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A third microendemic to the Iwokrama Mountains of central Guyana: a new “cryptic” species of *Allobates* Zimmerman and Zimmerman, 1988 (Anura: Aromobatidae)

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Abstract The aromobatid frog *Allobates amissibilis* sp. nov. is described from a very limited area in the Iwokrama Mountains at elevations between 160 and 950 m, in central Guyana, South America. The new taxon is diagnosed from other *Allobates* species by morphology, bioacoustics, and genetics, and can be distinguished readily from known congeners by cryptic colouration, small size (16.3–17.8 mm snout-vent length), absence of distinct dorsal pattern in living adult individuals, presence of a distinctly enlarged tubercle on each eyelid, diffuse broad oblique lateral stripe extending from groin to about midbody length, sexually dimorphic throat colouration (pinkish grey, suffused with dark pigment in male, immaculate cream to yellow in female), belly cream to yellow in both sexes, and distinct vocalisation formed by calls of usually 9–12 notes emitted between silent intervals of usually ca. 2–6 s, with a dominant frequency ranging from 5,064 to 5,845 Hz. The new species is the third microendemic reported from the Iwokrama Mountains together with the caecilian *Caecilita iwokramae* and the lizard *Gonatodes timidus*. We recommend considering the conservation status of the new species as Data Deficient, and highlight that environmental impact assessments are needed to refine its IUCN threat status.

Keywords *Allobates amissibilis* sp. nov · Bioacoustics · Guiana Shield · Microendemicity · Systematics · Taxonomy

Introduction

As currently recognised, the Neotropical frog genus *Allobates* Zimmerman and Zimmerman, 1988, includes 47 species distributed mostly east of the Andes, in lowland and cloud forests from the extreme south of Nicaragua to the Atlantic forests in Brazil, with one species native to the Caribbean island of Martinique (Fouquet et al. 2013; Frost 2013; Lötters et al. 2007; Simões et al. 2013). To date, only two *Allobates* species have been reported from Guyana (Cole et al. 2013), namely *A. femoralis* (Boulenger, 1884), which displays bright orangish red flash marks in groin and on arms and legs (a “near to aposematic colouration” according to Vences et al. 2003), and the cryptically coloured *A. spumaponens* Kok and Ernst, 2007.

Most *Allobates* species are regarded as “cryptic” species in the sense that distinct taxa masquerade under the same name due to poor morphological differentiation, but are usually still distinguishable based on non-morphological characters such as advertisement call. As noted by Simões et al. (2013), a plethora of new anuran species are discovered using the concept of “integrative taxonomy”, which suggests the use of several independent lines of evidence, such as morphology, bioacoustics, and genetics to recognize new taxa (Padial et al. 2010). Specifically in the genus *Allobates*, it has been demonstrated recently that morphology and bioacoustics may sometimes fail to identify hypothetical new taxa (Tsuji-Nishikido et al. 2012). Molecular data have been a useful tool

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in recognising Neotropical cryptic frog diversity (e.g. Fouquet et al. 2007, 2012a, b; Funk et al. 2011) and should, whenever possible, be used to detect and support the erection of new hypothetical "cryptic" species, or so called "candidate species" (Vieites et al. 2009). In this regard, it is interesting to note that the situation in the Guiana Shield lowlands usually strongly contrasts with that in the Guiana Shield highlands, where it has been demonstrated recently that genetic diversity is low among most species and populations, even those that are morphologically well defined (Kok et al. 2012).

Although Iwokrama is probably one of the best-surveyed areas of Guyana, relatively few publications have followed previous intensive surveys (see Kok 2012). Only *Allobates femoralis* has been formally reported from the area (under the name *Epipedobates femoralis*, see Donnelly et al. 2005a, b). Donnelly et al. (2005a, b) also reported a "*Colostethus* sp" collected at a single locality named Pakatau Creek situated at the extreme NW of the Iwokrama Forest Reserve, at the foothills of the Pakaraima Mountain Range. That specimen could be either an *Allobates* or more probably an *Anomaloglossus*, which is currently impossible to state given the absence of any published morphological data.

Two microendemic species to the Iwokrama Mountains have been discovered so far: the siphonopid caecilian *Caecilita iwokramae* Wake and Donnelly, 2010, and the sphaerodactylid lizard *Gonatodes timidus* Kok, 2012. Herein we report a third endemic taxon to the area, a new *Allobates* species, which was obtained from only two localities in the Iwokrama Mountains. The type locality, named "Turu Falls", has been designated as a site of potential ecotouristic value, notably due to its spectacular topography featuring small waterfalls and creeks with pools and cascades (Fig. 1).

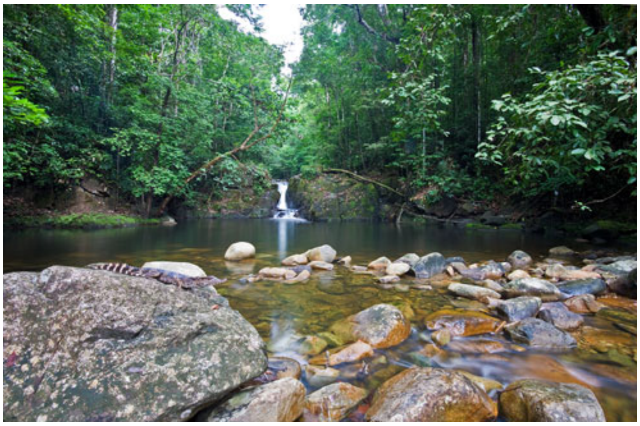


Fig. 1 Turu Falls and its large water reservoir, at the type locality of *Allobates amissibilis* sp. nov. (note the presence of a *Paleosuchus trigonatus* on the left rock). The area has been designated as a site of potential ecotouristic value due to aesthetic attractiveness. Photograph by P.J.R.K. (3 December 2012)

Materials and methods

Fieldwork and deposition of specimens

Specimens were collected by hand and euthanized by immersion in a 2 % lidocaine solution (Linisol), fixed in 10 % formalin for several days and transferred to 70 % ethanol for permanent storage. A piece of liver and/or thigh muscle was taken from most specimens prior to fixation and preserved in 95 % ethanol for later molecular analyses. Specimens were deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRSNB) and of the Senckenberg Naturhistorische Sammlungen Dresden (MTD). Tissue samples were deposited in the Amphibian Evolution Lab, Biology Department, Vrije Universiteit Brussel, and in MTD.

Morphology

All morphometric data were taken from the preserved specimens, to the nearest 0.01 mm and rounded to the nearest 0.1 mm, under a Leica stereo dissecting microscope using an electronic digital calliper or an ocular micrometer.

Abbreviations and standard measurements for adults are as follows: (1) snout-vent length (SVL); (2) head length from corner of mouth to tip of snout (HL); (3) head width at level of angle of jaws (HW); (4) snout length from anterior corner of eye to tip of snout (SL); (5) eye to naris distance from anterior corner of eye to posterior margin of naris (EN); (6) internarial distance (IN); (7) eye length (EL); (8) interorbital distance (IO); (9) greatest length of tympanum from its anterior margin to its posterior margin (TYM); (10) forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow (FAL); (11) length of Finger I from proximal edge of palmar tubercle to tip of finger (HAND I); (12) length of Finger II from proximal edge of palmar tubercle to tip of finger (HAND II); (13) length of Finger III from proximal edge of palmar tubercle to tip of finger (HAND III, also equivalent to hand length); (14) length of Finger IV from proximal edge of palmar tubercle to tip of finger (HAND IV); (15) width of disc on Finger III (WFD); (16) tibia length from outer edge of flexed knee to heel (TL); (17) foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV (FL); (18) width of disc on Toe IV (WTD). Relative lengths of fingers were compared according to Kaplan (1997), using the distance from the proximal edge of the palmar tubercle to the tip of each finger.

Colour in life is described from digital photographs and field notes. Sex and maturity were determined by the presence/absence of vocal slit(s) and confirmed by dissection when sex determination was doubtful. Internal soft anatomy was examined by dissection of preserved specimens.

Additional specimens examined are in the Appendix. Taxonomy follows Grant et al. (2006).

Bioacoustics

An uninterrupted advertisement call of about 6 min was recorded from the holotype at a distance of ca. 1.5 m using a Sennheiser ME66/K6 microphone attached to a Marantz PMD661 solid-state recorder. The call was analysed at a sampling rate of 44,100 Hz using Raven Pro version 1.4 for Mac OS X (Charif et al. 2010). Temporal variables measured included: call duration (beginning of first to the end of the last note of a call); note duration (beginning of the note to the end of the note); number of notes per call (a call is here defined as a series of identical notes emitted in groups between longer silent intervals); silent intervals (end of one call to the beginning of the next); inter-note interval (end of one note to beginning of the next); and call rate (= number of calls per minute) (Kok and Kalamandeen 2008). Peak of the dominant (emphasised) and of the highest frequencies of the note were measured from a spectral slice taken through the portion of the note with the highest amplitude (using the Blackman window function at a 3 dB filter bandwidth of 120 Hz) (Kok and Kalamandeen 2008). Air temperature at the call site was measured with a Hanna digital pH/thermometer and was 25 °C.

Institutional acronyms follow Frost (2013).

New species description

Allobates amissibilis sp. nov.

Allobates sp. "Iwokrama" Fouquet et al. 2013: tables 1–3, Fig. 3

(Figs. 2–5, Table 1)

Holotype IRSNB 4155 (field number PK 3672), an adult male collected by Philippe J. R. Kok, 3 December 2012 at 1030 hours, Turu Falls, base of Iwokrama Mountains, Potaro-Siparuni District, Guyana (04°24'46"N, 058°47'02"W, ca. 160 m elevation).

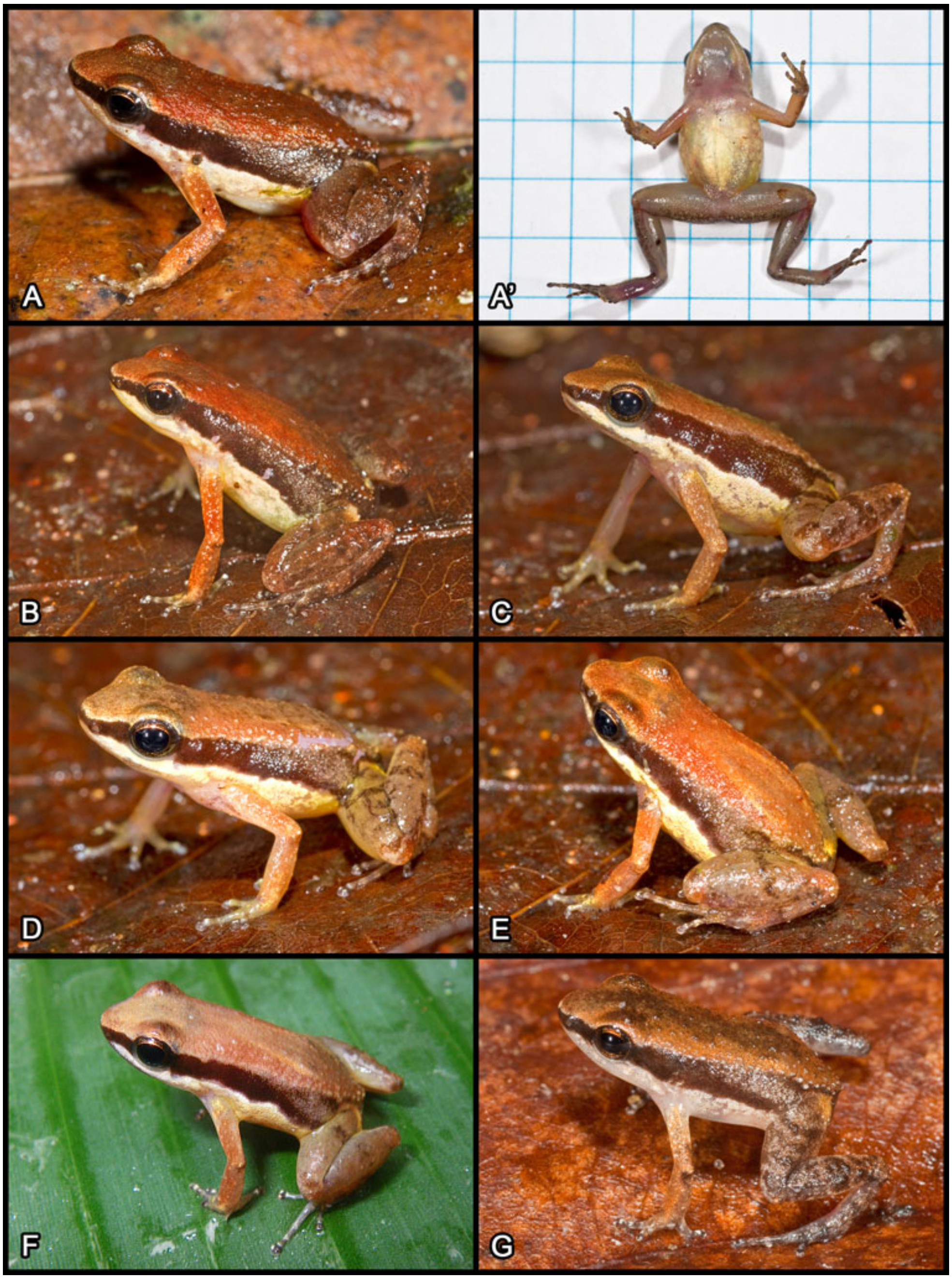
Paratopotypes (n=5) Three adult males (IRSNB 4157–59, field numbers PK 3796 and PK 3797–98), collected by Jonathan Clegg, and Philippe J. R. Kok and Armstrong Simon, respectively, with same data as holotype; one adult male (MTD 47884, field number 047), collected by E. Meyer, 25 May 2010, on Turu Falls trail, right bank of Turu creek going upstream to Turu Falls; and one adult female (IRSNB 4156, field number PK 3795, designated as the allotype), collected by Philippe J. R. Kok and Armstrong Simon with same data as holotype.

Referred specimen A juvenile (IRSNB 15915, field number PK 3526), collected by Philippe J. R. Kok and Lawrence Antoin, 19 March 2011, close to the top of one of the highest

Table 1 Measurements (in mm) of the type series of *Allobates amissibilis* sp. nov. Abbreviations are defined in the text

Character	IRSNB 4155 (holotype)	IRSNB 4156 (allotype)	IRSNB 4157	IRSNB 4158	IRSNB 4159	MTD 47884
Sex	Male	Female	Male	Male	Male	Male
SVL	16.3	17.8	17.5	16.4	16.9	17.4
HL	4.9	5.2	5.4	5.4	5.3	4.9
HW	5.4	5.8	5.7	5.6	5.4	5.5
SL	2.8	2.9	2.8	2.6	2.8	2.9
EN	1.5	1.7	1.5	1.4	1.3	1.7
IN	2.1	2.2	2.2	2.2	2.2	2.0
EL	2.2	2.4	2.2	2.2	2.4	2.4
IO	2.1	2.0	1.7	1.9	1.9	1.9
TYM	0.9	1.0	0.9	1.0	0.8	1.1
FAL	3.6	3.9	3.9	3.9	3.9	4.0
HAND I	3.3	3.0	3.2	3.1	3.2	3.0
HAND II	2.9	2.7	2.9	2.8	2.9	2.8
HAND III	3.8	3.8	4.0	3.9	4.0	3.8
HAND IV	2.4	2.3	2.5	2.4	2.5	2.3
WFD	0.4	0.4	0.4	0.4	0.5	0.4
TL	7.6	8.0	8.0	8.1	8.0	7.7
FL	6.7	6.7	6.6	6.3	6.5	6.6
WTD	0.7	0.6	0.7	0.6	0.6	0.5

Fig. 2 **a–g** *Allobates amissibilis* sp. nov., showing intraspecific variation in colour and pattern in life. **a** Dorsolateral view of IRSNB 4155, male holotype 16.3 mm snout-vent length (SVL) (**a'** Ventral view of the same specimen). **b** Dorsolateral view of IRSNB 4156, female allotype 17.8 mm SVL. **c** Dorsolateral view of IRSNB 4157, male paratype 17.5 mm SVL. **d** Dorsolateral view of IRSNB 4158, male paratype 16.4 mm SVL. **e** Dorsolateral view of IRSNB 4159, male paratype 16.9 mm SVL. **f** Dorsolateral view of MTD 47884, male paratype 17.4 mm SVL. **g** Dorsolateral view of IRSNB 15915, juvenile 10.5 mm SVL. Photographs by P.J.R.K.



peaks (unnamed) of the Iwokrama Mountains (04°20’11”N, 058°46’54”W, ca. 950 m elevation). One leg removed and preserved in 95 % ethanol for molecular analyses.

Etymology The specific name is considered a noun in apposition and is derived from the ecclesiastical Latin word *amissibilis* literally meaning “that may be lost”, in reference to the threats that this potentially highly restricted species may face in the near future as a result of increasing human pressure due to the aesthetic attractiveness of the locality where it occurs.

Definition and diagnosis The new species is characterised by the following unique combination of characters: (1) SVL small, adult males 16.9±0.6 mm (range 16.3–17.5 mm, $n=5$), adult female 17.8 mm ($n=1$); (2) in life skin on dorsum shagreen to granular, always more granular posteriorly; (3) median lingual process absent; (4) annulus tympanicus visible anteroventrally, tympanum posterodorsally barely visible; (5) vocal sac distinct, subgular; (6) maxillary teeth present, very small; (7) distal tubercle on Finger IV absent; (8) tip of Finger IV not reaching distal subarticular tubercle on Finger III when fingers adpressed; (9) Finger I 7–12 % longer than Finger II (*n*=6); (10) finger discs weakly expanded, middle section of last phalange of Finger III 80 % of Finger III disc width; (11) lateral fringes on fingers absent; (12) metacarpal ridge absent; (13) Finger III not swollen in male, overall morphology of Finger III identical in male and female; (14) supracarpal pad absent; (15) thenar tubercle conspicuous, weakly protuberant; (16) black arm gland absent; (17) nature of tarsal keel variable, usually short, tuberclelike, curved or directed transversely across tarsus and not extending from metatarsal tubercle, rarely straight or very weakly curved, extending proximolaterad from halfway between metatarsal tubercle and dermal thickening; (18) tarsal fringe absent; (19) Toe IV disc moderately expanded, middle section of last phalange of Toe IV 50–60 % of Toe IV disc width; (20) basal webbing only between Toes III–IV; (21) metatarsal fold absent; (22) weak pre- and postaxial fringes on Toes II–III (preaxial ones more conspicuous) and weak preaxial fringe on Toe IV (usually more conspicuous than on Toes II–III), present in male, more weakly developed (almost undetectable) in female; (23) body colouration cryptic with no distinct pattern on adult dorsum, but dorsal "hourglass" pattern in the single juvenile; (24) dorsolateral stripe absent or present, in which case as a diffuse narrow line, extending from tip of snout to vent area; (25) oblique lateral stripe present as a diffuse broad area, extending from groin to about midbody length; (26) ventrolateral stripe present, whitish to yellowish white, with no distinct dark blotches ventrolaterally; (27) paracloacal marks present, pale to orangish yellow; (28) enlarged cloacal tubercles absent; (29) distinctly enlarged tubercle on each eyelid; (30) throat colouration sexually dimorphic, pinkish grey, suffused with dark pigment in male, immaculate cream to yellow in female; (31) belly colouration not clearly sexually dimorphic, cream to yellow in both sexes; (32) dark dermal collar absent; (33) iris metallic copper with black reticulations in life, incomplete pupil ring (present only above the pupil); (34) large intestine unpigmented; (35) adult testes unpigmented; (36) mature oocytes pigmented; (37) diurnal habits, males calling by day; (38) advertisement call characterized by calls of usually 9–12 notes consisting of seven harmonics, emitted between silent intervals of usually ca. 2–6 s.

Generic allocation The new species is assigned unambiguously to the genus *Allobates* by the combination of the above characters # 2, 3, 10, 20, 23, 25, 32, 35 and based on molecular phylogenetic relationships (see Fig. 3 in Fouquet et al. 2013 in which the new species is listed as "*A.* sp. "Iwokrama"").

Morphological comparisons with congeneric species Available data converge to suggest that several cryptically coloured *Allobates* have relatively restricted distributions (the authors unpubl. data, see also Caldwell et al. 2002; Lima et al. 2009; Simões et al. 2013). *Allobates amissibilis* has only been collected at two localities in the Iwokrama Mountains despite the fact that several intensive surveys have been conducted by the authors and by independent research groups in the entire Iwokrama Forest and peripheral areas. All surveys conducted outside the Iwokrama Mountains area were unable to secure any additional specimen of the new species. Comparisons with congeners thus focus on *Allobates* species from the Guiana Shield region (sensu Señaris and MacCulloch 2005) and extralimital Amazonian species, but we also compare the new taxon with known species within the same phylogenetic clade (sensu Fouquet et al. 2013). Morphological comparisons are based on examination of museum specimens (see Appendix) and/or original descriptions/redescriptions.

Eight species of *Allobates* are currently reported from the Guiana Shield region (Señaris and MacCulloch 2005; Frost 2013): *A. femoralis*, widespread in the lowlands of the Amazon Basin and the Guianas; *A. granti* (Kok, MacCulloch, Gaucher, Poelman, Bourne, Lathrop, and Lenglet, 2006), from French Guiana and Suriname [some populations recently reported from Suriname by Ouboter and Jairam (2012) likely belong to an undescribed taxon; see also Fouquet et al. 2012a)]; *A. marchesianus* (Melin, 1941) reported as widespread in the Amazon Basin, but its presence outside the type locality (Missão Taracuá, upper Rio Uaupés, north of the Amazon river, Amazonas state, Brazil) is uncertain (see Caldwell et al. 2002); *A. myersi* (Pyburn, 1981), from the Amazonian lowlands of Colombia; *A. spumaponens*, disjunctly distributed in central Guyana and northern Pará, Brazil (Avila-Pires et al. 2010); *A. sanmartini* (Rivero, Langone, and Prigioni, 1986), endemic to Las Majadas, Bolívar state, Venezuela; *A. sumtuosus* (Morales, 2002), type locality (Reserva Biológica Río Trombetas) in Pará state, Brazil, a disjunct population reported from Loreto, Peru; and *A. undulatus* (Myers and Donnelly, 2001), endemic to Cerro Yutajé, Amazonas state, Venezuela.

Allobates amissibilis is immediately distinguished from *A. femoralis* and *A. myersi* by the absence of conspicuous flashmarks on dorsal surface of thighs, by the absence of dark mottling on venter (both present in *A. femoralis* and *A. myersi*), and by smaller size (max SVL less than 18.0 mm in *A. amissibilis* vs more than 20.0 mm in *A. femoralis* and *A. myersi*).

Allobates amissibilis is morphologically similar to *A. granti* and confusion between these species is easy, but the new species can be distinguished readily from *A. granti* by the following combination of characters (those of *A. granti* in parentheses): larger SVL in male (16.3–17.5 mm, *n*=5 vs 14.9–16.7, *n*=8 in *A. granti*), dorsal surface of hindlimbs light to moderately dark brown (dark bluish grey), belly colouration not clearly sexually dimorphic, cream to yellow in both sexes (strongly dimorphic, white in male, yellow in

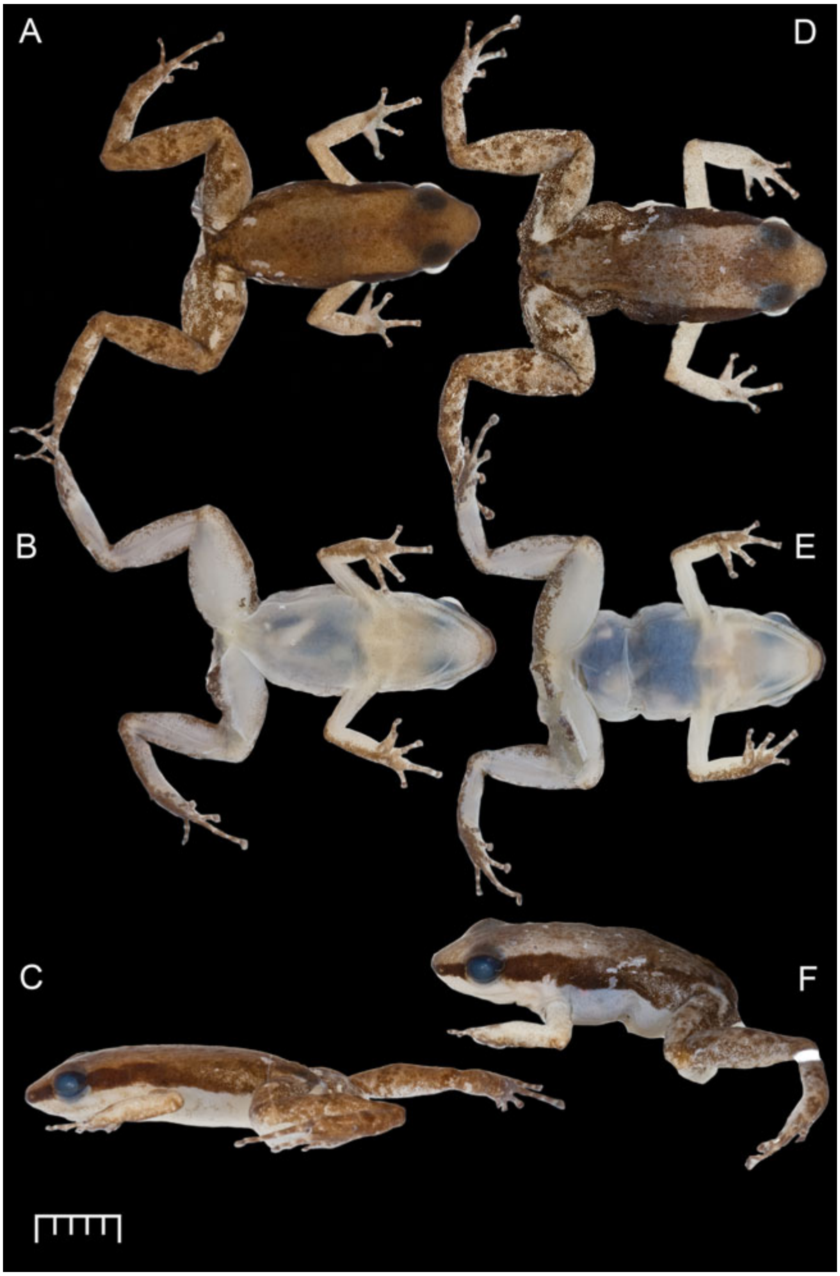


Fig. 3 **a–f** *Allobates amissibilis* sp. nov. **a** Dorsal, **b** Ventral, and **c** Lateral views of the male holotype (IRSNB 4155). **d** Dorsal, **e** Ventral, and **f** Lateral views of the female allotype (IRSNB 4156). Photographs by P.J.R.K. *Bar* 5 mm

female), oblique lateral stripe as a diffuse broad area, extending from groin to about midbody length (oblique lateral stripe less conspicuous, not reaching midbody length, usually barely distinct), and thenar tubercle weakly protuberant (distinctly protuberant).

Allobates amissibilis is immediately distinguished from *A. marchesianus* by lacking a broad distinct dorsolateral stripe (when present a diffuse narrow line in *A. amissibilis*), and in having cream to yellow belly in male (uniform grey in *A. marchesianus*).

Allobates amissibilis is also morphologically very similar to *A. spumaponens* (the geographically closest cryptically coloured *Allobates* species), but the new species can be readily distinguished from *A. spumaponens* by the following combination of characters (those of *A. spumaponens* in parentheses): slightly larger SVL in male (16.3–17.5 mm, *n*=5 vs 13.2–17.0, *n*=6 in *A. spumaponens*), belly colouration not clearly sexually dimorphic, cream to yellow in both sexes (strongly dimorphic, hyaline-white in male, yellow in female), throat colouration clearly sexually dimorphic, throat suffused with dark pigment in male, immaculate yellow in female (poorly dimorphic, pale with very discrete spotting on chin and margin of lower lip in male, immaculate in female), oblique lateral stripe as a diffuse broad area, extending from groin to about midbody length (oblique lateral stripe less conspicuous, not reaching midbody length), dorsolateral stripe usually absent, as a diffuse narrow line when present (dorsolateral stripe more conspicuous, broader), conspicuous dark grey blotches on flanks absent (present), and faint dark brown transverse crossbars on legs (absent).

Allobates amissibilis is easily distinguished from *A. sanmartini* in having a smaller SVL (maximum SVL 17.8 mm vs 25.4 mm in *A. sanmartini*), tympanum smaller than half the size of eye (larger than half the size of eye in *A. sanmartini*), and Finger I longer than II (shorter in *A. sanmartini*).

Allobates amissibilis is mainly distinguished from *A. sumtuosus* by having Finger III not swollen in male (reported as swollen in the original description of *A. sumtuosus*), a broad oblique lateral stripe extending from groin to about midbody length (reported as absent in the original description of *A. sumtuosus*), dorsolateral stripe usually absent, as a diffuse narrow line when present (dorsolateral stripe more conspicuous and broader in *A. sumtuosus*), throat suffused with dark pigment in male (reported as immaculate in *A. sumtuosus*), and faint dark brown transverse crossbars on legs (absent in *A. sumtuosus*).

Allobates amissibilis is distinguished readily from *A. undulatus* by having a smaller SVL (maximum SVL 17.8 mm vs 25.0 mm in *A. undulatus*), by lacking wavy-edged dorsal markings (present in *A. undulatus*), and a supracarpal pad atop wrist in male (present in *A. undulatus*).

Six extralimital species of *Allobates* are known to occur in Amazonia, in peripheral areas to the Guiana Shield region: *A. caeruleodactylus* (Lima and Caldwell, 2001), known only from three localities south of the Amazon river in Amazonas state, Brazil; *A. crombiei* (Morales, 2002), reported only from the drainage of the lower Río Xingú, south of the Amazon river, Pará state, Brazil; *A. grillisimilis* Simões, Sturaro, Peloso, and Lima, 2013, known only from south of the Amazon river, in the Madeira-Tapajós interfluve, Amazonas state, Brazil; *A. masniger* (Morales, 2002), known only from the lower drainages of the Río Tapajos, south of the Amazon river, Pará state, Brazil; *A. nidicola* (Caldwell and Lima, 2003), reported from south of the Amazon river in the Amazonas and Rondônia states, Brazil; and *A. paleovarzensis* Lima, Caldwell, Biavati, and Montanarin, 2010, reported from a few localities on both sides of the Amazon river, Amazonas state, Brazil (Kaefer and Lima 2012). Comparisons with these species are provided below.

Allobates amissibilis is distinguished immediately from *A. caeruleodactylus* by larger SVL in male (16.3–17.5 mm, *n*=5 vs 15.0–16.3, *n*=12 in *A. caeruleodactylus*), by lacking sky-blue digits and blue discs on toes in male (present in *A. caeruleodactylus*), and by having faint dark brown transverse crossbars on legs (absent in *A. caeruleodactylus*).

Allobates amissibilis is distinguished readily from *A. crombiei* by smaller SVL in male (16.3–17.5 mm, *n*=5 vs 17.4–19.0, *n*=n/a in *A. crombiei*), and by having a broad oblique lateral stripe extending from groin to about midbody length (absent in *A. crombiei*).

Allobates amissibilis differs from *A. grillisimilis* mainly by larger SVL in male (16.3–17.5 mm, n=5 vs 12.8–15.9, n=33 in *A. grillisimilis*), by having the belly colouration cream to yellow in both sexes (white to translucent in both sexes in *A. grillisimilis*), and the throat suffused with dark pigment in male (few melanophores located on chin only).

Allobates amissibilis is distinguished from *A. masniger* by the following combination of characters (those of *A. masniger* in parentheses): smaller SVL in male (16.3–17.5 mm, n=5 vs 17.9–19.5, n=n/a in *A. masniger*), absence of conspicuous dorsolateral stripe (usually present and conspicuous), presence of a broad oblique lateral stripe extending from groin to about midbody length (usually absent), absence of dark blotches ventrolaterally (present), belly cream to yellow (grey or light grey), and lighter throat colour (usually very dark).

Allobates amissibilis is distinguished from *A. nidicola* by smaller SVL in male (16.3–17.5 mm, *n*=5 vs 18.5–21.0, *n*=30 in *A. nidicola*), and by the same combination of characters mentioned above to distinguish *A. amissibilis* from *A. masniger* [*A. masniger* and *A. nidicola* are morphologically almost identical (Tsuji-Nishikido et al. 2012)].

Allobates amissibilis mainly differs from *A. paleovarzensis* by the combination of much smaller SVL in male (16.3–17.5 mm, *n*=5 vs 18.3–22.4, *n*=31 in *A. paleovarzensis*), Finger III not swollen in male (weakly swollen in *A. paleovarzensis*), and lack of a broad dorsolateral stripe (usually present in *A. paleovarzensis*, when present a diffuse narrow line in *A. amissibilis*).

Two described species have recently been assigned to a phylogenetic clade that is shared with *Allobates amissibilis* (see Fouquet et al. 2013, under the name *A.* sp "Iwokrama"): *A. conspicuus* (Morales, 2002), from eastern Peru and western Brazilian Amazonia; and *A. insperatus* (Morales, 2002), from the eastern slopes of the Andes in Ecuador.

Allobates amissibilis is distinguished immediately from *A. conspicuus* by the combination of a larger SVL in male (16.3–17.5 mm, *n*=5 vs 15.4–16.5, *n*=n/a in *A. conspicuus*), lack of a broad dorsolateral stripe (present in *A. conspicuus*, when present a diffuse narrow line in *A. amissibilis*), presence of a broad oblique lateral stripe extending from groin to about midbody length (reported as absent in the original description of *A. conspicuus*), and throat colour sexually dimorphic (not sexually dimorphic in *A. conspicuus*).

Allobates amissibilis is distinguished readily from *A. insperatus* by the lack of a broad dorsolateral stripe (present in *A. insperatus*, when present a diffuse narrow line in *A. amissibilis*), and a cream to yellow belly in male and female (white in both sexes in *A. insperatus*).

Description of the Holotype An adult male 16.3 mm SVL (Figs. 2a,b; 3a–c, additional measurements in Table 1) in good condition, except for a few superficial scars on posterior body and a large incision in the left thigh for tissue sample; body slender; head 1.1x wider than long; head length 30.0 % of SVL; head width 33.1 % of SVL; snout broadly rounded in dorsal view, acutely rounded in lateral view, extending past lower jaw, snout 57.1 % of head length. Nares located laterally, opening posterolaterally; canthus rostralis rounded, loreal region slightly concave, flaring slightly at upper lip; internarial distance 38.9 % of head width; eye-naris distance 30.6 % of head length; 68.2 % of eye length. Tympanum subcircular, directed posterolaterally, 40.1 % of eye length, separated from eye by a distance equal to 25.6 % of tympanum diameter; supratympanic fold absent, supratympanic area slightly concave; tympanic annulus visible anteroventrally, posterodorsal aspect of tympanum barely visible. Tongue attached anteriorly, broadly rounded posteriorly, longer than wide, median lingual process absent. Choanae very small, subcircular, lateral. Vocal slits long, lateral. Very small teeth present on maxillary and premaxillary, dentigerous process of vomers absent. Cloacal tubercles absent; vent at level of upper thighs, a small anal flap above it. Skin granular on dorsum, granules weakest on head, largest posteriorly; one distinctly enlarged tubercle on each eyelid; belly smooth.

Forelimb slender, skin smooth; metacarpal ridge absent; ulnar fold absent; hand length 23.3 % of SVL; Finger I longer than II when fingers adpressed; fingers unwebbed, lateral fringes absent; Finger III not swollen; tip of Finger IV not reaching distal subarticular tubercle on Finger III when fingers adpressed; terminal discs weakly expanded, slightly wider than long, equal to or slightly larger than the width of the distal phalanges; width of disc on Finger III 0.40 mm; discs with distinct dorsal scutes. Relative lengths of adpressed fingers III > I > II > IV; palmar tubercle large, ovoid, 0.56 mm in its largest diameter, 14.7 % of hand length, anterior periphery pigmented; thenar tubercle distinct, but not protuberant, ovoid, anterior periphery pigmented, about half the size of the palmar tubercle and narrowly separated from it. One subarticular tubercle on Fingers I, II, and IV; two subarticular tubercles on Finger III; subarticular tubercle on Finger I largest, subarticular tubercle on Finger II and basal subarticular tubercle on Finger III subequal; subarticular tubercle on Finger IV and distal subarticular tubercle on Finger III smaller, distal tubercle on Finger III smallest (Fig. 4).

Hindlimb robust, skin granular; tibia length 46.6 % of SVL; heels overlapping when hindlimbs are flexed at right angles to sagittal plane of body; foot length 41.1 % of SVL; relative length of adpressed toes IV > III > V > II > I; Toe I very short, its tip reaching the base of the subarticular tubercle on Toe II when toes are adpressed on left foot, failing to reach the base of the subarticular tubercle on Toe II when toes are adpressed on right foot; discs on Toes II, III, IV, and V larger than width of distal phalanges; disc on Toe I equal to width of distal phalange. Width of disc on Toe IV 0.70 mm; rudimentary webbing present only between Toes III-IV, webbing slightly pigmented; weak pre- and postaxial fringes on Toes II-III (preaxial ones more conspicuous) and weak preaxial fringe on Toe IV (more conspicuous than on Toes II-III). Inner metatarsal tubercle oval, 0.53 mm in length, distal portion pigmented, outer metatarsal tubercle round, projecting, 0.33 mm in diameter, entirely pigmented; medial metatarsal tubercle absent on both feet, a weak metatarsal "bump" on right foot. Two subarticular tubercles present on Toes III and V, here on Toe IV, and one on Toes I and II. Subarticular tubercles on Toes I and II largest; basal subarticular tubercle on Toe IV very small on both feet. Metatarsal fold absent. Tarsal keel well defined, short, tuberclelike, directed transversely across tarsus, located 1.10 mm from proximal edge of inner metatarsal tubercle, not extending from it (Fig. 4).

Fig. 4 *Allobates amissibilis* sp. nov. Left hand (*left*), and left foot (*right*) of the male holotype (IRSNB 4155) . Photographs by P.J.R.K. *Bar* 5 mm

Colour of the Holotype in life Dorsum chestnut brown with granules slightly darker than background; dorsal surface of head similar in colour to dorsum, but with a slight metallic tint. Wide lateral black band from tip of snout to vent, containing ca. two-thirds of tympanum, widening posteriorly from axilla. Very thin, barely distinguishable light line above the band, apparently extending from tip of snout to vent. Broad, diffuse pale oblique lateral stripe embedded in the black band, extending from groin to ca. midbody length. Flanks whitish; ventrolateral stripe present, whitish, barely visible. Upper lip whitish, suffused with tiny melanophores. Throat pinkish grey, suffused with dark pigment. Belly cream.

Upper surfaces of thighs and shanks dark brown, with a few darker blotches and three faint dark brown transverse crossbars (one on thigh, one on shank, and one on tarsus, which appear as a single stripe when legs are bent). Pale paracloacal marks present, pale orangish yellow. Pale yellow spot on groin. Forelimbs light orangish brown, with a short dark brown line tapering from arm insertion to elbow. Toes dark brown with some light grey blotches. Fingers light brown with some pale blotches. Palm brown, sole dark brown. Iris metallic copper with black reticulations, pupil ring present only above the pupil.

Colour of the Holotype in preservative Dorsum dark brown with granules slightly darker than background; dorsal surface of head slightly darker than body. Wide lateral black band from tip of snout to vent. Broad, diffuse pale oblique lateral stripe embedded in the black band, extending from groin and reaching arm insertion. Flanks white; ventrolateral stripe indistinct. Upper lip white, finely suffused with tiny melanophores (best seen under magnification). Throat white, finely suffused with dark pigment (best seen under magnification). Belly white.

Upper surfaces of thighs and shanks similar in colour to dorsum, with a few darker blotches, three faint dark brown transverse crossbars (one on thigh, one on shank, and one on tarsus). Pale paracloacal marks present. Forelimbs very light brown, with a short inconspicuous brown line tapering from arm insertion to elbow. Toes dark brown with some white blotches. Fingers very light brown with some white blotches. Palm light brown, sole dark brown.

Male secondary sexual characters Males are smaller than the only known female (mean SVL in males 16.9 mm, female 17.8 mm) and have a pinkish grey throat suffused with melanophores in life (throat immaculate yellow in living female) (Fig. 5). These melanophores are less conspicuous, but still well visible in preservative and allow distinction between sexes in preserved specimens. Lateral fringes on Toes II–IV (preaxial only on the latter) are weak but visible in males, almost undetectable in the single female.

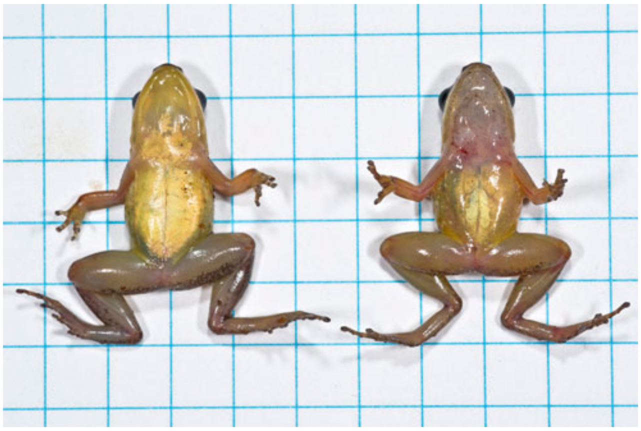


Fig. 5 *Allobates amissibilis* sp. nov. Ventral views of the female allotype (IRSNB 4156, *left*), and a male paratype (IRSNB 4158, *right*), showing sexually dimorphic throat colouration. Photographs by P.J.R.K. *Grid squares* 5 mm

Variation among paratypes Except the sexual dimorphism in size, the nature of lateral fringes on toes, the throat colour (see above), and insignificant differences in morphometrics (measurements of the type series are provided in Table 1), all paratypes conform to the description of the holotype, except as follows: in life, dorsal colour varies from light brown to chestnut brown; lateral dark band varies from dark brown to black; colour of upper surfaces of thighs and shanks varies from brown to dark brown; colour of forelimbs varies from very light brown to orangish brown; ventral colour varies from cream to bright yellow; in MTD 47884 (male) the oblique lateral stripe fails to reach midbody length (Fig. 2). In preservative, dorsal colour varies from light grey to dark brown (Fig. 3 shows this variation, which is not related to sex). The enlarged tubercle on eyelid was well visible in all specimens in life (see Fig. 2e for instance), but in some cases becomes less conspicuous in preserved specimens (that character is not sexually dimorphic as it can be observed in both males and females, however, whether the distinctness of the eyelid tubercle is subject to physiological plasticity cannot be fully assessed given the comparatively small sample size). A weak medial metatarsal tubercle is present in two specimens. The single juvenile collected (referred specimen) further differs in having an “hourglass” pattern on dorsum.

Advertisement call

Temporal structure 6 min, 20 s of call recorded from the holotype include 52 calls emitted between silent intervals and containing 1–19 notes each (Fig. 6). The most common number of notes within a call is 10 (27 % of calls) followed by 11 (21 %), 9 (15 %), and 12 (13 %). Additional calls of 1, 5, 6, 8, 13, 15, or 19 notes each represent 2 to less than 6 % of the total number of calls, and ca. 23 % of the total number of calls if considered altogether.

Eleven representative calls (covering the observed variation in number of notes/call) have been analyzed, totalling a sample of 109 notes (see Table 2 for measurements of acoustic parameters). Note duration ranges from 0.024–0.044 s (mean 0.035 s±0.005); call duration ranges from 0.029 to 7.976 s (mean 3.411 s±2.0); inter-note interval within a call ranges from 0.277 to 0.623 s (mean 0.344 s±0.06). Call rate is 8.3 calls/min in the call sequence recorded. Silent interval between calls ranges from 1.627 to 19.709 s (mean 3.715 s±2.72), and is usually ca. 2–7 s.

Amplitude modulations are variably evident in the oscillograms and range from none to two (Fig. 7).

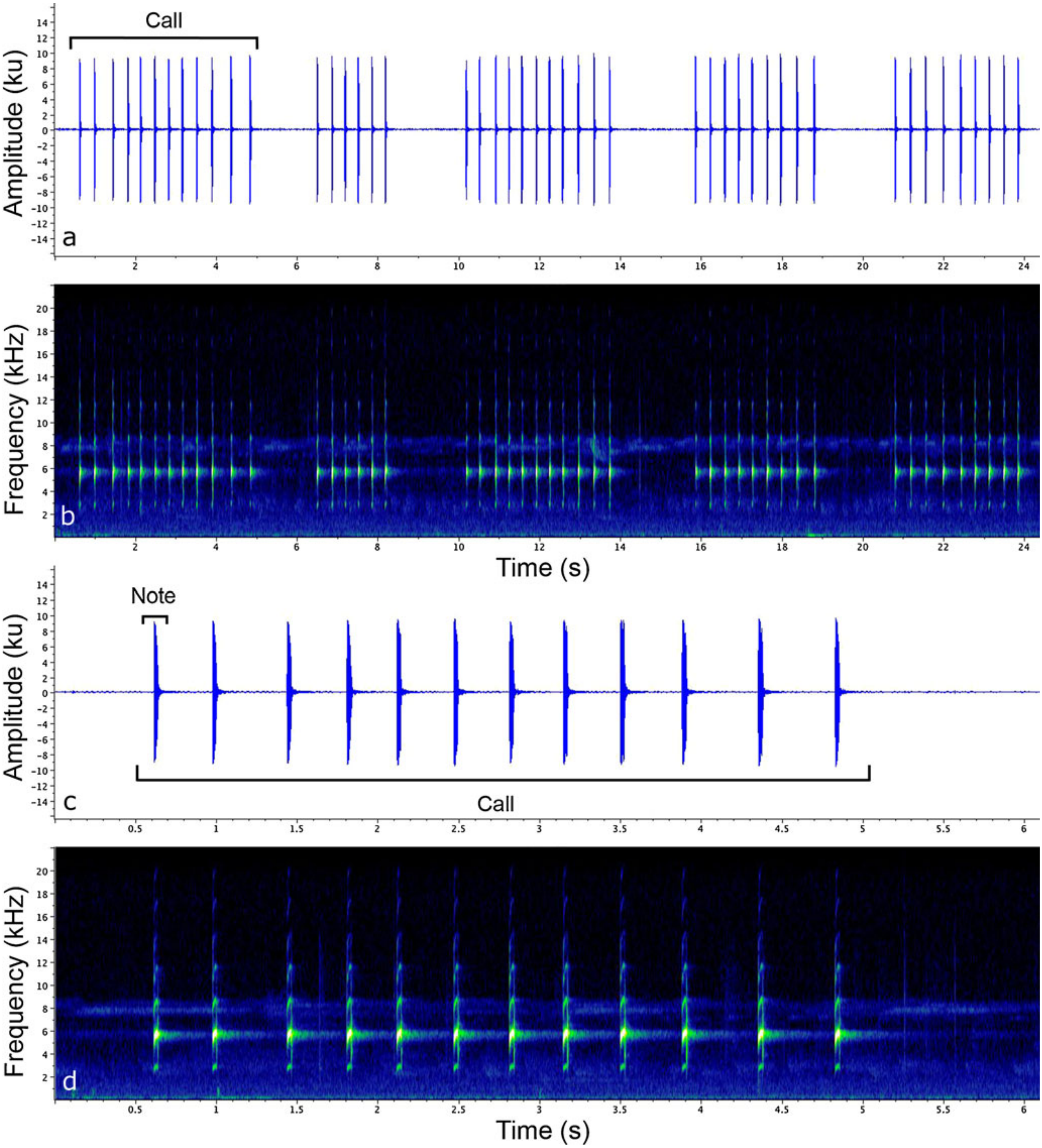


Fig. 6 **a–d** Vocalisation of *Allobates amissibilis* sp. nov., holotype. **a** Oscillogram showing five calls emitted between silent intervals (sequence of 24 seconds). **b** Spectrogram of the same sequence. **c** Oscillogram of a single call containing 12 notes. **d** Spectrogram of the same call. Temperature during recording was 25 °C

Spectral structure Seven harmonics are visible, with the dominant frequency being located in the second harmonic (Figs. 6–8); the highest (seventh) harmonic is sub-ultrasonic (spectral energy in the ultrasonic range, i.e. slightly above 20,000 Hz, on at least one occasion, see Table 2). The dominant frequency ranges from 5,064 to 5,845 Hz (mean 5,522.26 Hz±97.40); the frequency of the highest (seventh) harmonic ranges from 18,447 to 20,481 Hz (mean

Table 2 Measurements of acoustic parameters for the holotype of *Allobates amissibilis* sp. nov. See text for method

	Note #	Number of harmonics	Note duration (s)	Inter-note interval (s)	Call duration (s)	Dominant frequency (Hz)	Highest harmonic frequency (Hz)
1-note call	1	7	0.029		0.029	5,465	19,341
5-note call	1	7	0.033	0.485		5,418	19,555
	2	7	0.039	0.317		5,465	19,056
	3	7	0.032	0.345		5,418	18,913
	4	7	0.032	0.338		5,441	18,961
	5	7	0.033		1.653	5,489	19,531
6-note call	1	7	0.040	0.323		5,463	19,543
	2	7	0.033	0.293		5,512	19,543
	3	7	0.032	0.294		5,645	19,692
	4	7	0.043	0.292		5,645	19,708
	5	7	0.034	0.300		5,612	19,527
	6	7	0.043		1.728	5,629	19,576
8-note call	1	7	0.038	0.336		5,513	19,393
	2	7	0.036	0.300		5,513	19,709
	3	7	0.032	0.293		5,608	19,476
	4	7	0.032	0.296		5,513	19,593
	5	7	0.033	0.300		5,489	19,659
	6	7	0.041	0.346		5,536	19,526
	7	7	0.032	0.372		5,489	19,559
	8	7	0.032		2.519	5,489	19,493
9-note call	1	7	0.033	0.323		5,489	19,593
	2	7	0.032	0.367		5,536	19,460
	3	7	0.031	0.305		5,631	19,393
	4	7	0.033	0.289		5,465	19,692
	5	7	0.032	0.435		5,607	19,593
	6	7	0.032	0.331		5,489	19,476
	7	7	0.035	0.320		5,631	19,476
	8	7	0.036	0.365		5,513	19,725
	9	7	0.032		3.032	5,489	19,576
10-note call	1	7	0.032	0.291		5,631	19,460
	2	7	0.029	0.496		5,536	19,493
	3	7	0.029	0.328		5,513	19,642
	4	7	0.030	0.305		5,631	19,576
	5	7	0.037	0.309		5,631	19,659
	6	7	0.031	0.322		5,655	19,792
	7	7	0.031	0.315		5,631	19,676
	8	7	0.037	0.328		5,631	19,659
	9	7	0.037	0.323		5,631	19,659
	10	7	0.035		3.346	5,655	19,510
11-note call	1	7	0.029	0.297		5,631	19,346
	2	7	0.042	0.351		5,536	19,484
	3	7	0.042	0.290		5,845	20,481
	4	7	0.033	0.287		5,608	19,698
	5	7	0.044	0.309		5,465	19,079
	6	7	0.044	0.281		5,489	19,555
	7	7	0.044	0.285		5,512	18,984
	8	7	0.034	0.353		5,465	19,650
	9	7	0.037	0.358		5,465	19,460

Table 2 (continued)

	Note #	Number of harmonics	Note duration (s)	Inter-note interval (s)	Call duration (s)	Dominant frequency (Hz)	Highest harmonic frequency (Hz)
	10	7	0.033	0.342		5,489	19,508
	11	7	0.034		3.570	5,465	19,389
12-note call	1	7	0.032	0.327		5,346	18,910
	2	7	0.026	0.394		5,465	19,161
	3	7	0.032	0.311		5,441	19,493
	4	7	0.036	0.324		5,489	19,875
	5	7	0.033	0.339		5,489	19,593
	6	7	0.031	0.300		5,536	19,609
	7	7	0.031	0.378		5,489	19,427
	8	7	0.032	0.332		5,560	19,443
	9	7	0.031	0.312		5,655	19,476
	10	7	0.031	0.391		5,631	19,476
	11	7	0.031	0.402		5,655	19,627
	12	7	0.031		4.181	5,489	19,559
13-note call	1	7	0.037	0.315		5,612	19,443
	2	7	0.039	0.292		5,629	19,460
	3	7	0.032	0.324		5,529	19,443
	4	7	0.036	0.299		5,612	19,510
	5	7	0.032	0.324		5,596	19,526
	6	7	0.033	0.346		5,612	19,759
	7	7	0.035	0.292		5,612	19,759
	8	7	0.041	0.314		5,496	19,709
	9	7	0.031	0.317		5,596	19,626
	10	7	0.042	0.310		5,596	19,510
	11	7	0.036	0.444		5,612	19,642
	12	7	0.033	0.390		5,596	19,676
	13	7	0.033		4.428	5,496	19,360
15-note call	1	7	0.034	0.307		5,496	19,227
	2	7	0.038	0.304		5,479	19,377
	3	7	0.042	0.470		5,479	19,377
	4	7	0.041	0.375		5,496	19,410
	5	7	0.042	0.294		5,446	19,061
	6	7	0.042	0.329		5,463	19,410
	7	7	0.041	0.286		5,463	19,410
	8	7	0.041	0.303		5,430	19,360
	9	7	0.041	0.313		5,463	19,161
	10	7	0.043	0.290		5,463	19,344
	11	7	0.044	0.277		5,430	19,443
	12	7	0.041	0.291		5,463	19,360
	13	7	0.043	0.312		5,446	19,061
	14	7	0.041	0.295		5,463	19,078
	15	7	0.042		5.064	5,430	19,360
19-note call	1	7	0.024	0.413		5,064	18,447
	2	7	0.028	0.410		5,280	18,447
	3	7	0.031	0.406		5,380	18,929
	4	7	0.031	0.388		5,380	18,845
	5	7	0.031	0.403		5,430	19,028
	6	7	0.033	0.356		5,430	19,012

Table 2 (continued)

Note #	Number of harmonics	Note duration (s)	Inter-note interval (s)	Call duration (s)	Dominant frequency (Hz)	Highest harmonic frequency (Hz)
7	7	0.034	0.352		5,463	19,261
8	7	0.038	0.623		5,463	18,978
9	7	0.035	0.341		5,496	19,543
10	7	0.031	0.374		5,629	19,629
11	7	0.034	0.331		5,629	19,493
12	7	0.037	0.369		5,463	19,676
13	7	0.036	0.365		5,629	19,626
14	7	0.035	0.382		5,629	19,576
15	7	0.039	0.582		5,479	19,509
16	7	0.036	0.365		5,479	19,593
17	7	0.037	0.320		5,496	19,344
18	7	0.031	0.562		5,645	19,344
19	7	0.034		7.976	5,396	19,593

19,444.79 Hz±275.74). The dominant frequency is slightly modulated upward (Fig. 8).

Comparisons with calls of cryptically coloured congeneric species from the Guiana Shield and peripheral areas The advertisement calls of 9 of the 12 cryptically coloured *Allobates* species currently reported from the Guiana Shield and peripheral areas are known. However, comparison between species is often difficult because call descriptions are sometimes very brief or incomplete. Most analyses lack the necessary standardisation for reliable diagnoses. We relied on original descriptions for the comparisons provided below (except for *A. granti* and *A. spumaponens* for which we have call recordings).

The advertisement call of *Allobates amissibilis* is distinguished mainly from the call of *A. granti* (described by Kok et al. 2006, see also Kok and Ernst 2007) in having one pulse/note (two distinct pulses/note in *A. granti*), and a shorter note duration ranging from 0.024 from 0.044 s (0.068–0.070 s in *A. granti*) (see also Fig. 8); from the call of *A. spumaponens* (described by Kok and Ernst 2007) in being emitted in groups of notes between silent intervals (call continuous in *A. spumaponens*), in having a shorter note duration ranging from 0.024 to 0.044 s (0.060–0.070 s in *A. spumaponens*), and in having seven harmonics visible (two in *A. spumaponens*) (see also Fig. 8); from the call of *A. marchesianus* (described by Caldwell et al. 2002) by containing 1–19 notes per call (21–24 notes in *A. marchesianus*), in having longer inter-note interval ranging from 0.277 to 0.623 s (0.119–0.212 s in *A. marchesianus*), and in having seven harmonics visible (three in *A. marchesianus*); from the call of *A. undulatus* (described by Myers and Donnelly 2001) by containing 1–19 notes per call (2 notes in *A. undulatus*), and in having a higher dominant frequency ranging from 5,064 to 5,845 Hz (ca. 3,300–3,900 Hz in *A. undulatus*); from the call of *A. caeruleodactylus* (described by Lima and Caldwell 2001) in being emitted in groups of notes between silent intervals (call usually continuous in *A. caeruleodactylus*), and in having a dominant frequency below ca. 6,000 Hz (above ca. 6,000 Hz in *A. caeruleodactylus*); from the call of *A. grillisimilis* (described by Simões et al. 2013) in being much slower, with a call duration of ca. 3 s on average (always less than ca. 0.3 s in *A. grillisimilis*), and with much longer inter-note interval (within a same call) ranging from 0.277 to 0.623 s (0.010–0.043 s in *A. grillisimilis*); from the call of *A. masniger* (described by Tsuji-Nishikido et al. 2012) and the call of *A. nidicola* (described by Caldwell and Lima 2003, see also Tsuji-Nishikido et al. 2012) in being emitted in groups of notes between silent intervals (call continuous in *A. masniger* and *A. nidicola*), and in having a dominant frequency always above ca. 5,000 Hz (always below ca. 5,000 Hz in *A. masniger* and *A. nidicola*); and from the call of *A. paleovarzensis* (described by Lima et al. 2010) in being slower, with a call rate of 8.3 calls/min (12–20 calls/min in *A. paleovarzensis*), a call duration of ca. 3 s on average (always less than, or maximum ca. 3 s in *A. paleovarzensis*), and with much longer inter-note interval (within a same call) ranging from 0.277 to 0.623 s (0.065–0.266 s in *A. paleovarzensis*).

Distribution and ecology

Allobates amissibilis is currently known only from two localities: Turu Falls at the foothills of the Iwokrama Mountains, and close to the top of one of the highest unnamed peaks of the Iwokrama Mountains (Fig. 9), between 160 and 950 m elevation, in the Iwokrama Forest Reserve, Guyana. The species is not abundant at any of the known sites, and only a few males were heard calling, very sporadically, in March, May and December. Intensive surveys led in the Iwokrama Forest during the year 1997 (Donnelly et al.

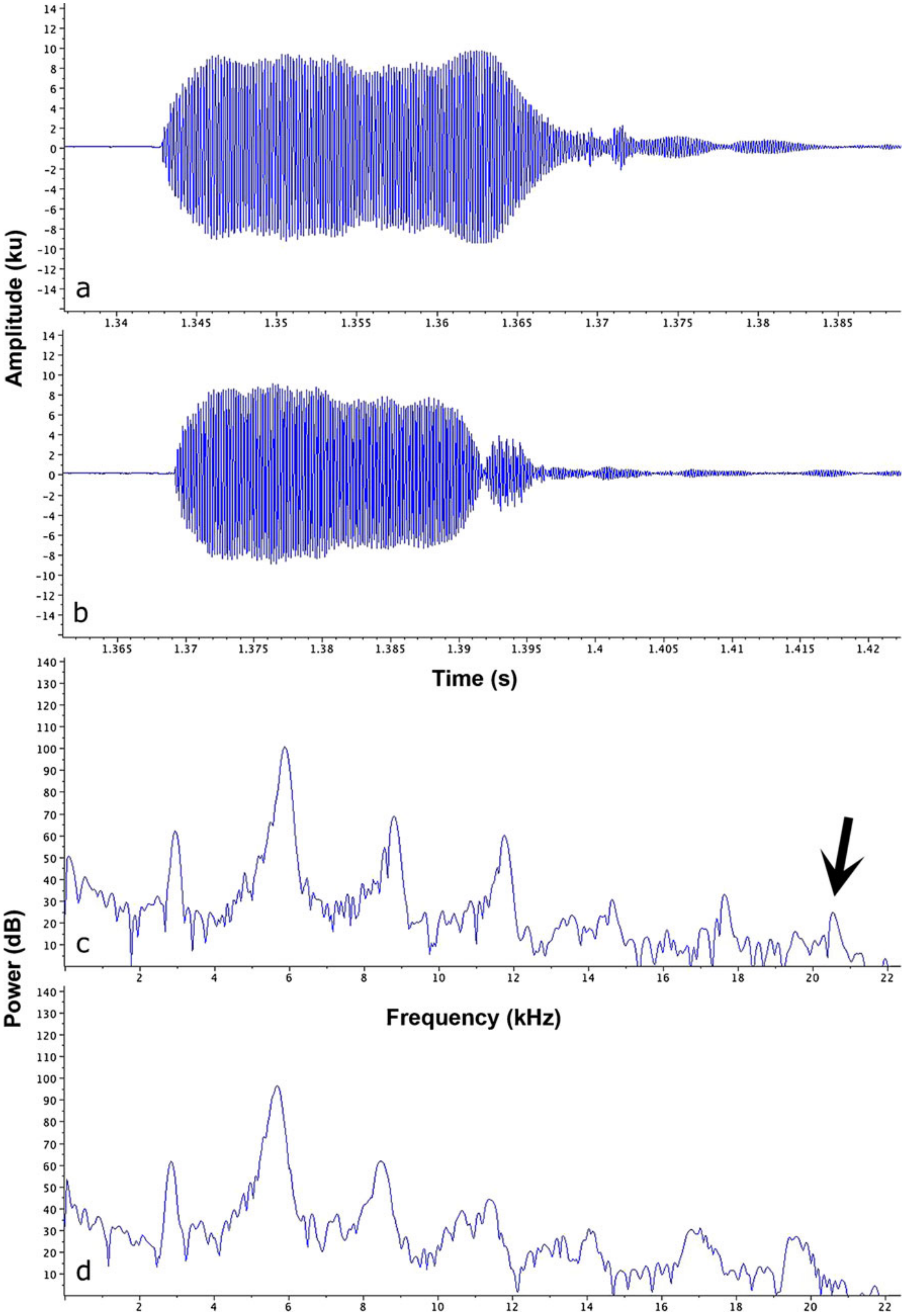


Fig. 7 **a–d** Vocalisation of *Allobates amissibilis* sp. nov., holotype. **a**,**b** Expanded oscillograms of two notes from different calls, showing variation in amplitude modulation. **c**,**d** Spectral slices of the same notes showing the seven harmonics. *Arrow* Spectral energy in the ultrasonic range (i.e. slightly above 20,000 Hz) for the last (seventh) harmonic. Temperature during recording was 25 °C

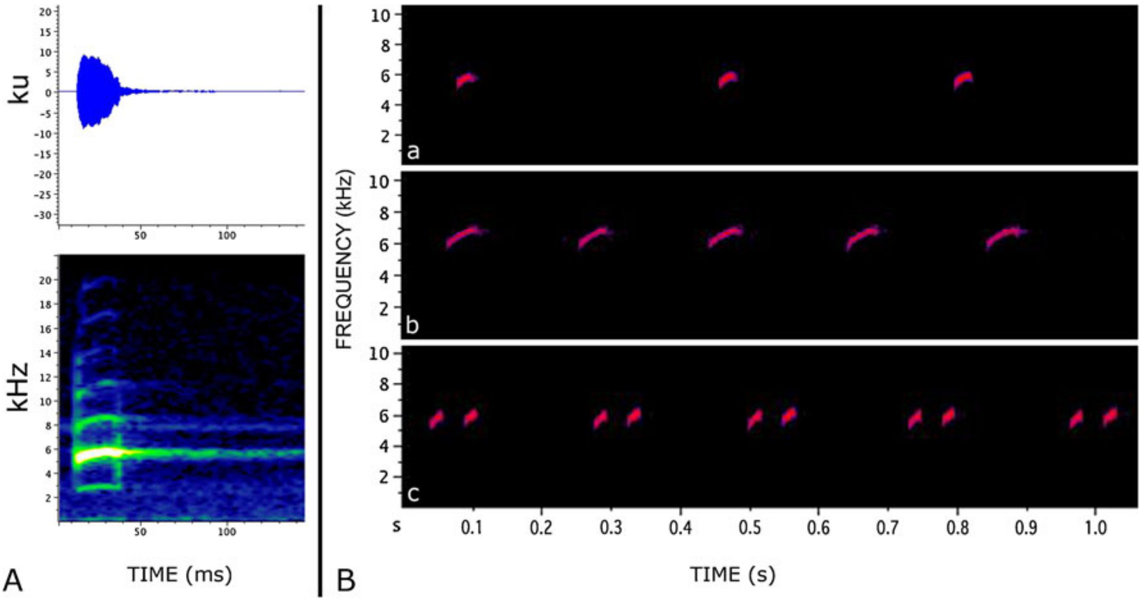


Fig. 8 **a** Vocalisation of *Allobates amissibilis* sp. nov., holotype. Slightly expanded oscillogram and spectrogram of one note, showing frequency modulation (slightly modulated upward). **b** Comparison between 1 s-call sequences (showing dominant frequency only) of three morphologically similar Guiana Shield *Allobates* species (*a*) *Allobates amissibilis* sp. nov. from Turu Falls, Guyana (holotype, IRSNB 4155) (*b*) *Allobates spumaponens* from Mabura Hill Forest Reserve, Guyana (holotype, SMNS 12511) and (*c*) *Allobates granti* from Haute Wanapi, French Guiana (paratype, MNHN 2005.0268, call recorded by Philippe Gaucher). Temperatures during recording were 25 °C [**a**, **b**(*a*), and **b**(*b*)], and ca. 24 °C (Bc)

2005a, b) were unable to collect any specimen of this species, which further suggests low population density and geographic restriction.

Allobates amissibilis was found in open mixed lowland forest and in premontane forest with low and open canopy, in the gorge and on one peak of the Iwokrama Mountains. Interestingly, at both sites *Allobates amissibilis* was found in close vicinity to freshly dropped tapir (*Tapirus terrestris*) faeces. Whether frogs benefit from the presence of tapirs by feeding on insects that are attracted by their faeces or by using water filled tapir foot prints/tracks as alternative larval/reproduction habitats is unknown.

Males call from the ground, often sitting slightly above the substrate, such as on a rock or an exposed root. Advertisement calls are apparently triggered by rain, but a few males were heard calling during dry periods. No male carrying tadpoles has been found, the tadpole is unknown, and virtually nothing is known about the reproductive biology of the species.

Phylogenetic relationships

Molecular phylogenetic relationships of the new species are illustrated in Fouquet et al. (2013: Fig. 3, under the name *Allobates* sp. "Iwokrama" using sequence data from the paratype MTD 47884). We therefore refrain from presenting a separate phylogenetic analysis until additional data on species not included in Fouquet et al. (2013) are available. These authors highlighted a sister relationship between the new species (under the name *Allobates* sp. "Iwokrama") and a clade containing *A. conspicuus*, *A. insperatus*, and an undescribed species from Cuyabeno (NW Ecuador). The clade containing these four species is sister to the *trilineatus* clade of Grant et al. (2006).

Discussion

Although the genus *Allobates* is renowned as a taxonomically difficult group, there is strong converging evidence to consider *A. amissibilis* as distinct from all known congeners by combining morphology, bioacoustics and genetics. This underlines yet again the usefulness of so-called "integrative taxonomy", especially in taxonomically challenging groups.

The new species is the third microendemic reported from the Iwokrama Mountains together with the caecilian *Caecilita iwokramae* and the lizard *Gonatodes timidus*. The occurrence of three species belonging to very distantly related taxa sharing a very restricted range is remarkable and suggests that the Iwokrama Mountains could be an area of endemism. The possible mechanisms behind this phenomenon will be further addressed in a separate publication.

The phylogenetic position of the new species is no less noteworthy because it was recovered as the sister taxon of a group of geographically very distant species (eastern slopes of the Andes in Ecuador [*A. insperatus*], eastern Peru and western Brazilian Amazonia [*A. conspicuus*], and northwestern Ecuador [*A.* sp "Cuyabeno"]). However, the non-inclusion of some taxa (e.g. *A. sanmartini*, *A. sumtuosus*, *A. crombiei*, and

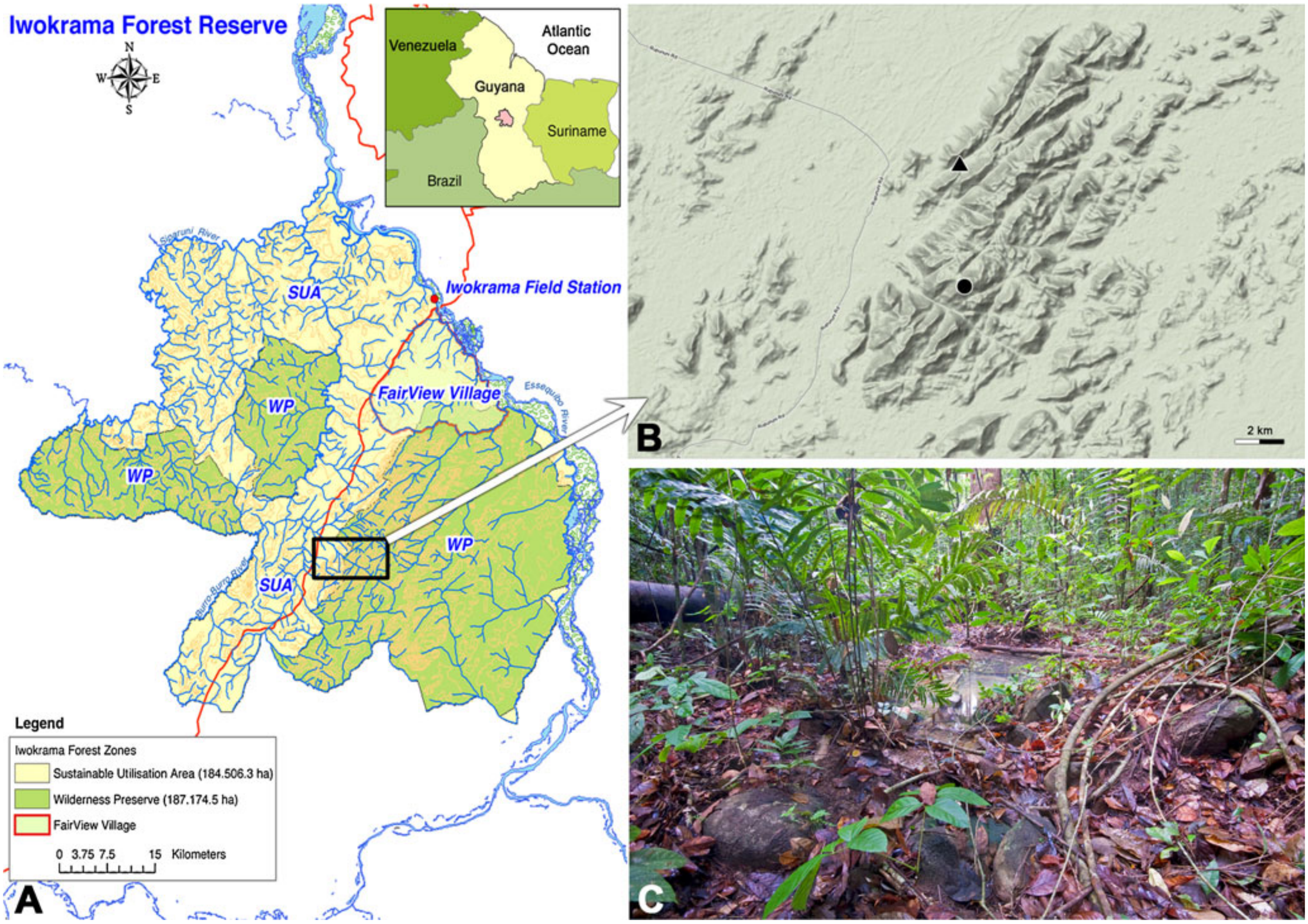


Fig. 9 **a–c** Distribution and habitat of *Allobates amissibilis* sp. nov. **a** Map of the Iwokrama Forest Reserve in Guyana. *Black rectangle* Iwokrama Mountains (enlarged in **b**). The *line* crossing the Reserve is the road between Linden and Lethem. **b** The two sites where the new species was collected in the Iwokrama Mountains. *Triangle* Type locality (Turu Falls), *dot* unnamed summit where an additional specimen was obtained. **c** Macrohabitat of *Allobates amissibilis* sp. nov. at the type locality. Photograph by P.J.R.K. Map in **a** courtesy of Iwokrama International Centre for Rainforest Conservation and Development, map in **b** © Google Map

A. grillisimilis) in the phylogenetic analyses is currently an obstacle to phylogenetic accuracy, and prevents us from drawing concluding affinity and biogeographic inferences at this point.

The presence of a distinctly enlarged tubercle on each eyelid is of potential diagnostic value since similar eyelid tubercles were not observed in comparative material (see Appendix). But confirming the presence or absence of a similar structure in other congeneric species would require a systematic assessment of large series of additional material, which is beyond the scope of this study.

Because appropriate data on population sizes and possible decline are currently insufficient to make any sound assessment of its risk of extinction, we suggest that *Allobates amissibilis* be classified as "Data Deficient" (DD) in accordance with IUCN (2001). However, because of its apparent very limited distribution it is likely that the species status could be raised to "Vulnerable" (VU), "Endangered" (EN), or even "Critically Endangered" (CR), and although the Iwokrama Mountains lie in a Wilderness Preserve (WP) area (where even sustainable uses of the forest are forbidden), environmental impact assessments should be implemented to determine whether the species should be considered vulnerable and prone to population decline, or even extinction. This appears particularly important in the light of the prospective development of Turu Falls as an ecotourism site, which, if not planned carefully, could alter this ecosystem substantially and put the long-term viability of these populations at stake.

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Experiments comply with the current laws of the country in which they were performed.

Conflict of interest The authors declare that they have no conflict of interest.

Appendix: Additional specimens examined

Allobates femoralis

FRENCH GUIANA: Regina: Pic Matécho (03°44' N, 53°29' W), IRSNB 13025. Roura: Crique Bagot, IRSNB 12682. Saül: Saül, Montagne Belvédère (3°37' N, 53°10' W, elevation ca. 250 m), ca. 7 km SE from the village, IRSNB 12910, IRSNB 12930. GUYANA: no other locality, IRSNB 7507.

Allobates granti

FRENCH GUIANA: Grand Santi: Montagne Kotika (elevation 700 m), MNHN 2005.0272–74 (paratypes); MNHN 2005.0276–77 (tadpoles). Maripasoula: Haut Marwani (02°36' N, 54°01' W, elevation 159 m), MNHN 2005.0269–71 (paratypes); Maripasoula, Haute Wanapi (02°30' N, 53°49' W, elevation 192 m), MNHN 2005.0268 (paratype). Saül: Saül, Montagne Belvédère (3°37' N, 53°10' W, elevation ca. 250 m), ca. 7 km SE from the village, IRSNB 1932 (holotype), IRSNB 1933 (paratype), IRSNB 1935–36 (paratypes), ULABG 6816 (ex-IRSNB 1937) (paratype); Saül, along the trail between the airstrip and the village, IRSNB 1934 (paratype); Saül, Chemin des Gros Arbres, MNHN 2005.0275 (paratype). St-Georges: Piton Armontabo (elevation 150 m), Layon Est, MNHN 2005.0266–67 (paratypes).

Allobates spumaponens

GUYANA: Upper Demerara-Berbice: Mabura Hill Forest Reserve (5°09' N, 58°41' W, elevation ca. 100 m), SMNS 12511 (holotype), SMNS 12510, SMNS 12512–16 (paratypes), MTD 47771.

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