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A New Nurse Frog from Brazil (Aromobatidae: *Allobates*), with Data on the Distribution and Phenotypic Variation of Western Amazonian Species

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Abstract. Limited knowledge about species diversity restricts inferences about biogeography and macroecology in Amazonia, where biodiversity documentation has become particularly pressing due to anthropogenic impacts. An emblematic example of poorly known Amazonian amphibian diversity is that of *Allobates* nurse frogs, in which species boundaries and ranges are unclear. Based on genetic, morphological and call data from samples collected in 14 poorly known sites in Brazil, we identify and describe a new, broadly distributed western Amazonian nurse frog. In the light of the genetic data, combined with examination of more than 400 museum specimens, we also assess the distribution and levels of phenotypic variation in poorly known species from Amazonian lowlands, namely *A. flaviventris*, *A. gasconi*, *A. subfolionidificans*, and *A. trilineatus*. Lastly, our morphological examinations point to inconsistencies and heterospecific samples in the type series of *A. fuscellus*, *A. gasconi*, and *A. vanzolinus*, as revealed by large variation in key traits. By improving knowledge about species ranges and identifications, we hope that this study will support biodiversity inventories and stimulate further investigations of understudied western Amazonian nurse frogs.

Keywords. Amazon; Amphibia; South America; Systematics; Taxonomy.

Resumo. Um conhecimento limitado sobre a diversidade de espécies restringe inferências sobre biogeografia e macroecologia na Amazônia, onde documentar padrões de biodiversidade tornou-se particularmente urgente devido a impactos antropogênicos. Um exemplo emblemático de anfíbios amazônicos cuja diversidade é mal conhecida é o das rãs-cuidadoras do gênero *Allobates*, para as quais as distribuições e os limites entre espécies ainda não estão claros. Com base em dados genéticos, morfológicos e de vocalização de espécimes amostrados em 14 localidades pouco exploradas no Brasil, identificamos e descrevemos uma nova espécie de *Allobates* de ampla distribuição na Amazônia ocidental. À luz dos dados genéticos, em combinação com o exame de mais de 400 espécimes de museus, também examinamos a distribuição e a variação fenotípica em espécies pouco conhecidas das planícies amazônicas, nomeadamente *A. flaviventris*, *A. gasconi*, *A. subfolionidificans* e *A. trilineatus*. Por último, a análise de espécimes depositados em coleções zoológicas aponta para inconsistências e amostras heteroespecíficas na série tipo de *A. fuscellus*, *A. gasconi* e *A. vanzolinus*, como revelado por uma grande variação em caracteres-chave. Ao melhorar o conhecimento sobre as distribuições e identificações de espécies, esperamos que este estudo apoie inventários de biodiversidade e estimule novas investigações sobre as pouco conhecidas rãs-cuidadoras da Amazônia ocidental.

INTRODUCTION

Recent biodiversity inventories in the Neotropics have led to an increasing number of taxonomic discoveries, indicating that we still have a limited understanding of species diversity in Earth's most biodiverse region (Pimm et al., 2010; Scheffers et al., 2012). This knowledge gap restricts our comprehension of species ranges and inferences about the ecological and evolutionary drivers of diversification (Angulo and Icochea, 2010). This is the case of Amazonian amphibians, for which integrated molecular and phenotypic analyses have significantly changed our understanding of species diversity (Padiá

and de la Riva, 2009). Several taxa once viewed as wide-ranged have been shown to correspond to multiple, divergent, spatially restricted lineages, some of which received formal taxonomic descriptions (e.g., Peloso et al., 2014, 2016; Fouquet et al., 2015, 2016; Caminer et al., 2017). The possibility that amphibian diversity is structured in geographic space has exciting and potentially transformative implications for biogeographic and macroecological investigations in Amazonia.

An emblematic example of poorly understood Amazonian diversity is that of nurse frogs, genus *Allobates* Zimmerman and Zimmerman, 1988. Identifying species is a challenging task in these mostly cryptically colored,

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leaf-litter anurans (Grant et al., 2006). Unclear species boundaries and diagnoses have resulted in the incorporation of poorly identified DNA and occurrence data into public databases, including GenBank (NCBI, 2017) and the Red List of Threatened species (IUCN, 2016). This lack of taxonomic clarity may have concrete impacts in many fields of expertise (Harris, 2003). Biodiversity assessments, such as those that aim to evaluate the impact of hydropower dams and transmission lines in Brazil (e.g., CONAMA, 1986; CONAMA, 1997; IBAMA, 2007), are extremely vulnerable to such poorly diagnosed samples, because they rely on species-level taxonomies to assess the rarity and vulnerability of the impacted fauna. In the face of the anthropogenic impacts currently faced by Amazonia, proper description and documentation of biodiversity in this region have become particularly pressing (Myers et al., 2000).

In the early 2000's, systematic morphological comparisons led to the description of several new *Allobates* species (Grant and Rodríguez, 2001; Lima and Caldwell, 2001; Myers and Donnelly, 2001; Morales, 2002; Caldwell and Lima, 2003; La Marca et al., 2004). However, the use of genetic data later revealed that some of those names do not correspond to natural groups, and that some of those type series likely represent species composites (Grant et al., 2006). More recently, the use of mitochondrial DNA barcodes, along with information about vocalizations and coloration in life, led to a pulse of new descriptions based on samples from Brazil (Lima et al., 2007, 2010, 2014, 2015; Simões et al., 2010, 2013a; Melo-Sampaio et al., 2013; Simões, 2016). Despite these efforts, the distribution of most lowland *Allobates* species is still poorly known, and published species lists generally fail to provide identification at the species level for nurse frogs (e.g., Bernarde et al., 2011, 2013; Pantoja and Fraga, 2012; Waldez et al., 2013; Vaz-Silva et al., 2015).

On the basis of biodiversity inventories in 14 poorly known Brazilian localities, examination of specimens deposited in museum collections, and new and previously published molecular data (e.g., Grant et al., 2006; 2017; Santos et al., 2009; Simões et al., 2010, 2013a; Simões, 2013b; 2016; Fouquet et al., 2013; Lima et al., 2014, 2015), we describe a widely distributed species of western Amazonian *Allobates*. Molecular and morphological analyses also provide information about the distribution, phenotypic variation, and phylogenetic relationships of additional western Amazonian species, namely *A. flaviventris* Melo-Sampaio et al., 2013, *A. gasconi* (Morales, 2002), *A. subfolionidificans* (Lima et al., 2007), and *A. trilineatus* (Boulenger, 1883), improving the identification of samples included in previous studies. We also take the opportunity to report inconsistencies in the type series of *A. fuscillus* (Morales, 2002), *A. gasconi* (Morales, 2002), and *A. vanzolinii* (Morales, 2002).

Our analysis incorporates molecular data generated by previous phylogenetic assessments of *Allobates*, yet we do not reexamine the group's systematics beyond our target taxa. Instead, we refer to the much more extensive work of Grant et al. (2017).

MATERIALS AND METHODS

Field sampling

Newly sampled specimens of *Allobates flaviventris*, *A. gasconi*, *A. trilineatus*, and the new species were collected during several field expeditions from November 2009 to March 2016 in western Brazilian Amazonia (Fig. 1–2). A total of 14 sites were sampled (Table S1).

Adult frogs were killed with a topic solution of lidocaine hydrochloride and subsequently fixed in 10% formalin for 24 hours and transferred to 70% ethanol for permanent storage. Liver samples were taken prior to fixation and stored in absolute ethanol for molecular analyses. Specimens were deposited in Museu Nacional, Rio de Janeiro (MNRJ) and Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCP).

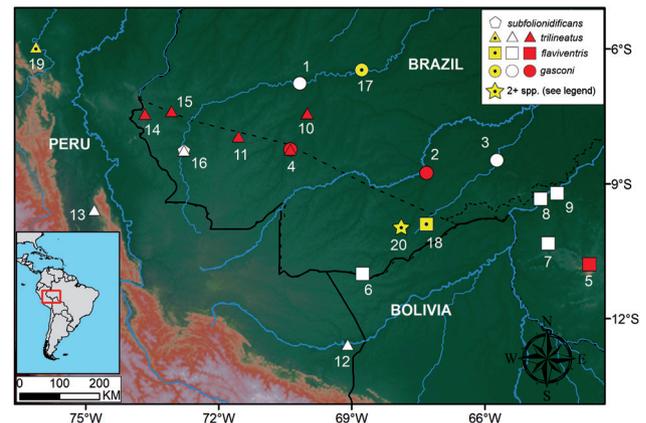


Figure 1. Samples of *Allobates flaviventris*, *A. gasconi*, *A. subfolionidificans*, and *A. trilineatus* used in phylogenetic analyses. Newly-sampled specimens (red symbols) and samples obtained from GenBank (white symbols) are shown. For reference, the type locality of each species is also indicated (yellow symbols with a dot). The yellow star corresponds to Rio Branco, state of Acre (AC) in Brazil, from which we generated molecular data of *A. trilineatus* and *A. gasconi*, as well as obtained sequences of *A. subfolionidificans* from GenBank (corresponding to this species' type locality). Numbers indicate the following sites: (1) Eirunepé, state of Amazonas (AM), Brazil; (2) Boca do Acre, AM; (3) Rio Ituxí, Lábrea, AM; (4) Feijó, AC; (5) Parque Nacional Serra dos Pacaás Novos, state of Rondônia (RO), Brazil; (6) Cobija, Bolivia; (7) Parque Estadual Guajará-Mirim (RO); (8) Cachoeira do Jirau, Porto Velho (RO); (9) Jaci-Paraná, Porto Velho (RO); (10) Envira, AM; (11) Tarauacá, AC; (12) Cuzco Amazónico, Puerto Maldonado, Peru; (13) Rio Llullapichis, Panguana, Peru; (14) Parque Nacional Serra do Divisor, Mâncio Lima (AC); (15) Mâncio Lima (AC); (16) Porto Walter (AC); (17) Jaiuu, IPIXUNA (AM); (18) Fazenda Bonal, Senador Guimard (AC); (19) Huallaga River, Yurimaguas, Peru; (20) Rio Branco (AC).

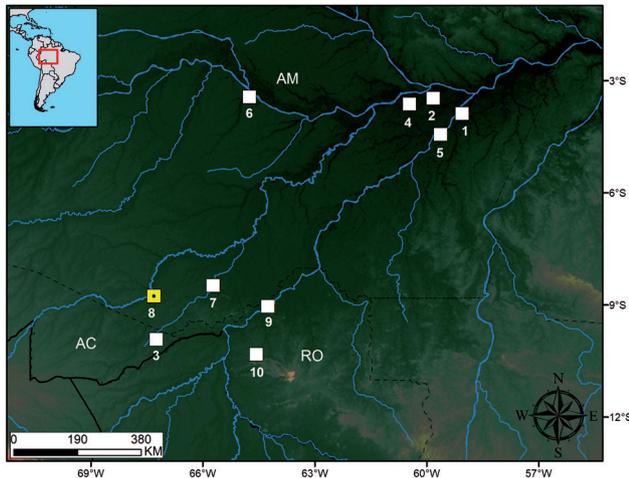


Figure 2. Known distribution of *Allobates tinae* sp. nov. The type locality is indicated by a yellow square with a central dot. Numbers indicate the following sites: (1) Nova Olinda do Norte, state of Amazonas (AM), Brazil; (2) Careiro, AM; (3) Fazenda Bonal, Senador Guiomard, state of Acre (AC), Brazil; (4) Manaquiri, AM; (5) Borba, AM; (6) Tefé, AM; (7) Rio Ituxi, Lábrea, AM; (8) Boca do Acre, AM; (9) Cachoeira do Morrinhos, Porto Velho, state of Rondônia (RO), Brazil; (10) Rio Formoso, Parque Estadual de Guajará-Mirim, Nova Mamoré, RO.

Molecular sampling and analyses

We generated new DNA sequences for 27 specimens of *Allobates flaviventris*, *A. gasconi*, *A. trilineatus*, and the new species and combined these data with published sequences of 58 individuals. This sample encompasses 32 of the 50 named species of *Allobates* (see Results). We refrained from using a large number of GenBank sequences attributed to *Allobates* for which we had no access to the corresponding museum vouchers and that were not clearly assigned to a species. However, we did include unidentified GenBank samples when we had access to the corresponding vouchers (or to vouchers from the same locality) and could therefore test whether they correspond to our focal taxa (*A. flaviventris*, *A. gasconi*, *A. subfolionidificans*, *A. trilineatus*, and the new species) also based on morphological attributes. We also limit the inclusion of multiple samples from a given locality that correspond to a demonstrably monophyletic species, based on preliminary phylogenetic analyses and previous studies. As outgroups, we included one representative of each of the other four aromobatid genera, namely *Anomaloglossus stepheni* (Martins, 1989), *Aromobates nocturnus* Myers et al., 1991, *Mannophryne collaris* (Boulenger, 1912), and *Rheobates palmatus* (Werner, 1899). To root our tree, we considered *Allobates* as the sister of a clade composed by the remaining Aromobatidae, following the revisionary work of Grant et al. (2017).

Matching available datasets (e.g., Grant et al., 2006, 2017; Santos et al., 2009; Fouquet et al., 2013; Simões, 2016), we generated sequences of the mitochondrial genes 16S subunit ribosomal RNA (16S) following Palum-

bi et al. (1996), *cytochrome oxidase I* (COI) as per Folmer et al. (1994), and *cytochrome b* (CYTB) following Santos et al. (2009). Moreover, because our sampled taxa (including the newly described species) have been previously sampled for nuclear data, our dataset also incorporated sequences of seven additional genetic markers (totaling 10 genes and 6,723 base pairs), as follows: the nuclear genes 28S ribosomal RNA (28S), *histone H3* (HH3), *recombination activating gene 1* (RAG1), *rhodopsin* (RHO), *seventh in absentia* (SIA), and *tyrosinase* (TYR), as well as the mitochondrial 12S rRNA gene (12S). We opted for not using published data of six additional genes (BDNF, BMP2, NCX1, NT3, POMC, ZFX1) because sequences of only seven *Allobates* samples are available for them, which would lead to extreme levels of missing data for those genes in our dataset (i.e., > 90%). Specimen and locality information of newly sequenced specimens (including GenBank accession numbers) is provided in Table S1, while samples obtained from GenBank are detailed in Table S2.

Sequences were edited using Geneious Pro 6 (Kearse et al., 2012) and aligned with MAFFT 7.309 (Katoh and Standley, 2013) as implemented in Geneious using default settings. We refrained from manually modifying alignments to avoid subjective changes, but visual inspection suggested no alignment anomalies. Our final concatenated alignment is provided in the online supporting information (Text S1). Models of nucleotide evolution and best-fit partition schemes were determined with PartitionFinder 2.1.1 (Lanfear et al., 2016), implementing PhyML for likelihood estimation (Guindon et al., 2010) and the Bayesian Information Criterion for model selection (Sullivan and Joyce, 2005). Based on PartitionFinder results, codon partitioning was used for the protein coding genes. We performed phylogenetic inference under a Bayesian framework using MrBayes 3.2.6 (Ronquist et al., 2012), implementing three independent runs of four Markov chains of 20 million generations each and sampling every 1,000 steps. We assessed stationarity of model parameters (i.e., effective sample sizes > 200) and convergence among runs using Tracer 1.6, combined runs in LogCombiner 1.8.4 (with 10% discarded as burn-in), and summarized a maximum clade credibility tree in TreeAnnotator 1.8.4 (Drummond et al., 2012). Resulting topologies were visualized in FigTree 1.4.3 (Drummond et al., 2012).

Examination of museum specimens

Unique combinations of morphological characters among sampled individuals and molecular phylogenetic patterns suggested the occurrence of an undescribed species of *Allobates* (see Results). To test species identification, we examined preserved specimens housed in several herpetological collections in the light of the pertinent

literature, focusing on the type series of Amazonian *Allobates* species and samples incorporated in previous molecular phylogenetic analyses (see Appendix 1). Visited institutions included the Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA-H), Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP), Museu Paraense Emílio Goeldi, Belém (MPEG), and Universidade Federal do Acre, Rio Branco (UFAC-RB), all in Brazil, and Museo de la Universidad San Marcos, Lima, Peru (MUSM). We also examined high-resolution photographs of specimens deposited in the Sam Noble Museum of Natural History of the University of Oklahoma (OMNH), United States of America.

Morphological measurements

Preserved adult specimens were measured under a stereo-microscope. To determine maturity, we performed gonadal inspection to visualize mature oocytes in females (when it was not possible to see the oocytes through the skin); for males, we observed calling activity at the field or the presence of vocal slits in preserved specimens. We used a digital caliper to take morphometric measurements to the nearest 0.1 mm. Morphological characters were scored in all specimens following definitions and terminology suggested by Grant et al. (2006), Barrio-Amorós and Santos (2009), and Simões (2016). Measurements were: snout–vent length (SVL); head length, from jaw articulation to the tip of the snout (HL); head width, at the level of the jaw articulation (HW); interorbital distance (IOD); eye–snout distance, from the anterior corner of the eye to the tip of snout (ETS); internarial distance (IND); eye diameter (ED); diameter of tympanum (TD); forearm length (FAL); upper arm length (UAL); hand length, from the proximal edge of palmar tubercle to the tip of Finger III (HandIII); width of the disc of Finger III (WDFIII); tibia length (TL); foot length, from the proximal edge of the metatarsal tubercle to the tip of Toe IV (FL); width of the disc of Toe IV (WDTIV). Following the traditional scheme adopted in *Allobates* taxonomy in recent years, we numbered fingers as I–IV. Data on color in life were taken from field notes and digital photographs.

Analyses of vocalizations

We recorded advertisement calls of seven adult males (six of them vouchered) with a total of 45 calls (4–13 per male). Calls from the new species were recorded in Boca do Acre (state of Amazonas, Brazil) on 13 February 2013, between 15:30–18:00 h. We used a Marantz PMD661 digital recorder with a Sennheiser ME 66 uni-directional microphone, 44 kHz sample rate, and 8-bit sample format. Air temperature in Boca do Acre was not

measured. Additional recordings were conducted in Tefé (03°25'52"S, 64°44'49"W), state of Amazonas, Brazil. These recordings were obtained on 11 February 2011, between 07:55–09:25 h with a Marantz PMD660 recorder and a Sennheiser ME 66 microphone, using 44.1 kHz sample rate and 16-bit sample format. Temperature at the time of recording in Tefé was 25.2–27°C.

Calls were analyzed in Raven 1.4 (Bioacoustics Research Program, 2011) with a 256 spectrogram window size and different values of brightness and contrast for a better visualization of audio files. Temporal and spectral traits were measured from waveform and spectrogram, respectively. Dominant frequency was measured with the “peak frequency” measurement and bandwidth 90% (i.e., the bandwidth where 90% of the energy of the call concentrates) with the “bandwidth 90%” measurement. Waveforms and spectrograms were generated with the same software. Advertisement call terminology for temporal and spectral call parameters follow the definitions presented by Köhler et al. (2017). Calls of all recorded males of the new species were pooled for descriptive statistics.

RESULTS

Phylogenetic relationships

Our phylogenetic analysis (Fig. 3) recovered *Allobates olfersioides* (Lutz, 1925) (sensu Verdade and Rodrigues, 2007) from the Atlantic Forest of coastal Brazil as the sister of all remaining *Allobates*. We recovered a clade composed of two species that occur west of the Andes, *A. talamancae* (Cope, 1875) from Central America, and *A. niputidea* Grant et al., 2007 from Colombia, as the sister of a large clade that encompasses the *Allobates* species distributed east of the Andes. This latter clade includes all sampled Amazonian species.

Cryptically colored lowland Amazonian *Allobates* did not compose a clade. We recovered one major clade composed of large-bodied species distributed south of the Amazon River (Fig. 3), as follows: *A. flaviventris*, sampled by us in the Parque Nacional Serra dos Pacaás Novos and along the upper Madeira River, which nested with samples from Parque Estadual Guajará-Mirim, state of Rondônia (in agreement with Grant et al., 2017), as well as from the upper Acre River in Departamento Pando, Bolivia (referred as *Colostethus* cf. *trilineatus* in Vences et al., 2000); *A. magnussoni* Lima et al., 2014, known from the Tapajós River basin in Brazil; *A. nidicola* Caldwell and Lima 2002, found on the left bank of the Madeira River in Brazil; and *A. masniger* (Morales, 2002), from the Madeira-Tapajós interfluvium in Brazil. Moreover, we recovered another major *Allobates* clade that included an expanse of species that occur in the Amazonian lowlands, Andes, and Guiana

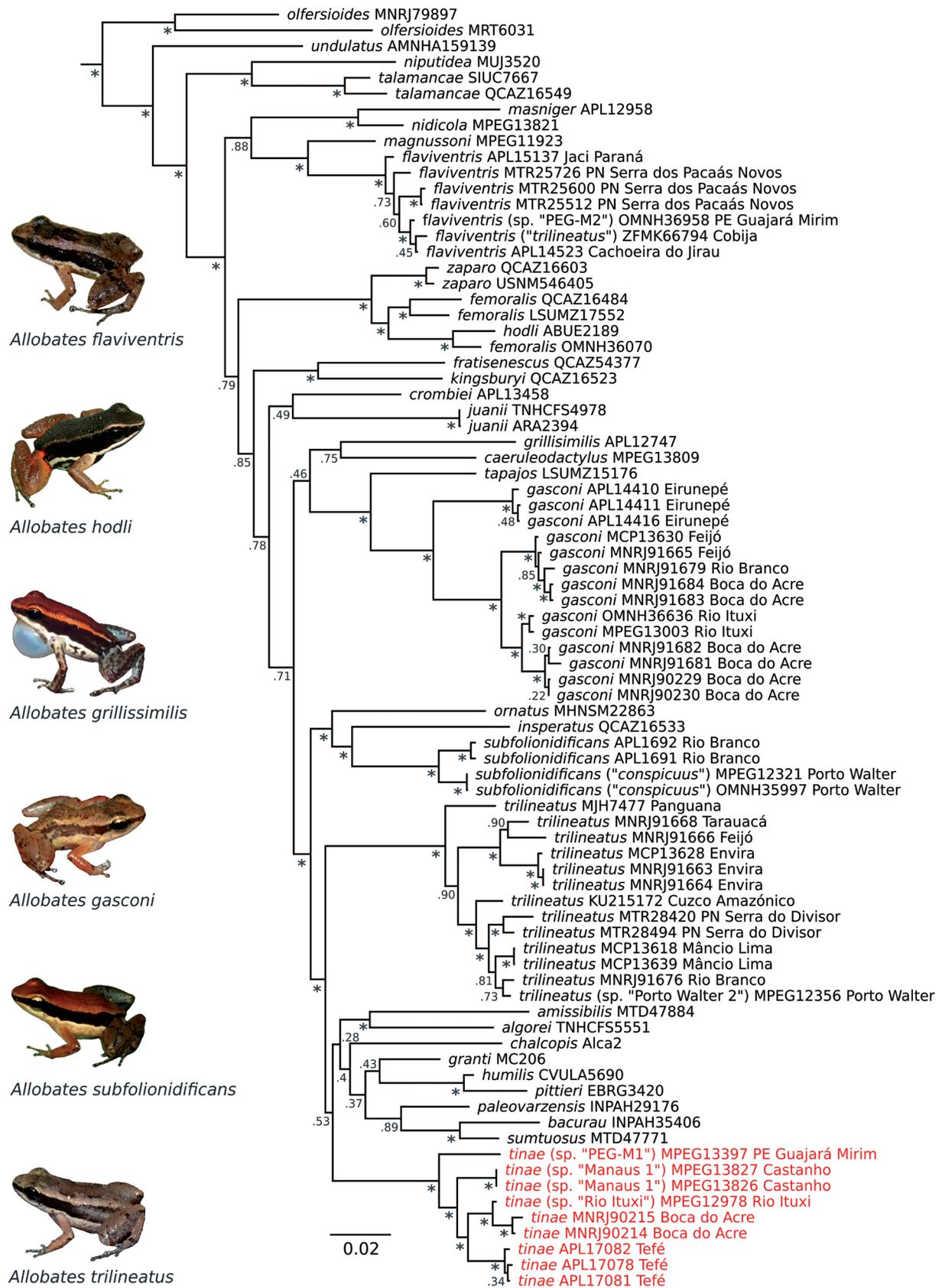


Figure 3. Phylogenetic relationships of *Allobates* estimated under a Bayesian framework based on 10 molecular markers. Asterisks denote posterior probabilities > 0.95. Names in parentheses correspond to the designation given to sampled specimens in previous studies. Terminals in red correspond to *Allobates tinae* **sp. nov.**

Shield, including our samples of *A. gasconi*, *A. trilineatus*, and the new taxon described in this study (see below).

Our samples from Feijó (Acre, Brazil), Rio Branco (Acre, Brazil) and Boca do Acre (Amazonas, Brazil), which we assign to *Allobates gasconi* based on morphological attributes (see below), composed a clade along with previously sampled *A. gasconi* from Eirunepé (Simões et al., 2013b) and with samples from the Ituxi River (referred to as *Allobates* sp. “Rio Ituxi” in Grant et al., 2006), both in Amazonas, Brazil.

Allobates subfolionidificans from Acre, Brazil, including samples previously assigned to *A. conspicuus* (Morales, 2002; see below), is closely related to *A. insperatus* (Morales, 2002), from Ecuador, and *A. ornatus* (Morales, 2002), from the Andean foothills in Peru, with high support (Fig. 3).

Samples collected by us and assigned to *Allobates trilineatus* (from Envira, state of Amazonas; and Tarauacá, Feijó, Parque Nacional Serra do Divisor, Mâncio Lima, and Rio Branco, all in state of Acre, Brazil) based on morphological attributes (see below) formed a highly supported clade along with specimens of *A. trilineatus* sampled by previous investigations (from Panguana and Cuzco Amazónico in Peru; Grant et al., 2006). Other samples in this clade have been referred to as *Allobates* sp. “Porto Walter 2” (Grant et al., 2006) and *A. gasconi* (Santos et al., 2009); we confirm that these samples correspond to *A. trilineatus* based on morphological examinations of museum specimens (see below).

The phylogenetic analysis also recovered a highly supported clade composed of previously and newly sampled individuals of a broadly distributed yet unnamed species (Fig. 3). We collected this species along the Juruá-Madeira interfluvium in Brazil, from Senador Guimard in Acre north into Tefé in Amazonas. It has been previously referred to as *Allobates* sp. “Manaus 1” from Castanho in Amazonas, Brazil (Grant et al., 2006), *A. “gasconi”* and *A. “marchesianus”* from the Ituxi River in Amazonas, Brazil (Grant et al., 2006; Santos et al., 2009), and *Allobates* sp. “PEG-M1” (Grant et al., 2006) and *Allobates* sp. “Small” (Santos et al., 2009) from Parque Estadual Guajará-Mirim in Rondônia, Brazil. We confirm that these samples are conspecific also based on morphological attributes; a formal taxonomic description is provided below.

This new species formed a poorly supported clade along with taxa that occur mostly north of the Amazon River, namely *A. amissibilis* Kok et al., 2013 and *A. granti* (Kok et al., 2006) from northern South America tepuis (table mountains), *A. algorei* Barrio-Amorós and Santos, 2009, *A. humilis* (Rivero, 1980) and *A. pittieri* (La Marca et al., 2004) from the Venezuelan Andes, *A. chalcopis* (Kaiser et al., 1994) from the lesser Antillean island of Martinique, *A. paleovarzensis* Lima et al., 2010 from central Brazilian Amazonia, and *A. sumtuosus* (Morales, 2002) and *A. bacurau* Simões, 2016 from central Brazilian Amazonia.

These species formed a highly supported clade along with *A. trilineatus* (Fig. 3).

Morphological examination of type series

An examination of the material deposited in herpetological collections revealed incorrectly identified specimens and inconsistencies in the type series of *Allobates fuscillus*, *A. gasconi*, and *A. vanzolinus* (Morales, 2002; Fig. S1), as detailed below.

We found 14 paratypes of *Allobates fuscillus* whose morphological attributes disagree with the species’ diagnosis, as proposed by Morales (2002), and which more closely resemble *A. trilineatus* or *A. gasconi* (Fig. S1A–D). For instance, several paratypes (e.g., INPA 2312, 2333, 2534, 3127, 4042, 4510, 4555, 4556) show transversal stripes on thighs and have marbled flanks (absent from the holotype and other paratypes of *A. fuscillus*), and Finger II approximately the same length as Finger IV (Finger II larger than Finger IV in *A. fuscillus*). Moreover, in agreement with Grant and Rodríguez (2001), we found the SVL of male paratypes INPA 2312 (15.0 mm), INPA 4556 (16.0 mm), INPA 4042 (16.2 mm), and INPA 2333 (16.3 mm) to be substantially smaller than that of the holotype of *A. fuscillus* (INPA 2532; 17.2 mm), overlapping with the known size range of *A. trilineatus* (15.0–17.7 mm; provided by Grant and Rodríguez, 2001).

Other paratypes of *Allobates fuscillus* lack a second, small tubercle close to the main external metatarsal tubercle, a trait present in the holotype of *A. fuscillus*. One paratype (INPA 3514) lacks ventrolateral and dorsolateral stripes (present in the holotype and paratypes INPA 2531, 3250, 3270 and 3514 of *A. fuscillus*); and another paratype (INPA 2351, a female; Fig. S1C) has a faded hourglass pattern on a slightly granular dorsum, a dark brown lateral stripe vanishing at the level of arm insertion and faded towards the groin, and small size (SVL = 15.0 mm). This combination of characters is known solely in *A. gasconi*.

Our observations also indicate that *Allobates vanzolinus*, paratype INPA 3073 from Jaiú (Amazonas, Brazil) is a male of *A. gasconi* (Fig. S1E), as indicated by small SVL (15.5 mm), presence of a pale lateral stripe on flanks, and a dark brown hourglass pattern on dorsum (in *A. vanzolinus*, minimum SVL 21.5 mm, pale dorsolateral stripe absent, dorsum uniformly brown; Fig. S1F–G).

In the case of *Allobates gasconi* (Fig. S1D), measurements reported for the holotype in the species’ description (Morales, 2002) do not match our re-examination of the same specimen. For instance, its SVL was originally reported as 13.9 mm, contrasting with 15.0 mm measured by us. Similarly, the SVL range originally reported for the type series was 14.3–17.3 mm, while our measurements indicate 13.1–17.4 mm (considering both sexes).

Lastly, our morphological observations revealed that specimens OMNH 35997 and MPEG 12321, identified by Victor Morales as *Allobates conspicuus* (see Grant et al., 2006: 129) and therefore treated as such in subsequent phylogenetic studies (Grant et al., 2006; Santos et al., 2009), more closely match the diagnosis of *A. subfolionidificans* (Fig. S1H–I), as indicated by the presence of a uniformly brown dorsum without pale dorsolateral stripes and presence of a supranumerary tubercle between the subarticular tubercle of Toe V and the external metatarsal tubercle (pale dorsolateral stripe present, supranumerary tubercle absent on foot in *A. conspicuus* [Morales, 2002]).

***Allobates tinae* sp. nov.**
(Fig. 4A–C, 5A–C)

Allobates sp. Grant et al., 2006: 299, fig. 73 (clades “Manaus 1”, “PEG-M1”, and “Rio Ituxi”). – Simões, 2016: 519, fig. 12H–I. – Santos et al., 2009: fig. S3A (clades “Small”, “sp. 1”, and “gasconi”).

Allobates aff. *conspicuus* Melo-Sampaio et al., 2013: 339.

Allobates flaviventris Melo-Sampaio et al., 2013: 338 (in part).

Allobates sp. Grant et al., 2017: S29, fig. 21 (clades “PEGM1”, “small”, “Rio Ituxi”, “Manaus 1” and “Castanho”).

Holotype (Fig. 4A–C, 5A–C)

MNRJ 90214 (field number BA 123), an adult male from Platô do Piquiá, municipality of Boca do Acre, state

of Amazonas, Brazil, (08°45′35.28″S, 67°18′32.04″W), collected by Paulo Roberto Melo Sampaio, Ivan Prates, Simone Arruda de Matos and Josimar Costa da Silva on 15 February 2013.

Paratypes (Fig. 4D–F, 5D–F)

To avoid the risk of composite series masked by cryptic diversity, a prevalent issue in *Allobates*, we conservatively restrict the type series of *A. tinae* sp. nov. to sites around the type locality in the states of Acre and Amazonas in Brazil, from which we have call and color in life data. We also limit the type series to adult specimens. Paratypes are listed below.

MNRJ 90218, 90220, 90222, 90224 and 90226, adult males, with same collecting site and date as the holotype. UFAC-RB 4604, an adult male from Fazenda Bonal, municipality of Senador Guimard, state of Acre, Brazil (09°53′45.1″S, 67°18′14.8″W), collected by Paulo Roberto Melo Sampaio, Bruno Luiz Alencar de Souza Melo and Auristo da Conceição on 2 April 2010 (incorrectly labeled as a paratype of *Allobates flaviventris* during the curatorial process). UFAC-RB 4636–37, two adult males from Fazenda Bonal, municipality of Senador Guimard, state of Acre, Brazil (09°53′45.1″S, 67°18′14.8″W), collected by Paulo Roberto Melo Sampaio on 8 May 2010. UFAC-RB 4625, an adult male from BR-317 ~km 164, “ramal em frente ao Bode Preto”, municipality of Boca do Acre, state of Amazonas, Brazil, (09°00′22.82″S, 67°10′56.75″W), collected by Moisés Barbosa de Souza, Paulo Roberto Melo

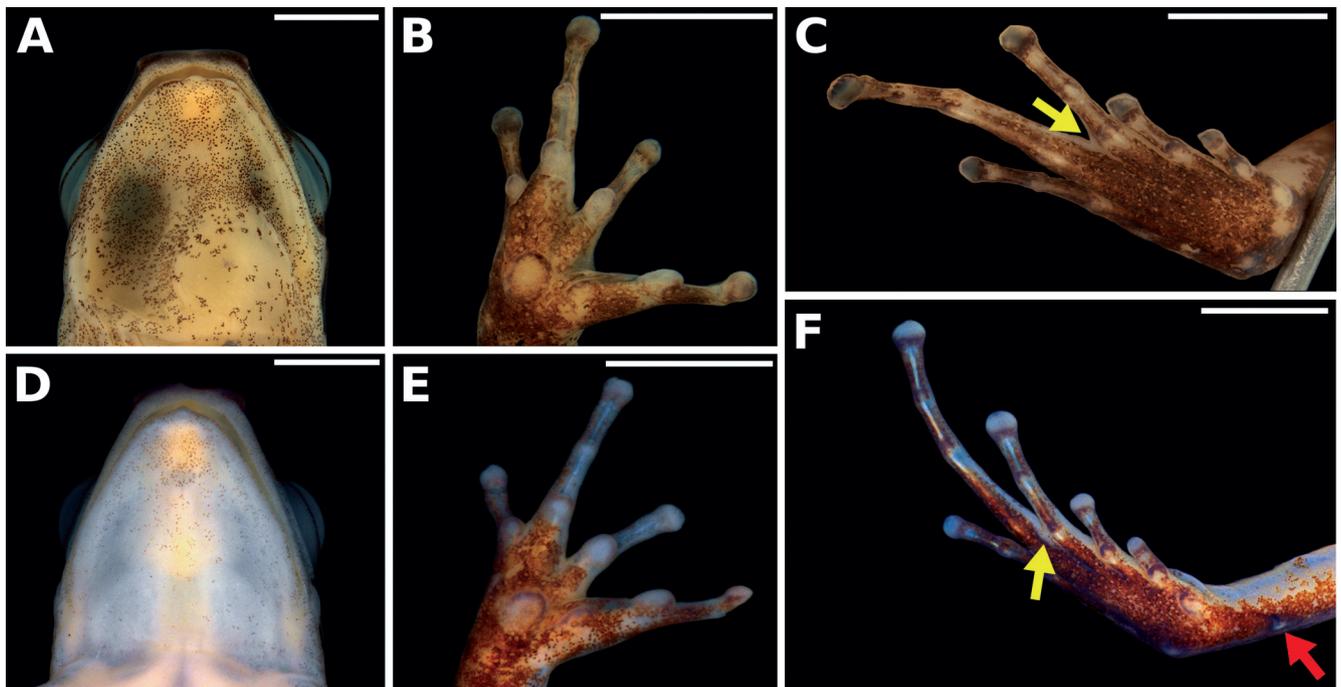


Figure 4. Ventral view of head, hand and foot of (A–C) male (holotype MNRJ 90214) and (D–F) female (paratopotype MNRJ 90228) *Allobates tinae* sp. nov. Yellow arrows indicate basal webbing between Toes III and IV. Red arrow indicates tarsal tubercle. Bars = 2 mm.

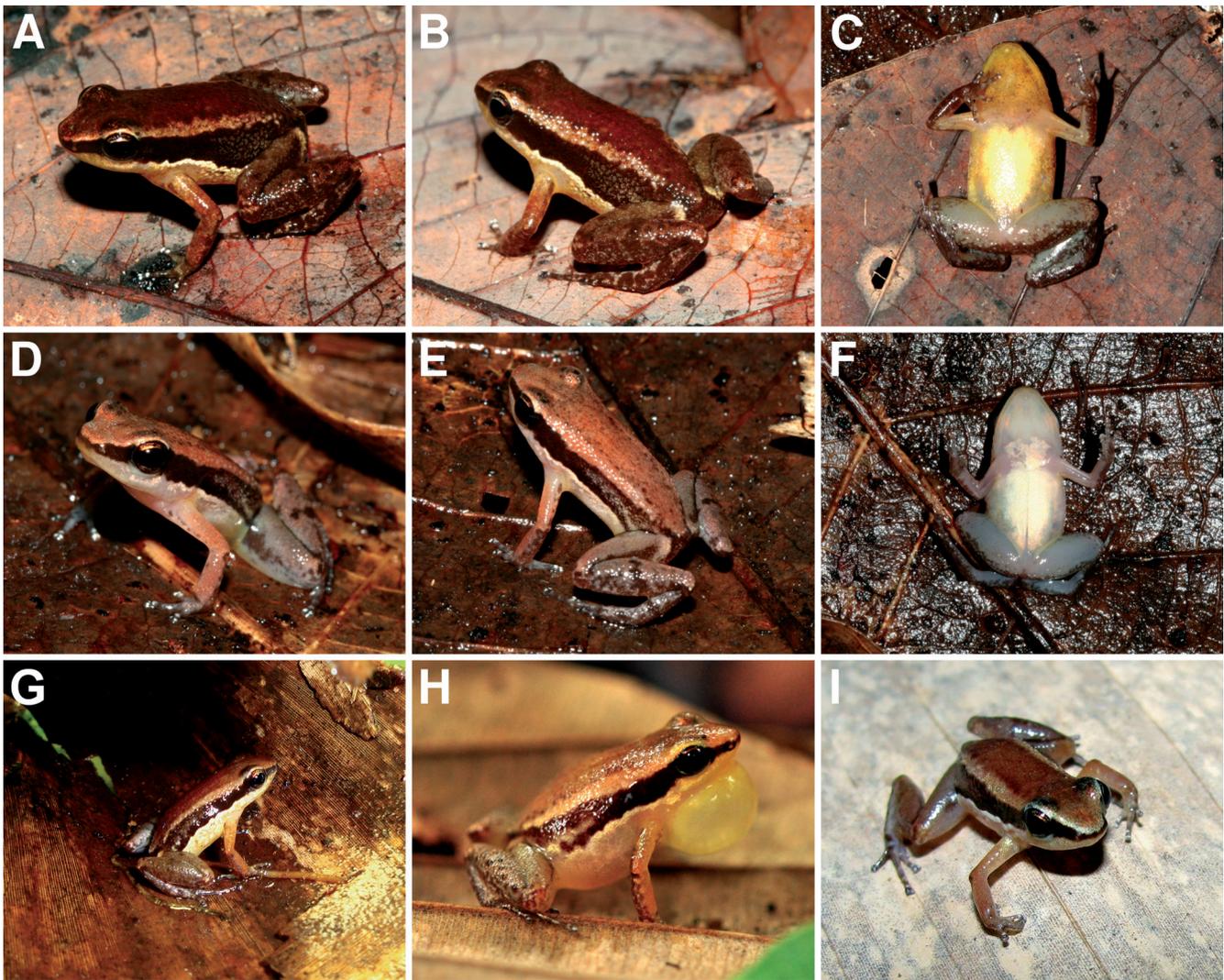


Figure 5. *Allobates tinae* sp. nov. in life. (A–C) Male holotype MNRJ 90214 from Boca do Acre, Amazonas, Brazil. (D–F) A female paratopotype MNRJ 90215. (G) Male UFAC-RB 4604 from Fazenda Bonal, Senador Guimard, Acre, Brazil (incorrectly listed as a paratype of *A. flaviventris* in Melo-Sampaio et al., 2013). (H) Male specimen from Careiro da Várzea, Amazonas, Brazil (photo: Pedro I. Simões). (I) Male UFAC-RB 4637 from Fazenda Bonal, Senador Guimard, Acre, Brazil.

Sampaio and Nathocley Mendes Venâncio on 17–19 November 2009. MNRJ 90215–17, 90219, 90221, 90223, 90225, 90227–28, adult females, with same collecting site and date as the holotype.

Referred specimens

Other samples referred to *Allobates tinae* sp. nov. include UFAC-RB 4638, female juvenile from Fazenda Bonal, municipality of Senador Guimard, state of Acre, Brazil (09°53'45.1"S, 67°18'14.8"W), collected by Paulo Roberto Melo Sampaio on 8 May 2010. MNRJ 90213 (field number BA 125), a juvenile female, from approximately 12 km into “ramal do 26”, municipality of Boca do Acre, state of Amazonas, Brazil (08°55'12.72"S, 67°08'49.92"W), collected by Paulo Roberto Melo Sampaio, Ivan Prates, Simone Arruda de Matos and Josimar Costa da Silva on

15 February 2013. MPEG 13397–13404, from Parque Estadual de Guajará-Mirim, municipality of Nova Mamoré, state of Rondônia, Brazil, collected by Janalee P. Caldwell and team between January and March 1998. MPEG 12957–12979, from Madereira Scheffer, Rio Ituxi, municipality of Lábrea, state of Amazonas, Brazil (ca. 08°20'S, 65°43'W), collected by Janalee P. Caldwell, Laurie J. Vitt and team between February and March 1997.

Diagnosis

The new species is included in the genus *Allobates* on the basis of the phylogenetic results (Fig. 3) and overall similarity with congeners (Fig. 4–5). *Allobates tinae* sp. nov. is diagnosed by the following combination of characteristics: (i) snout rounded in lateral and dorsal views; (ii) a medium-sized species, mean SVL of males

15.2 mm (range 14.2–15.9 mm), mean SVL of females 15.8 mm (range 14.8–17.2 mm); (iii) dorsal surface of snout uniformly light brown, same color extending posteriorly until eye level; dorsum tan brown in life; (iv) skin texture of dorsum granular, flat small granules scattered from the level of the eyes to the urostyle region; (v) dark brown lateral stripe with well delimited upper and lower edges; (vi) pale dorsolateral stripe present in preserved specimens, conspicuous in life; (vii) oblique lateral stripe absent, pale cream spots scattered on inguinal region of the dark brown lateral stripe, reaching up to two thirds of it towards the forelimbs; (viii) iridescent white ventrolateral stripe conspicuous in live and preserved specimens, unbroken from tip of snout to inguinal region; (ix) bright paracloacal mark present, half-moon shaped; (x) sexual dimorphism in throat and chest coloration of live specimens (golden yellow in males, white in females); (xi) abdominal

surfaces cream, reaching towards the flanks (xii) dorsal surface of legs uniform, without transversal dark stripes; (xiii) iris metallic gold, without a pupil ring; (xiv) vocal sac distinct, single, subgular; (xv) maxillary teeth present; (xvi) Finger III not swollen in males; (xvii) basal webbing present between Toes III and IV; (xviii) fringes absent on toes; (xix) diurnal habits, males calling in daytime; (xx) advertisement calls characterized by the emission of tonal notes ranging between 4,875–6,029 Hz.

Description of the holotype

Holotype measurements are presented in Table 1. Adult male, SVL 14.8 mm, head slightly wider than long (HL 90% of HW), HW 33% of SVL, HL 29% of SVL, snout rounded in dorsal and lateral view; ETS 39.3% of HL, IND 35.3% of HW, ETS 114% of ED, nares opening posterolaterally; TD

Table 1. Morphological measurements (in mm) of the type series of *Allobates tinae* sp. nov. Asterisk indicates the holotype. Measurement abbreviations are presented in the Materials and Methods.

Females												
	MNRJ 90215	MNRJ 90216	MNRJ 90217	MNRJ 90219	MNRJ 90221	MNRJ 90223	MNRJ 90225	MNRJ 90227	MNRJ 90228	Range	Mean ± SD	
SVL	14.78	15.23	16.4	15.37	17.2	16.07	15.72	16.49	15.39	14.8–17.2	15.9 ± 0.8	
HL	4.3	4.42	4.62	4.6	4.74	4.55	4.37	4.77	4.67	4.3–4.8	4.6 ± 0.2	
HW	4.83	4.95	4.97	4.98	5.11	4.75	4.92	4.94	4.81	4.8–5.1	4.9 ± 0.1	
IOD	3.38	3.48	3.31	3.15	3.6	3.18	3.15	3.52	3.15	3.2–3.6	3.3 ± 0.2	
ETD	2.63	2.68	2.6	2.55	2.7	2.63	2.6	2.7	2.67	2.6–2.7	2.6 ± 0.1	
IND	1.93	2.13	2.01	1.96	2.14	2.06	2.03	2.17	2.09	1.9–2.2	2.1 ± 0.1	
ED	2.12	2.13	2.15	2.06	2.21	2.18	2.13	2.17	2.13	2.1–2.2	2.1 ± 0	
TD	0.77	0.94	0.95	0.86	1	0.98	0.99	0.87	0.86	0.8–1	0.9 ± 0.1	
FAL	3.55	3.84	3.58	3.67	3.69	3.59	3.54	3.95	3.83	3.5–4	3.7 ± 0.1	
UAL	3.12	3.78	3.46	3.7	3.81	3.73	3.78	3.63	4.08	3.1–4.1	3.7 ± 0.3	
HAI	3.36	3.53	3.41	3.51	3.47	3.43	3.5	3.63	3.61	3.4–3.6	3.5 ± 0.1	
WDF	0.47	0.53	0.41	0.38	0.34	0.38	0.41	0.46	0.42	0.3–0.5	0.4 ± 0.1	
TL	7.62	7.8	8.42	7.87	8.29	8.36	7.8	8.11	8.47	7.6–8.5	8.1 ± 0.3	
FL	6.42	6.87	6.94	6.01	6.1	6.67	6.76	6.99	7.14	6–7.1	6.7 ± 0.4	
WDT	0.67	0.61	0.57	0.53	0.54	0.47	0.43	0.44	0.56	0.4–0.7	0.5 ± 0.1	
Males												
	MNRJ 90214*	MNRJ 90218	MNRJ 90220	MNRJ 90222	MNRJ 90224	MNRJ 90226	UFAC-RB 4625	UFAC-RB 4636	UFAC-RB 4637	UFAC-RB 4604	Range	Mean ± SD
SVL	14.78	15.36	15.36	14.19	15.49	15.89	14.45	14.4	14.84	15.81	14.2–15.9	15.1 ± 0.6
HL	4.35	4.37	4.47	4.5	4.32	4.28	4.42	4.39	4.33	4.3	4.3–4.5	4.4 ± 0.1
HW	4.84	4.82	4.98	4.78	4.74	4.79	5	4.76	5.05	4.85	4.7–5.1	4.9 ± 0.1
IOD	3.07	3.08	3.28	3.08	3.15	3.03	2.97	3.3	3.38	3.21	3–3.4	3.2 ± 0.1
ETD	2.57	2.59	2.53	2.53	2.6	2.53	2.61	2.45	2.45	2.46	2.5–2.6	2.5 ± 0.1
IND	1.71	2.1	1.97	1.84	1.91	1.83	1.98	2.11	2.12	1.97	1.7–2.1	2 ± 0.1
ED	2.25	2.1	2.01	1.97	2.09	2.02	2.06	2.11	2.12	2.11	2–2.3	2.1 ± 0.1
TD	1	0.91	0.94	0.99	0.85	0.82	1.04	0.84	0.83	0.92	0.8–1	0.9 ± 0.1
FAL	3.82	3.58	3.7	3.7	3.53	3.66	3.38	3.46	3.84	3.58	3.4–3.8	3.6 ± 0.1
UAL	3.38	3.8	3.84	3.57	3.56	3.46	3.3	3.34	3.57	3.53	3.3–3.8	3.5 ± 0.2
HAI	3.55	3.4	3.33	3.45	3.38	3.62	3.46	3.29	3.49	3.53	3.3–3.6	3.5 ± 0.1
WDF	0.49	0.4	0.44	0.43	0.37	0.4	0.46	0.41	0.47	0.42	0.4–0.5	0.4 ± 0
TL	7.58	7.68	8.2	7.87	7.34	7.73	7.25	7.18	7.57	7.64	7.2–8.2	7.6 ± 0.3
FL	6.82	6.45	6.82	6.71	6.7	6.7	6.63	6.37	6.6	6.98	6.4–7	6.7 ± 0.2
WDT	0.54	0.45	0.54	0.53	0.46	0.47	0.61	0.55	0.55	0.56	0.5–0.6	0.5 ± 0.1

44.4% of ED, tympanic annulus incomplete, with skin concealing posterodorsally; Tongue nearly twice long than wide, attached anteriorly, rounded posteriorly; Vocal slits present; Tongue cream-colored; Median lingual process absent.

Forearm thicker than upper arm, FAL 113% of UAL; Finger III length 24% of SVL; tip of Finger IV reaching proximal subarticular tubercle of Finger III when fingers are appressed; Finger II reaching the medial subarticular tubercle of Finger III; relative length of fingers III > I > II > IV; Finger III not swollen; basal webbing and lateral fringes absent on fingers; palmar tubercle nearly ovoid; a single subarticular tubercle present on Finger I, II and IV, two subarticular tubercles on Finger III. Discs of Fingers I, II, III, and IV moderately expanded, all with distinct dorsal scutes; width of disc on Finger III 0.49 mm.

Tibia length 51% of SVL; relative length of toes IV > III > V > II > I; basal webbing present between Toes III–IV. Tip of Toe I reaching proximal subarticular tubercle of Toe II when toes are appressed; tip of Toe III reaching medial tubercle of Toe IV. Inner metatarsal tubercle ovoid, outer metatarsal tubercle rounded. Metatarsal fold weak; Tarsal keel tubercle-like and curved, located about 0.8 mm from proximal edge of inner metatarsal tubercle and not connected by fold. A single subarticular tubercle present on Toe I; two subarticular tubercles present on Toes III and V; three subarticular tubercles present on Toe IV. Skin smooth ventrally, granular on dorsum (Fig. 4). Small flat granules scattered on dorsum from the level of the eyes to the urostyle region, more conspicuous posteriorly. Cloacal tubercles absent.

Holotype color in preservative

Dorsal surface of body uniformly tan brown, partially darker only near snout and above the orbits. A pale dorsolateral stripe is present, characterized by a narrow line (1.2 mm wide at mid-abdomen level; distance between dorsolateral lines 4.2 mm); inner edge of pale dorsolateral stripe well marked. Lateral surface of body characterized by a solid dark brown lateral stripe, extending from tip of snout to groin. Pale ventrolateral line present, cream-colored, extending from anterior portion of tympanum to groin, wider and more conspicuous around arm insertion. Throat, gular, and anterior pectoral regions light brown, with evenly scattered melanophores. Posterior pectoral region, abdomen and ventral surface of thigh insertion uniformly cream. Distal portion of thigh and knees with scattered melanophores. Arms cream to pale brown in dorsal view, melanophores concentrated in small and regular light brown blotches on the posterior surface of upper arm, forearm and hand. Tip of fingers light brown. Paired scutes on finger discs cream. Upper arm cream in ventral view. Forearm and hand tan brown in ventral view.

Area immediately surrounding vent solid dark brown, bounded by an unpigmented, half-moon shaped

transverse band, corresponding to the pale paracloacal mark. Thigh light brown in dorsal view, with no transversal stripes. Inner and outer dorsolateral surfaces of thigh dark brown. Dorsal surface of shank tan brown, with irregular dark brown transversal blotches. Outer dorsal surface of tarsal region lighter than overall pattern of legs, with scattered dark brown blotches. Toes light brown, with irregularly distributed melanophores. Ventral surface of shank and tarsal region predominantly cream to translucent. Dark brown marbling appears along inner and outer ventrolateral edges and on knee. Ventral surface of metatarsal regions uniformly dark brown.

Variation in preserved specimens

Variation in body measurements among specimens in the type series is presented in Table 1. In general, dorsal coloration matching that of holotype, but sometimes with slight variation in shades of brown (lighter in males MNRJ 90218, 90220, 90224 and 90226, and females MNRJ 90215, 90216 and 90219). Pale dorsolateral and ventrolateral stripes vary in outline and distinctness (less visible in females MNRJ 90215 and 90219, and males MNRJ 90218 and 90220). Cream markings on flanks vary in size and shape, sometimes being almost imperceptible (MNRJ 90227). Melanophores with dark brown pigmentation present only on chin in female specimens. Melanophores with dark brown pigmentation present on chin and throat, decreasing at level of insertion of arm in male specimens.

Color in life

Dorsum uniformly dark to pale tan brown, generally darker at the tip of skin granules (Fig. 5). Pale dorsolateral stripe conspicuous, bright tan brown or cream. Lateral surface of body surrounded by a dark brown lateral stripe from tip of snout to groin. Dark brown lateral stripe stippled with pale spots, sometimes resembling a diffuse oblique stripe on groin region, but never forming a complete or solid oblique lateral stripe. Ventrolateral stripe present along lower margin of dark brown lateral stripe. Ventrolateral stripe iridescent white in female specimens. Ventrolateral stripe iridescent yellow from tip of snout to level of arm insertion and iridescent white posteriorly in male specimens. Irregular iridescent white blotches (same color as ventrolateral stripe) present below ventrolateral stripe, towards the abdomen. Throat and chest surfaces golden yellow in males. Throat and chest of females pinkish-white. Vocal sac of males bright yellow when inflated. Abdomen yellow posteriorly in males, white in females.

Upper arm yellow proximally and tan brown distally. Forearms tan brown with irregular dark brown blotches. Carpal and metacarpal regions light brown in dorsal view, brown in ventral view. Fingers brown with irregular yel-

Table 2. Call parameters of *Allobates tinae* sp. nov. Values within brackets in table header refer to the number of calls analyzed by each male. Data in parentheses represent mean ± SD.

Male [Number of Calls]	MNRJ 90220 [4]	Unvouchered [4]	APL 17078 [5]	APL 17079 [8]	APL 17080 [6]	APL 17081 [5]	APL 17082 [13]	Pooled Global [45]	Pooled Topotypical [8]
T (°C)	-	-	25.2	25.6	25.6	25.6	26.9	25.2–26.9	-
SVL (mm)	15.4	-	-	-	-	-	-	-	-
Call Duration (s)	1.766	1.667	1.554	1.187	1.328	1.576	1.578	0.285–2.27 (1.497 ± 0.45) n = 45	1.057–2.147 (1.716 ± 0.33) n = 8
Note Duration (s)	0.058 n = 31	0.055 n = 29	0.053 n = 31	0.056 n = 41	0.053 n = 32	0.06 n = 30	0.054 n = 85	0.044–0.072 (0.055 ± 0.004) n = 279	0.044–0.072 (0.057 ± 0.005) n = 60
Dominant Frequency (Hz)	4875	5250	5512	5426	6029	5340	5327	4875–6029 (5413 ± 328) N = 45	4875–5250 (5062 ± 200) N = 8
Bandwidth 90% (Hz)	1125	750–1125	861	689–861	1033	861	1033–861	689–1125	750–1125
Inter-note Interval (s)	0.189 n = 27	0.199 n = 25	0.234 n = 26	0.217 n = 33	0.24 n = 26	0.243 n = 25	0.22 n = 72	0.131–0.387 (0.22 ± 0.037) n = 234	0.131–0.278 (0.194 ± 0.034) n = 52
Interval Between Calls (s)	34.572 n = 4	43.7 n = 3	17 n = 3	11.359 n = 8	19.793 n = 6	20.075 n = 4	17.178 n = 14	4.741–53.283 (21.401 ± 10.84) n = 42	25.569–53.283 (38.486 ± 9.88) n = 7
Notes Per Call (mode)	8	5,7,8,9	7	6	7	6	6	2–9 (7) n = 45	5–9 (8) n = 8

low patches in dorsal view. Paired scutes on finger discs iridescent white.

Dorsal surfaces of thighs uniformly yellowish-brown, with blue shades. Thighs with dark brown blotches only along inner and outer edges. Dorsal surface of shank same color as thigh, with irregular dark brown blotches. Ventral surfaces of thigh and shanks cream. Tarsal region cream in ventral view. Toes with gray, dark brown and iridescent white patterning. Paired scutes on toe discs iridescent white.

Advertisement call

Call parameters (Fig. 6) are described on the basis of seven recorded males, two from the type locality, Boca do Acre (paratype MNRJ 90220 and one unvouchered specimen), and five from Tefé (APL 17078–82), both locali-

ties in the state of Amazonas, Brazil. Results presented here correspond to all seven males recorded (Table 2). The advertisement call (n = 45) is composed of groups of tonal notes with ascending frequency modulation emitted between long and variable time silent intervals (4.741–53.283 s; 21.401 ± 10.84 s; n = 42). Number of notes in each call is 2–9 (mode = 8; n = 45). Call duration is 0.285–2.27 s (1.497 ± 0.45 s; n = 45) and note duration is 0.044–0.072 s (0.055 ± 0.004 s; n = 279). Inter-note interval is 0.131–0.387 s (0.22 ± 0.037 s; n = 234). Dominant frequency of the entire call is 4,875–6,029 Hz (5,413 ± 328 Hz; n = 45). Bandwidth where 90% of the energy of the call concentrates 689–1125 Hz.

Comparisons with other Amazonian lowland *Allobates* species

We present comparisons between *Allobates tinae* sp. nov. and other species of *Allobates* that occur in Amazonian lowlands.

Morphological comparisons

Allobates tinae sp. nov. differs from *A. femoralis* (Boulenger, 1883), *A. hodli* Simões et al., 2010, *A. myersi* (Pyburn, 1981) and *A. zaparo* (Silverstone, 1976) by the absence of red, orange, or yellow flash marks on the dorsal surface of thigh, and by the absence of black and white marbling on the abdomen.

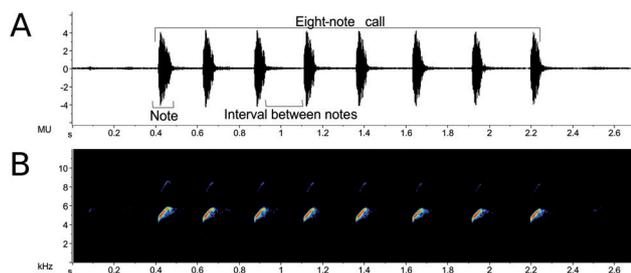


Figure 6. *Allobates tinae* sp. nov. advertisement call. Waveform (A) and spectrogram (B) of a typical eight-note call. The spectrogram shows the evident ascending frequency modulation.

The bright yellow throat of live males of *Allobates tinae* **sp. nov.** distinguishes this species from species that exhibit a dark throat, namely *A. amissibilis*, *A. flaviventris*, *A. fuscillus*, *A. granti*, *A. magnussoni*, *A. marchesianus* (Melin, 1941), *A. masniger*, *A. melanolaemus* (Grant and Rodríguez, 2001), *A. nidicola*, *A. paleovarzensis*, *A. trilineatus* and *A. vanzolinus*. Smaller body size distinguishes *A. tinae* **sp. nov.** (maximum SVL of adult males = 15.8 mm) from *A. amissibilis*, *A. flaviventris*, *A. fuscillus*, *A. magnussoni*, *A. masniger*, *A. melanolaemus*, *A. nidicola*, *A. paleovarzensis*, and *A. vanzolinus* (minimum SVL of adult males > 16.0 mm). Additionally, *A. tinae* **sp. nov.** is distinguished from *A. trilineatus* by the absence of swelling in Finger III (swollen Finger III in *A. trilineatus*), from *A. granti* by the presence of a dorsolateral stripe (absent in *A. granti*), and from *A. marchesianus* by the presence of a ventrolateral stripe (absent in *A. marchesianus*).

Allobates tinae **sp. nov.** is diagnosed from *A. crombiei* (Morales, 2002), *A. gasconi*, and *A. ornatus* by lacking a rhombus or hourglass-shaped dark brown pattern on dorsum and by lacking a transversal dark brown bar on dorsal surface of thigh (present in *A. crombiei*, *A. gasconi* and *A. ornatus*). *Allobates tinae* **sp. nov.** is smaller than *A. crombiei* (maximum SVL of adult males = 15.8 mm in *A. tinae* **sp. nov.**, SVL of males of *A. crombiei* > 16.0 mm). Moreover, *A. tinae* is distinguished from *A. gasconi* and *A. ornatus* by Finger III not swollen in males (swollen in *A. gasconi* and *A. ornatus*).

Considering the *Allobates* species that exhibit smaller body sizes, *A. tinae* **sp. nov.** is distinguished from *A. caeruleodactylus* (Lima and Caldwell, 2001) by lacking sky-blue colors on fingers of live specimens and by the presence of well-defined pale dorsolateral and ventrolateral stripes (fingers sky-blue, pale dorsolateral and ventrolateral stripes absent in *A. caeruleodactylus*). *Allobates tinae* **sp. nov.** is distinguished from *A. conspicuus*, *A. grillisimilis* and *A. subfolionidificans* by lacking dark brown transverse bars on dorsal surface of thigh (dorsal surface of thigh with a single transverse dark brown bar in *A. conspicuus*; with a variable number of transverse dark brown bars in *A. grillisimilis* and *A. subfolionidificans*) and by a yellow throat in live male specimens (throat white to translucent in male *A. grillisimilis*, white in male *A. subfolionidificans*). Preserved specimens of *A. tinae* **sp. nov.** also have a pale dorsolateral stripe (absent in *A. subfolionidificans*). *Allobates tinae* **sp. nov.** is similar in size to *A. tapajos* Lima et al., 2015 but is distinguished by its uniformly brown dorsum and thighs without transverse stripes and the presence of a continuous pale ventrolateral stripe (dorsum with scattered dark brown blotches, pale ventrolateral stripe diffuses and dark transverse stripes in thighs in *A. tapajos*).

Allobates tinae **sp. nov.** is distinguished from *A. bacurau* by slightly larger female size (minimum SVL > 14.7 in *A. tinae* **sp. nov.**; maximum SVL < 14.8 mm in *A. ba-*

curau) and absence of swollen Finger III (swollen Finger III present in *A. bacurau*). *Allobates tinae* **sp. nov.** is distinguished from *A. sumtuosus* by the presence of dorsolateral stripes, granular texture of dorsum and yellow throat color (dorsolateral stripes absent in life, smooth skin with white to translucent throat in *A. sumtuosus*).

Vocalization comparisons

The emission of tonal notes distinguishes the call of *Allobates tinae* **sp. nov.** from that of *A. granti* (pulsed notes; Kok and Ernst, 2007). The multiple note call (sensu Kohler et al., 2017) of *A. tinae* **sp. nov.** is divergent from single note calls emitted by *A. subfolionidificans*, *A. nidicola*, *A. caeruleodactylus*, and *A. marchesianus* (Lima and Caldwell, 2001; Caldwell and Lima, 2003; Lima et al., 2007; Tsuji-Nishikido et al., 2012; in the case of *A. marchesianus*, compared to discrete call; see Caldwell et al., 2002 for details about two call types in this species). Calls of *A. bacurau* (6.92–11.07 s) and *A. marchesianus* (3.39–4.40 s in the “continuous call” type) are longer (see Caldwell et al., 2002; Simões 2016) than that of *A. tinae* **sp. nov.**; calls of *A. magnussoni* (0.065–0.104 s), *A. grillisimilis* (0.173–0.267 s), *A. nidicola* (0.034–0.050 s), *A. masniger* (0.047–0.064 s), *A. caeruleodactylus* (0.062 s) are shorter than that of *A. tinae* **sp. nov.** (Lima and Caldwell, 2001; Tsuji-Nishikido et al., 2012; Simões et al., 2013a; Lima et al., 2014). Number of notes in multiple note calls is different from that of *A. tinae* **sp. nov.** in *A. bacurau* (61–81), *A. crombiei* (25–59), *A. sumtuosus* (23–35) and *A. marchesianus* (21–24, in the case of the “continuous call” of *A. marchesianus*; Caldwell et al., 2002; Lima et al., 2012; Simões et al., 2013b; Simões, 2016). Notes are shorter than those of *A. tinae* **sp. nov.** in *A. amissibilis* (0.024–0.044 s), *A. grillisimilis* (0.021–0.026 s), *A. subfolionidificans* (0.024–0.043 s), *A. crombiei* (0.021–0.037 s) and *A. marchesianus* (0.034–0.044 s; Caldwell et al., 2002; Lima et al., 2007; 2012; Kok et al., 2013; Simões et al., 2013a). *Allobates magnussoni* (4,273–4,704 Hz), *A. flaviventris* (3,617–4,651 Hz), *A. masniger* (4,362–4,694 Hz), and *A. melanolaemus* (3,840–4,560 Hz) have a lower dominant frequency than *A. tinae* **sp. nov.** (Grant and Rodríguez, 2001; Tsuji-Nishikido et al., 2012; Melo-Sampaio et al., 2013; Lima et al., 2014), while *A. grillisimilis* has higher dominant frequency than *A. tinae* **sp. nov.** (6,460–6,546 Hz; Simões et al., 2013a). The only call trait that distinguishes *A. paleovarzensis* and *A. tinae* **sp. nov.** is the interval between calls (0.26–3.65 s; Lima et al., 2010). Even using eight acoustic characteristics (note structure, call pattern, call duration, number of notes per call, note duration, dominant frequency, bandwidth 90% and interval between calls), we cannot distinguish *A. tinae* **sp. nov.** from *A. trilineatus* based solely on advertisement calls (see Grant and Rodríguez, 2001).

Etymology

The specific epithet honors Dr. Albertina Pimentel Lima, a professor at the Instituto Nacional de Pesquisas da Amazônia (INPA), for her extensive contributions to *Allobates* taxonomy. Dr. Lima has described or re-described with colleagues more than a dozen species of nurse frogs. Her work has inspired the first author to investigate *Allobates* taxonomy.

Distribution

The new species is known from lowland western Amazonia in Brazil to the south of the Amazon River (Fig. 2) in the states of Acre (municipality of Senador Guimard), Amazonas (Boca do Acre, Borba, Careiro, Careiro da Várzea, Lábrea, Manaquiri, Nova Olinda do Norte and Tefé), and Rondônia (Nova Mamoré and Porto Velho). In its type locality (Boca do Acre, Amazonas), *Allobates tinae* **sp. nov.** is syntopic with *A. gasconi* and *A. femoralis*. To the south (e.g., Fazenda Bonal, Acre), it co-occurs with *A. hodli*, *A. subfolionidificans*, and *A. trilineatus*. To the east (e.g., in the middle course of the Madeira River), *A. tinae* **sp. nov.** is sympatric with *A. caeruleodactylus*, *A. flaviventris*, *A. grillisimilis*, *A. masniger*, and *A. nidicola* (see Simões 2016).

DISCUSSION

Based on genetic, morphological, and call data, we identify and describe *Allobates tinae* **sp. nov.**, a broadly distributed, western Amazonian lowland nurse frog. The data also help to refine the distribution of poorly known species from western Amazonian lowlands, namely *A. flaviventris*, *A. gasconi*, *A. subfolionidificans*, and *A. trilineatus*. Lastly, our examination of museum specimens points to inconsistencies in the type series of *A. fuscillus*, *A. gasconi*, and *A. vanzolinus*, as suggested by pronounced variation in traits that have been shown to strongly correlate with species boundaries in *Allobates*, such as the color of throat in reproductive males, presence of dorsolateral stripes, hourglass-shaped dorsal pattern and SVL (Simões et al., 2010, 2013a,b, 2016; Lima et al., 2014, 2015). By improving knowledge about species ranges and identifications, we hope this study will support biodiversity inventories and stimulate further investigations of understudied western Amazonian nurse frogs.

Notes on *Allobates gasconi*

In the light of the genetic data, our morphological examinations indicate some phenotypic variation within widely distributed western Amazonian *Allobates*. This is

the case, for instance, of *A. gasconi*. Based on morphological attributes, we assign to this species several of our newly sampled specimens from the states of Acre and Amazonas in Brazil (Fig. 3). In agreement with this proposed identification, these frogs are phylogenetically close to previously sampled *A. gasconi* from Eirunepé in Amazonas, Brazil, which is the closest sampled site from this species' type locality (Simões et al., 2013b). There is, however, some phenotypic variation across this species' range. Some of our *A. gasconi* samples differ from the holotype in male throat pigmentation (dark in the type of *A. gasconi*, often white to moderately pigmented in other specimens), extent of dark brown lateral stripe (extending anteriorly to arm insertion in *A. gasconi*, often not reaching the arm in other specimens), and degree of swelling of Finger III (highly swollen in *A. gasconi*, not swollen to moderately swollen in other specimens). However, this variation seems to be continuous across adjacent sites. As such, evidence of undescribed diversity within this taxon is currently equivocal. Further appraisals of morphological variation within *A. gasconi* will benefit from genetic and call data from this species' type locality (Jainu in Amazonas, Brazil), which are currently not available.

Notes on *Allobates trilineatus*

We also detected phenotypic variation in *Allobates trilineatus*. Our molecular phylogenetic analysis included two samples from Panguana and Cuzco Amazónico in Peru that were previously assigned to this species (Fig. 3). These samples are phylogenetically close to newly sampled frogs from Rio Branco, Serra do Divisor, Mâncio Lima, and Porto Walter (all in Acre, Brazil). Other newly sampled individuals from Envira (Amazonas, Brazil), Feijó, and Tarauacá (Acre, Brazil) are morphologically consistent with, and phylogenetically close to, those samples of *A. trilineatus*. However, they are somewhat distinct, mostly lacking transversal stripes on thighs and having grayish limbs. Typical *A. trilineatus* is known to occur geographically close to these samples, in the municipality of Sena Madureira in Acre (Melo-Sampaio, 2015).

Phenotypic variation within *Allobates trilineatus* has been also reported by previous studies. For instance, some specimens present an hourglass-shaped pattern on the dorsum (e.g., AMNH-FS 8689), yet this trait seems to be infrequent, and is not observed in the holotype (Boulenger, 1883; Grant and Rodríguez, 2001). Moreover, the holotype (BMNH.1947.2.14.20, a male) is substantially larger (SVL = 17.2 mm) than other adult males from the same site (e.g., MUSM 15611, SVL = 16.1 mm; AMNH FS 8689, SVL = 16.0 mm). Morphological variation may explain why specimens assigned to *A. trilineatus* by Grant and Rodríguez (2001; e.g., KU 182124–25 and KU 183529) were considered paratypes of *A. insperatus* by

Morales (2002), even though *A. trilineatus* and *A. insperatus* are not closely related phylogenetically (Fig. 3). Assessing levels of phenotypic variation within *A. trilineatus* will benefit from future sampling of genetic data from the type locality (Yurimaguas, Peru). Currently, our *A. trilineatus* samples from Parque Nacional da Serra do Divisor in Acre are the geographically closest specimens from this species' type locality.

Notes on *Allobates subfolionidificans*

Morphological diagnoses also indicate that samples from western Acre (Porto Walter) treated as *Allobates conspicuus* in previous phylogenetic investigations (e.g., Grant et al., 2006; Santos et al., 2009) in fact correspond to *A. subfolionidificans*. The original identification of these samples as *A. conspicuus* was made by Morales (2002; see Grant et al., 2006: 129); however, *A. subfolionidificans* was described one year later (which may justify Morales' identification). Here, we substantially extend the known range of this species to the west (previously known solely from Rio Branco in eastern Acre). Consistent with this scenario, our own fieldwork has found evidence of *A. subfolionidificans* in Feijó, central Acre, as suggested by egg clutches deposited on the inferior surface of leaves (Fig. S1J), which are typical of, and currently known solely in, *A. subfolionidificans* (Souza et al., 2017). Moreover, we have found that several specimens housed at the Coleção Herpetológica da Universidade Federal do Acre fit the description of *A. subfolionidificans*, suggesting that this species is widespread across the state of Acre in Brazil (see Appendix 1).

Notes on *Allobates flaviventris*

Our phylogenetic analysis also confirms that, as suggested by Melo-Sampaio et al. (2013), *Allobates flaviventris* occurs in Bolivia. A sample previously collected in Cobija, Departamento Pando (ZFMK 66794), and referred to as *Colostethus* cf. *trilineatus* (Vences et al., 2000: 36), clustered together in our tree with several new and previously sampled specimens of *A. flaviventris* from Rondônia in Brazil. Information about color in life presented for this specimen by Gonzales et al. (1999: 185, plate 5A and 5B; referred to as *Colostethus* sp.) is consistent with the diagnosis provided by Melo-Sampaio et al. (2013) for females of *A. flaviventris*.

Notes on *Allobates fuscellus*

To resolve the composite series of *Allobates fuscellus*, we conservatively restrict this name to populations occurring in Penedo, municipality of Ipixuna (INPA 2532 holo-

type and INPA 2531 paratype), and Jainu, municipality of Itamarati (INPA 3250, 3270 and 3514), both in the state of Amazonas, Brazil (Table S3).

On the basis of these specimens, we propose a new diagnosis for *Allobates fuscellus*, as follows: medium-sized species (SVL 17.2–17.8 mm in males; 18.8–19.5 mm in females); dark to solid dark throat in males; swollen Finger III in adult males; dorsolateral and ventrolateral stripes distinct; reduced Finger IV; transverse stripe in thighs absent; posterior surfaces of thighs dark.

Notes on *Allobates tinae* sp. nov.

Most *Allobates* species appear to have limited geographic ranges (see Simões 2016), but *A. tinae* sp. nov. is widespread in western Brazilian Amazonia. This wide range spans both banks of the Madeira River, which appears to be an important barrier for other nurse frogs, as is the case of *A. hodli* (Simões et al., 2010). It remains to be seen whether this distribution pattern, which may have implications for our understanding of the role of biogeographic barriers in Amazonia, is also shared by other widespread nurse frog species, such as *A. gasconi* and *A. trilineatus*. Although widely distributed, *A. tinae* sp. nov. is presently not known to occur in any conservation unit. Inventories in Reserva Extrativista Arapixi (PRMS, unpublished data) and Reserva Extrativista do Médio Purus (Waldez et al. 2013) failed to detect this species. However, given the proximity between protected areas and sites where *A. tinae* is known to occur, this species may currently be protected. Inventories in conservation units such as Flona do Iquiri, Flona Mapiá-Inauini, Parque Estadual do Matupiri and Parque Nacional Mapiuari are necessary to clarify whether this species is in fact protected in southern Brazilian Amazonia, which corresponds to the arc of deforestation.

Concluding remarks

The revisionary work of Morales (2002) based solely on preserved specimens suffered from poorly defined characters, brief descriptions, inaccurate diagnoses, and absence of comparisons. While the recognition of species boundaries in *Allobates* based on morphological attributes is possible, it should rely on extensive, careful comparisons (e.g., Kok et al., 2006; Lima et al., 2007). Moreover, it has become clear that this task is better informed by the integration of diverse types of data, including vocalizations, DNA sequences, and coloration in life (Simões et al., 2010, 2013a,b; Simões, 2016; Melo-Sampaio et al., 2013; Lima et al., 2014, 2015). As a result, to address standing issues in the taxonomy of Amazonian *Allobates*, it will be essential to re-sample the type localities of many

species to gather much-needed genetic, acoustic, and coloration in life data. Moreover, several nurse frogs have not yet been included in comprehensive studies, with potential consequences for the phylogenetic relationships of the Amazonian taxa. For some species, a proposed assignment to the genus *Allobates* requires further testing, which is the case of *A. ranoides* (Boulenger, 1918), *A. sanmartini* (Rivero et al., 1986) and *A. wayuu* (Acosta-Galvis et al., 1999). Accordingly, it has been recently shown that some species tentatively allocated in the genus *Allobates* (e.g., Grant et al., 2006) are in fact nested within *Hyloxalus*, as is the case of *H. cepedai* (Morales, 2002) and *H. picachos* (Ardila-Robayo et al., 2000) (Grant et al., 2017).

With the description of *Allobates tinae* **sp. nov.**, 28 nurse frog species are currently known to occur in Amazonian lowlands (Frost, 2017), a number that will certainly continue rising. In the light of new biological inventories and improved species identifications, this study points to a diverse *Allobates* fauna in the poorly-known lowlands of western Amazonia. This emerging picture of species ranges in *Allobates* will benefit from further sampling in regions that are seemingly rich in nurse frogs, some of which harbor unique environments. This is the case, for instance, of the white-sand forests (campinaranas) along the Javari River banks, where previous inventories have discovered a number of new species (Perez-Peña et al., 2010; Rojas et al., 2015). Nevertheless, obtaining the diverse datasets needed to improve *Allobates* taxonomy may represent a significant challenge for herpetologists sampling such remote regions.

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ONLINE SUPPORTING INFORMATION

The following Supporting Information is available for this article online:

Table S1. Newly sampled specimens used in phylogenetic analyses of *Allobates*, including voucher numbers, locality information, and GenBank accession numbers.

Table S2. Genetic samples obtained from GenBank for phylogenetic analyses of *Allobates*, including voucher numbers, locality information, and GenBank accession numbers.

Table S3. New identifications proposed for specimens in the type series of *Allobates flaviventris*, *A. fuscullus* and *A. vanzolinus*.

Figure S1. Morphological examinations of the type series of western Amazonian lowland *Allobates*. **(A)** Dorsal view of the holotype of *A. fuscullus* (INPA 2532); **(B)** ventral view of the same specimen (INPA 2532); **(C)** paratypes of *A. fuscullus* (from left to right, INPA 2333, 2351 and 2537) showing marked morphological variation. Note the presence of dark transversal stripes on the thigh of specimens INPA 2333 and 2535, and faded lateral band in INPA 2351; **(D)** holotype of *A. gasconi* (INPA 3082); **(E)** *A. gasconi* (INPA 3073) described originally as a paratype of *A. vanzolinus*; **(F)** holotype of *A. vanzolinus* (INPA 4896); **(G)** ventral view of the same specimen (INPA 4896); **(H)** holotype of *A. subfolionidificans* (INPA 13760); **(I)** a specimen of *A. subfolionidificans* from Porto Walter (MPEG 12321) previously identified as *A. conspicius*; **(J)** egg clutch of *A. subfolionidificans* in Feijó, Acre, Brazil.

Text S1. Concatenated alignment used in phylogenetic analyses (in nexus format).

APPENDIX

Examined specimens. Underlined voucher numbers correspond to new records.

Allobates alessandroi ($n = 3$): PERU: **Cusco**: Paucartambo: MUSM 15609 (holotype), MUSM 17737 (paratype); **Puno**: MUSM 15608 (paratype).

Allobates brunneus ($n = 16$): BRAZIL: **Mato Grosso**: Chapada dos Guimarães: INPA-H 10116–18, 10120–21, 10123, 10127, 10129–31, 10131, 10133, 10136, 10140–42, 10148.

Allobates caeruleodactylus ($n = 9$): BRAZIL: **Amazonas**: Autazes: km 12 on the road to Autazes, INPA-H 7238 (holotype), 7229–32, 7234–37 (paratypes).

Allobates conspicuus ($n = 2$): PERU: **Madre de Dios**: Manu: MUSM 24238. MUSM 31601.

Allobates femoralis ($n = 14$): BRAZIL: **Acre**: Sena Madureira: UFAC-RB 4714; **Amazonas**: Careiro da Várzea: MPEG 13806–17; **Rondônia**: Porto Velho: INPA-H 16728.

Allobates flaviventris ($n = 60$): BRAZIL: **Acre**: Rio Branco: Bambuzal do João, UFAC-RB 5536; Senador Guiomard: Fazenda Experimental Catuaba, UFAC-RB 4650 (holotype), 4599–4601, 4640–4641, 4671, 4678 (paratypes), 4603, 4633–4635, 4649, 4657, 4659–4660, 4670, 4675–4677, 4602, 4631–4632, 4658, 4661–4666, 4669 (paratypes); **Rondônia**: Parque Estadual de Guajará-Mirim: MPEG 13348–75.

Allobates fuscellus ($n = 6$): BRAZIL: **Amazonas**: Ipixuna: Penedo, right bank of Juruá river, INPA 2532 (holotype), 2531; Itamarati: Jainu, Juruá River, INPA 3114, 3250, 3270, 3514 (paratypes).

Allobates gasconi ($n = 52$): BRAZIL: **Acre**: Feijó: MCP 13630; Nova Vida: INPA 4726 (paratype); Rio Branco: Parque Ambiental Chico Mendes, MNRJ 91679 (PRMS 215); **Amazonas**: Boca do Acre: Estrada do Cruzeirozinho próximo ao platô do Piquiá, MNRJ 90229–40; Itamarati: Jainu, left bank of Juruá River, INPA 3082 (holotype), 3079, 3085, 3090, 3150–51, 3172, 3249, 3406, 3415, 3483–84, 3491, 3494, 3496, 3512–13 (paratypes), 3073 (as a paratype of *A. vanzolinus*); Lábrea: Rio Ituxi, MPEG 12992–13010.

Allobates goianus ($n = 1$): BRAZIL: **Goiás**: Chapada dos Veadeiros: 30 km from Alto Paraíso, MZUSP 76652 (holotype; former WCAB 47779).

Allobates grillisimilis ($n = 8$): BRAZIL: **Amazonas**: Nova Olinda do Norte: Ramal do Curupira, INPA-H 30809–30810 (paratypes); Borba: Ramal Novo Horizonte, about 5 km southwest of the city of Borba on the right bank of the Madeira River, INPA-H 30784, 30794, 30799–30801, 30804 (paratopotypes).

Allobates hodli ($n = 34$): BRAZIL: **Acre**: Senador Guiomard: Fazenda Bonal, UFAC-RB 4654–56; Fazenda Experimental Catuaba, UFAC-RB 4674; **Rondônia**: Porto Velho: Cachoeira do Jirau, on the left bank of the upper Madeira River, INPA-H 16555 (holotype), INPA-H 16541, 16553–68 (paratopotypes); Fortaleza do Abunã, about 160 km upstream from the city of Porto Velho, INPA-H 16622; Mutum-Paraná, left bank of the upper Madeira River across the river from the village, 121 km upstream from the city of Porto Velho, Mutum-Paraná, 34 km upstream from Cachoeira do Jirau, INPA-H 16818; Mutum-Paraná, about 121 km upstream from the city of Porto Velho, INPA-H 16788, 16767, 16756, 16805, 16758, 16788, 16739, 16771, 16777, 16730 (paratypes).

Allobates magnussoni ($n = 30$): BRAZIL: **Pará**: Santarém: Alter do Chão, Curuá-Una, MPEG 11921–50.

Allobates marchesianus ($n = 9$): BRAZIL: **Amazonas**: Missão Taracuá: INPA-H 7970–72, 7976–77, 7988, 10212, UFAC-RB 4181 (topotypes); São Gabriel da Cachoeira: UFAC-RB 4812.

Allobates melanolaemus ($n = 4$): PERU: **Loreto**: MUSM 17741 (holotype), MUSM 16507 (paratype), AMNH FS 11920, 11922 (paratypes).

Allobates nidicola ($n = 3$): BRAZIL: **Amazonas**: Castanho: Approximately 40 km S Manaus, INPA 8093 (holotype), MPEG 13820–21.

Allobates olfersioides ($n = 9$): BRAZIL: **Alagoas**: Mangabeiras: MZUSP 73707 (former WCAB 2801; holotype of *Colostethus alagoanus*); **Bahia**: Ibirapitanga: MNRJ 28952; **Espírito Santo**: Linhares: MNRJ 40420–21; Linhares: Refúgio Sooretama, Lagoa Macuco, MZUSP 73752 (former WCAB 1952; holotype of *Colostethus capixaba*); Santa Teresa: MNRJ 32425; **Rio de Janeiro**: Angra dos Reis: MNRJ 8094 (topotype); Teresópolis: MNRJ 23722–23.

Allobates paleovarzensis ($n = 1$): BRAZIL: **Amazonas**: Castanho: Near the town of Careiro da Várzea, INPA-H 20904 (holotype).

Allobates sp. ($n = 15$): BRAZIL: **Rondônia**: Parque Estadual de Guajará-Mirim: MPEG 13381–95.

Allobates subfolionidificans ($n = 74$): BRAZIL: **Acre**: Brasiléia: Reserva Extrativista Chico Mendes, UFAC-RB 5869; Colocação Santa Terezinha: Parque Nacional da Serra do Divisor, Rio Ouro Preto, UFAC-RB 3810; Cruzeiro do Sul: Mâncio Lima, Parque Nacional da Serra do Divisor, Igarapé Ramon, UFAC-RB 2785; Reserva Extrativista do Alto Juruá, trail to Mato Grosso, UFAC-RB 828, 855, 857, 2020, 2022, 2155, 2164; Reserva Extrativista do Alto Juruá, Rio Amônia/Montevidéo (Mr. Zeli), UFAC-RB 2663; Reserva Extrativista do Alto Juruá, Rio Amônia/Quieto (Ms. Auzira), UFAC-RB 5618; Manoel Urbano: Parque Estadual Chandless, “trail 7”, UFAC-RB 4540, 4542; Marechal Thaumaturgo: Reserva Extrativista do Alto Juruá, foz do Rio Breu, UFAC-RB 2316–2317; Reserva Extrativista do Alto Juruá, caminho do Rio Arara, UFAC-RB 2429, 2433, 2479; Reserva Extrativista do Alto Juruá, mouth of Rio Bagé, UFAC-RB 2613, 2615; Porto Acre: Reserva Florestal Humaitá, UFAC-RB 982; Porto Walter: MPEG 12318–12326; Rio Branco: Chácara de Jesus, UFAC-RB 4874; Parque Zoológico de Universidade Federal do Acre, INPA-H 13760 (holotype), UFAC-RB 4616–4617, 4682–4683, 4700–4701; Tarauacá: Complexo das florestas Estaduais do Gregório, “site 5”, UFAC-RB 5647; Complexo das florestas Estaduais do Gregório, “site 8”, ca. 20 km far from Rio Gregório, UFAC-RB 5668; PERU: **Loreto**: Genaro Herrera: MUSM 15612.

Allobates sumtuosus ($n = 10$): BRAZIL: **Amazonas**: Manaus: Reserva Florestal Adolpho Ducke, INPA-H 31949–31951; **Pará**: Reserva Biológica Trombetas: USNM 303591 (holotype, through photographs), INPA-H 31954–55, 31959–60; **Roraima**: São João da Baliza: INPA-H 31956–57, (former AMNH 20210–11).

Allobates tapajos ($n = 7$): BRAZIL: **Amazonas**: INPA-H 36509–10, 36512, 36518, 36548, 36563, 36581.

Allobates trilineatus ($n = 56$): BRAZIL: **Acre**: Cruzeiro do Sul: Mâncio Lima, MCP 13618, 13639; Senador Guiomard: UFAC-RB 0160, 0162–64; Porto Walter: MPEG 12328–12360; Rio Branco: Parque Zoológico, Universidade Federal do Acre, UFAC-RB 3550, 4605–4615, 5203; Sena Madureira: Bairro Segundo Distrito, margem direita do Rio Iaco, UFAC-RB 4703–04, 5557; **Amazonas**: Envira: MCP 13628. PERU: **Madre de Dios**: Cocha Cashu: MUSM 15618. **San Martín**: Yurimaguas: MUSM 15611.

Allobates vanzolinius ($n = 7$): BRAZIL: **Amazonas**: Ipixuna: Jainu, INPA 3381, 3413 (paratypes); Vai-Quem-Quer: INPA 4896 (holotype), 4903, 4904, 4905, 4912 (paratypes).