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Two new species of *Allobates* of the *trilineatus* clade (Anura: Aromobatidae) from the Eastern Guiana Shield

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Abstract

The actual diversity of anurans occurring in Amazonia remains only partly described. This is notably the case of the species of the genus *Allobates* despite a fast rate of species description in this genus during the last decade. This increasing taxonomic effort has been particularly facilitated by the availability of DNA sequences throughout the region. These data suggest for instance the existence of three lineages in the Guiana Shield that may correspond to unnamed species. We examined morphology and calls of these putative species and compared them to related nominal species, which confirmed that two of these lineages not only differ genetically but also morphologically and bioacoustically. These two species are thus named and described herein. *Allobates vicinus* sp. nov. from northern Suriname forms a clade with another candidate species from southern Suriname and Northern Pará, (Brazil) and with *A. granti* that occurs in French Guiana. *Allobates ripicolus* sp. nov. occurs throughout the eastern Guiana Shield and is nested within the *A. tapajos* complex which otherwise occurs in southeastern Amazonia and comprises *A. tapajos* and *A. kamilae* along with three additional candidate species.

Keywords: Acoustics; Amazonia; Amphibia; Morphology; Neotropics; Taxonomy

Introduction

With 60 currently valid nominal species, *Allobates* Zimmermann and Zimmermann, 1988 is a highly diverse genus of frogs (Frost 2023), particularly in Amazonia (>85% of nominal species) where the genus started to diversify some 25 Ma (Réjaud et al. 2020). The distributions and the relationships among *Allobates* species provide a striking example of regional endemism within Amazonia and how hydrological changes during the Neogene affected the diversification of the Amazonian lineages (Réjaud et al. 2020). With 20 (35%) of the nominal species having been described since 2010 (e.g. Lima et al. 2020; Melo-Sampaio et al., 2020; Souza et al. 2020; Gagliardi-Urrutia et al. 2021; Moraes & Lima 2021; Ferrão et al. 2022; Silva et al. 2022) and with the existence of many additional putatively unnamed species (Réjaud et al. 2020; Vacher et al. 2020; Ferrão et al. 2022), this genus also exemplifies the large proportion of yet undocumented diversity of frogs inhabiting Amazonia. This pattern has been highlighted many times already, notably in the Guiana Shield by DNA-based estimations (e.g. Vacher et al. 2020) and the fast pace of species description in the region (e.g. Guerra et al. 2020; Rivera-Correa et al. 2021).

Several previous studies (Vences et al. 2003; Fouquet et al. 2007; Vacher et al. 2020; Réjaud et al. 2020) have identified mtDNA lineages of *Allobates* from the Guiana Shield that could not be assigned to any known taxon or that were misidentified. For instance, a species from French Guiana has been erroneously identified as *Colostethus beebei* (Noble, 1923) (Lescure & Marty 2000), a species that is in fact endemic to the uplands of Guyana and later assigned to the genus *Anomaloglossus* Grant et al. 2006 while the French Guiana species was

later described as *Colostethus* (= *Allobates*) *granti* (Kok, MacCulloch, Gaucher, Poelman, Bourne, Lathrop, and Lenglet, 2006). Subsequently, related populations from Suriname and northern Pará (Brazil) were either considered conspecific or as belonging to a candidate species because of the substantial mtDNA divergence with French Guiana populations (Fouquet et al. 2007; 2012; 2015a; Grant et al. 2017; Vacher et al. 2020; Réjaud et al. 2020). Réjaud et al. (2020: Fig. S2) identified two major lineages, one in French Guiana and another one in Suriname and northern Pará but mistakenly assigned these last populations to *A. granti* instead of to a candidate species. Moreover, a subdivision exists between northern Suriname vs. southern Suriname and northern Pará that may hide additional species boundaries. The absence of allele sharing on a nuclear locus (Fouquet et al. 2012) between French Guiana and northern Suriname and a divergence estimated to date back to some 4 Ma (Réjaud et al. 2020) also support the hypothesis that at least two species exist within *Allobates granti* sensu lato but morphological and acoustic data remain to be examined (Fig. 1).

Additionally, another lineage related to *Allobates tapajos* Lima, Simões, and Kaefer, 2015 was documented from French Guiana (Vences et al. 2003; Fouquet et al. 2007; 2012) and more populations were later found in Suriname (Fouquet et al. 2015a) and northern Pará (identified as *A. spumaponens* Kok and Ernst, 2007 by Avila-Pires et al. 2010). This lineage is nested within a clade formed by populations from the southern margin of the Amazon River (Réjaud et al. 2020; Ferrão et al. 2022; Fig. 1), which altogether form six major lineages: two are found in the Tapajós-Xingu interfluvium including *A. tapajos* (Lima et al. 2015), three in the Madeira-Tapajós interfluvium including *A. kamilae* Ferrão, Hanken, and Lima, 2022, leaving possibly four candidate species remaining unnamed within the complex. The divergence between the Guiana Shield populations and their closest southern relatives is estimated to date back some 5 Ma, thus suggesting that they might correspond to distinct species (Réjaud et al. 2020). It is noteworthy, that three other nominal species occur in the eastern lowlands of the Guiana Shield: *Allobates femoralis* (Boulenger, 1884) which is widespread in Amazonia; *Allobates sumtuosus* (Morales, 2002) which occurs on the western part of the region and *Allobates amissibilis* Kok, Hölting, and Ernst, 2013 which is only known from Iwokrama in Guyana.

Phenotypic data of these new lineages found in the Guiana Shield has never been examined. Therefore, we compared the morphology and calls of *Allobates granti* from French Guiana (type locality) with *A. aff. granti* populations from Suriname, as well as of *A. tapajos* from Pará (type locality) and *A. kamilae* from Rondônia (type locality) with *A. aff. tapajos* populations from French Guiana and Suriname. We discovered unambiguous differences among them advocating to consider them as two new species. We therefore describe and name them herein.

Material and Methods

Field work and deposition of specimens

We undertook extensive field work between 2013 and 2019 in French Guiana and in Suriname (notably Sipaliwini, Nassau, Bakhuis, Brownsberg, Voltzberg), collecting specimens, tissue samples, recording advertisement calls and ecological data of numerous *Allobates* populations. Frogs were collected by hand and euthanized with an intraperitoneal injection of Xylocaine® (lidocaine hydrochloride). All specimens were individually tagged, fixed in 10 % formalin, and then transferred to a solution of 70 % ethanol for permanent storage. Newly collected type specimens were deposited in the Museum National d'Histoire Naturelle (Paris, France) (MNHN-RA-2022.0065–0100).

Molecular analyses

We gathered all the 16S sequences available in GenBank forming the *A. granti* and the *A. tapajos* complexes according to Vacher et al. (2020) and Ferrão et al. (2022) (Appendix 1). We employed BLASTN to verify that no other 16S sequence deposited on GenBank after these works clustered with the species used in this study. These sequences were aligned with a sequence of *Allobates femoralis* (KX686026) as the outgroup, on the MAFFT7 online server under default parameters except the E-INS-i strategy, which is designed for sequences with multiple conserved domains and long gaps (Kato et al. 2017). We trimmed the alignment to keep only the region where most sequences overlap, resulting in a final alignment of 546 base pairs (bp). We investigated the phylogenetic relationships among a total of 135 terminals under Maximum Likelihood (ML), applying a GTRCAT model with RAxML v.8.2.4 (Stamatakis 2014). All RAxML analyses were performed on the CIPRES Science Gateway online server (Miller et al. 2010). Nonparametric bootstrapping values (Felsenstein 1985) were estimated using 1,000 pseudoreplicates.

Morphometric analysis

We measured 12 adult males of *Allobates granti* sensu stricto, seven of which were genotype-in previous papers and seven of them had their calls recorded; from the new species *A. aff. granti* (*A. vicinus* sp. nov.) we measured 14 adult specimens (10 males and four females), five of which were genotyped in previous paper and five had their calls recorded; two adult males of *A. aff. granti* 2, both genotyped; and one with its call recorded; from the new species of *A. aff. tapajos* (*A. ripicolus* sp. nov.) we measured 20 adult specimens (14 males and six females), seven of which were genotyped in previous papers and five were recorded (Appendix 2). The measurements of the latter specimens were compared to the related *A. tapajos* sensu stricto and *A. kamilae* using the data of Ferrão et al. (2022).

Sex was determined either in the field via calling activity, or in the laboratory by examining the presence of a vocal sac, vocal slits and gonads. We measured preserved specimens to the nearest 0.01 mm with digital calipers under a dissecting stereomicroscope. Terminology, diagnostic characters, and measurements generally follow Caldwell et al. (2002), with some modifications from Grant and Rodríguez (2001) to facilitate comparison with other *Allobates* species. The following measurements were recorded: snout-vent length (SVL); head length from corner of mouth to tip of snout (HL); head width at level of angle of jaws (HW); snout length from anterior corner of naris to tip of snout (SL); eye to naris distance from anterior corner of eye to center of naris (EN); internarial distance (IN); eye length (EL); interorbital distance between anterior edges of eyes (IO); diameter of tympanum (TYM); forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow (FAL); hand length from proximal edge of palmar tubercle to tip of Finger III (HAND); width of disc on Finger III (WFD); thigh length from flexed knee to cloaca (ThL); 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).

We examined the variation of morphometric data among adult males through a principal component analysis (PCA) via FactoMineR package in R v.3.2.4 (Lê et al. 2008; R Development Core Team 2016). To control for variation in body-size among individuals we performed additional analyses on a size-corrected dataset (residuals) obtained by linear-regressing the original morphometric measures of each variable on SVL (Strauss 1985). For the comparison between *A. aff. tapajos*, *A. tapajos* and *A. kamilae* we removed SL and IO because these measurements were taken differently in Ferrão et al. (2022).

Acoustic analysis.

We gathered call recordings of seven males of *Allobates granti* (including from populations near the type locality), five males of *A. aff. granti*, one male of *A. aff. granti* 2, nine males of *Allobates aff. tapajos*, seven males of *A. tapajos* from the type locality and 26 of *A. kamilae* (from Ferrão et al. 2022). Calls consisted of single (*A. aff. tapajos*) or clusters of notes (in the other species) emitted at a relatively fast pace and with pronounced upward frequency modulation. Considering these single or clustered notes as “calls”, following a call-centered definition of Köhler et al. (2017), we used Audacity v.2.1.1 with the following configuration: window = Blackman, Discrete Fourier Transform = 1,024 samples and measured the following six variables for *A. aff. tapajos* (single note calls): number of notes per call (NC), call length (CL), silence between calls (SC), dominant frequency (DF1), minimum frequency (MiF1), maximum frequency (MxF1). These variables were compared to the variables of the first notes of the calls emitted by *A. tapajos* and *A. kamilae*. We measured 12 variables for the *A. granti* complex, since they emit pairs of notes: call length (CL), silence between calls (SC), silence between notes (SN), first and second note length (NL1&2), dominant frequency of the first and the second note (DF1&2), minimum frequency of the first and the second note (MiF1&2), maximum frequency of the first and the second note (MxF1&2), and the delta of maximum dominant frequency between the first and second notes (DMxF1–2). Four calls of each recorded male were measured, and the average was considered as a single measurement. Dominant frequency was measured using the Peak frequency function; maximum and minimum frequencies were measured 20dB below the peak frequency to avoid background noise interference. We undertook PCAs using bioacoustics variables independently for the two species complexes. Call recordings of *A. granti*, *A. aff. granti* and the new species were deposited at www.sonotheque.mnhn.fr (Appendix 3; MNHN-SO-2023-124–143); those from *A. kamilae* (FNJV50564–50593) and *A. tapajos* (FNJV50556–50562) are deposited in the Fonoteca Neotropical Jacques Viellard (University of Campinas, Campinas, Brazil; <https://www2.ib.unicamp.br/fnjv/>).

Results

Phylogenetic relationships

The relationships among species inferred from the ML analysis are poorly supported at most nodes (Fig. 1). However, sequences from individuals corresponding to the different putative species form strongly supported clades. Populations previously identified as *A. granti* form three distinct lineages. All the samples from French Guiana form a clade corresponding to the nominal species as the sister to the populations from Suriname and northern Pará (4.0–4.4% mean p distance) with poorly supported relationships. The populations from northern Suriname (*A. aff. granti* = *A. vicinus* sp. nov.) and the ones from southern Suriname and northern Pará (*A. aff. granti* 2) form two distinct additional lineages (3.4% p distance). These results are similar to the results of Réjaud et al. (2020).

The populations previously identified as *Allobates* aff. *tapajos* from the Guiana Shield (French Guiana, Suriname, Northern Pará and Amapá) are nested within a clade formed by five other major lineages from the south of the Amazon River. The relationships among these six lineages are poorly supported. *Allobates* aff. *tapajos* (*A. ripicolus* sp. nov.) displays the lowest mean p-distance with *A. kamilae* and *A. aff. tapajos* 3 (4.5% and 4.6%, Table 3), which are the closest species according to Réjaud et al. (2020) and Ferrão et al. (2022) who used more genomic data than in the present study.

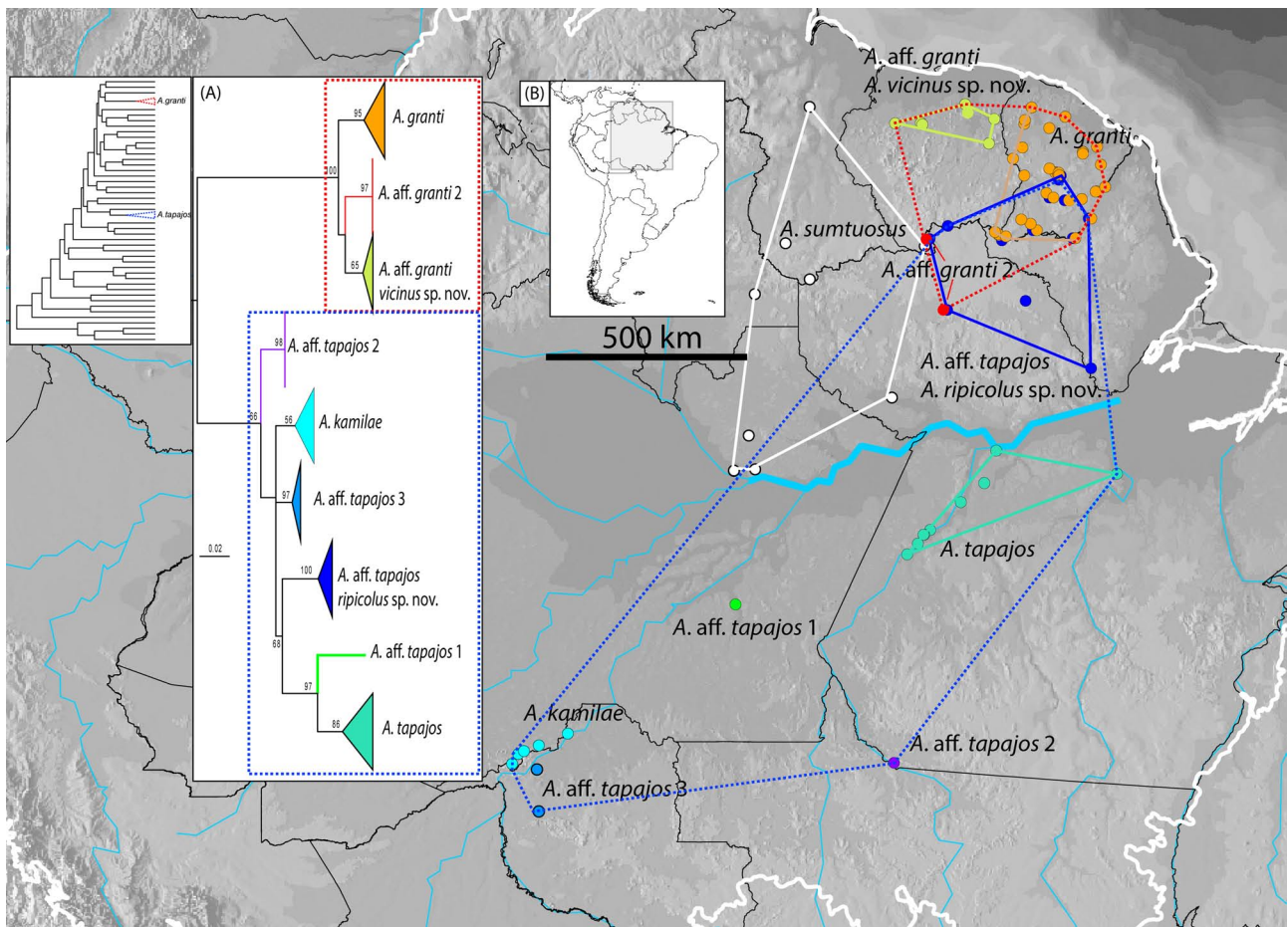


FIGURE 1. (A) Maximum Likelihood phylogenetic tree obtained from the analysis of 135 sequences of 16S (546 bp) of *Allobates* belonging to the *A. granti* and the *A. tapajos* complexes. Bootstraps > 50 % are indicated on the left side of the nodes. A backbone mitogenomic phylogeny adapted from Réjaud et al. (2020) indicates the respective phylogenetic positions of the two species complexes within the genus. For the sake of clarity, branches within species are collapsed (full tree available in Appendix 4). (B) Distribution of the different species included in the molecular dataset (plus *A. sumtuosus* to illustrate the spatial pattern) are depicted by polygons and the limits of the two complexes with dotted lines. The limit of Amazonia is depicted as a white line.

TABLE 1. Mean, minimum and maximum values of morphometric measurements in mm.

			SVL	HL	HW	SL	EN	IN	ED	IO	TD	FAL	HAND	WFD	LL	TL	FL	WTD
<i>A. vicinus</i> sp. nov.	Male (n=10)	Mean	15.5	5.3	5.2	1.1	1.5	2.1	2.0	3.6	1.0	3.4	3.7	0.4	6.9	7.2	6.4	0.6
		Max	16.5	5.5	5.5	1.3	1.6	2.2	2.2	3.8	1.2	3.6	4.0	0.5	7.3	7.5	6.7	0.6
		Min	14.6	5.1	4.9	1.0	1.3	1.9	1.9	3.4	0.9	3.3	3.4	0.4	6.6	6.8	6.0	0.5
	Female (n=4)	Mean	16.6	5.6	5.3	1.1	1.5	2.3	2.1	3.6	1.0	3.7	3.5	0.4	7.4	7.5	6.5	0.6
		Max	17.1	5.6	5.4	1.2	1.6	2.3	2.3	3.8	1.2	3.8	3.6	0.4	7.8	7.7	6.8	0.6
		Min	16.0	5.5	5.2	1.1	1.3	2.2	2.0	3.4	0.9	3.6	3.2	0.4	6.9	7.2	6.1	0.6
<i>A. ripicolus</i> sp. nov.	Male (n=14)	Mean	15.8	5.2	5.1	1.1	1.5	2.1	1.9	3.6	0.9	3.3	3.6	0.4	7.1	7.5	6.9	0.6
		Max	16.4	5.4	5.2	1.2	1.5	2.2	2.1	3.8	1.0	3.6	3.9	0.5	7.4	7.9	7.6	0.7
		Min	15.0	4.9	4.9	1.0	1.4	2.0	1.8	3.5	0.8	3.1	3.1	0.4	6.8	7.1	6.5	0.5
	Female (n=5)	Mean	16.4	5.4	5.2	1.2	1.5	2.3	2.0	3.7	0.9	3.5	3.7	0.5	7.4	7.7	7.0	0.6
		Max	16.8	5.7	5.6	1.3	1.7	2.4	2.0	4.0	1.0	3.7	3.9	0.5	7.8	8.1	7.6	0.6
		Min	15.5	5.3	4.9	1.1	1.3	2.2	1.9	3.5	0.8	3.2	3.2	0.4	7.1	7.2	6.3	0.6

Morphometric analyses.

The PCA based on raw morphometric measurements of the *A. granti* complex accumulated 65.5 % of the total variation in the first two components (Fig. 2A). The first principal component (PC1) explains 52.8 % of the variation, all variable coefficients are highly positively correlated with body size, which segregate *A. aff. granti 2* from the two others that largely overlap (Table 1; Fig. 2A). The second principal component (PC2) explains 12.7% of the variation and also does not separate the different species. Using residuals, all three species largely overlap on both PCs. *Allobates granti* and *A. aff. granti* (*A. vicinus* sp. nov.) cannot be differentiated through morphometric measurements. Nevertheless, differences in coloration and calls exist (see below).

The PCA based on raw measurement of the *A. tapajos* complex accumulated 48.0 % of the total variation in the first two components (Fig. 2C). The first principal component (PC1) explains 29.9 % of the variation, all variable coefficients are highly positively correlated with body size which does not segregate any of the three species. However, the second principal component (PC2) explains 18.1 % of the variation and segregates *A. tapajos* from the two others, which largely overlap between them, mostly because of its larger WTD and smaller HL. The first two components of the PCA based on size-corrected morphometric measurements (residuals) account for 45.1 % (Fig. 2D) and segregate *A. aff. tapajos* (*A. ripicolus* sp. nov.) from both *A. kamilae* and *A. tapajos*. Although limited overlap with *A. kamilae* remains, all size corrected variables overlap among the three species, thus not providing diagnostic characters. However, differences in coloration and calls exist between the new species and *A. kamilae* (see below).

Acoustic analysis.

The calls of *Allobates granti*, *A. aff. granti* (*A. vicinus* sp. nov.) and *A. aff. granti 2* are segregated within the bidimensional space formed by the two first components of the PCA, which account for 75.9 % of the total variation (Fig. 3C). *Allobates aff. granti* and *A. aff. granti 2* notably produce two notes with distinct maximum dominant frequencies (range of DMxF1–2 : 190–347 Hz in *A. aff. granti*; 207 Hz in *Allobates aff. granti 2* vs. -44–90 Hz in *A. granti*) (Fig3D). Moreover, the intervals between calls are longer in *Allobates aff. granti* than in the two others (range of SC: 233–374 ms vs 151–202 ms in *A. granti* and 168 in *A. aff. granti 2*.)

The calls of *Allobates tapajos*, *A. aff. tapajos* (*A. ripicolus* sp. nov.) and *A. kamilae* are partly segregated within the bidimensional space formed by the two first components of the PCA, which account for 69.1 % of the total variation (Fig. 4C). *Allobates kamilae* is well-segregated but *Allobates tapajos* and *A. aff. tapajos* notably overlap despite the fact that their calls clearly differ by the number of notes per call (always a single note in *A. aff. tapajos* vs. 1–3 notes in *A. tapajos* but 1 note calls are rare; and *A. kamilae* always emits more than two notes). Further analyses excluding *A. kamilae* provided total segregation between *Allobates aff. tapajos* and *A. tapajos* along the two first PCs (78.8% of the variation).

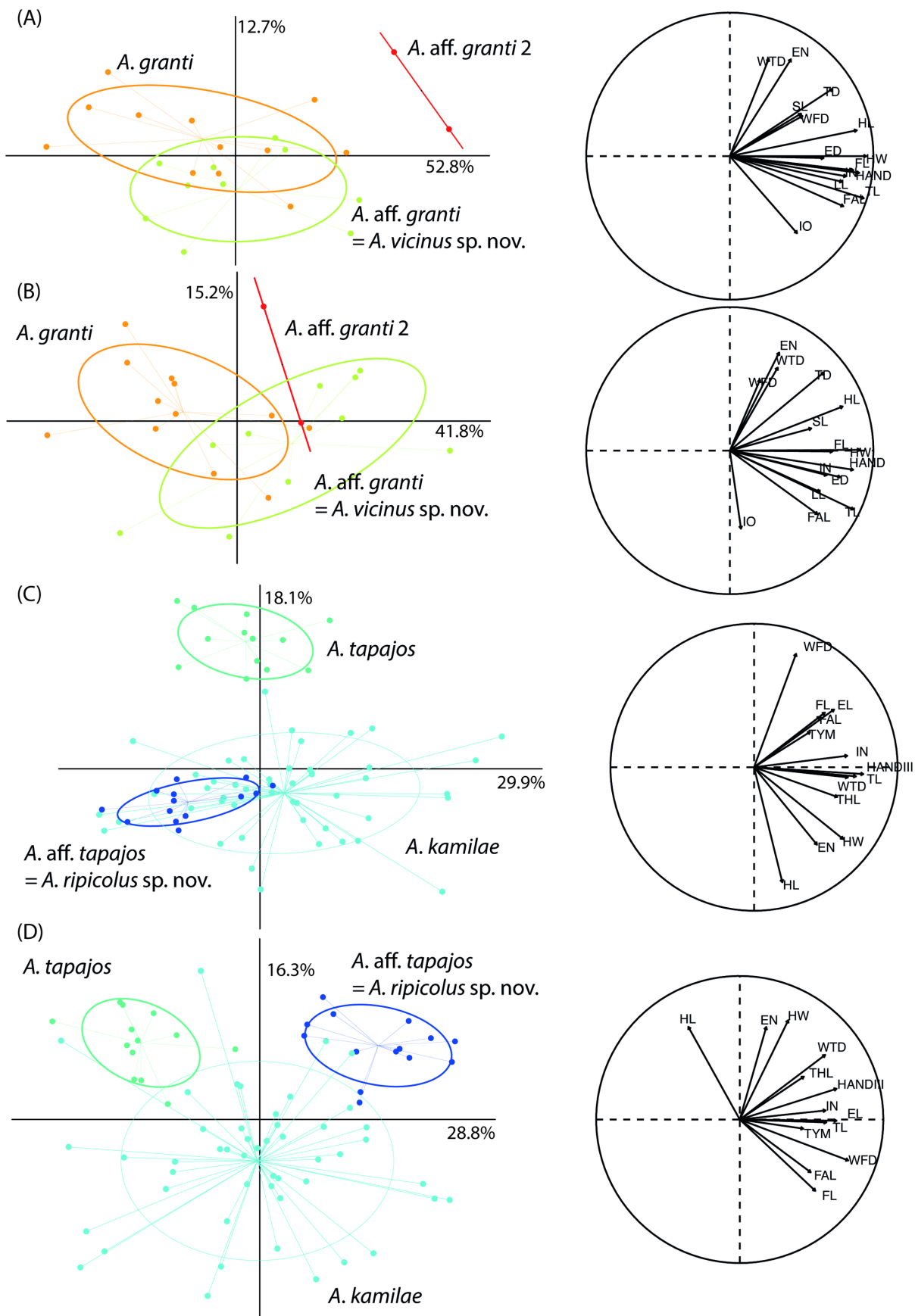


FIGURE 2. Morphometric analyses: Principal Component Analysis (PCA) plot of the two first PCs and the correlation circle representing variable contributions for (A) the *Allobates granti* complex using raw data and (B) size-corrected data, (C) the *A. tapajos* complex using raw data and (D) size-corrected data.

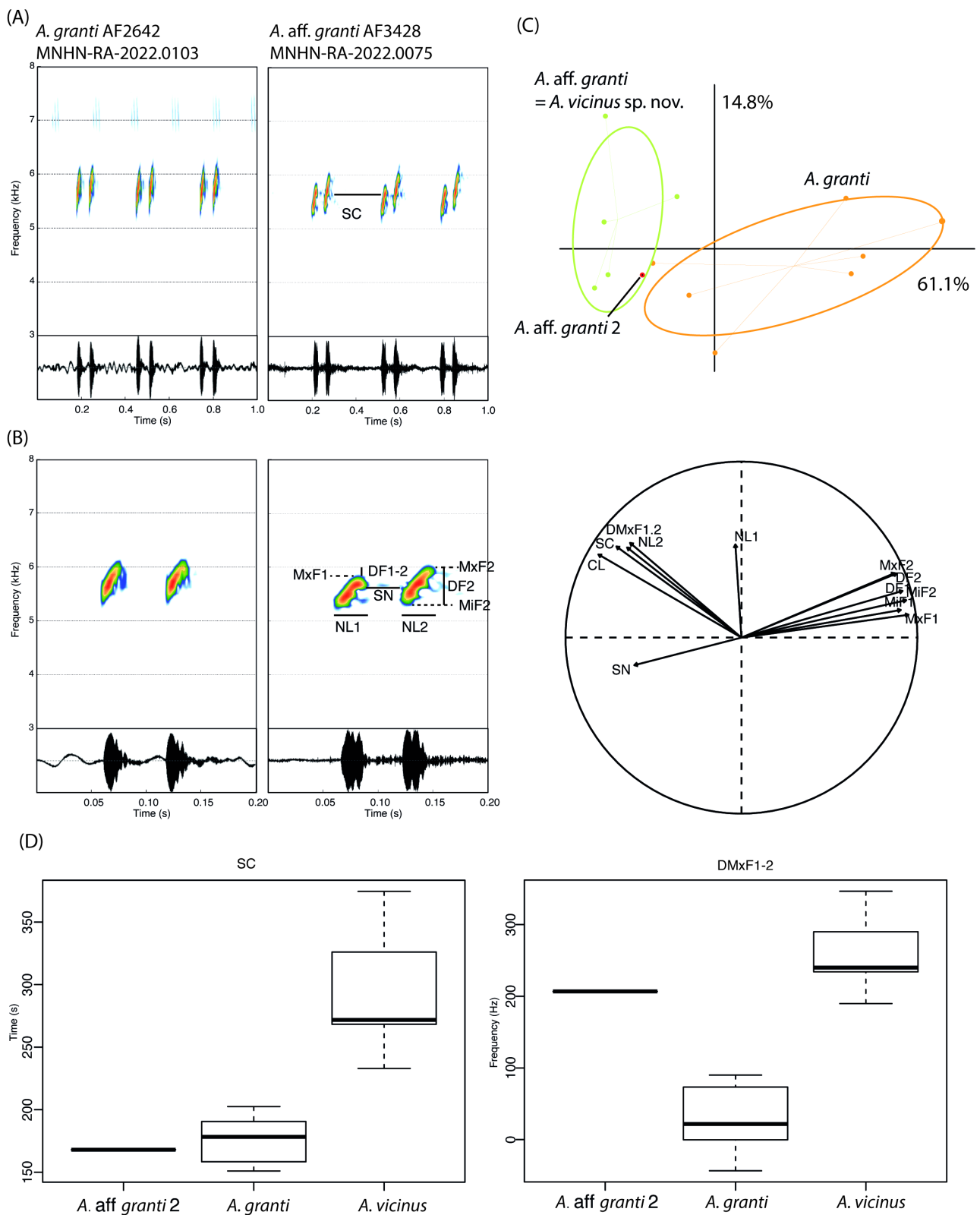


FIGURE 3. Examples of sonograms of *Allobates granti* and *A. aff. granti*: (A) depicting a series of calls on a 1 s window and (B) focusing on a single call on a 0.2 s window; (C) PCA plot of the two first PCs and the correlation circle representing variable contributions. The measured variables are illustrated on the call of *A. aff. granti*. (D) Box plot of two selected variables whose values do not overlap among species.

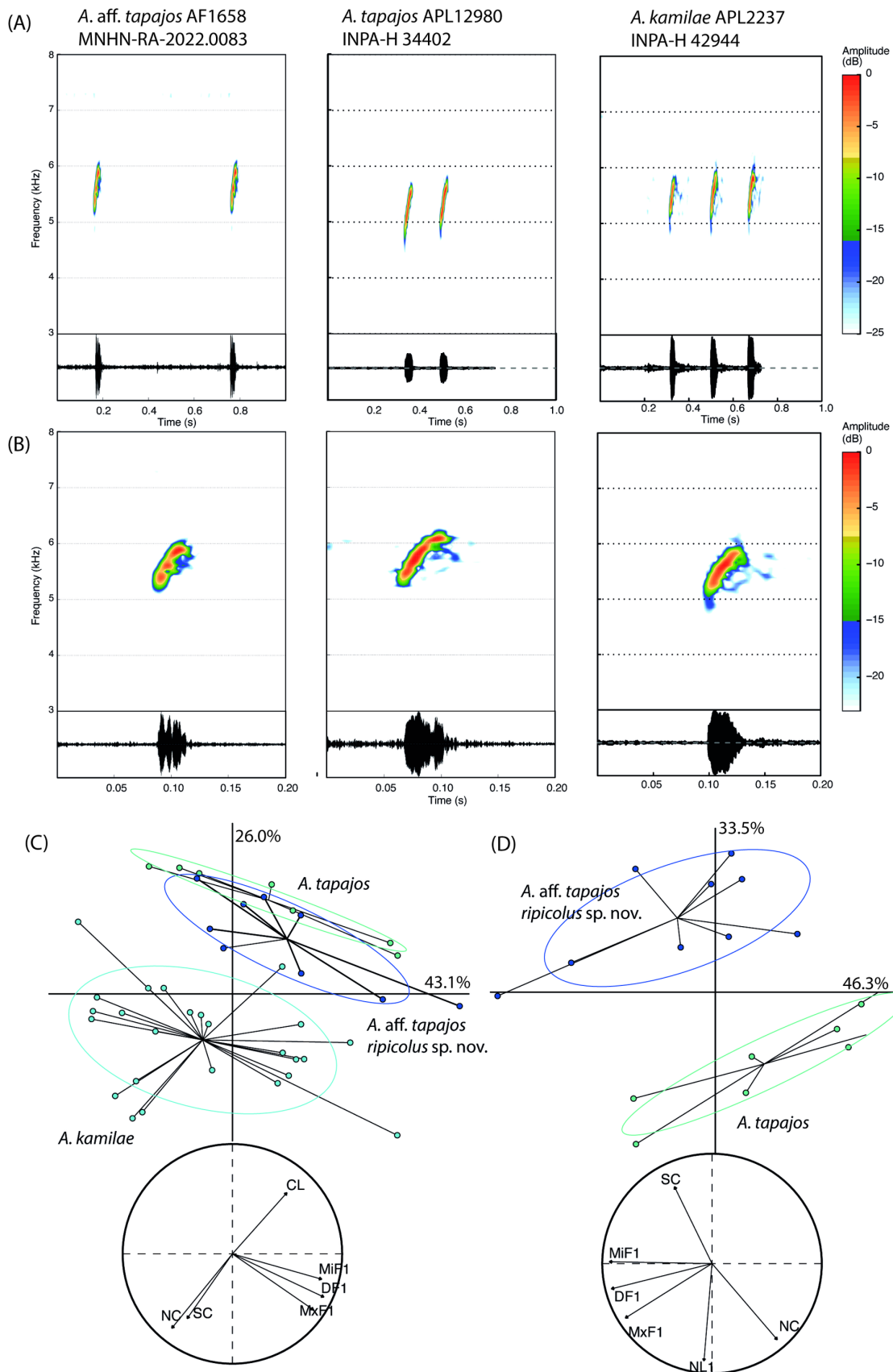


FIGURE 4. Examples of sonograms of *Allobates* aff. *tapajos*, *A. tapajos* and *A. kamilae*: (A) depicting a series of calls (a single call in *A. tapajos* and *A. kamilae*) on a 1s window and (B) focusing on a single note on a 0.2 s window; (C) PCA plot of the two first PCs and the correlation circle representing variable contributions, and (D) excluding *A. kamilae*. Only the range of the number of notes per call (NC) do not overlap across the three species.

Allobates vicinus sp. nov.
MNHN-RA-2022.0079 (AF3771)
Voltzberg Suriname

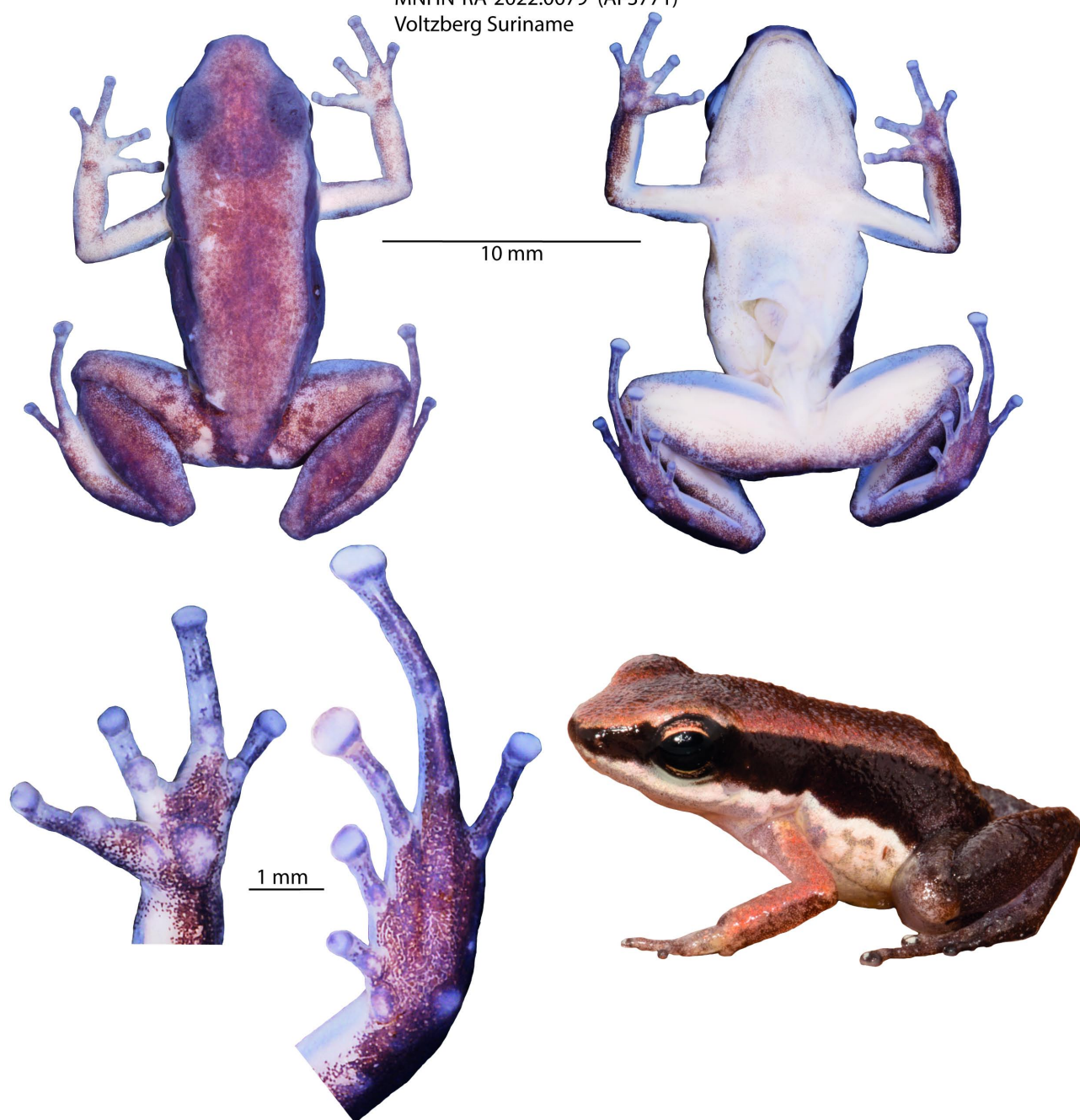


FIGURE 5. Dorsal, ventral, left palmar and left plantar views of preserved holotype of *Allobates vicinus* sp. nov. and dorsolateral view of the holotype in life.

Taxonomy

We acknowledge that differences are subtle among these species but considering the congruence among mtDNA, calls, morphometrics and qualitative morphological differences, we name and describe two new species below. However, considering too little material is available for *A. aff. granti* ² we refrain from taking a taxonomic decision for that species.

Since most *Allobates* have restricted geographic distributions, interspecific comparisons here are focused on cryptically-colored nominal *Allobates* species occurring in the Guiana Shield and to related species south of the Amazon River for *A. aff. tapajos*.

TABLE 2. Mean values of acoustic variables. Asterisks indicate variables that were not taken, because the structure of the calls are distinct.

		CL	NC	SC	NL1	NL2	SN	MiF1	MxF1	DF1	MiF2	MxF2	DF2	DMxF1-2
<i>A. vicinus</i> sp. nov.	Mean	93.95	2	294.7	24.3	33.7	34.5	5082	5832	5531	5221	60925	5747	260
	Min	88.2	2	233.0	13.0	26.8	30.5	4786	5635	5422	5006	5869	5586	190
	Max	110.2	2	374.5	31.0	43.0	38.8	5295	6035	5785	5454	6275	6020	347
<i>A. aff. granti</i> 2	n=1	92.5	2	168.0	13.0	39.5	36.3	5015	5973	5492	5298	6180	5741	207
<i>A. granti</i>	Mean	80.3	2	175.6	24.4	25.2	31.0	5450	6332	5927	5550	6363	5986	31
	Min	72.2	2	151.0	19.3	20.5	23.8	5095	5875	5479	5185	5965	5612	-44
	Max	94	2	202.5	29.8	29.8	39.3	5733	6931	6471	5806	6953	6454	90
<i>A. ripicolus</i> sp. nov.	Mean	*	1	550.4	36.8	*	*	5250	6090	5770	*	*	*	*
	Min	*	1	390.7	26.5	*	*	4914	5875	5519	*	*	*	*
	Max	*	1	686.2	45.0	*	*	5745	6465	6072	*	*	*	*
<i>A. tapajos</i>	Mean	*	1.8	407.2	45.0	*	*	5041	6112	5721	*	*	*	*
	Min	*	1.4	326.5	40.5	*	*	4795	5814	5413	*	*	*	*
	Max	*	2	477.0	48.0	*	*	5315	6565	6064	*	*	*	*
<i>A. kamilae</i>	Mean	*	3.7	736.9	31.4	*	*	5067	6184	5745	*	*	*	*
	Min	*	2.7	406.1	19.3	*	*	4874	5669	5340	*	*	*	*
	Max	*	6.2	1860.5	43.6	*	*	5682	6585	6129	*	*	*	*

Allobates vicinus sp. nov.

Allobates granti Fouquet et al. 2007; 2012; Vacher et al. 2020; Grant et al. 2017

Allobates cf. *granti* Fouquet et al. 2015a

Allobates aff. *granti* Réjaud et al. 2020

Holotype. MNHN-RA-2022.0079 (field n° AF3771), an adult male from Voltzberg, Suriname (4.68169 N 56.18568 W, 100 m asl) collected by A. Fouquet and R. Jairam on 25/01/2016 (Fig. 5).

Paratopotypes. two adults: NZCSA1181 (field n° AF3777) a male and MNHN-RA-2022.0080 (field n° AF3805), a female collected with the holotype.

Paratypes. Twelve adults: MNHN-RA-2022.0070–74 (field n° AF2476; AF2479; AF2510; AF2513; AF2515), five males and MNHN-RA-2022.0067–68 (field n° AF2416; AF2421; AF2474), three females from Nassau, Suriname (4.80262 N 54.61502 W, 580 m asl) collected by A. Fouquet and R. Jairam on 20/12/2014; MNHN-RA-2022.0075–78 (field n° AF3428–9; AF3431; AF3436), four males from Bakhuis, Suriname (4.70646 N 56.77943 W, 340 m asl) collected by A. Fouquet and R. Jairam on 05/01/2015.

Etymology. The specific epithet “vicinus” is a latin word that means “neighbor”, referring to the two sister species *A. granti* in French Guiana and *A. vicinus* sp. nov. in Suriname facing each other on each side of the Maroni River.

Generic placement. The new species is assigned unambiguously to the genus *Allobates* because the tip of finger IV does not reach the distal subarticular tubercle of finger III, toe IV with basal webbing and lateral fringe on its preaxial side, pale paracloacal marks (characters 5, 43 and 50 of Grant et al. 2017, respectively) and its phylogenetic relationship as assessed by molecular data.

Definition. A small species of cryptically-colored *Allobates*. (1) Mean SVL of males 15.5 mm (range 14.6–16.5 mm); mean SVL of females 16.6 mm (range 16.0–17.1 mm); (2) In life, dorsal surface light brown with diffuse dark brown irregular blotches often forming an hourglass pattern and sometimes only scattered from interorbital to urostyle region; background color of dorsal surfaces of legs light brown to gray; diffuse, transverse dark brown bands present across dorsal surfaces of thigh (on its proximal region), irregular bands on shank (at mid-level), tarsus and

foot (at mid-level); posterior surface of thigh and groin dark brown; (3) skin texture of dorsum granular, with numerous and large tubercles scattered throughout dorsum, more abundant on the posterior half and legs; (4) lateral dark brown band with sharp upper and lower edge, as large as the posterior edge of the eye; (5) pale dorsolateral stripe poorly delimited dorsally by the hourglass pattern and sharply delimited ventrally by the dark brown colouration of the flanks; (6) oblique lateral stripe inconspicuous not reaching midbody length reduced to inguinal region of the lateral dark brown band; (7) pale ventrolateral stripe present only in live specimens, extending from the inguinal region to the snout, sometimes interrupted and irregular forming a marbled pattern extending ventrally; (8) white or cream comma-shape paracloacal mark; (9) throat and chest of males cream in preserved specimens, translucent in life, with uniformly distributed melanophores from the chin to the anterior half of the abdomen; (10) abdominal surfaces white centrally, yellow towards the flanks and ventral surface of legs in live males; (11) throat, chest and abdomen uniformly white in preserved specimens and bright yellow in live females, without any melanophores; (12) dark throat collar absent; (13) iris metallic copper, without a pupil ring; (14) median lingual process absent; (15) vocal sac distinct, subgular; (16) maxillary teeth present; (17) third phalanx of Finger III slightly swollen pre-axially in males; (18) distal tubercle absent on Finger IV; (19) tip of Finger IV not reaching the distal subarticular tubercle of Finger III; (20) tip of Finger II reaching the distal edge of distal subarticular tubercle of Finger III; (21) terminal discs weakly expanded; (22) rudimentary basal webbing present between Toes III and IV; (23) fringes on toes inconspicuous; (24) Toe I very short, its tip reaching the base of the subarticular tubercle on Toe II; (25) mature oocytes pigmented; (26) diurnal habits, males calling in daytime; (27) advertisement calls characterized by the continuous emission of note pairs; notes with ascending frequency modulation with dominant frequencies between 5,422–5,785 Hz for the first note and 5,586–6,020 Hz for the second, split by regular silent intervals of approximately 233–374 ms between calls.

Morphological comparisons with other *Allobates*. The character states of compared species are shown in parenthesis. *Allobates vicinus* differs from its closest relative *A. granti* (Fig. 6) by (1) its brown legs (gray-blueish); (2) its dorsum with numerous and large tubercle (finely granular); (3) its hourglass darker pattern on a light brown coloured back (brick or reddish-brown, rarely with an hourglass pattern); (4) by its dark brown lateral band, in life and preservative (uniformly black, exceptionally dark brown); (5) by its call consisting of two notes with distinct maximum dominant frequencies DMxF1–2 : 190–347 Hz (very similar values between the two notes DMxF1–2: -44–90 Hz in *A. granti*) (Fig. 3D) and longer intervals between calls SC: 233–374 ms (151–202 ms in *A. granti*) (Fig. 4).

See below the comparison with the other species of *Allobates* occurring in the Guiana region.

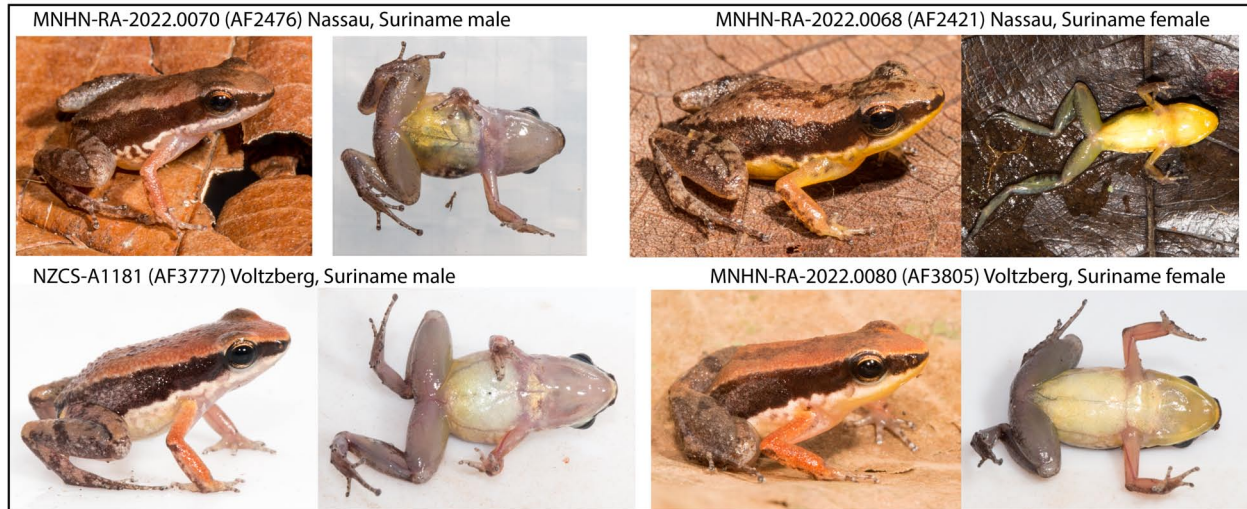
According to the literature *Allobates vicinus* differs from *A. sumtuosus* (Morales 2002; Kok & Ernst 2007; Simões et al. 2013) by (1) its throat uniformly covered with melanophores in males (melanophores restricted to tip and sides of chin in *A. sumtuosus* males); (2) the presence of transverse dark brown marks on thigh, shank and tarsus (absent or brown irregular spots); (3) its call consisting of pairs of notes (3.9–5.9 s long trills of 23–35 single notes) with dominant frequency of 5,422–6,020 Hz (vs. 6,172–6,480 Hz).

According to the literature *Allobates vicinus* differs from *A. amissibilis* Kok, Hölting, and Ernst, 2013 by (1) its belly coloration in life clearly sexually dimorphic being white in male, yellow in females, (cream to yellow in both sexes); (2) its oblique lateral stripe inconspicuous, not reaching midbody length (diffuse broad area extending from groin to about midbody length); (3) its calls consisting of pairs of notes (0.03–7.98 s long series of 1–19 single notes).

Description of the holotype. An adult male 15.5 mm SVL (Fig. 5; Table 1) in good condition, with a few superficial scars on dorsum and a large incision in the abdomen for tissue sample; body slender; head as wide as long (HL/HW= 1.0); head length 33.4 % of SVL; snout broadly subacuminate in dorsal view, acutely rounded in lateral view, extending past lower jaw. Nares located laterally, opening posterolaterally; canthus rostralis concave, loreal region slightly concave, flaring slightly at upper lip; internarial distance 40.1 % of head width (IN/HW); eye-naris distance 29.8 % of head length (EN/HL); 77.0 % of eye length (EN/ED). Tympanum subcircular, directed posterolaterally, 45.0 % of eye length (TD/ED); 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, with scattered larger granules becoming denser posteriorly, more easily visible in life; one distinctly enlarged tubercle on each eyelid; belly smooth.

A. vicinus sp. nov.



A. granti

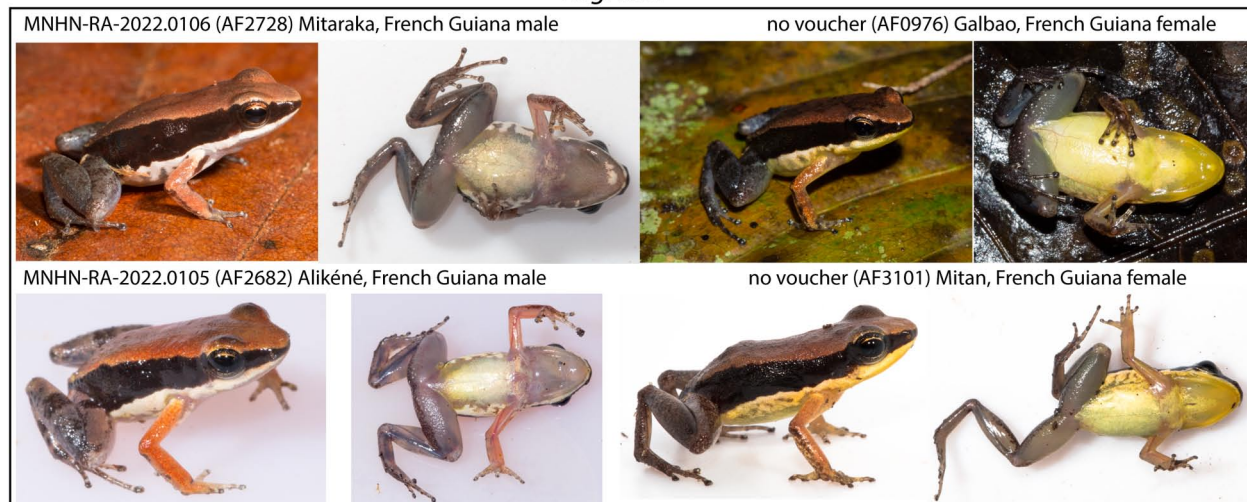


FIGURE 6. Additional specimens in life illustrating the variation on coloration within *Allobates vicinus* sp. nov. and *A. granti*.

Forelimb slender, skin smooth; metacarpal ridge absent; ulnar fold absent; hand length 22.2 % of SVL; Finger I longer than II when fingers adpressed; fingers unwebbed, preaxial edge of Finger III slightly swollen; tip of Finger IV not reaching distal subarticular tubercle on Finger III when fingers adpressed; terminal discs weakly expanded, slightly wider than long; width of disc on Finger III 0.38 mm; discs with distinct dorsal scutes. Relative lengths of adpressed fingers III > I > II > IV; palmar tubercle large, ovoid, 0.65 mm in its largest diameter, 18.9 % of hand length, periphery pigmented; thenar tubercle conspicuous but not protuberant, ovoid, anterior periphery pigmented, about a quarter 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 tubercles on Finger I and II subequal and largest, distal tubercle on Finger III smallest (Fig. 5).

Hindlimb robust, skin granular; thigh length 42.9 % of SVL; tibia length 45.9 % of SVL; heels overlapping when hindlimbs are flexed at right angles to sagittal plane of body; foot length 40.2 % 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; discs on Toes II, III, IV, and V larger than width of distal phalanges; disc on Toe I equal to width of distal phalanx. Width of disc on Toe IV 0.60 mm; rudimentary webbing present only between Toes III–IV, webbing not pigmented; lateral fringes inconspicuous. Inner metatarsal tubercle oval, 0.40 mm in length, distal portion pigmented, outer metatarsal tubercle round, projecting, 0.32 mm in diameter. Three subarticular tubercles on Toe IV, two subarticular tubercles on Toes III and V, and one on Toes I and II. Subarticular tubercles on Toes I and II

largest; distal and basal subarticular tubercles on Toe IV smallest. Metatarsal fold absent. Tarsal keel well defined, short, tubercle like, directed transversely across tarsus, located 0.90 mm from proximal edge of inner metatarsal tubercle, not extending from it (Fig. 5).

Color of holotype in life. Color in life of the holotype is shown in Fig. 5. Dorsal coloration is brown with a dark brown diffuse hourglass pattern from the scapular region to the urostyle; laterally a wide dark brown (almost black) band from tip of snout to around the body and above the vent, as wide as the eye at the level of its posterior edge; inconspicuous dorsolateral stripe above this band. The upper surface of tympanum is black, the lower surface white. The oblique lateral stripe embedded in the dark brown band consists of a diffuse lighter area extending from the groin to about one-third of the distance to the arm insertion. Flanks are creamish white below the lateral dark brown band forming a ventrolateral stripe extending ventrally along flanks. Upper lip is creamish white. Throat is gray entirely covered with scattered melanophores. Belly is immaculate creamish white anteriorly with tiny scattered melanophores and yellowish posteriorly without melanophores. Forelimbs are light reddish with a dark brown line on the posterior surface of forearms from elbow to wrist. A black blotch is present on the dorsal side of wrists. Upper surfaces of thighs and shanks are dark brown with inconspicuous black bands and blotches. A pale comma-shape paracloacal mark is present. Digits are dark gray with a few white dots. Fingers are dark gray with a few small white shaped dots. The iris is copper.

Color of the holotype in preservative. After six years in preservative (70% ethanol), the colors of the specimen have faded. The dorsum is light brown; the lateral band is dark brown and the diffuse oblique lateral stripe is barely distinguishable. Flanks, belly, and upper lips are immaculate white. Throat is white; the melanophores are visible. Upper surface of thighs is brown with dark brown blotch or dark brown band. The pale paracloacal mark is still visible. Forelimbs are white. Fingers and digits are light brown.

Variation in the type series. Apart from sexual dimorphism and dichromatism (males are slightly smaller than females and the ventral surface of females in life is bright yellow and without melanophores), most of the specimens have a clear dark brown dorsal hourglass pattern, although in a few specimens the pattern is only diffused (holotype) or reduced to irregular blotches (MNHN-RA-2022.0068; Fig 6). The dorsal surface of legs varies in coloration from dark grey to light brown with more or less conspicuous dark brown bands and blotches. The ventrolateral stripe is interrupted in some individuals (MNHN-RA-2022.0070; Fig 6) and does not extend ventrally in most females (MNHN-RA-2022.0068; Fig 6). Ventral surface is posteriorly immaculate white to yellow.

Advertisement call. The call consists of pairs of high pitched notes and is emitted regularly (without clear clusters) every 295 ms (233–374 ms) and sounds like a cricket chirp. The two notes within a call are spaced by 34 ms (30–39 ms) with the first note being shorter 24 ms (13–31 ms) than the second one 34 ms (27–43 ms). These notes have an upward frequency modulation, i.e. the first note varies from 5,422–5,785 Hz as dominant frequency (DF1) and second note varies from 5,586–6,020 Hz (DF2) but differs more clearly in maximum frequencies (190–247 Hz) (DMxF1–2). The maximum frequency of the first note is lower (5,635–6,035 Hz) than of the second note (5,869–6,275 Hz) (Fig. 3a).

Natural history and distribution. It is a diurnal and terrestrial species inhabiting the leaf litter of mature forest on moderate hills and massifs. It is particularly abundant along the slopes of swampy streams where the males transport the tadpoles to complete their development. *Allobates vicinus* probably has a breeding ecology similar to its sister species *A. granti*, where the tadpoles are deposited in small collections of water formed along swampy streams and at the base of trees or by the stems of fallen palms. This species can also be observed far from any permanent water body. Males are territorial and defend territories of a few square meters throughout the rainy season. When an intruder approaches, the occupant emits a vocalization distinct from the usual advertisement call. The calling activity is concentrated in the morning between 7 and 10 am and at the end of the afternoon between 4 and 7 pm. One male can keep several clutches during the same period and could be replaced by the female for guarding of the eggs as well as transport to a water body.

The species described herein is known from seven localities in Suriname; three from which type material is included: Voltzberg, Nassau, and Bakhuis mountains; and four more from molecular data: Lely mountain, Brownsberg, Raleighvallen and the Gros Rosebel area. The range of *Allobates vicinus* probably extends throughout the forested area of Suriname. However, it reaches its eastern boundaries along the Maroni River. Southward, *A. vicinus* may enter in contact with the third related lineage remaining unnamed (*A. aff. granti* 2) and with *A. sumtuosus*. A similar pattern of distribution and degree of molecular divergence between *A. granti* and *A. vicinus* was recently described in *Pristimantis grandoculis* from Suriname and its sister undescribed species (*P. sp.* “Guianas” East) from

French Guiana, although the lack of phenotypic divergence advocates to consider the French Guiana populations as conspecific (Fouquet et al. 2022). There are also many other examples of species that similarly display pronounced genetic divergence across the Maroni River (Fouquet et al. 2012).

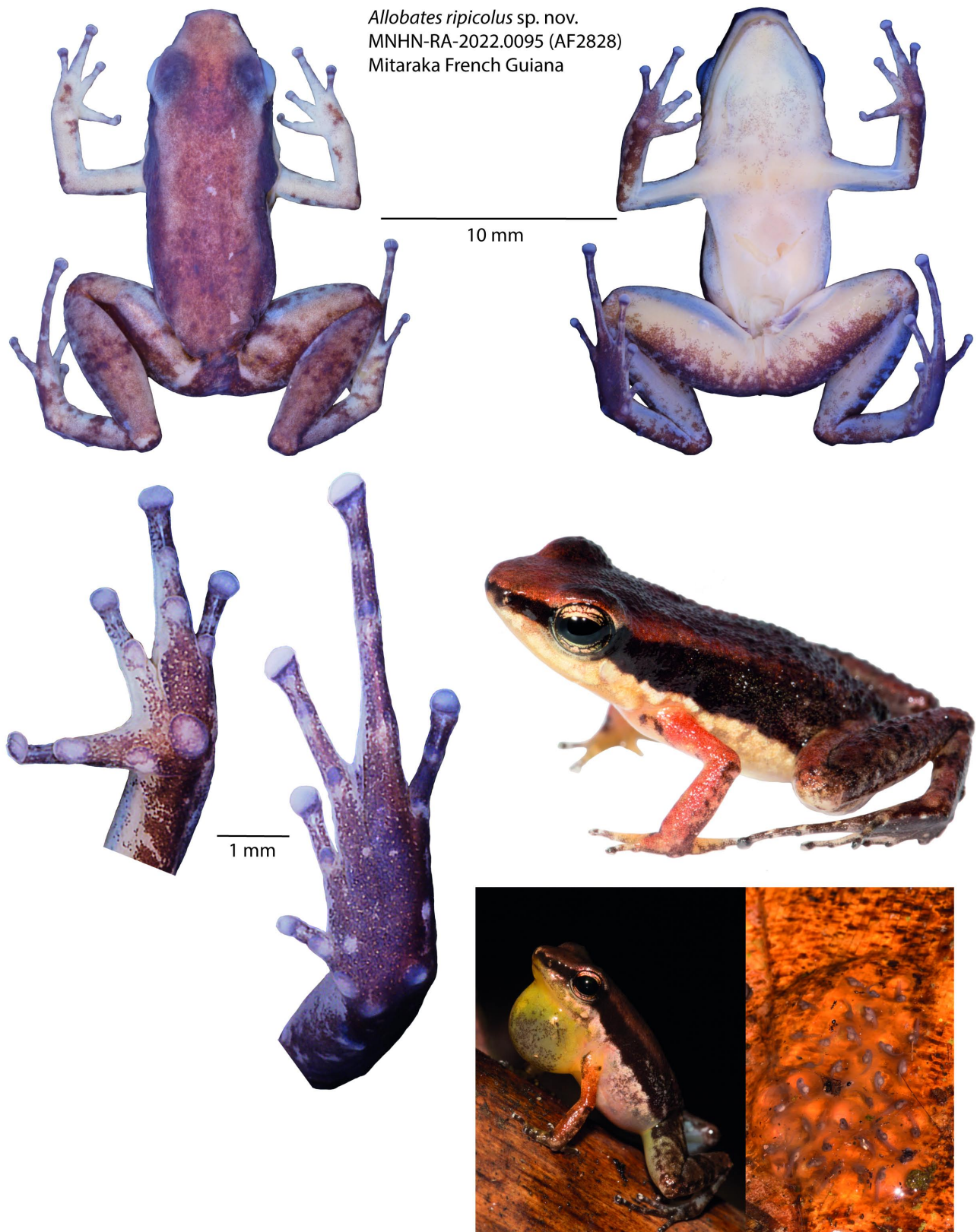


FIGURE 7. Dorsal, ventral, left palmar and left plantar views of preserved holotype of *Allobates ripicolus* sp. nov. and lateral view of the holotype in life. Additional uncollected specimen of a calling male from Sipaliwini, Suriname and a clutch found nearby.

Allobates ripicolus sp. nov.

Colostethus aff. *marchesianus* Vences et al. 2003

Allobates granti Fouquet et al. 2007

Allobates spumaponens Avila-Pires et al. 2010

Allobates sp. Saul Fouquet et al. 2012

Allobates sp. gr. *trilineatus* Fouquet et al. 2015a

Allobates aff. *tapajos* 4 Vacher et al. 2020

Allobates aff. *tapajos* 2 Réjaud et al. 2020

Allobates aff. *tapajos* Moraes and Lima 2021

Allobates tapajos Clade D Ferrão et al. 2022

Holotype. MNHN-RA-2022.0095 (field n° APA-973-1-AF2828), an adult male from Mitaraka, French Guiana (2.23577 N 54.44928 W, 300 m asl), collected by A. Fouquet and M. Dewynter on 01/03/2015 (Fig. 7).

Paratopotypes. Two adults: MNHN-RA-2022.0094 and 0096 (field n° APA-973-1-AF2789 and APA-973-1-AF2855), two females collected with the holotype.

Paratypes. Sixteen adults: MNHN-RA-2022.0081 (field n° AF1048), a male from Gros Arbres, Saul, French Guiana (3.62573 N 53.28052 W, 220 m asl), collected by A. Fouquet, K. Pineau, E. Courtois, B. Villette and C. Bedeau on 16/03/2013; MNHN-RA-2022.0083–84 (field n° AF1658; AF1686), two males from Crique Limonade, Saul, French Guiana (3.56311 N 53.19083 W, 280 m asl), collected by A. Fouquet, E. Courtois and J.P. Vacher on 23/02/2014; MNHN-RA-2022.0085 (field n° AF1905), a male, and MNHN-RA-2022.0086 (field n° AF1907), a female from Flat de la Waki, French Guiana (3.0835 N 53.41257 W, 180 m asl), collected by J.P. Vacher on 05/04/2014; MNHN-RA-2022.0092–93; 0088–89 (field n° AF2072–3; AF2216; AF2218), four males and MNHN-RA-2022.0087; 0090–91 (field n° AF1962; AF2276; AF2290), three females from Sipaliwini, Suriname (2.03253 N 56.11449 W, 280 m asl), collected by A. Fouquet and J.P. Vacher on 25/04/2014; MNHN-RA-2022.0097 (field n° AF3221), a male from Mitan, French Guiana (2.62840 N 52.55404 W, 100 m asl) collected by A. Fouquet and P. Nunes on 26/03/2015; MNHN-RA-2022.0098 (field n° AF3587), a male from Itoupé, French Guiana (3.02647 N 53.07983 W, 800 m asl), collected by A. Fouquet, E. Courtois, B. Villette and M. Dewynter on 07/01/2016; MNHN-RA-2022.0100 (field n° AF5397), a male from Camp Saut Richard, French Guiana (3.47363 N 53.20857 W, 200 m asl), collected by E. Courtois and M. Dewynter on 03/05/2019; MNHN-RA-2022.0099 (field n° AF5476), a male from Trois-Saut, French Guiana (2.19689 N 52.90168 W, 180 m asl), collected by E. Courtois and M. Dewynter on 28/04/2019.

Etymology. The specific epithet “ripicolus” is derived from a Latin word which means river banks, referring to the ecology of the species that is generally found nearby mid-sized rivers, on the ground of the frequently flooded major bed.

Generic placement. The new species is assigned unambiguously to the genus *Allobates* because the tip of finger IV does not reach the distal subarticular tubercle of finger III, toe IV with basal webbing and lateral fringe on its preaxial side, pale paracloacal marks (characters 5, 43 and 50 of Grant et al. 2017), respectively) and its phylogenetic relationship as assessed by molecular data.

Definition. A small species of cryptically-colored *Allobates*. (1) Mean SVL of males 15.8 mm (range 15.0–16.4 mm); mean SVL of females 16.4 mm (range 15.5–16.8 mm); (2) In life, dorsal surface of snout light brown, same color extending posteriorly until eye level; dorsum light brown laterally, with diffuse dark brown blotches scattered from interorbital region to urostyle region; background color of dorsal surfaces of legs light brown to gray; conspicuous diffuse transverse bands or blotches of a darker brown color present across dorsal surfaces of thigh (on its proximal region), shank (at mid-level) and foot (at mid-level); posterior surface of thigh and groin dark brown; (3) skin texture of dorsum granular, with larger granules on the posterior half of dorsum and legs; (4) lateral dark brown band with diffuse upper and lower edges particularly on posterior parts; (5) pale ill-defined dorsolateral stripe only reaching midbody; (6) oblique lateral stripe inconspicuous reaching midbody, reduced to a paler inguinal region within the lateral dark brown band; (7) cream ventrolateral stripe present, extending from the inguinal region to the snout, at times interrupted; (8) pale paracloacal mark present; (9) throat and chest of males white in preserved specimens, yellow in life, with melanophores concentrated on the posterior half of the throat; (10) abdominal surfaces white centrally, yellow towards the flanks in live males; (11) throat translucent without any melanophores, chest and abdomen uniformly white in preserved and live females; (12) dark throat collar absent; (13) iris is metallic gold, without a pupil ring; (14) median lingual process absent; (15) vocal sac distinct, subgular; (16) maxillary teeth

present; (17) third phalanx of Finger III slightly swollen preaxially in males; (18) distal tubercle absent on Finger IV; (19) tip of Finger IV not reaching the distal subarticular tubercle of Finger III; (20) tip of Finger II reaching the base of distal subarticular tubercle of Finger III; (21) terminal discs clearly expanded; (22) basal webbing present between Toes III and IV; (23) weak lateral fringes preaxially on Toe II and III; (24) Toe I very short, its tip not reaching the base of the subarticular tubercle on Toe II; (25) mature oocytes pigmented; (26) diurnal habits, males calling in daytime; (27) advertisement calls characterized by the continuous emission of single notes; notes with ascending frequency modulation and dominant frequencies between 5,519–6,072 Hz, split by regular silent intervals of approximately 391 to 686 ms between calls.

Morphological comparisons with other *Allobates*. The character states of compared species are shown in parenthesis. *Allobates ripicolus* differs from *A. granti* and *A. vicinus*, the two other co-occurring species of cryptically colored *Allobates* in the eastern Guiana Shield by (1) its dark brown lateral band with diffuse edges and not as wide as the eye (lateral band as wide as the eye with sharp edges, black in *A. granti* and dark brown in *A. vicinus*); (2) its longer feet but small arms FL/FAL= 44–45% (46–49% in *A. granti* and *A. vicinus*); (3) the presence of melanophores concentrated on the posterior half of throat in males and yellow throat in life, females with white ventral surface (from chin to mid-belly and translucent throat, females ventral surface yellow); (4) its single-note call (two-notes call).

Allobates ripicolus differs from the closely related *A. tapajos* occurring south of the Amazon River by (1) the absence of basal webbing between Toes II and III (present); (2) the presence of melanophores concentrated on the posterior half of throat (no melanophores); (3) its cream ventrolateral stripe continuous or interrupted (absent); (4) its call composed exclusively by a single note (usually composed of two notes [73% of calls], less frequently of one note [23% of calls] and rarely three notes [4% of calls]; Lima et al. (2005)) (Fig. 4).

Allobates ripicolus differs from the closely related *A. kamilae* by (1) its throat entirely translucent without melanophores in females (yellowish anteriorly with melanophores) (Fig. 7,8); (2) its Finger III slightly swollen preaxially in males (Finger III not swollen); (3) its call composed exclusively of a single note (frequently 2–5 notes and rarely 6–17 notes per call) (Fig. 4).

Allobates ripicolus differs from *A. sumtuosus* by (1) the presence of diffuse irregular dark brown blotches scattered on dorsum from eye level to urostyle region (dorsum uniformly brown); (2) its throat and chest yellow with melanophores concentrated on the posterior half of throat in males (white translucent uniformly covered with melanophores only in the throat margins); (3) its single note call with dominant frequency 5,519–6,072 Hz (call consisting of a trill of 23–35 notes and dominant frequency 6,172–6,480 Hz). *Allobates ripicolus* differs from *A. amissibilis* by (1) the presence of diffuse irregular dark brown blotches scattered on dorsum from eye level to urostyle region (dorsum uniformly brown); (2) its throat and chest yellow with melanophores concentrated on the posterior half of throat in males (white translucent uniformly covered with melanophores); (3) its single note call (call consisting of a trill of 1–19 notes).

Description of the holotype. An adult male 16.2 mm SVL (Fig. 7; Table 1) in good condition, with a few superficial scars on dorsum and snout and a large incision in the abdomen for tissue sample; body slender; head slightly longer than wide (HL/HW=1.05); head length 33.0 % of SVL; snout broadly rounded in dorsal view, acutely rounded in lateral view, extending past lower jaw. Nares located laterally, opening posterolaterally; canthus rostralis concave, loreal region slightly concave, flaring slightly at upper lip; internarial distance 41.2 % of head width (IN/HW); eye-naris distance 28.2 % of head length (EN/HL); 79.5 % of eye length (EN/ED). Tympanum sub circular, directed posterolaterally, 54.2 % of eye length (TD/ED); 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, sub circular, 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, with scattered larger granules becoming denser posteriorly, more easily visible in life; 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 as long as II when fingers adpressed; fingers unwebbed, proximal edge of Finger III conspicuously swollen; tip of Finger IV not reaching distal subarticular tubercle on Finger III when fingers adpressed; terminal discs clearly

expanded, discs of Fingers III and IV widest; width of disc on Finger III 0.44 mm; discs with distinct dorsal scutes. Relative lengths of adpressed fingers III > I = II > IV; palmar tubercle large, ovoid, 0.67 mm in its largest diameter, 17.7 % of hand length, periphery pigmented; thenar tubercle conspicuous but not protuberant, ovoid, periphery pigmented, about a third the size of the palmar tubercle and largely separated from it. One subarticular tubercle on Fingers I, II, and IV; two subarticular tubercles on Finger III; subarticular tubercles on Finger I largest, distal tubercle on Finger III smallest (Fig. 7).

Hindlimb robust, skin granular; thigh length 44.8 % of SVL; tibia length 48.9 % of SVL; heels overlapping when hindlimbs are flexed at right angles to sagittal plane of body; foot length 46.0 % of SVL; relative length of adpressed toes IV > III > V > II > I; Toe I very short, its tip not reaching the base of the subarticular tubercle on Toe II when toes are adpressed; discs on Toes II, III, IV, and V larger than width of distal phalanges; disc on Toe I equal to width of distal phalanx. Width of disc on Toe IV 0.55 mm; basal webbing present only between Toes III–IV, posteriorly pigmented; weak lateral fringes preaxially on Toe III and IV. Inner metatarsal tubercle oval, 0.40 mm in length, periphery pigmented, outer metatarsal tubercle round, projecting, 0.33 mm in diameter. Two subarticular tubercles present on Toes III, IV and V, and one on Toes I and II, basal tubercle of Toe IV barely visible on the right toe and very small (about 0.05 mm) and located postaxially on the left one. Subarticular tubercles on Toe I largest; distal subarticular tubercle on Toe IV smallest. Metatarsal fold absent. Tarsal keel well-defined, short, tubercle-like, directed transversely across tarsus, located 0.62 mm from proximal edge of inner metatarsal tubercle, not extending from it (Fig. 7).

Color of holotype in life. Color in life of the holotype is shown in Fig. 7. Dorsal coloration medium brown with dark brown scapular region and diffuse dark brown blotches on dorsum; dorsum light brown laterally from eye level to midbody forming an ill-defined dorsolateral band; laterally a wide dark-brown band from tip of snout around the body to the groin with ill-defined boundaries posterodorsally. The oblique lateral stripe embedded in the black band consists of a diffuse lighter area extending from the groin to about two-third of the distance to the arm insertion. Flanks are creamish white below the lateral dark brown band forming an interrupted ventrolateral stripe extending ventrally along flanks. Upper lip is creamish white. Throat is yellow with scattered tiny melanophores particularly concentrated on the posterior half. Belly is immaculate creamish with scattered tiny melanophores. Upper surfaces of thighs and shanks are brown with ill-defined dark brown transverse bands or blotches. A pale paracloacal mark is present. Forelimbs are reddish anterodorsally and dark gray on the posterior surface of forearms from elbow to wrist. A gray blotch is present on the wrists. Digits are dark gray with a few white dots. The upper surface of tympanum is black, the lower surface white. The iris is copper.

Color of holotype in preservative. After seven years in 70 % ethanol, colors of the specimen have faded, the dorsum is light brown; the lateral band is dark brown and the diffuse oblique lateral stripe is barely distinguishable. Flanks, belly, and upper lips are immaculate white. Throat is white; the melanophores are visible. Upper surface of thighs and shanks are brown with dark brown blotches and dark brown bands. The pale paracloacal mark is still visible. Forelimbs are white. Fingers and digits are light brown. (Fig. 7).

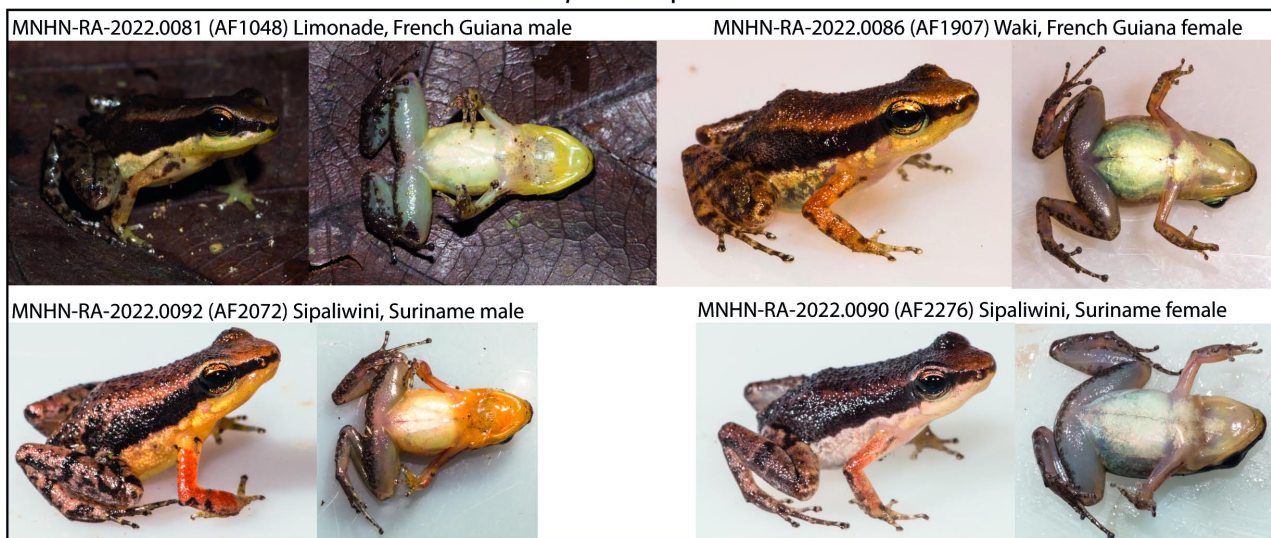
Variation in the type series. Apart from sexual dimorphism and dichromatism (males are slightly smaller than females and throat of females is translucent white and without melanophores), there is considerable variation in size, conspicuousness and distribution of dark brown blotches on dorsum and legs (Fig 8). The dorsal surface of legs varies in coloration from dark gray to light brown with more or less conspicuous dark brown bands and blotches. The ventrolateral stripe is continuous (MNHN-RA-2022.0081) or interrupted in some individuals (MNHN-RA-2022.0086; Fig 8). Ventral surface is immaculate white to yellowish.

Advertisement call. The call consists of a single high pitched note emitted regularly every 550 ms (391–686 ms) and lasting 37 ms (26–45 ms). These notes have an upward frequency modulation, with a minimum starting frequency of about 5,250 Hz (4,914–5,745) and as maximum ending frequency of about 6,090 Hz (5,875–6,465), which represents a 463 Hz (352–613 Hz) difference (MxF1–MiF1) (Fig 4a).

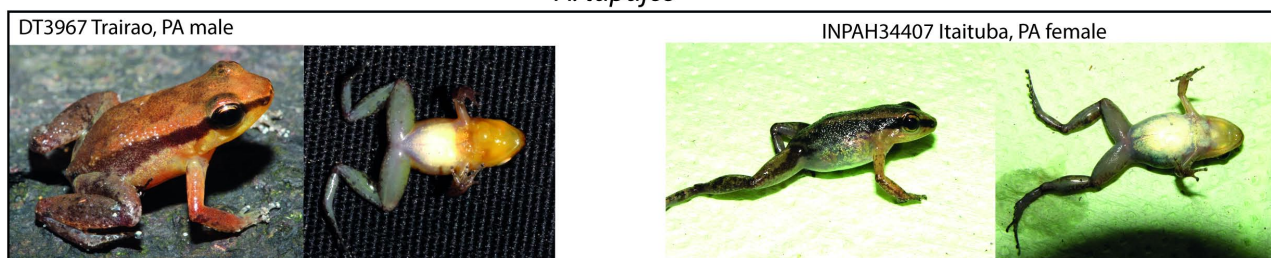
Natural history and distribution. *Allobates ripicolus* is generally associated with the temporary flooded banks of medium-sized rivers where males form patches of two to three individuals. But it is also found on bauxite plateaus such as Itoupé, where individuals were found around a temporary pond at 800 m. Males are territorial and call mainly in the morning and late afternoon. Two egg clutches were found in Sipaliwini (Suriname). They were deposited within folded dead leaves of *Cecropia* spp. One was very recent and contained 18 eggs (Fig 7). The male was calling 40 cm from it. The second one was cloudy and contained 37 well developed embryos, possibly in fact corresponding to two different clutches. The tadpoles are probably carried to a nearby water body by the male.

Allobates ripicolus occupies the southern half of French Guiana (Saul, upper Oyapock, Itoupé, Mitaraka) and is absent from the northern half. It also occurs in the west of Amapá (Brazil), the south of Suriname and the north of Pará (Brazil). It is therefore an endemic species of the eastern part of the Guiana region. Its distribution is similar to that of *Rhinella* aff. *magnussoni* which also has its sister species south of the Amazon River, Brazil (Vacher et al. 2020).

A. ripicolus sp. nov.



A. tapajos



A. kamilae

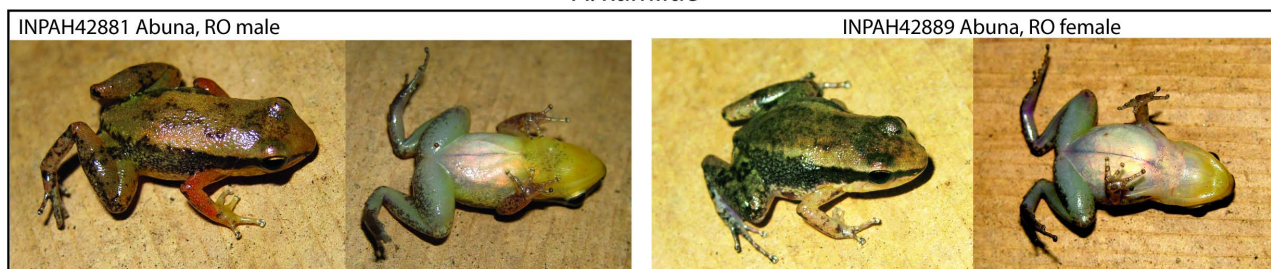


FIGURE 8. Additional specimens in life illustrating the variation of coloration within *Allobates ripicolus* sp. nov., *A. tapajos* (photos L.J.C.L. Moraes and A.P. Lima) and *A. kamilae* (photos A.P. Lima).

Discussion

We herein name and describe two new species of nurse frog from the eastern Guiana Shield. The first one, *Allobates vicinus*, was previously hypothesized to represent the sister species of *Allobates granti* based on molecular data (~~mt+nuDNA~~) (Fouquet et al. 2012; Vacher et al. 2020; Réjaud et al. 2020). We demonstrate here the existence of subtle but concordant phenotypic and acoustic differences, thus justifying its taxonomic description. This case illustrates how a careful examination of morphology and calls of specimens known to harbor genetic differences that nevertheless remain low enough to be ambiguous, can identify clear phenotypic differences and confirm boundaries between closely related species. This practice essentially corresponds to the guidelines of the integrative taxonomy advocated by many authors (e.g. Padial et al. 2010).

The other species, *Allobates ripicolus*, has been known to represent an undescribed species for two decades in French Guiana (Vences et al. 2003) and even after the description of the related *Allobates tapajos* in 2015 (Lima et al. 2015) and *A. kamilae* in 2022 (Ferrão et al. 2022), the differences between their calls was evident. Many species in the eastern Guiana Shield are in a similar situation. In fact, this is the case of another *Allobates* species, *A. femoralis*, which has been documented to harbor distinct calls across its vast distribution notably between Peru and the eastern Guiana Shield (Amezquita et al. 2009). Since this species is described from northwestern Peruvian Amazonia, the populations of the eastern Guiana Shield likely represent an undescribed species. The case of *Amazophrynella* sp. recently documented in Moraes et al. (2022) is even more striking since it represents a lineage more closely related to the species from southern Peru than to the species of the Guiana Shield. There are many other examples and the actual number of undescribed species in the eastern Guiana Shield remains unknown. Despite the continuous progress made in recent years, with no less than 20 frog species described since 2013, species awaiting description probably still represent a third of the species occurring in the region (Vacher et al. 2020).

TABLE3. Mean p-distances among main mtDNA lineages.

	<i>ripicolus</i>	<i>tapajos</i>	<i>tapajos3</i>	<i>kamilae</i>	<i>tapajos2</i>	<i>tapajos1</i>	<i>granti</i>	<i>aff.granti2</i>	<i>vicinus</i>
<i>A. ripicolus</i> sp. nov.									
<i>A. tapajos</i>	0.066								
<i>A. aff. tapajos3</i>	0.046	0.053							
<i>A. kamilae</i>	0.045	0.056	0.034						
<i>A. aff. tapajos2</i>	0.049	0.057	0.034	0.039					
<i>A. aff. tapajos1</i>	0.054	0.053	0.069	0.063	0.078				
<i>A. granti</i>	0.134	0.134	0.123	0.123	0.122	0.126			
<i>A. aff. granti 2</i>	0.127	0.133	0.119	0.115	0.112	0.136	0.044		
<i>A. vicinus</i> sp. nov.	0.125	0.134	0.120	0.120	0.117	0.137	0.040	0.034	

With each newly described species the congruence across distributional patterns of frogs in the region becomes more evident, notably the existence of three main bioregions within the eastern Guiana Shield that were delimited by Vacher et al. (2020). The two new species described herein and *Allobates granti* are each endemic to one of these regions, the easternmost one corresponding to Amapá, French Guiana, Suriname and northern Pará. Conversely, *Allobates sumtuosus*, that enters in contact with *A. vicinus* and *A. ripicolus* in southern Suriname, is circumscribed to the two other Guiana bioregions, whereas *A. amissibilis* is endemic to the northwestern bioregion. This pattern mirrors other frog groups, notably species of the *Pristimantis* gr. *unistrigattus* (Fouquet et al. 2022). The boundaries between these regions do not correspond to any conspicuous landscape features and Vacher et al. (2020) hypothesized that they could mainly result from current and/or past environmental heterogeneity. The eastern Guiana Shield is nowadays characterized by a dry corridor observed from southern Guyana to the state of Pará (Mayle & Power 2008) where relict savannahs are found (e.g. Sipaliwini), which is where *Allobates* species enter in contact. Moreover, neotropical climatic fluctuations during the Miocene and Pliocene are thought to have played a crucial role for in-situ diversification (Antonelli et al. 2010) through landscape modifications that have acted as barriers to dispersal (Carnaval & Bates 2007).

However, the divergence between *Allobates granti* and *A. vicinus* appear to have occurred across the Maroni River, thus, within the easternmost bioregion. The role of the Maroni River as a barrier forming a range boundary or a break between lineages within species of frogs was already identified by Fouquet et al. (2012), including in *Allobates granti*. Contrasting evidence for the importance of rivers has been reported, suggesting permeability of rivers to gene flow could depend on river course vagility over time (Lundberg et al. 1998) and species life history traits such as type of habitat (Fouquet et al. 2015b). The species of *Allobates* illustrate very well the role of ecology in the relative importance of rivers as barriers since *Allobates granti* does not seem to occur on the right bank of the Oyapock River and faces *A. vicinus* across the Maroni River. By contrast, in *A. ripicolus* which is associated with river beds, originates from a trans-amazon dispersal some 4 Ma (Réjaud et al. 2020) and displays little genetic structure within the Eastern Guiana Shield, suggesting that rivers represent less effective barriers.

The perception that Amazonian species are not only vastly underestimated in numbers but also much more narrowly distributed (regional endemism) raises conservation concerns since climatic and land use changes (e.g. Malhi

et al. 2008) represent major threats for amphibians in the region. Considering the range of these two new species, they should be considered as Least Concern according to the IUCN criteria (IUCN 2022). Nevertheless, they are narrowly distributed and require pristine habitats and could therefore undergo decline in the upcoming years.

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Declarations

Conflict of Interests/Competing Interests. The authors have no competing interests to declare that are relevant to the content of this article.

Availability of data and material.

All new call recordings have been deposited in public repositories.

Ethics approval.

Experiments have been conducted in accordance with relevant national legislation on the use of animals for research.

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APPENDIX 1. Details (accession numbers, localities and collectors) regarding the molecular data analyzed in this study

GB Accession	Field N	Voucher	Species	Locality	State	Lat	Lon
KDQF01000783	AF1998		<i>A. aff. granti</i> 2	Sipaliwini, Apalagadi	Suriname	2.1728	-56.0969
KDQF01000792	AF2015	MNHN-RA-2022.0065	<i>A. aff. granti</i> 2	Sipaliwini, Apalagadi	Suriname	2.1728	-56.0969
KDQF01000793	AF2016	MNHN-RA-2022.0066	<i>A. aff. granti</i> 2	Sipaliwini, Apalagadi	Suriname	2.1728	-56.0969
KDQF01002947		MPEG30888	<i>A. aff. granti</i> 2	ESEC Grao Para, centro	PA	0.63028	-55.7285
JN690935	MTR10084		<i>A. aff. tapajos</i> 1	Santa Maria Rio Aripuana	AM	-5.7978	-60.26527
OK349680		CHUFPB30308	<i>A. aff. tapajos</i> 2	Teles River, Jacareacanga	PA	-9.2583	-56.8057
OK349679	AAGARDA12452		<i>A. aff. tapajos</i> 2	Teles River, Jacareacanga	PA	-9.2583	-56.8057
DQ502241		MPEG13383	<i>A. aff. tapajos</i> 3	Parque Estadual Guajara-Mirim	RO	-10.3213	-64.5633
KDQF01002638	HJ285		<i>A. aff. tapajos</i> 3	UHE Jirau,	RO	-8.7484	-63.9034
MZ667618	APL20015		<i>A. aff. tapajos</i> 3	Porto Velho, Jaci-Parana	RO	-9.4125	-64.4425
MZ667619	APL20042		<i>A. aff. tapajos</i> 3	Porto Velho, Jaci-Parana	RO	-9.4125	-64.4425
AY263233	RBE495		<i>A. granti</i>	Saul	French_Guiana	3.6255	-53.2072
EU201066	CM185		<i>A. granti</i>	Trijonction	French_Guiana	2.3333	-54.6
EU201067	RB38		<i>A. granti</i>	St Eugene	French_Guiana	4.85	-53.06667

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APPENDIX 1. (Continued)

GB Accession	Field N	Voucher	Species	Locality	State	Lat	Lon
JN690927	CM231		<i>A. granti</i>	Saul	French_Guiana	3.6256	-53.2072
JN690928	PG301		<i>A. granti</i>	Haut Marwini	French_Guiana	2.6067	-54.0257
JN690929	PG233		<i>A. granti</i>	Haute Wanapi	French_Guiana	2.5134	-53.8211
JN690930	CM302		<i>A. granti</i>	Toponowini	French_Guiana	3.0521	-52.705
JN690931	PG125		<i>A. granti</i>	Toponowini	French_Guiana	3.0521	-52.705
JN690932	PG175		<i>A. granti</i>	Armontabo	French_Guiana	3.8044	-52.2886
KDQF01000105	AF0275		<i>A. granti</i>	Nouragues, Camp Inselberg	French_Guiana	4.0833	-52.6833
KDQF01000106	AF0276		<i>A. granti</i>	Nouragues, Camp Inselberg	French_Guiana	4.0833	-52.6833
KDQF01000125	AF0519		<i>A. granti</i>	CisameG	French_Guiana	4.195265	-52.3720
KDQF01000130	AF0528		<i>A. granti</i>	Nouragues, Camp Inselberg	French_Guiana	4.08501	-52.6809
KDQF01000352	AF0976		<i>A. granti</i>	Saul, Galbao	French_Guiana	3.63592	-53.2725
KDQF01000370	AF1018		<i>A. granti</i>	Saul, Galbao	French_Guiana	3.625727	-53.2805
KDQF01000383	AF1050		<i>A. granti</i>	Saul, gros arbres	French_Guiana	3.615576	-53.2270
KDQF01000403	AF1102		<i>A. granti</i>	Ilet Lezard rive D	French_Guiana	5.054438	-53.7977
KDQF01000419	AF1135		<i>A. granti</i>	Nouragues, Parare	French_Guiana	4.04203	-52.6806
KDQF01000424	AF1160	MNHN-RA-2022.0101	<i>A. granti</i>	Trinite, aya	French_Guiana	4.6025	-53.4143
KDQF01000610	AF1628		<i>A. granti</i>	Saul, Limonade	French_Guiana	3.57317	-53.19851
KDQF01000740	AF1904	MNHN-RA-2022.0102	<i>A. granti</i>	Flat de la Waki	French_Guiana	3.08466	-53.41019
KDQF01001034	AF2642	MNHN-RA-2022.0103	<i>A. granti</i>	Atachi Bakka	French_Guiana	3.5671	-53.96164
KDQF01001055	AF2682	MNHN-RA-2022.0105	<i>A. granti</i>	Alikene	French_Guiana	3.21515	-52.4019
KDQF01001078	AF2728	MNHN-RA-2022.0106	<i>A. granti</i>	Mitaraka	French_Guiana	2.23577	-54.44928
KDQF01001134	AF2914	MNHN-RA-2022.0108	<i>A. granti</i>	Memora G	French_Guiana	3.31774	-52.19329
KDQF01001236	AF3095		<i>A. granti</i>	Mitan G	French_Guiana	2.6284	-52.55404
KDQF01001239	AF3100		<i>A. granti</i>	Mitan G	French_Guiana	2.6284	-52.55404
KDQF01001444	AF3635		<i>A. granti</i>	Itoupe	French_Guiana	3.02302	-53.09547
KDQF01001578	AG393		<i>A. granti</i>	Dekou dekou	French_Guiana	4.6968	-53.9598

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APPENDIX 1. (Continued)

GB Accession	Field N	Voucher	Species	Locality	State	Lat	Lon
KDQF01001631	AG467		<i>A. granti</i>	Alikene	French_Guiana	3.2200	-52.37855
KDQF01001634	AG476		<i>A. granti</i>	Saul, Monts Belvedere	French_Guiana	3.7193	-53.4128
KDQF01001639	AG482		<i>A. granti</i>	Saul, Monts Belvedere	French_Guiana	3.7193	-53.4128
KDQF01001652	AG506		<i>A. granti</i>	Saul, Monts Belvedere	French_Guiana	3.719347	-53.4128
KDQF01001869	BOAM025		<i>A. granti</i>	Borne 4	French_Guiana	2.3709	-53.7728
KDQF01001872	BOAM029		<i>A. granti</i>	Borne 4	French_Guiana	2.3709	-53.7728
KDQF01001888	BOAM052		<i>A. granti</i>	Borne 4	French_Guiana	2.3709	-53.7728
KDQF01001989	BPN1586		<i>A. granti</i>	Saul	French_Guiana	3.62556	-53.2072
KDQF01001990	BPN1612		<i>A. granti</i>	Saul	French_Guiana	3.62556	-53.2072
KDQF01001993	BPN1687		<i>A. granti</i>	Saul	French_Guiana	3.62556	-53.2072
KDQF01002254	CM206		<i>A. granti</i>	Saul	French_Guiana	3.62556	-53.2072
KDQF01002327	CM405		<i>A. granti</i>	Lucifer	French_Guiana	4.7774	-53.9475
KDQF01002328	CM406		<i>A. granti</i>	Lucifer	French_Guiana	4.7774	-53.9475
KDQF01003835	PG166		<i>A. granti</i>	Armontabo	French_Guiana	3.8044	-52.2881
KDQF01003851	PG299		<i>A. granti</i>	Haut Marwini	French_Guiana	2.6067	-54.0257
KDQF01003852	PG300		<i>A. granti</i>	Haut Marwini	French_Guiana	2.6067	-54.0257
KDQF01003868	PG406		<i>A. granti</i>	Kotika, Mont	French_Guiana	3.93472	-54.20472
KDQF01003874	PG467		<i>A. granti</i>	Kotika, Mont	French_Guiana	3.93472	-54.20472
KDQF01003875	PG468		<i>A. granti</i>	Kotika, Mont	French_Guiana	3.9347	-54.2047
KDQF01003901	PG591		<i>A. granti</i>	Mitaraka	French_Guiana	2.2911	-54.5342
KDQF01004321	T3041		<i>A. granti</i>	Mitaraka	French_Guiana	2.26667	-54.51667
KDQF01004461	WAAM010		<i>A. granti</i>	Flat de la waki	French_Guiana	3.18341	-53.4775
AY263232	RBE492		<i>A. ripicolus</i>	Saul	French_Guiana	3.6255	-53.2072
EU201069	AG092		<i>A. ripicolus</i>	Saul, Crique Limonade	French_Guiana	3.5667	-53.2167
KDQF01000622	AF1658	MNHN-RA-2022.0083	<i>A. ripicolus</i>	Saul, Limonade	French_Guiana	3.56311	-53.19083
KDQF01000741	AF1906		<i>A. ripicolus</i>	Flat de la Waki	French_Guiana	3.0835	-53.41257

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APPENDIX 1. (Continued)

GB Accession	Field N	Voucher	Species	Locality	State	Lat	Lon
KDQF01000821	AF2072	MNHN-RA-2022.0092	<i>A. ripicolus</i>	Sipaliwini, Apalagadi	Suriname	2.17816	-56.08521
KDQF01001115	AF2828	MNHN-RA-2022.0095	<i>A. ripicolus</i>	Mitaraka, layon B	French_Guiana	2.23577	-54.44928
KDQF01001311	AF3221	MNHN-RA-2022.0097	<i>A. ripicolus</i>	Mitan G	French_Guiana	2.6284	-52.55404
KDQF01002022	BPN2892		<i>A. ripicolus</i>	RAP Basecamp 1	Suriname	2.46554	-55.62955
KDQF01002914		MPEG30384	<i>A. ripicolus</i>	REBIO Maicuru	PA	0.82861	-53.93120
KDQF01002915		MPEG30385	<i>A. ripicolus</i>	REBIO Maicuru	PA	0.82861	-53.93120
KDQF01002948		MPEG30890	<i>A. ripicolus</i>	ESEC Grao Para centro	PA	0.63028	-55.7285
KDQF01003825	PG100		<i>A. ripicolus</i>	Saul	French_Guiana	3.5667	-53.21667
KDQF01003826	PG101		<i>A. ripicolus</i>	Saul	French_Guiana	3.5667	-53.21667
KDQF01004176	RBE494		<i>A. ripicolus</i>	Saul	French_Guiana	3.6255	-53.2072
KDQF01004394	UHE144		<i>A. ripicolus</i>	UHE SANTO ANTONIO	AP	-0.64559	-52.5005
KDQF01004395	UHE145		<i>A. ripicolus</i>	UHE SANTO ANTONIO	AP	-0.645593	-52.5005
KDQF01004468	WAAM017		<i>A. ripicolus</i>	Flat de la waki	French_Guiana	3.18341	-53.4775
DQ502110	MJH3973		<i>A. tapajos</i>	Rio Curua-Una	PA	-3.1500	-54.8333
EU342545		LSUMZ15296	<i>A. tapajos</i>	Rio Curua-Una	PA	-3.1500	-54.8333
EU342546		LSUMZ15291	<i>A. tapajos</i>	Rio Curua-Una	PA	-3.1500	-54.8333
KDQF01001798	BM004		<i>A. tapajos</i>	UHE Belo Monte	PA	-2.9505	-51.9366
KDQF01001805	BM032		<i>A. tapajos</i>	UHE Belo Monte	PA	-2.9505	-51.9366
KR047027	APL12965	INPA-H 34404	<i>A. tapajos</i>	Parque Nacional da Amazonia, Itaituba	PA	-4.47027	-56.28444
KR047028	APL12968	INPA-H 34409	<i>A. tapajos</i>	Parque Nacional da Amazonia, Itaituba	PA	-4.47027	-56.28444
KX524470		INPA-H 36565	<i>A. tapajos</i>	Itaituba	PA	-4.171477	-56.0155
KX524471		INPA-H 36533	<i>A. tapajos</i>	Itaituba	PA	-4.171477	-56.0155
KX524472		INPA-H 36519	<i>A. tapajos</i>	Itaituba	PA	-4.171477	-56.0155
KX524473		INPA-H 36577	<i>A. tapajos</i>	Itaituba	PA	-4.171477	-56.0155
KX524474		INPA-H 36528	<i>A. tapajos</i>	Itaituba, Parana-Mirim	PA	-4.5825	-56.6617
KX524475		INPA-H 36570	<i>A. tapajos</i>	Itaituba, Parana-Mirim	PA	-4.5825	-56.6617
KX524476		INPA-H 36559	<i>A. tapajos</i>	Itaituba, Parana-Mirim	PA	-4.5825	-56.6617
KX524477		INPA-H 36526	<i>A. tapajos</i>	Itaituba, Parana-Mirim	PA	-4.5825	-56.6617
KX524478		INPA-H 36537	<i>A. tapajos</i>	Itaituba, Sao Luis do Tapajos	PA	-4.27246	-56.14532
KX524479		INPA-H 36525	<i>A. tapajos</i>	Itaituba, Sao Luis do Tapajos	PA	-4.27246	-56.14532
KX524480		INPA-H 36560	<i>A. tapajos</i>	Itaituba, Vila Rayol	PA	-4.273093	-56.16128
KX524481		INPA-H 36587	<i>A. tapajos</i>	Itaituba, Vila Rayol	PA	-4.273093	-56.16128
KX524482		INPA-H 36515	<i>A. tapajos</i>	Itaituba, Vila Rayol	PA	-4.273093	-56.16128
KX524483		INPA-H 36573	<i>A. tapajos</i>	Itaituba, Vila Rayol	PA	-4.273093	-56.16128

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APPENDIX 1. (Continued)

GB Accession	Field N	Voucher	Species	Locality	State	Lat	Lon
KX524484		INPA-H 36549	<i>A. tapajos</i>	Itaituba, Vila Rayol	PA	-4.273093	-56.161285
KX524485		INPA-H 36542	<i>A. tapajos</i>	Itaituba, Vila Rayol	PA	-4.273093	-56.16128
KX524486		INPA-H 36562	<i>A. tapajos</i>	Aveiro, Brasilia legal	PA	-3.562892	-55.34562
KX524487		INPA-H 36544	<i>A. tapajos</i>	Belterra	PA	-2.445911	-54.57293
KX524488		INPA-H 36584	<i>A. tapajos</i>	Belterra	PA	-2.445911	-54.57293
KX524489		INPA-H 36568	<i>A. tapajos</i>	Belterra	PA	-2.445911	-54.57293
EU201068	AF0148		<i>A. vicinus</i>	Brownsberg	Suriname	4.936527	-55.194826
JN690923	BPN1054		<i>A. vicinus</i>	Lely Mountain	Suriname	4.26667	-54.73333
JN690924	BPN1055		<i>A. vicinus</i>	Lely Mountain	Suriname	4.26667	-54.73333
JN690925	BPN1056		<i>A. vicinus</i>	Lely Mountain	Suriname	4.26667	-54.73333
JN690926	BPN0778		<i>A. vicinus</i>	Ralleighvallen	Suriname	4.71667	-56.21667
KDQF01000062	AF0154		<i>A. vicinus</i>	Brownsberg	Suriname	4.93653	-55.19483
KDQF01000064	AF0158		<i>A. vicinus</i>	Brownsberg	Suriname	4.93653	-55.19483
KDQF01000968	AF2476	MNHN-RA-2022.0070	<i>A. vicinus</i>	Nassau, trail camp	Suriname	4.80262	-54.61502
KDQF01000971	AF2479	MNHN-RA-2022.0071	<i>A. vicinus</i>	Nassau	Suriname	4.80262	-54.61502
KDQF01001414	AF3428	MNHN-RA-2022.0075	<i>A. vicinus</i>	Bakhuis, Slope 5k	Suriname	4.70646	-56.77943
KDQF01001415	AF3429	MNHN-RA-2022.0076	<i>A. vicinus</i>	Bakhuis, Slope 5k	Suriname	4.70646	-56.77943
KDQF01003782	NZCS69		<i>A. vicinus</i>	rosebel,	Suriname	5.12439	-55.24925
KDQF01003783	NZCS70		<i>A. vicinus</i>	rosebel	Suriname	5.12439	-55.24925
MZ667621	APL22564	INPA-H 42888	<i>A. kamilae</i>	Porto Velho, Morrinhos	RO	-9.076111	-64.24611
MZ667622	APL22565	INPA-H 42896	<i>A. kamilae</i>	Porto Velho, Morrinhos	RO	-9.076111	-64.24611
MZ667623	APL22570	INPA-H 42895	<i>A. kamilae</i>	Porto Velho, Morrinhos	RO	-9.076111	-64.24611
MZ667624	APL22571		<i>A. kamilae</i>	Porto Velho, Morrinhos	RO	-9.076111	-64.24611
MZ667625	APL22572	INPA-H 42922	<i>A. kamilae</i>	Porto Velho, Morrinhos	RO	-9.076111	-64.24611
MZ667630	APL14972	INPA-H 42948	<i>A. kamilae</i>	Porto Velho, Pedras	RO	-9.167074	-64.629109
MZ667626	APL14791	INPA-H 42919	<i>A. kamilae</i>	Porto Velho, Bufalos	RO	-9.133275	-64.497260
MZ667629	APL14700	INPA-H 42965	<i>A. kamilae</i>	Porto Velho, Jirau Esquerdo	RO	-9.317073	-64.743354
MZ667631	APL14970	INPA-H 42920	<i>A. kamilae</i>	Porto Velho, Pedras	RO	-9.167074	-64.629109
MZ667627	APL14758	INPA-H 42964	<i>A. kamilae</i>	Porto Velho, Bufalos	RO	-9.133275	-64.497260
MZ667633	APL14701	INPA-H 42901	<i>A. kamilae</i>	Porto Velho, Jirau Esquerdo	RO	-9.317073	-64.743354
MZ667632	APL14609	INPA-H 42967	<i>A. kamilae</i>	Porto Velho, Jirau Esquerdo	RO	-9.317073	-64.743354
MZ667628	APL14838	INPA-H 42937	<i>A. kamilae</i>	Porto Velho, Bufalos	RO	-9.133275	-64.497260
MZ667620	APL15879	INPA-H 42921	<i>A. kamilae</i>	Porto Velho, Morrinhos	RO	-9.076111	-64.246111

APPENDIX 2. Additional material examined.

Allobates granti (all males): MNHN-RA-2022.0101 (AF1160) Trinité; MNHN-RA-2022.0104 (AF2643) Atachi Bakka; MNHN-RA-2022.0105 (AF2682) Alikéné; MNHN-RA-2022.0108 (AF2914) Mémora ; MNHN-RA-2022.0109 (AF3212) Mitan ; MNHN-RA-2022.0110 (AF3586) Itoupe; MNHN-RA-2022.0112 (AF5455) Trois-Saut ; MNHN-RA-2022.0111 (AF3636) Itoupe ; MNHN-RA-2022.0102 (AF1904) Flat de la Waki ; MNHN-RA-2022.0103 (AF2642) Atachi Bakka; MNHN-RA-2022.0106 (AF2728) Mitaraka; MNHN-RA-2022.0107 (AF2768) Mitaraka

Allobates aff. granti 2 (2 adults): Suriname: Sipaliwini: Apalagadi MNHN-RA-2022.0065-6

Allobates kamilae (75 adults): Brazil: Rondônia: Porto Velho: west bank of the upper Madeira River INPA-H 42923 (holotype), INPA-H 42902, 42919, 42937, 42943 , 42952, 42963–64, 42886 (paratopotypes), and INPA-H 42879, 42881–82, 42887, 42889, 42899, 42906, 429–13, 42917, 42920, 42925–26, 42929, 42931, 42936, 42938–39, 42944–45, 42947–50, 42956, 42965–67 (paratypes); east bank of the upper Madeira River INPA-H 42877–78, 42880, 42884–85, 42890, 42892–94, 42897, 42900, 42903–05, 42908–09, 42911, 42914–16, 42924, 42927–28, 42930, 42932–35, 42940–42, 42953, 42955, 42957–59, 42961–62 (paratypes).

Allobates tapajos (24 adults): Brazil: Pará: INPA-H 34425 (holotype) and 34402–24 (paratypes) Parque Nacional da Amazônia.

APPENDIX 3. Details (accession numbers, localities and collectors) regarding the acoustic data analyzed in this study

Accession	Species	locality	collector	File name
MNHN-SO-2023-124	<i>A. vicinus</i>	Voltzberg	A. Fouquet	160125_0777
MNHN-SO-2022-126	<i>A. vicinus</i>	Bakhuis	A. Fouquet	LS110037 AF3428
MNHN-SO-2022-125	<i>A. vicinus</i>	Bakhuis	A. Fouquet	LS110038 AF3429
MNHN-SO-2022-129	<i>A. aff. granti 2</i>	Apalagadi	A. Fouquet	LS110117 AF2015
MNHN-SO-2022-128	<i>A. vicinus</i>	Nassau	A. Fouquet	LS110405
MNHN-SO-2022-127	<i>A. vicinus</i>	Nassau	A. Fouquet	LS110428
MNHN-SO-2022-130	<i>A. granti</i>	Itoupe	M. Dewynter	400 m Itoupe 2010
MNHN-SO-2022-131	<i>A. granti</i>	Itoupe	A. Fouquet	160112_0722 AF3636
NA	<i>A. granti</i>	NA	Marty and Gaucher 2000	Track 14 C beebei
MNHN-SO-2019-17	<i>A. granti</i>	Mitaraka	A. Fouquet	LS110467 AF2728
MNHN-SO-2022-132	<i>A. granti</i>	Waki	J.-P. Vacher	STE-014_5_4_2014_AF1904
MNHN-SO-2022-133	<i>A. granti</i>	AtachiBakka	J.-P. Vacher	STE-128_09-02-2015_AF2642
MNHN-SO-2022-134	<i>A. granti</i>	Alikene	J.-P. Vacher	STE-164_5-02-2015_AF2682
MNHN-SO-2022-135	<i>A. ripicolus</i>	Itoupe	A. Fouquet	160107_0698
MNHN-SO-2022-136	<i>A. ripicolus</i>	Itoupe	A. Fouquet	AF3587_175820
MNHN-SO-2022-137	<i>A. ripicolus</i>	Itoupe	M. Dewynter	800 m Itoupe 2010
MNHN-SO-2022-138	<i>A. ripicolus</i>	Saul	A. Fouquet	LS110023 AF1686
MNHN-SO-2022-139	<i>A. ripicolus</i>	Borne 4	M. Dewynter	LS110059 Borne 4 Mael
MNHN-SO-2022-140	<i>A. ripicolus</i>	Sipaliwini	A. Fouquet	LS110091
MNHN-SO-2022-141	<i>A. ripicolus</i>	Sipaliwini	A. Fouquet	LS110133 AF2072
MNHN-SO-2022-142	<i>A. ripicolus</i>	Mitaraka	A. Fouquet	LS110524
MNHN-SO-2022-143	<i>A. ripicolus</i>	Waki	J.-P. Vacher	STE-016_5_4_2014_AF1906

APPENDIX 4. Full ML tree

