarin 2010 by the absence of a distinct dark, diamond-shaped or hourglass pattern on dorsum, or dark brown markings on the head (Fig. 2). *Allobates grillisimilis* differs from *A. olfersioides* (Lutz 1981) and *A. goianus* (Bokermann 1975) in lacking a cross-like pattern on dorsum. *Allobates grillisimilis* is distinguished from *A. nidicola* (Caldwell & Lima 2003), *A. masniger* (Morales 2000 "2002") and *A. vanzolinius* (Morales 2000 "2002") by its smaller size (maximum SVL < 16.0 mm, males and females pooled) and unpigmented throat and belly (adult *A. nidicola*, *A. masniger* and *A. vanzolinius* with minimum SVL > 20.0 mm, and dark-gray to black throat and belly). The new species differs from *A. fuscellus* (Morales 2000 "2002")*, A. marchesianus* (Melin 1941), and *A. trilineatus*

(Boulenger 1883) in having unpigmented throat and belly, and males with Finger III not swollen (throat and belly gray, and a swollen Finger III in males of *A. fuscellus*, *A. marchesianus* and *A. trilineatus*).

Preserved specimens of *Allobates grillisimilis* are most easily confounded with *A. caeruleodactylus* (Lima & Caldwell 2001), *A. conspicuus* (Morales, 2000 "2002"), *A. granti* (Kok *et al.* 2006), *A. spumaponens* Kok & Ernst 2007, *A. subfolionidificans* (Lima, Sanchez & Souza 2007), and *A. sumtuosus* (Morales 2000 "2002"), and therefore more detailed comparisons between them and the new species is warranted.

Males of *Allobates caeruleodactylus* have sky-blue fingers in life, uniformly dark-gray in preservative (fingers light brown with pale scutes in *Allobates grillisimilis*). Color of throat and belly of female *A. granti* and *A. spumaponens* are yellowish in life (uniformly white to translucent in *Allobates grillisimilis*). Finger I is much longer than Finger II in *A. conspicuus*, *A. sumtuosus* and *A. spumaponens* (Finger I almost the same length of Finger II in *Allobates grillisimilis*). Dorsal surface of legs and arms without distinct dark brown transverse bars in *A. caeruleodactylus*, *A. spumaponens* and *A. sumtuosus* (legs and arms with a variable number of transverse bars in *Allobates grillisimilis*). Among these species, advertisement calls consist of a single note emitted in a continuous (in *A. caeruleodactylus* and *A. subfolionidificans*) or interrupted series (*A. spumaponens*), or by two notes emitted in a continuous series (*A. granti*). Advertisement call of *Allobates grillisimilis* consists of a trill of 3–15 short notes (mode = 4–5 notes, depending on sampling locality), emitted between silent intervals. Tadpoles of *A. granti*, *A. spumaponens*, and *A. subfolionidificans* are distinguished from those of *Allobates grillisimilis* by having short to moderately elongate papillae on posterior labium (moderately to very elongate in *Allobates grillisimilis*). Tadpoles of *A. sumtuosus* also have short, round papillae on posterior labium (Simões & Lima 2012). Tadpoles of *A. caeruleodactylus* have P-3 tooth row distinctively shorter than P-2 and P-1 rows (tooth rows with same length in *Allobates grillisimilis*).

Allobates conspicuus differs from *Allobates grillisimilis* by the generally larger size of reproductive males and females (minimum SVL of *A. conspicuus* = 15.4 mm, and maximum SVL of *Allobates grillisimilis* = 16.0 mm, with 85% of analyzed individuals being smaller than 15.0 mm), and by the presence of lateral fringes on toes (fringes absent in *Allobates grillisimilis*). Finger I is also distinctively longer than Finger II in *A. conspicuus*, as indicated in Fig. 12 of Morales (2000 "2002") (Finger I and Finger II have almost the same length in *Allobates grillisimilis*). The call, color in life, and tadpole of *A. conspicuus* are unknown. However, it is unlikely that *A. conspicuus* occurs in locations geographically close to *Allobates grillisimilis*, as the former has not been recorded within at least 1500 km of the known distribution of the new species.

Description of the holotype. Measurements of the holotype are presented in Table 1. Body robust, head slightly wider than long (HL/HW = 0.91), head length corresponding to 0.31 times the snout-to-vent length (Fig. 3A). Eye diameter conspicuously larger than distance from nostril to anterior corner of the eye (EN/EL = 0.66). Nares located posterolaterally to tip of snout, directed anterolaterally, visible in ventral, lateral, and anterior views. Nostrils not visible dorsally. Internarial distance equivalent to 42% of head width. Canthus rostralis convex from tip of snout to nostril, straight from nostril to anterior corner of the eye. Loreal region vertical. Tympanum round, corresponding to approximately 0.4 times the maximum diameter of the eye. Anteroventral margin of tympanum distinct, all other margins indistinct (Fig. 3C). Maxillary teeth present. Tongue roughly triangular, slightly longer than wide, anterior tip attached to mouth floor. Median lingual process absent. Choanae round, positioned anterodorsally to eye bulge. A single vocal sac present, corresponding to most of the area of the medial and posterior subgular region. Vocal sac round when expanded. Lateral vocal slits present at level of maxillary articulation when vocal sac is retracted.

Palmar tubercle drop-shaped, tip projecting towards the base of Finger II. Thenar tubercle weakly developed, oval to elliptic, evident in ventral view of hand, but not protuberant. Maximum diameter of thenar tubercle 75% of maximum diameter of palmar tubercle. Subarticular tubercles of Fingers II, II and IV are round to oval, small, never exceeding the width of phalanges. Subarticular tubercle on Finger I oval, 1.1 times larger than thenar tubercle in maximum diameter. Distal subarticular tubercle absent on Finger IV. Supernumerary tubercles absent. Carpal and metacarpal ridges absent. No fringes or webbing on fingers. Length of Finger II approximately 90% the length of Finger I. Tip of Finger IV does not reach distal subarticular tubercle of Finger III when fingers are pressed against each other. Relative lengths of fingers: IV < II < I < III. Finger III not swollen. Disc of Finger IV moderately expanded, width of disc 1.6 times the width of adjacent phalanx. Discs of Fingers I, II, III and IV moderately to weakly expanded, width of discs corresponding to 1.2, 1.3, 1.7 and 1.6 times the width of adjacent phalanx, respectively (Fig. 4A).

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TABLE 1. Measurements (in mm) of *Allobates grillisimilis* holotype (INPA-H 30779, an adult male) and type series. Males and females present size dimorphism, females being generally slightly larger than males. Significant differences in snout-to-vent length are also observed between sampling localities. Therefore, all measures are presented separately according to sex and sampling locality. Values in type series columns represent mean ± standard deviation (minimum value observed in the series – maximum value observed in the series).

| | Holotype | Borba | | Nova Olinda do Norte | | Maués |
		Males (n = 22)	Females (n = 8)	Males (n = 10)	Females (n = 5)	Males (n = 7)
SVL	14.0	13.9 ± 0.5 (12.8–14.9)	14.6 ± 0.7 (13.8–16.0)	13.3 ± 0.4 (12.9–14.3)	13.9 ± 0.9 (12.8–15.1)	15.1 ± 0.70 (13.8–15.9)
HL	4.3	4.4 ± 0.2 (4.0–4.6)	4.5 ± 0.1 (4.2–4.7)	4.1 ± 0.1 (4.0–4.3)	4.3 ± 0.2 (4.1–4.5)	4.6 ± 0.2 (4.1–4.7)
HW	4.7	4.9 ± 0.1 (4.7–5.1)	5.0 ± 0.1 (4.9–5.2)	4.7 ± 0.2 (4.5–4.9)	4.9 ± 0.2 (4.5–5.0)	4.1 ± 0.3 (3.6–4.6)
SL	2.2	2.1 ± 0.1 (1.7–2.3)	2.3 ± 0.2 (2.0–2.4)	2.1 ± 0.2 (1.7–2.5)	2.2 ± 0.1 (2.0–2.2)	2.5 ± 0.2 (2.2–2.8)
EN	1.4	1.3 ± 0.1 (1.2–1.5)	1.4 ± 0.1 (1.3–1.5)	1.3 ± 0.1 (1.1–1.3)	1.3 ± 0.1 (1.2–1.5)	1.3 ± 0.1 (1.1–1.5)
IN	2.0	2.0 ± 0.1 (1.8–2.2)	2.1 ± 0.1 (2.0–2.3)	2.1 ± 0.1 (1.9–2.4)	2.1 ± 0.1 (2.0–2.2)	1.8 ± 0.1 (1.6–2.0)
EL	2.1	2.2 ± 0.1 (2.0–2.3)	2.2 ± 0.1 (2.1–2.3)	2.1 ± 0.1 (1.9–2.3)	2.2 ± 0.1 (2.0–2.3)	1.8 ± 0.2 (1.6–2.1)
IO	4.6	4.4 ± 0.2 (4.0–4.9)	4.4 ± 0.1 (4.2–4.6)	4.2 ± 0.1 (4.1–4.4)	4.3 ± 0.1 (4.1–4.5)	3.1 ± 0.2 (2.7–3.3)
TYM	0.9	0.9 ± 0.1 (0.7–1.1)	0.9 ± 0.2 (0.7–1.1)	0.9 ± 0.1 (0.7–1.0)	0.9 ± 0.1 (0.7–0.9)	0.8 ± 0.1 (0.7–0.9)
FAL	3.3	3.2 ± 0.1 (3.0–3.5)	3.3 ± 0.1 (3.0–3.4)	3.0 ± 0.1 (3.0–3.2)	3.1 ± 0.1 (3.0–3.3)	3.4 ± 0.2 (3.0–3.7)
UAL	4.4	4.0 ± 0.2 (3.5–4.5)	4.2 ± 0.2 (4.0–4.5)	4.0 ± 0.1 (4.0–4.2)	4.0 ± 0.0 (4.0–4.0)	3.9 ± 0.2 (3.6–4.2)
HANDI	2.9	2.9 ± 0.2 (2.5–3.5)	3.0 ± 0.2 (2.6–3.5)	2.9 ± 0.3 (2.6–3.5)	2.8 ± 0.2 (2.6–3.0)	2.8 ± 0.2 (2.5–3.0)
HAND II	2.6	2.6 ± 0.1 (2.3–2.9)	2.6 ± 0.2 (2.5–2.9)	2.6 ± 0.1 (2.5–2.7)	2.6 ± 0.1 (2.4–2.7)	2.5 ± 0.2 (2.3–2.8)
HAND III	3.7	3.7 ± 0.2 (3.2–4.0)	3.7 ± 0.2 (3.5–4.2)	3.6 ± 0.1 (3.5–3.9)	3.6 ± 0.1 (3.5–3.8)	3.5 ± 0.2 (3.1–3.8)
HAND IV	2.5	2.5 ± 0.1 (2.3–2.7)	2.5 ± 0.2 (2.2–2.9)	2.5 ± 0.1 (2.5–2.7)	2.5 ± 0.05 (2.5–2.6)	2.5 ± 0.1 (2.4–2.7)
WFD	0.5	0.5 ± 0.1 (0.3–0.5)	0.6 ± 0.1 (0.5–0.6)	0.4 ± 0.2 (0.4–0.4)	0.5 ± 0.2 (0.4–0.9)	0.4 ± 0.1 (0.3–0.6)
WPF	0.3	0.3 ± 0.05 (0.2–0.4)	0.3 ± 0.05 (0.2–0.4)	0.3 ± 0.01 (0.3–0.3)	0.3 ± 0.01 (0.3–0.3)	0.4 ± 0.1 (0.3–0.5)
DPT	0.4	0.5 ± 0.1 (0.3–0.6)	0.5 ± 0.05 (0.4–0.5)	0.5 ± 0.05 (0.4–0.6)	0.5 ± 0.1 (0.4–0.6)	0.6 ± 0.1 (0.5–0.7)
LL	7.2	7.1 ± 0.3 (6.5–7.7)	7.2 ± 0.3 (6.6–7.7)	6.8 ± 0.2 (6.5–7.0)	6.7 ± 0.2 (6.4–6.9)	7.0 ± 0.3 (6.5–7.5)
TL	7.8	7.4 ± 0.3 (7.0–8.0)	7.6 ± 0.3 (7.3–8.0)	7.2 ± 0.2 (6.9–7.5)	7.3 ± 0.2 (7.1–7.6)	7.4 ± 0.3 (7.0–7.7)
FL	7.0	6.9 ± 0.4 (6.3–7.5)	7.0 ± 0.4 (6.5–7.5)	6.6 ± 0.1 (6.5–6.8)	6.5 ± 0.3 (6.0–6.9)	6.3 ± 0.2 (6.0–6.7)
WTD	0.5	0.6 ± 0.05 (0.5–0.6)	0.6 ± 0.1 (0.4–0.7)	0.5 ± 0.01 (0.5–0.5)	0.5 ± 0.05 (0.5–0.6)	0.5 ± 0.1 (0.4–0.6)
WTT	0.3	0.3 ± 0.05 (0.2–0.4)	0.3 ± 0.1 (0.2–0.4)	0.3 ± 0.1 (0.2–0.4)	0.3 ± 0.05 (0.2–0.3)	0.4 ± 0.1 (0.4–0.5)
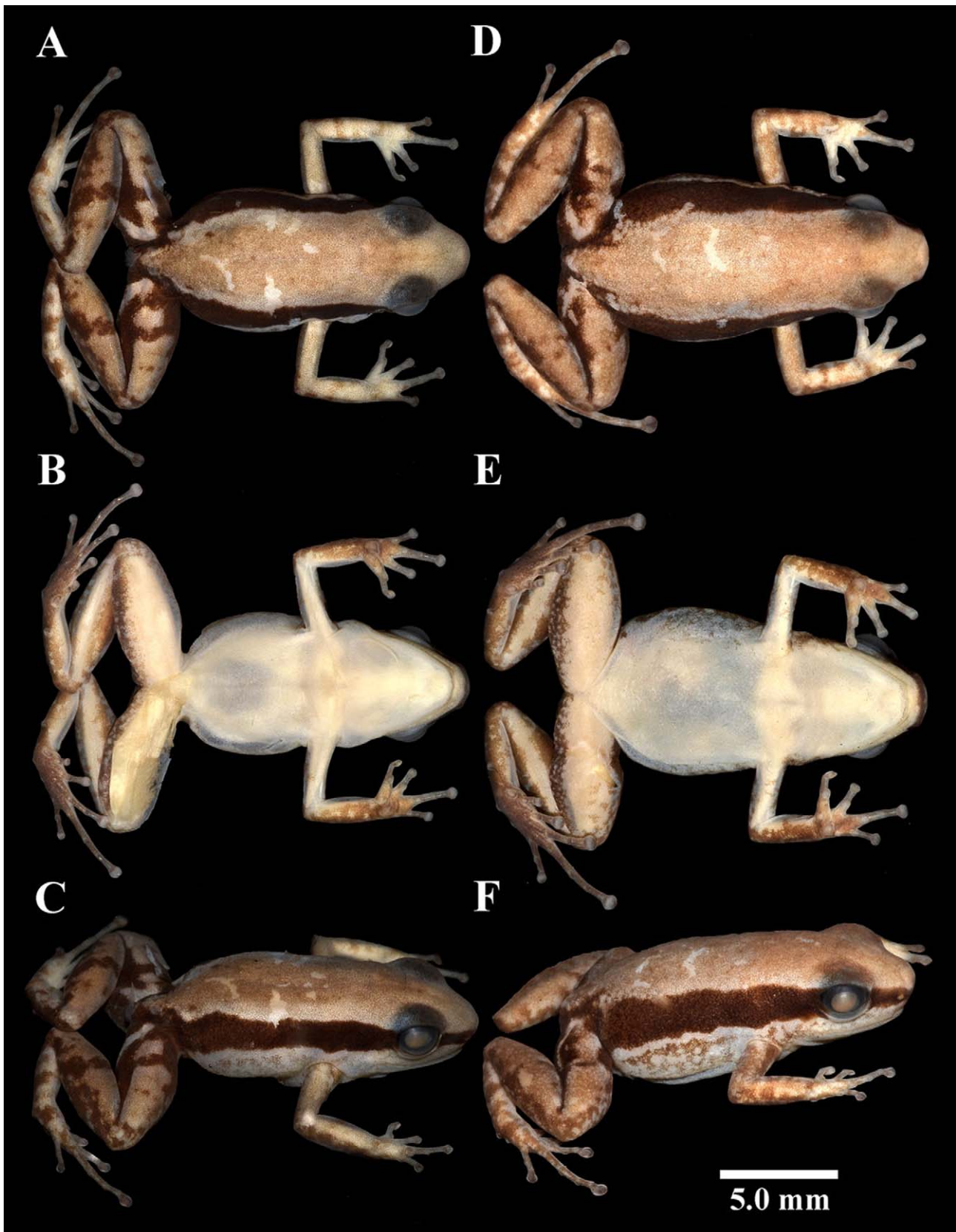
FIGURE 3. *Allobates grillisimilis* from Borba, Amazonas, Brazil. (A) Dorsal, (B) ventral, and (C) lateral views of *Allobates grillisimilis* holotype (INPA-H 30779, male). (D) Dorsal, (E) ventral, and (F) lateral views of *Allobates* sp nov. allotype (INPA-H 30780, female). Both individuals have incisions on ventral surface of thighs, made during removal of muscle tissue samples. Scratches on dorsum of both individuals were caused by manipulation.
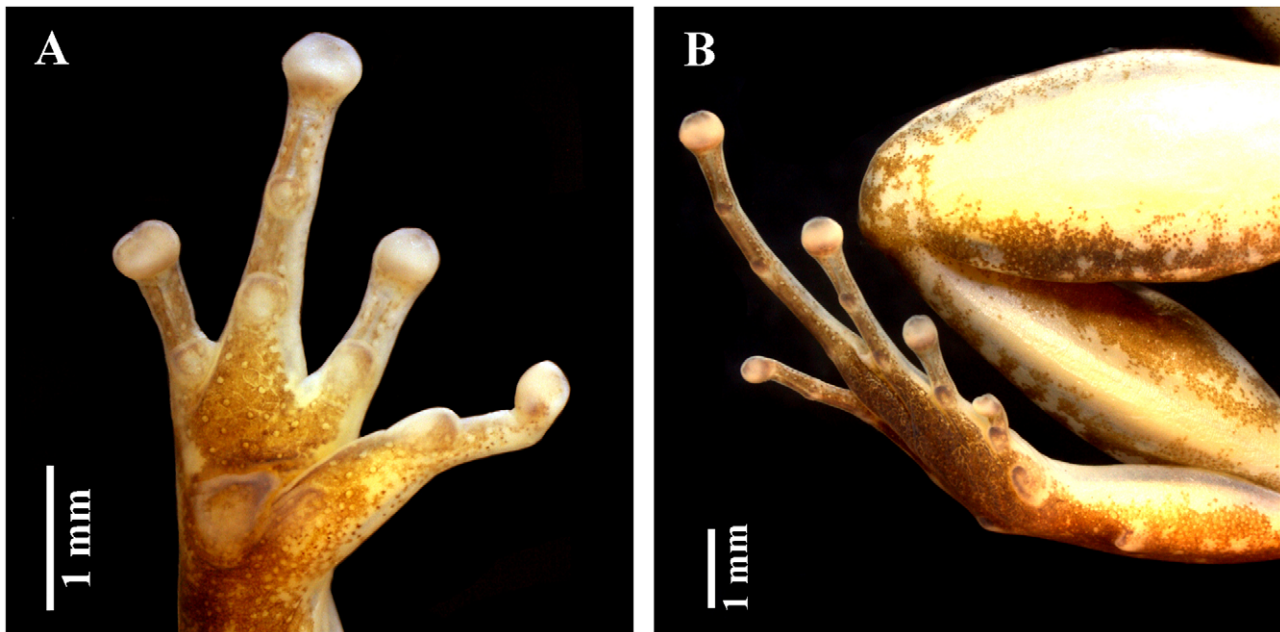
FIGURE 4. *Allobates grillisimilis* from Borba, Amazonas, Brazil (INPA-H 30779, holotype, male) (A) Right hand and (B) Right foot.

Tibia length equivalent to 0.6 times the snout-to-vent length. Tarsal keel present, tubercle-like, strongly curved at its proximal end, flattening and straightening towards metatarsal tubercle. Metatarsal fold absent. A short, weak dermal thickening is observed on the outer edge of the sole, but it does not extend as a continuous ridge from postaxial edge of the base of Toe V to outer metatarsal tubercle. Preaxial edge of tarsus smooth, with no fringe. Basal webbing present only between Toes III and IV. Relative lengths of toes: I < II < V < III < IV. Discs of Toes I, II, III, IV and V moderately expanded, width of discs corresponding to 1.6, 1.7, 1.9, 1.7 and 1.4 times the width of adjacent phalanx, respectively (Fig. 4B).

Skin generally smooth on dorsum. Small and unpigmented granules in a small number, barely evident on dorsal surface of urostyle region and shanks. Skin smooth ventrally and laterally (Fig. 3A,B,C). Dermal flap above cloaca absent.

Variation in type series. Males from Borba, Nova Olinda do Norte, and Maués differed significantly in snout-to-vent length (ANOVA, $F_{2,36}$ = 24.71, P < 0.01), with specimens from Maués being slightly larger. Therefore, variation in individual morphometric measurements is presented separately according to sampling locality (Table 1).

In localities where males and females were collected (Borba and Nova Olinda do Norte), females had generally longer snout-to-vent length when compared to males (ANOVA, $F_{1,43}$ = 4.65, P < 0.01). Significant differences in body proportions according to sex were found in head measurements relative to body size, HL/SVL and HW/SVL ratios being usually larger in males (HL/SVL ANOVA, $F_{1,43}$ = 12.69, P = 0.03; HW/SVL ANOVA, $F_{1,43}$ = 7.42 , P < 0.01), indicating that males have relatively more robust heads relative to overall body size. Males also have proportionally longer tibiae (TL/SVL ANOVA, $F_{1,43}$ = 9.18 , P < 0.01).

Head length 88% of head width in average, considering pooled samples from Borba and Nova Olinda do Norte. Head longer than wide only in males from Maués, which have an average HL/HW ratio of 1.08.

Skin texture of dorsum is smooth to weakly granular posteriorly in 45 individuals. Twelve individuals have slightly protuberant round granules, with dark brown pigmented tips in the posterior region of dorsum.

Color in life. Males and females do not present fixed dimorphism in relation to color or color pattern in life (Fig. 2C, D, E, F). Dorsal surface of body is solid tan brown. Lateral surface of body is solid dark brown. Small spots of darker brown, same color as lateral surface of body, can be present posteriorly on dorsum, on top of larger granules. A pale dorsolateral stripe with diffuse inner edge is present in most individuals, but is variable in width and melanophore density, making it more or less conspicuous among individuals. A white, iridescent ventrolateral

stripe is present along the lower margin of the dark brown flanks, from tip of snout to the groin, wider and more conspicuous from behind the eye to groin (Fig 2A, C, D, E). Ventrolateral stripe is often diffuse or interrupted. Pale iridescent marbling, same color as of ventrolateral stripe, is present below ventrolateral stripe, towards the abdomen, over a light brown or gray background. Throat, gular and pectoral regions and abdomen are uniformly white to translucent (Fig. 2B, F). In males, vocal sac is white to translucent when inflated (Fig. 2C, E). A few brown melanophores are often present, scattered on chin and anterior margin of vocal sac. Iris metallic gold with tiny black flecks and a pupil ring.

Dorsal surface of upper and forearm predominantly light brown to khaki, white only around arm-body insertion. A few dark brown blotches may be present laterally on upper arm. A variable number of dark brown blotches or incomplete transverse bars are present on dorsal and lateral surfaces of forearm. Upper arm white to translucent, same color as chest in ventral view. Forearm, carpal and metacarpal regions are dark brown in ventral view, with a few light blotches. Fingers uniformly dark brown in ventral view, light brown with dark brown flecks in dorsal view. Paired scutes on finger discs are iridescent white.

The area immediately adjacent to vent is solid dark brown, flanked by a light cream paraclocal mark. Distal edge of paracloacal mark is limited by a solid or interrupted dark brown transverse bar, evident in dorsal view and extending along the inner lateral surface of thigh. Dorsal surface of thigh is light brown to khaki, with a variable number of dark brown transverse bars or irregular blotches (transverse bars absent or interrupted in some individuals). Dorsal surface of shank same color as that of thigh, also with a variable number of dark brown transverse bars or blotches. Ventral surface of thigh and shank generally white to translucent, same color as abdomen, with dark brown marbling along inner and outer edges. Tarsal region is light brown with dark brown flecks in dorsal view, uniformly dark brown in ventral view. Toes with dark brown and light brown patterning. Paired scutes on toe discs are iridescent white.

Color of the holotype in preservative. Dorsal surface of body is uniformly brown, darker only above the orbits (Fig 3A). Lateral surface of body is solid dark brown. A pale dorsolateral stripe is present, characterized by a narrow line (~ 0.3 mm) adjacent to the dark lateral surface of body where the density of melanophores is reduced, gradually increasing towards the center of the dorsum (*i.e.* the inner edge is diffuse). A narrow bright white ventrolateral stripe is present from tip of snout to groin, wider and more conspicuous from behind the eye to groin. Small patches the same color of ventrolateral line form a marbling pattern on ventrolateral region, towards the abdomen, on darker, light brown background (Fig. 3C). Throat, gular region, pectoral region, abdomen and ventral surface of thighs are uniformly white to translucent (Fig. 3B). A few melanophores are present only on chin. Tongue is cream-colored.

Arms pale brown in dorsal view, melanophores more concentrated in some areas of the forearm, forming faint blotches or banding patterns. Paler areas are visible on the axilla and metacarpal region, especially on Fingers I and II. Tip of fingers light brown, finger discs with pale scutes. Upper arm pale to translucent in ventral view, continuous with color pattern of chest. Forearm, carpal and metarcarpal regions are tan brown in ventral view, with a few irregular pale blotches. Surface of lateral edge of forearm, carpal and metacarpal regions same color as their ventral surface, extending laterally from elbow to ventral surface of palm and fingers.

The area immediately around vent is solid dark brown, flanked by an unpigmented transverse band, corresponding to the pale paracloacal mark. Distal edge of paracloacal mark is margined by a solid dark brown transverse bar (continuous on right thigh, interrupted on the left), extending along the whole inner lateral surface of thigh. Thigh is brown in dorsal view, with a single solid dark brown transverse bar and a few smaller dark brown blotches appearing on a light brown background. Dorsal surface of shank same color as thigh, with a single dark brown transverse bar. Outer dorsolateral surface of shank with irregular dark brown blotches and patches. Outer dorsal surface of tarsal region is lighter than overall pattern of legs. Inner dorsal surface of tarsal region with dark brown blotches. Toes are generally light brown, with irregularly distributed melanophores. Ventral surface of thigh and shank predominantly white to translucent, same color as abdomen. Dark brown marbling appears along inner and outer edges and around the knee. Ventral surface of tarsal and metatarsal regions is uniformly dark brown. Toes are dark brown in ventral view, with uniformly pale discs.

Color variation in the type series. Allotype same color as holotype except for a pale paracloacal mark flanked distally by a solid dark transverse bar which is interrupted medially (Fig. 3D). The allotype also lacks solid dark transverse bars on dorsal surface of thigh and shank. Only a few, weakly marked dark brown blotches are present on dorsal surface of these regions.

The presence of a pale dorsolateral line is highly variable among specimens in the type series (Fig. 5). It is present in eight, absent in 18, and barely distinguished in four specimens from Borba; present in 14 and absent in one individual from Nova Olinda do Norte; and present in four out of seven specimens from Maués.

Dark transverse bars on dorsal surface of thighs are also highly variable in number and width among individuals (Fig. 5). Five of the 52 individuals examined (including the allotype) completely lack transverse bars on dorsal surface of thighs. One, and up to five dark transverse bars may be present on thighs of the remaining individuals. Transverse bars vary from solid, dark brown stripes, to medially interrupted stripes, or diffuse brown blotches. The number and pattern of dark brown transverse bars are also variable on dorsal surfaces of shanks and forearms.
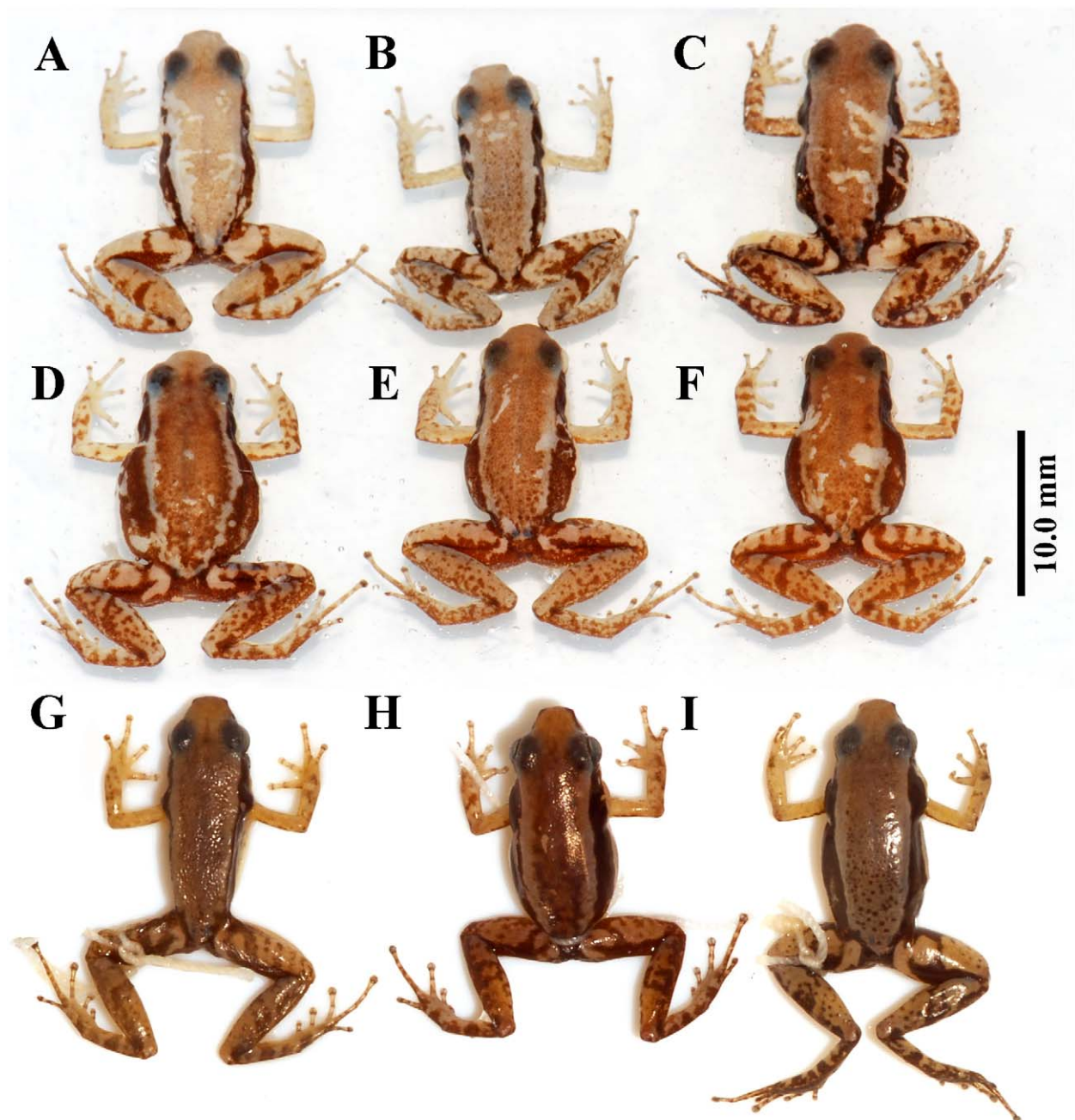
FIGURE 5. Variation in color pattern of dorsal surface of body and legs between individuals from the type-series of *Allobates grillisimilis*. Specimens in upper line from type locality in Borba, Amazonas, Brazil: (A) INPA-H 30784, male; (B) APL30787, male; (C) INPA-H 30798, male. Specimens in middle line from Nova Olinda do Norte, Amazonas, Brazil: (D) INPA-H 30816, female; (E) INPA-H30817, male; (F) INPA-H 30823, male. Specimens in lower line from Maués, Amazonas, Brazil, all males: (G) MPEG 28536; (H) MPEG 28545; (I) MPEG 28535.

FIGURE 6. Tadpole of *Allobates grillisimilis* from Borba, Amazonas, Brazil, collected from an egg clutch in January 2008. From top to bottom: dorsal, ventral, and lateral views of preserved tadpole in developmental stage 27 (INPA-H 30827), used in the detailed description (see text).

Five males and five females were dissected for close examination of color of internal organs and oocytes. The large intestine is not pigmented. Testes are not pigmented. Mature oocytes are pigmented, with light brown pigments concentrated in a single pole.

Tadpole description. Tadpole measurements were obtained from 91 tadpoles at different developmental stages (Table 2), maintained in lots with the same collection numbers (INPA-H 30828: Stage 25; INPA-H 30827: Stages 26–28; INPA-H 30824, 30825: Stages 35–37; INPA-H 30826: Stages 38–40). One tadpole at stage 27 was used for a detailed description (Fig. 6, Fig. 7A,B). Tadpoles collected from the backs of males and preserved immediately were all at developmental stage 25, with conspicuous and fully developed spiracle and oral disc.

Body depressed dorsoventrally, body width (4.5 mm) larger than body depth (2.3 mm), 6.5 mm in length. Snout is nearly round in dorsal view, flattened anteriorly in dorsal view, and anterodorsally in lateral view, from the level of nostrils to the tip of snout. Nares are small, directed dorsolaterally, 0.7 mm anterior to the eye, and 0.4 mm posterior to tip of snout. Nostrils narrowly spaced, distance between nostrils (1.0 mm) only slightly shorter than distance between orbits (1.1 mm). Eyes dorsal, directed dorsolaterally, 0.6 mm in maximum length, and located 1.2 mm posterior to tip of snout. Spiracle single, sinistral, forming a free short tube opening posterodorsally, about level of body axis in lateral view, 4.1 mm posterior to tip of snout. Vent tube medial, free, 1.0 mm in length, opening dextrally.

Musculature of tail is deeper (1.2 mm) along the first third of tail length and wider at body-tail insertion (1.3 mm). Ventral fin originates at body-tail insertion. Dorsal fin originates slightly anterior (0.3 mm) to body-tail insertion, and reaches maximum height 12.0 mm from tip of snout, approximately at middle tail length. At maximum depth of tail, depth of musculature is 1.0 mm, dorsal fin 1.0 mm and ventral fin 0.5 mm.

TABLE 2. Measurements (in mm) of *Allobates grillisimilis* tadpoles from Borba, Amazonas, Brazil, in January 2008. Tadpoles were raised in laboratory until they reached later developmental stages. Tadpole classification in different developmental stages followed Gosner (1960): Stage 25 = no hind limb buds; Stages 26–28 = development of hind limb buds (but no toe differentiation); Stages 35–37 = advanced toe differentiation with increasing separation between toes, but no metatarsal tubercle; Stages 38–40 = development of metatarsal tubercle, followed by development of remaining foot tubercles. *n* = number of tadpoles measured. *Clutches* = number of different clutches from which tadpoles proceeded.

	Stage 25	Stages 26-28	Stages 35-37	Stages 38-40
n	20	17	25	29
Clutches	2	2	5	5
TL	10.50 ± 2.52 (7.50–15.33)	19.14 ± 0.88 (17.50–20.67)	20.46 ± 0.38 (20.18–21.33)	20.43 ± 0.12– (20.17–20.60)
BL	3.59 ± 0.85 (2.60–5.20)	6.82 ± 0.36 (6.20–7.60)	8.28 ± 0.30 (7.50–8.90)	8.37 ± 0.31 (7.40–8.90)
TAL	6.58 ± 1.58 (4.75–9.75)	11.98 ± 0.71 (10.63–13.13)	13.88 ± 0.83 (12.50–15.63)	14.95 ± 0.88 (12.63–16.13)
BW	2.28 ± 0.58 (1.55–3.35)	4.58 ± 0.39 (3.95–5.35)	5.97 ± 0.21 (5.45–6.35)	6.10 ± 0.17 (5.60–6.35)
BH	1.07 ± 0.24 (0.73–1.60)	1.96 ± 0.22 (1.67–2.33)	2.37 ± 0.24 (1.67–2.67)	2.40 ± 0.26 (2.00–3.27)
HWLE	2.53 ± 0.56 (2.00–3.60)	4.44 ± 0.23 (4.10–4.80)	5.24 ± 0.30 (4.70–6.00)	5.43 ± 0.27 (5.00–6.00)
TMW	0.86 ± 0.10 (0.67–1.00)	1.34 ± 0.09 (1.23–1.57)	1.78 ± 0.18 (1.57–2.30)	2.13 ± 0.21 (1.83–2.53)
MTH	1.57 ± 0.32 (1.20–2.13)	2.69 ± 0.12 (2.53–2.93)	3.21 ± 0.23 (2.73–3.63)	3.37 ± 0.20 (2.83–3.70)
TMH	0.95 ± 0.11 (0.83–1.23)	1.36 ± 0.10 (1.26–1.56)	1.81 ± 0.15 (1.57–2.13)	2.02 ± 0.14 (1.70–2.30)
IOD	0.69 ± 0.15 (0.53–0.97)	1.14 ± 0.07 (1.00–1.26)	1.27 ± 0.08 (1.13–1.40)	1.33 ± 0.07 (1.17–1.50)
IND	0.61 ± 0.13 (0.40–0.87)	1.03 ± 0.04 (0.96–1.06)	1.20 ± 0.09 (1.00–1.37)	1.26 ± 0.08 (1.10–1.40)
END	0.35 ± 0.08 (0.27–0.53)	0.67 ± 0.08 (0.60–0.97)	0.75 ± 0.06 (0.67–0.83)	0.75 ± 0.09 (0.67–1.03)
NSD	0.39 ± 0.08 (0.33–0.53)	0.70 ± 0.06 (0.67–0.83)	0.82 ± 0.07 (0.67–0.97)	0.87 ± 0.08 (0.67–0.97)
ED	0.56 ± 0.05 (0.47–0.63)	0.73 ± 0.04 (0.67–0.77)	0.99 ± 0.09 (0.87–1.20)	1.18 ± 0.09 (1.00–1.30)
VTL	0.31 ± 0.21 (0.00–0.65)	0.84 ± 0.17 (0.50–1.05)	1.29 ± 0.09 (1.20–1.50)	1.23 ± 0.21 (1.00–2.00)
STL	0.57 ± 0.09 (0.50–0.75)	1.00 ± 0.17 (0.70–1.25)	1.22 ± 0.13 (1.00–1.45)	1.25 ± 0.17 (1.00–1.75)

TABLE 3. Advertisement call measurements of *Allobates grillisimilis* holotype (INPA-H 30779) and males recorded at three distinct localities in the northern Madeira-Tapajós interfluve, in central Brazilian Amazonia. Values in columns represent mean ± one standard deviation (minimum value observed in the series – maximum value observed in the series). Air temperature at time of recording of the holotype was 25°C. Air temperature at time of recording ranged from 24.9–27.9°C in Borba, from 24.2–24.9°C in Nova Olinda do Norte, and from 25.0–26.5°C in Maués.

|	Holotype	Borba	Nova Olinda do Norte	Maués
N° Individuals	1	10	6	4
Calls analyzed	8	80	48	32
N° Notes/call (Mode)	5	5	4	5
N° Notes/call (Range)	4–7	3–10	3–15	3–6
SIC (s)	1.693 ± 0.466 (1.125–2.485)	1.525 ± 0.312 (0.920–1.999)	0.912 ± 0.229 (0.695–1.347)	1.192 ± 0.248 (0.899–1.403)
SIF (s)	0.010 ± 0.001 (0.010–0.012)	0.014 ± 0.002 (0.01–0.02)	0.020 ± 0.002 (0.017–0.023)	0.020 ± 0.003 (0.015–0.002)
SIM (s)	0.016 ± 0.001 (0.015–0.019)	0.017 ± 0.002 (0.013–0.019)	0.023 ± 0.003 (0.020–0.027)	0.026 ± 0.012 (0.018–0.043)
DC (s)	0.200 ± 0.054 (0.137–0.267)	0.178 ± 0.035 (0.122–0.244)	0.227 ± 0.053 (0.170–0.305)	0.149 ± 0.011 (0.141–0.165)
DFN (s)	0.030 ± 0.001 (0.029–0.034)	0.022 ± 0.006 (0.016–0.030)	0.015 ± 0.003 (0.012–0.020)	0.016 ± 0.003 (0.013–0.021)
DCN (s)	0.023 ± 0.002 (0.021–0.026)	0.019 ± 0.004 (0.012–0.024)	0.0167 ± 0.002 (0.0128–0.0196)	0.017 ± 0.002 (0.015–0.019)
DLN (s)	0.022 ± 0.002 (0.019–0.025)	0.019 ± 0.004 (0.013–0.023)	0.016 ± 0.003 (0.012–0.020)	0.016 ± 0.002 (0.014–0.019)
PFC (Hz)	6497.6 ± 35.9 (6460.0–6546.1)	6394.2 ± 169.4 (6200.2–6651.0)	6219.9 ± 153.9 (6011.7–6363.2)	5964.7 ± 96.3 (5867.8–6061.6)
LFC (Hz)	5715.6 ± 119.5 (5589.0–5874.9)	5690.4 ± 142.8 (5518.8–5913.3)	5609.9 ± 106.5 (5446.1–5738.7)	5282.8 ± 178.3 (5056.6–5437.6)
HFC (Hz)	6989.4 ± 19.4 (6962.0–7016.9)	6906.2 ± 217.4 (6654.8–7414.9)	6631.3 ± 165.5 (6411.7–6797.6)	6425.1 ± 111.8 (6304.7–6528.4)
PFFN (Hz)	6250.0 ± 74.3 (6201.6–6416.9)	6230.2 ± 185.3 (5881.2–6488.2)	6016.3 ± 108.9 (5834.9–6127.9)	5815.3 ± 111.0 (5671.3–5902.8)
LFFN (Hz)	5520.7 ± 60.4 (5424.7–5611.3)	5664.7 ± 158.2 (5494.7–5908.3)	5559.3 ± 102.5 (5405.5–5698.6)	5283.0 ± 161.6 (5085.7–5427.3)
HFFN (Hz)	6978.4 ± 15.5 (6951.0–6994.9)	6774.2 ± 295.9 (6450.3–7430.0)	6374.0 ± 79.6 (6237.6–6449.4)	6178.6 ± 153.4 (5982.3–6318.1)
PFCN (Hz)	6492.2 ± 38.2 (6416.9–6546.1)	6434.9 ± 161.3 (6247.3–6714.3)	6228.2 ± 150.6 (6007.8–6360.3)	6014.5 ± 90.7 (5924.3–6093.9)
LFCN (Hz)	5843.3 ± 63.3 (5710.2–5896.8)	5900.1± 164.4 (5642.2–6108.9)	5781.9 ± 173.2 (5538.5–5951.3)	5507.6 ± 164.2 (5298.1–5698.2)
HFCN (Hz)	6974.3 ± 18.9 (6951.0–7005.9)	6864.3 ± 178.2 (6636.6–7207.7)	6588.8 ± 130.6 (6400.5–6736.4)	6358.9 ± 109.6 (6245.8–6462.2)
PFLN (Hz)	6411.5 ± 106.6 (6244.6–6503.0)	6359.8 ± 146.3 (6153.1–6602.6)	6221.8 ± 149.7 (6011.7–6343.7)	6026.6 ± 97.2 (5929.7–6118.1)
LFLN (Hz)	5861.1 ± 117.5 (5578.4–5940.8)	5848.8 ± 159.9 (5570.9–6100.6)	5788.9 ± 185.7 (5526.7–5989.7)	5564.8 ± 129.9 (5404.2–5720.3)
HFLN (Hz)	7005.9 ± 24.9 (6984–7060.8)	6806.1 ± 215.7 (6487.8–7206.3)	6570.4 ± 138.8 (6404.4–6761.3)	6365.8 ± 108.9 (6270.3–6473.9)
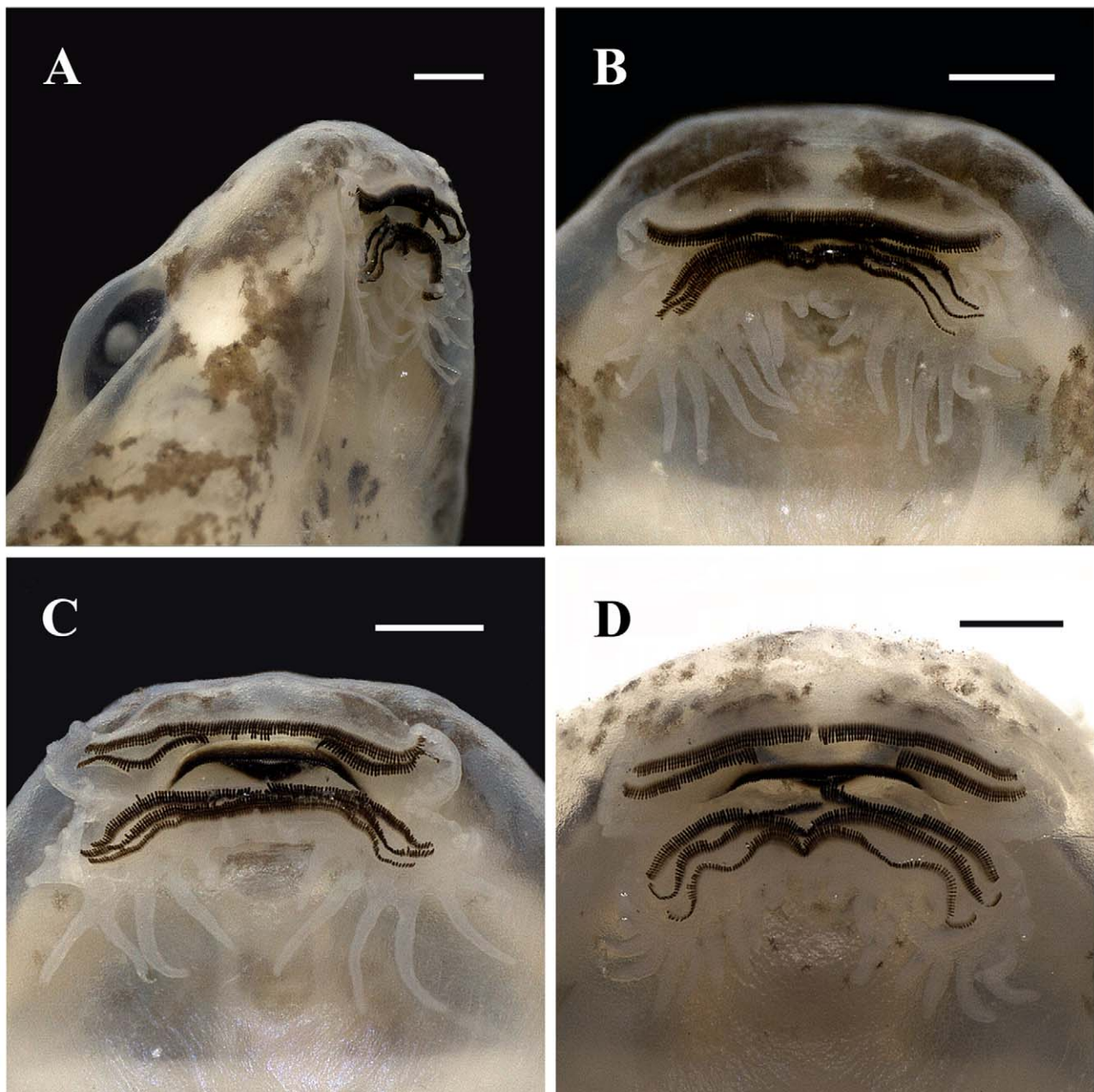
FIGURE 7. Oral discs of *Allobates grillisimilis* tadpoles from Borba, Amazonas, Brazil, collected in January 2008. (A) Oblique and (B) ventral views of oral disc of tadpole at developmental stage 27. (C) Tadpole at stage 38, photographed on dark background, emphasizing distribution and length of papillae. (D) A second tadpole at stage 38, photographed on white background, emphasizing relative length of tooth rows. Scale bars correspond to 0.5 mm.

Oral disc is positioned anteroventrally, emarginate laterally, transversely elliptical, 1.7 mm in transverse width. Anterior labium 1.7 mm in length, continuous with snout, but delimited by a shallow depression. Round to pyramidal marginal papillae absent dorsally on anterior labium (gap 1.2 mm, 70% of total anterior labium length), but present laterally, on its outer margins. Posterior labium free from body wall, 1.6 mm in length, with a single row of marginal papillae. First five papillae adjacent from lateral emargination are pyramidal to moderately elongate. The following eight papillae are very elongate (up to 0.5 mm long). The most central (posterior) three papillae are moderately elongate.

Labial tooth row formula is 2(2)/3(1). Rows A-1 and A-2 with same length (1.2 mm), A-2 with a large medial gap (0.4 mm). Rows P-1, P-2 and P-3 with same length (1.4 mm), P-1 presenting a very narrow medial gap (< 0.1 mm), evidenced by a break between subjacent tooth ridges. Upper jaw sheath flat medially, with lateral flexures,

0.7 mm in length (41 % of oral disc width), < 0.1 mm in width. Cutting edge serrate, with serrations not extending to lateral process of the upper jaw. Lower jaw sheath deeper than upper jaw, arch (or V) shaped, 0.6 mm in length, with serrate cutting edge.

Morphology of oral disc is constant throughout all developmental stages examined. Elongate papillae are evident at least from stage 25 to stage 40. The number of marginal papillae on the posterior labium is slightly variable among individuals (Fig. 7B,C,D): lateral papillae 4–6, elongate latero-posterior papillae 6–9. Moderately elongate central posterior papillae 3–5.

Color in formaldehyde is grayish brown, body darker than tail (Fig. 6). Body tegument is translucent. Brown melanophores are scattered in blotches on dorsum and lateral surfaces, absent on ventral surface (except for small aggregations approximately the level of the eyes). Intestine coils are visible through skin. Tail musculature is light cream. Tail fins are translucent, with scattered brown melanophores forming irregular blotches.

In life, iridescent, nearly golden pigments are visible on dorsal and lateral surfaces of the body. Shades of red and pink appear on medial region of body, as internal organs and blood vessels are visible through translucent skin (Fig. 8).
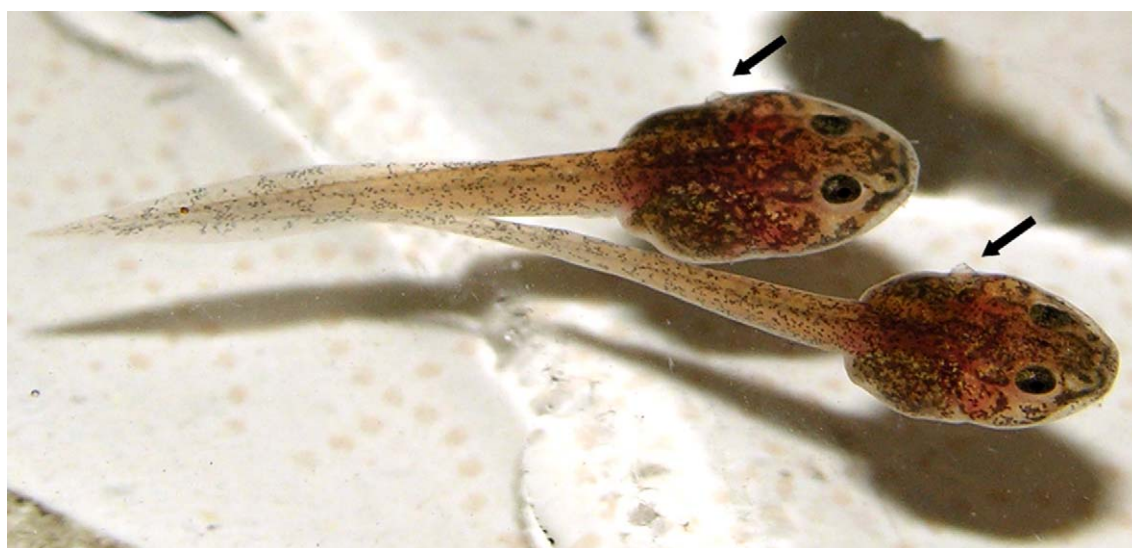

FIGURE 8. Living tadpoles of *Allobates grillisimilis* from Borba, Amazonas, Brazil, showing color in life and position of spiracle (indicated by black arrows).

Call description and variation. The advertisement call of *Allobates grillisimilis* consists of groups of very short tonal notes, highly similar in duration, emitted between short silent intervals (Fig. 9). Call parameters measured from calls of the holotype, and from 20 males recorded at the three sampling sites are presented in Table 3.

The number of notes in each call varied from three to 15 among all samples analyzed. At the type locality, the number of notes in each call ranged from four to seven, resulting in average call duration of 0.178 ± 0.035 s. Average peak frequency of calls considering all notes was 6497.6 ± 35.9 Hz at the type locality. Calls were usually longer (0.227 ± 0.053 s in average) and had overall lower peak frequencies (6219.9 ± 153.9 Hz in average) among individuals sampled in Nova Olinda do Norte. Calls were shorter (0.149 ± 0.011 s in average) and had even lower peak frequencies (5964.7 ± 96.3 Hz) among males recorded in Maués.

Considering all call samples, frequency modulation is slightly similar among first, central, and last pulses. The first pulse of each call generally present higher frequency modulation (average difference between lower and higher frequencies = 998.9 ± 239.7 Hz) than central, and last pulses (average difference between lower and higher frequencies = 905.1 ± 143.2 Hz, and 891.4 ± 178.0 Hz, respectively).

Reproductive behavior. At the type locality, males were found calling from sites slightly elevated from the forest floor, such as tree roots, logs, lianas, old termite nests or leaves laying on the ground (Fig. 10A). Height of calling sites ranged from three to 48 cm (mean 19.6 cm, *N*=18 observations), the first corresponding to a dead leaf on the ground and the latter to the roots of a palm tree.
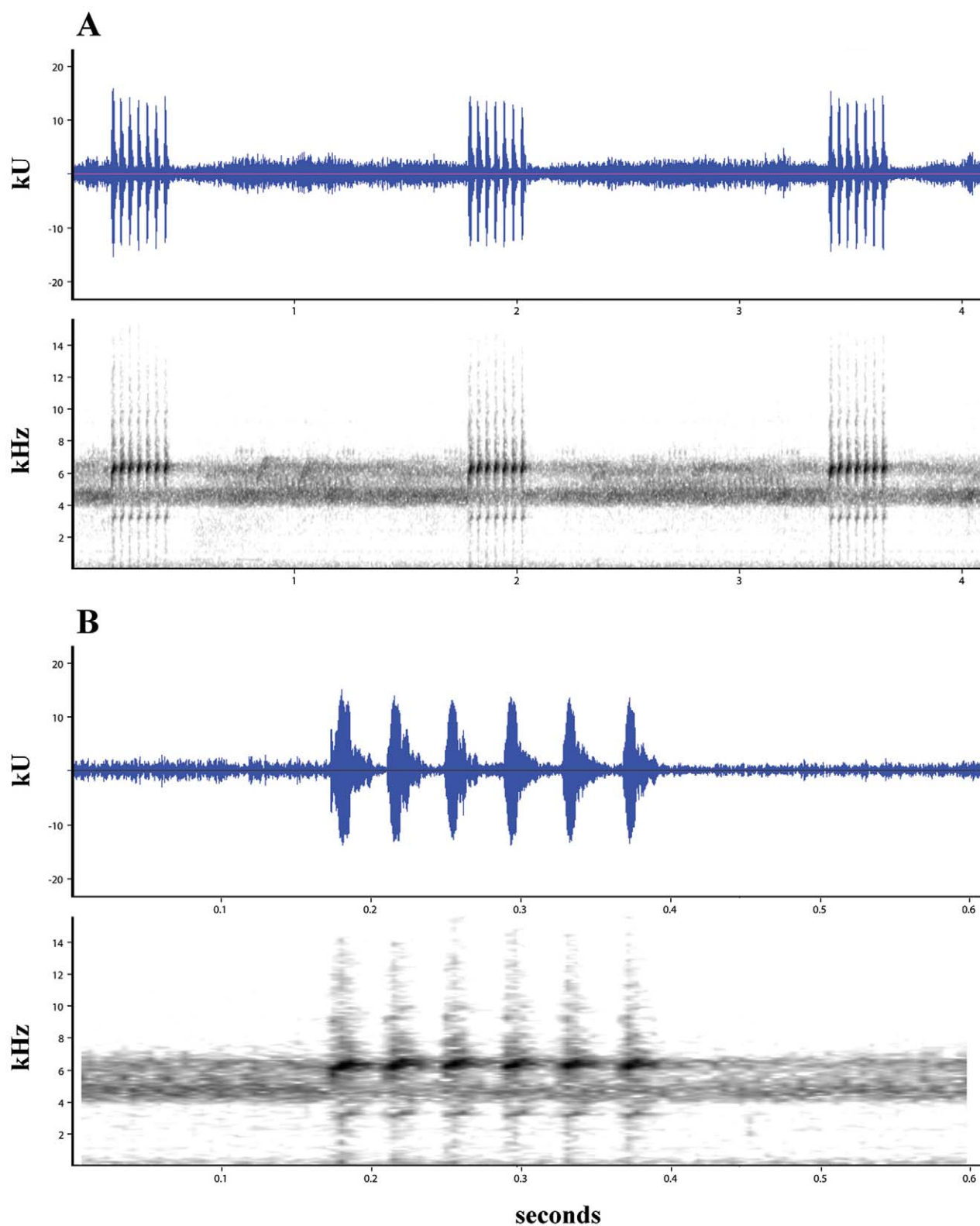
FIGURE 9. Advertisement call of *Allobates grillisimilis* holotype (INPA-H 30779) recorded in Borba, Amazonas, Brazil, on 12th of January 2008, at 07:28 h and 25°C. (A) Waveform (upper graph) and sonogram (lower graph) of a 4 s segment of advertisement calls, denoting the arrangement of calls, which consist in groups of very short tonal notes. The number of notes is generally variable between calls in the same calling bout. (B) Detailed view (0.6 s) of a single call, consisting of a group of six short notes.

FIGURE 10. Reproductive behavior of *Allobates grillisimilis* (A) Female (upper left) attracted by a courting male in Nova Olinda do Norte, Amazonas, Brazil. Courtship did not result in oviposition. (B) Female inside a curled dead leaf, used as an oviposition site. (C) Jelly nest containing 13 eggs deposited by the same female. (D) *Allobates grillisimilis* male collected while transporting tadpoles. All tadpoles being transported were at developmental stage 25 of Gosner (1960). (B), (C), and (D) from type locality in Borba, Amazonas, Brazil, photographed in January 2008.

Eggs are deposited in terrestrial nests, usually on the inner surface of a curled dead leaf on the forest floor (Fig. 10B,C), but also on flat dead leaves. Jelly egg masses contained six to thirteen embryos (mean = 9±2 embryos, *N*=13 egg masses observed).

Two courtships were observed by A. P. Lima on January 18 and 19, 2008. Both occurred in the morning, starting approximately at 07:30 to 08:00. Previous to both successful courtships (*i.e.* those that resulted in oviposition), the two observed females were spotted in the territories of other males, but left some time after being led to potential oviposition sites, and before males attempted amplexus. The following courtship pattern is described based on steps common to the two subsequent courtships, recorded from their outset until oviposition.

The female moved towards a second male who was calling nearby. As the female reached the second male's sight distance (about 1 m), he changed the calling pattern (alternating advertisement with what is probably a courtship call) and moved inside a small curled dead leaf on the forest floor. The female accompanied, and both stood side by side on the leaf for a few minutes, with the male emitting both types of calls, but no body contact. After this step, the male left the nest formed by the curled leaf and continued calling and moving around his territory, either alone (female remaining inside the nest) or followed by the female. On a second try, the male (while still calling), approached the same nest and was followed inside by the female. In one of the observations, male and female could be clearly observed inside the nest, and the pair gathered in cephalic amplexus for approximately one minute. In the second observation, no tactile interactions could be observed inside the nest. On both observations, males left immediately after pairing, returning to a nearby calling site and emitting advertisement calls. Both females stayed inside the nest for around 20 minutes (first female 07:41–08:01 h; second female: 09:25–09:50 h) laying eggs. First female laid 13 eggs and the second, nine eggs.

Distribution. *Allobates grillisimilis* was only found in primary *terra-firme* forests of the northwestern Madeira-Tapajós interfluve, in Brazil (Fig. 1). Its known distribution is limited west and north by the large Madeira and Amazon rivers, respectively. The species is not known to occur in localities south of the municipality of Borba, although an equivalent amount of time was spent in field work by the authors in other sites of adequate habitat around the city of Novo Aripuanã.

From November 2004 to July 2011, the authors conducted field work targeting the study of diurnal frogs in several sampling points a) south of the Aripuanã River, on the right bank of the Madeira River, until the Brazilian border with Bolivia; b) along the left bank of the Madeira River, from the Municipality of Careiro da Várzea to the Brazilian border with Bolivia; c) north of the Amazon River, in the Manaus and Itacoatiara regions, as well as localities in the states of Roraima and Pará; d) in the region of Parque Nacional da Amazônia, on the left bank of Tapajós River, and east of the presumed *Allobates grillisimilis* distribution. In none of these occasions we were able to detect the new species. Further data were obtained from the Brazilian Program for Biodiversity Research-PPBio online database (http://ppbio.inpa.gov.br). The database is updated frequently with data proceeding from intensive species surveys carried out at standardized sampling grids. The new species has not been recorded at any sampling grid where anuran surveys have been carried out (Fig. 1A).

Thus, the available records strongly suggest that the new species has a restricted geographic range, occupying areas on the right bank of the Madeira River, and reaching eastwards, between the Aripuanã River and the Municipality of Maués in central Brazilian Amazonia (Fig. 1B).

Discussion

Allobates grillisimilis is the 20th species in the genus *Allobates* to be detected in Brazil (Segalla *et al.* 2012; see Simões & Lima 2011 for an additional record of *A. myersi*), and the 15th to be described from the Brazilian Amazon basin, maintaining a steady trend in species discoveries following more intensive field work in relatively unexplored localities of the Amazonian lowlands (Morales 2000 "2002"; Lima & Caldwell 2001; Caldwell & Lima 2003; Lima *et al.* 2007; 2010; Simões *et al.* 2010).

Although the new species has the smallest body size among species currently assigned to genus *Allobates* (considering the average and minimum values for SVL among reproductive individuals), SVL variation range overlaps with those of nine species that also occur in the Brazilian Amazon (*A. brunneus*, *A. caeruleodactylus*, *A. conspicuous*, *A. fuscellus*, *A. gasconi*, *A. marchesianus*, *A. spumaponens*, *A. subfolionidificans*, *A. sumtuosus*). Additionally, some morphological characters classically used in comparisons between *Allobates* species (*e.g.* presence of pale dorsolateral stripe, presence of well developed granules on posterior surface of dorsum, head proportions) also proved to be highly variable when considering a large series of specimens, having potentially limited use as diagnostic traits.

We argue that, when based only on preserved adult specimens, the identification of *Allobates* can be difficult and demand extensive knowledge of the complete body of literature regarding the genus' taxonomy, including species descriptions, and recent systematic rearrangements. As shown repeatedly in the past, the use of acoustic parameters, larval morphology and reproductive behavior traits proved to be essential characters allowing for a direct and unambiguous species diagnosis (Caldwell & Lima 2003; Kok *et al.* 2006; Kok & Ernst 2007). Detailed

morphological analysis is still useful for comparisons between preserved individuals belonging to a few species, somewhat similar in relation to color patterns and body size, and for which data on calls, tadpoles and behavior are scarce or unavailable. Thus, we urge researchers currently conducting anuran surveys in the Amazon region to build call and photo databases linked to their reference collections. Ideally, such databases should also include information on the species larval stages and reproductive behavior. Whenever possible, information from all these sources should integrate new species descriptions by anuran taxonomists, helping field biologists to diagnose and catalogue their reference collections. A molecular screening of all known *Allobates* species will also be much useful to help to sort out this complicated group. Tissue samples should be collected routinely together with voucher specimens, and deposited in an accredited institution, that has a long term plan for preservation of genetic material.

The discovery of *Allobates grillisimilis* draws attention once again to the existence of geographically restricted anuran species in the Amazonian lowlands and the importance of considering ecological sub-structuring within the interfluves of large rivers. While Amazonian rivers are well known boundaries for the distribution of some vertebrates (Cracraft & Prum 1988; Ron 2000), considering each of their interfluves as a single and continuous area of endemism means adopting a dangerous paradigm, as unique sedimentary compartments may harbor restricted or locally adapted groups of species.

A second problem arises from the existence of cryptic species complexes (a group of closely related species currently classified as a single taxon) and by our inability to diagnose new taxa based exclusively on morphological characters in some anuran genera (Lemmon *et al.* 2007; Brown & Twomey 2009; Angulo & Icochea 2010; Peloso 2010). These will often generate imprecise distribution records that in the long term will feed distribution models and maps portraying taxa as geographically widespread, when they are actually constituted by two or more independent and geographically restricted evolutionary lineages.

Accurate estimates of the geographic distributions of species are often critical to effective conservation planning at the regional level (Angulo & Icochea 2010) based on beta-diversity, including the choice between alternative areas for the establishment of conservation units (Margules *et al.* 2002). As general recommendations for the development of more reliable databases on anuran species distributions, we suggest a greater investment in taxonomic and systematic studies aiming at clarifying species boundaries, as well as surveys with sampling designs that reflect the geomorphologic or biogeographic substructuring existing across apparently continuous stretches of lowland forests.

Acknowledgements

References

Altig, R. & McDiarmid, R.W. (1999) *Tadpoles: the biology of anuran larvae.* The University of Chicago Press, Chicago, 444 pp.

Angulo, A. & Icochea, J. (2010) Cryptic species complexes, widespread species and conservation: lessons from Amazonian frogs of the *Leptodactylus marmoratus* group (Anura: Leptodactylidae). *Systematics and Biodiversity*, 8(3), 357–370. http://dx.doi.org/10.1080/14772000.2010.507264

Barrio-Amorós, C.L. & Santos, J.C. (2009) Description of a new *Allobates* (Anura, Dendrobatidae) from the eastern Andean piedmont, Venezuela. *Phyllomedusa*, 8(2), 89–104.

Barrio-Amorós, C.L., Rivas, G. & Kaiser, H. (2006) New Species of *Colostethus* (Anura, Dendrobatidae) from the Península de Paria, Venezuela. *Journal of Herpetology.* 40, 371–377. http://dx.doi.org/10.1670/0022-1511(2006)40[371:NSOCAD]2.0.CO;2

Brown, J.L. & Twomey, E. (2009) Complicated histories: three new species of poison frogs of the genus *Ameerega* (Anura: Dendrobatidae) from north-central Peru. *Zootaxa*, 2049, 1–38.

Caldwell, J.P., Lima, A.P. & Keller, C. (2002) Redescription of *Colostethus marchesianus* (Melin, 1941) from its type locality. *Copeia*, 2002, 157–165. http://dx.doi.org/10.1643/0045-8511(2002)002[0157:ROCMMF]2.0.CO;2

Caldwell, J.P. & Lima, A.P. (2003) A new Amazonian species of *Colostethus* (Anura: Dendrobatidae) with a nidicolous tadpole. *Herpetologica*, 59, 219–234. http://dx.doi.org/10.1655/0018-0831(2003)059[0219:ANASOC]2.0.CO;2

Charif, R.A., Clark, C.W. & Fristrup, K.M. (2004) *Raven 1.2 User's Manual*. Cornell Laboratory of Ornithology, Ithaca, NY.

Costa, J.B.S., Bemerguy, R.L., Hasui, Y. & Borges, M.S. (2001) Tectonics and paleogeography along the Amazon River. *Journal of South American Earth Sciences*, 14, 335–347. http://dx.doi.org/10.1016/S0895-9811(01)00025-6

Cracraft, J. & Prum, R.O. (1988) Patterns and processes of diversification: speciation and historical congruence in some Neotropical birds. *Evolution,* 42(3), 603–620. http://dx.doi.org/10.2307/2409043

DNPM - Departamento Nacional da Produção Mineral – Brasil (1978) *Projeto RADAMBRASIL – Levantamento dos recursos naturais*, *Vol.19, Folha SB 20, Purus: Geologia, geomorfologia, pedologia, vegetação e uso potencial da terra.* Departamento Nacional da Produção Mineral , Rio de Janeiro.

Frost, D.R. (2011) Amphibian Species of the World: an Online Reference. Version 5.5. American Museum of Natural History, New York, USA. Available at http://research.amnh.org/vz/herpetology/amphibia/ (accessed 05 May 2012).

Geurgas, S.R. & Rodrigues, M.T. (2010) The hidden diversity of *Coleodactylus amazonicus* (Sphaerodactylinae, Gekkota) revealed by molecular data. *Molecular Phylogenetics and Evolution*, 54, 583–593. http://dx.doi.org/10.1016/j.ympev.2009.10.004

Gosner, K.L. (1960) A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, 16, 183–190.

Grant, T., Frost, D.R., Caldwell, J.P., Gagliardo, R., Haddad, C.F.B., Kok, P.J.R., Means, B.D., Noonan, B.P., Schargel, W. & Wheeler, W.C. (2006) Phylogenetic systematics of dart-poison frogs and their relatives (Anura: Athesphatanura: Dendrobatidae). *Bulletin of the American Museum of Natural History*, 299, 1–262. http://dx.doi.org/10.1206/0003-0090(2006)299[1:PSODFA]2.0.CO;2

Grant, T., Acosta, A. & Rada, M. (2007). A name for the species of *Allobates* (Anura: Dendrobatoidea: Aromobatidae) from the Magdalena Valley of Colombia. *Copeia,* 2007, 844–854.
http://dx.doi.org/10.1643/0045-8511(2007)7[844:ANFTSO]2.0.CO;2

Kok, P.J.R., MacCulloch, R.D., Gaucher, P., Poelman, E.H., Bourne, G. R., Lathrop, A. & Lenglet, G.L. (2006) A new species of *Colostethus* (Anura, Dendrobatidae) from French Guiana with a redescription of *Colostethus beebei* (Noble, 1923) from its type locality. *Phyllomedusa* 5, 43–66.

Kok, P.J.R. & Ernst, R. (2007) A new species of *Allobates* (Anura: Aromobatidae: Allobatinae) exhibiting a novel reproductive behaviour. *Zootaxa*, 1555, 21–38.

Lemmon, E.M., Lemmon, A.R., Collins, J.T., Lee-Yaw, J.A. & Cannatella, D.C. (2007) Phylogeny-based delimitation of species boundaries and contact zones in the trilling chorus frogs (*Pseudacris*). *Molecular Phylogenetics and Evolution,* 44, 1068–1082. http://dx.doi.org/10.1016/j.ympev.2007.04.010

Lima, A.P. & Caldwell, J.P. (2001) A new Amazonian species of *Colostethus* with sky blue digits. *Herpetologica*, 57, 133–138.

Lima, A.P., Sanchez, D.E.A. & Souza, J.R.D. (2007) A new Amazonian species of frog genus *Colostethus* (Dendrobatidae) that lays its eggs on undersides of leaves. *Copeia* 2007, 1, 114–122. http://dx.doi.org/10.1643/0045-8511(2007)7[114:ANASOT]2.0.CO;2

Lima, A.P., Caldwell, J.P. & Strussmann, C. (2009) Redescription of *Allobates brunneus* (Cope) 1887 (Anura: Aromobatidae: Allobatinae), with a description of the tadpole, call, and reproductive behavior. *Zootaxa*, 1988, 1–16.

Lima, A.P., Caldwell, J.P., Biavati, G. & Montanarin, A. (2010) A new species of *Allobates* (Anura: Aromobatidae) from Paleovárzea Forest in Amazonas, Brazil. *Zootaxa*, 2337, 1–17.

Margules, C.R., Pressey, R.L. & Williams P.H. (2002) Representing biodiversity: data and procedures for identifying priority areas for conservation. *Journal of Biosciences*, 27(4 – suppl. 2), 309–326.

Morales, V.C. (2000, "2002") Sistemática y biogeografía del grupo *trilineatus* (Amphibia, Anura, Dendrobatidae, *Colostethus*), con descripcíon de once espécies nuevas. *Publicaciones de La Asociacíon de Amigos de Doñana*, 13, 1–59.

Morrone, J.J. (2006) Biogeographic areas and transition zones of Latin America and the Caribbean Islands based on panbiogeographic and cladistic analyses of the entomofauna. *Annual Review of Entomology*, 51, 467–94. http://dx.doi.org/10.1146/annurev.ento.50.071803.130447

Padial, J. M., Miralles, A., De la Riva, I. and Vences, M. (2010) The integrative future of taxonomy. *Frontiers in Zoology*, 2010, 16. http://dx.doi.org/10.1186/1742-9994-7-16

Peloso, P.L.V. (2010) A safe place for amphibians? A cautionary tale on the taxonomy and conservation of frogs, caecilians and salamanders in the Brazilian Amazonia. *Zoologia*, 27(5), 667–673.

Roosmalen, M.G.M. van, Roosmalen, T. van & Mittermeier, R.A. (2002) A taxonomic review of the Titi Monkeys, genus *Callicebus,* Tomas, 1903, with the description of two new species, *Callicebus bernhardi* and *Callicebus stephennashi*, from Brazilian Amazonia. *Neotropical Primates*, 10 (Suppl.), 1–52.

Ron, S. (2000) Biogeographic area relationships of lowland Neotropical rainforest based on raw distributions of vertebrate groups. *Biological Journal of the Linnean Society*, 71, 379–402. http://dx.doi.org/10.1111/j.1095-8312.2000.tb01265.x

Rossetti, D.F., de Toledo, P.M. & Góes, A.M. (2005) New geological framework for Western Amazonia (Brazil) and implications for biogeography and evolution. *Quaternary Research*, 63, 78–89. http://dx.doi.org/10.1016/j.yqres.2004.10.001

Segalla, M.V., Caramaschi, U., Cruz, C.A.G., Garcia, P.C.A., Grant, T., Haddad, C.F.B & Langone, J. (2012) *Brazilian amphibians – List of species*. Sociedade Brasileira de Herpetologia, Curitiba, Brazil. Available at http://www.sbherpetologia.org.br/ (accessed 20 June 2012).

Silva, J.M.C., Rylands, A.B. & Fonseca, G.A.B. (2005) The fate of the Amazonian areas of endemism. *Conservation Biology*, 19(3), 689–694. http://dx.doi.org/10.1111/j.1523-1739.2005.00705.x

Simões, P.I., Lima, A.P. & Farias, I.P. (2010) The description of a cryptic species related to the pan-Amazonian frog *Allobates femoralis* (Boulenger 1883) (Anura: Aromobatidae). *Zootaxa*, 2406, 1–28.

Simões, P.I. & Lima, A.P. (2011) The complex advertisement calls of *Allobates myersi* (Pyburn, 1981) (Anura: Aromobatidae) from São Gabriel da Cachoeira, Brazil. *Zootaxa*, 2988, 66–68.

Simões, P.I. & Lima, A.P. (2012) The tadpole of *Allobates sumtuosus* (Morales, '2000' 2002) (Anura: Aromobatidae) from its type locality at Reserva Biológica do Rio Trombetas, Pará, Brazil. *Zootaxa*, 3499, 86–88.

Wilkinson, L. (1990) *SYSTAT: the system for statistics*. SYSTAT inc., Evanston.

APPENDIX I. Material examined.

Allobates alessandroi.—PERU: *CUSCO*: Paucartambo, Cosñipata, San Pedro, 13°03'18"S/71°32'36"W, 1480 m.a.s.l. (AMNH 157004: paratype)

Allobates brunneus.—BRAZIL: *MATO GROSSO*: Chapada dos Guimarães (INPA-H 10111–48; tadpoles, INPA-H 10025–27, 10029–30, 10032–37, 10039, 10041, 10043–44.)

Allobates caeruleodactylus.— BRAZIL: *AMAZONAS*: Km 12 on road to Autazes. INPA-H 7238: holotype; INPA-H 7229–32, males, 7234–37; OMNH 35837–44; tadpoles, INPA-H 8037–42, 8042–46, 8085.

Allobates crombiei.– BRAZIL: *PARÁ*: Cachoeira do Espelho, on the right bank of Xingu River, 54 km from Altamira (3°39'00.4" S; 52° 22'33.2" W). INPA-H 30457, 30461–62, 30464, 30471–77, males; INPA-H 30458–60, 30463, 30465–70, females.

Allobates marchesianus.—BRAZIL: *AMAZONAS*: Missão Taracuá (INPA-H 7959–90; tadpoles INPA-H 7943–50, 7992, 7998, 8084); São Gabriel da Cachoeira (INPA-H 7991, 7993, 8000–07).

Allobates masniger.—BRAZIL: *AMAZONAS*: Maués, Floresta Nacional de Pau-Rosa, Rio Paraconi, Comunidade Bragança (MPEG 28615–28619); *PARÁ*: Itaituba, Parque Nacional do Amazonas, Rio Tapajós (INPA-H 28109, 28193, 28196, 28200, 28206–08, 28213–28214); Ca 75 km SW of Itaituba, Parque Nacional do Amazonas, Rio Tapajós (USNM 303585: holotype, USNM 303584, 303587, 303589-90).

Allobates mcdiarmidi.—BOLIVIA: *COCHABAMBA*: Chapare, San Onofre (USNM 257805: holotype, USNM 257804, USNM 257806).

Allobates melanolaemus.—PERU: *LORETO*: Río Ampiyacu, Estirón (AMNH 114924–45).

Allobates nidicola.—BRAZIL: *AMAZONAS*: Km 12 on road to Autazes (INPA-H 8093: holotype; INPA-H 8094, 7253–59, 7261–62; MPEG 13818–25, OMNH 37419–26, 37422)

Allobates olfersioides.—BRAZIL: *RIO DE JANEIRO*: Angra dos Reis (USNM 96539–96540: syntypes). Nichtheroy (USNM 96412: syntype). Rio de Janeiro, Tijuca (AMNH 72445–47)

Allobates paleovarzensis.— BRAZIL: *AMAZONAS*, Castanho, 34km S Manaus, 03°22'26.3''S/59°52'06.4''W (INPA-H 20904: holotype, INPA 20876–903, 20905, 20861-75)

Allobates spumaponens.—GUYANA: Berbice River Camp, ca. 30km SW of Kwakwa, 5°5'6"N/58°14'14"W (AMNH 166470–75)

Allobates stepheni.—BRAZIL: *AMAZONAS*:, Manaus, Reserva florestal Adolfo Ducke (AMNH 136197–204, 139289–90)

Allobates subfolionidificans.—BRAZIL: *ACRE*: Rio Branco: Parque Zoobotânico da Universidade do Acre (INPA-H 13760: holotype; INPA-H 11958–74, 13749–13754, 13756–13759, 13761–62).

Allobates sumtuosus.—BRAZIL: *PARÁ*:Reserva Biológica Rio Trombetas, Igarapé Jacaré (USNM 303591: holotype, USNM 303592–93)

Allobates vanzolinius.—BRAZIL: *AMAZONAS*: Vai-Quem-Quer and Jainu Rio Juruá (INPA-H 4896: holotype, INPA-H 4903–05, 4912, 3381, 3413.