# A new species of Anomaloglossus (Anura: Aromobatidae) of the stepheni group with the redescription of A. baeobatrachus (Boistel and de Massary, 1999), and an amended definition of A. leopardus Ouboter and Jairam, 2012

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# Article

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## Abstract

*Anomaloglossus* is a species-rich genus of frogs endemic to the Guiana Shield that still harbors several unnamed species. Within the *A. stepheni* species group (which includes four valid nominal species), *A. baeobatrachus* has an uncertain taxonomic status, notably because the holotype was an unvouched species depicted in a popular journal. Another member of this group, *A. leopardus*, was only superficially described, lacking information on the sex of specimens in the type series and on advertisement calls. Therefore, these two taxa need clarifications in order to allow the description of the extant undescribed species. In this paper, we redescribe *A. baeobatrachus* based on newly collected material from the species type locality and provide information about its reproductive ecology. We also provide an amended definition of *A. leopardus* using newly collected material from its type locality. These two species form a clade along with a third species from the Eastern Guiana Shield, which is also described herein. The reproductive biology of *A. baeobatrachus* and *A. stepheni* is very similar. Both species have endotrophic and nidicolous tadpoles, despite being distantly related, suggesting independent evolution of this breeding mode. The new species and *A. leopardus*, on the other hand, have exotrophic tadpoles.

**Key words**: Amazonia, Endemism, Endotrophy, Guiana Shield, Reproductive mode, Taxonomy

## Introduction

*Anomaloglossus* Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel, and Wheeler, 2006 currently contains 29 valid nominal species from the Guiana Shield (Frost 2018). As almost half of these species have been described after the year 2000, there has been a sharp increase in the recognized diversity within this genus. Nevertheless, many species remain undescribed and unnamed, most notably in the *A. stepheni* group (Vacher *et al.* 2017). This clade contains four valid taxa: *A. stepheni* Martins, 1989, *A. baeobatrachus* (Boistel & de Massary, 1999), *A. leopardus* Ouboter & Jairam, 2012 and *A. apiau* Fouquet, Souza, Nunes, Kok, Curcio, Carvalho, Grant & Rodrigues, 2015 that are distributed throughout the eastern lowlands of the Guiana Shield. The taxonomic status of *A. baeobatrachus* and *A. leopardus* are problematic and hamper the naming of other undescribed species in the group. These two nominal species—together with the still unnamed *Anomaloglossus* sp. "Mitaraka"—form a subclade within the *stepheni* species group (Vacher *et al.* 2017, Fouquet *et al.* 2019), distributed in the easternmost part of the Guiana Shield. Additional candidate species within the *stepheni* species group have been detected further west, in Suriname and Brazil, but they seem to be more distantly related to this

subclade (Vacher *et al.* 2017).

*Anomaloglossus baeobatrachus* has a particularly complex taxonomic history. The name *Colostethus baeobatrac*hus was first coined by Edwards (1974) and referred to a species from the Manaus region, in central Brazilian Amazonia. However, Edwards never published his work beyond his thesis manuscript, which therefore does not content any formal nomenclatural act. Fifteen years later, this species was formally described as *Colostethus stepheni* by Martins (1989). Apparently ignoring the description of Martins, Boistel & de Massary (1999) published, in a popular journal, a succinct description of a *Colostethus* from French Guiana that they identified as Edwards' *Colostethus baeobatrachus*. Although apparently not intended to formally describe a new species, this publication was a valid description according to the *International Code of Zoological Nomenclature* (ICZN), even if no holotype nor type locality were designated. To date, the only type material of *A. baeobatrachus* referred in the literature is a photograph provided by Boistel & de Massary (1999), illustrating an individual from Saint Eugène, French Guiana (Boistel R. pers. com.). This problem was highlighted by Kok (2000*a*) who proposed a redescription of *C. baeobatrachus* based on 10 individuals from Saül (Montagne Belvédère) and the county of Roura (vicinity of the village of Cacao), French Guiana. Subsequently, Kok (2000*b*) rediscovered the existence of Martins' description of *C. stepheni* and, not finding any morphological differences between specimens from Manaus and French Guiana, considered *C. baeobatrachus* as a synonym of *C. stepheni*. In 2006, Grant *et al.* provided molecular evidence of the distinctiveness of *C. stepheni* and *C. baeobatrachus* and resurrected the latter. The same publication, Grant *et al.* (2006) erected the genus *Anomaloglossus* for the *Colostethus* species possessing a median lingual process, which is the case of *C. baeobatrachus*. Subsequently, *Anomaloglossus* populations from French Guiana (Fouquet *et al.* 2012), Suriname (Ouboter & Jairam 2012), and Northern Pará (Avila-Pires *et al.* 2011) and Amapá (Fouquet *et al.* 2012) in Brazil, were considered as belonging to *A. baeobatrachus*. However, Vacher *et al.* (2017) recently demonstrated that *A. stepheni* is distributed from the Manaus region to Suriname and that many cryptic species are actually confused with *A. baeobatrachus*.

Juncá *et al.* (1994) and Juncá (1996; 1998) extensively described the reproductive biology of *A. stepheni* whose tadpoles are endotrophic (morphologically characterized by reduced mouth parts and a median vent tube) and nidicolous (developing within a terrestrial nest). Grant *et al.* (2006) later reported the observation of phoresy in *A. baeobatrachus* from Serra do Navio, Amapá, Brazil, where a male was carrying three fully-developed exotrophic tadpoles (with well-developed mouth parts and dextral vent tubes), thus adding strong evidence for the distinction between *A. stepheni* and *A. baeobatrachus*. Deschamps (2005), in an unpublished manuscript, provided detailed information on the development and the breeding ecology of northern French Guiana populations of *A. baeobatrachus*, showing that these populations have a reproductive biology similar to *A. stepheni*, i.e., with nidicolous and endotrophic tadpoles. Later, Vacher *et al.* (2017) demonstrated that two co-occurring (notably in Serra do Navio) phenotypes exist within what they previously considered as *A. baeobatrachus*, which explains the observation reported by Grant *et al.* (2006). These two phenotypes differ in body size, calls, habitat and larval development (endotrophic vs. exotrophic). Fouquet *et al.* (2019) showed that they correspond to at least two different species that have repeatedly hybridized during their recent history without signs of present introgression. Moreover, only the endotrophic phenotype occurs in northwestern French Guiana where the type locality of *A. baeobatrachus* is located.

*Anomaloglossus leopardus* was recently described by Ouboter & Jairam (2012) based on three specimens collected in Apalagadi (southern Suriname) thirteen years earlier. The description does not mention the sex of the type specimens, provides very little information on the morphological variation, and none on living coloration, ecology or calls. However, Vacher *et al.* (2017) were able to confirm that *A. leopardus* is distinct from any other described species in the *A. stepheni* group based on molecular, acoustic and morphological data. They also demonstrated that it is closely related to *A. baeobatrachus* and to at least one undescribed species from southeastern French Guiana. This last candidate species, which was identified by Vacher *et al.* (2017) based on DNA, call, and morphology, has an exotrophic tadpole development mode and occurs in the Mitaraka massif at the border between Suriname and French Guiana. Molecular data demonstrated that this population is distinct from the other exotrophic populations of French Guiana and Amapá (Brazil) with which it probably has a history of admixture (Fouquet *et al.* 2019).

A thorough and updated redescription of *A. baeobatrachus* based on material collected in the type locality is greatly needed because the actual diversity within the *A. stepheni* group has been shown to be much larger than previously thought. Herein we fill this gap, by examining adult morphology and calls of genotyped individuals

including topotypical material and designating a neotype for *A. baeobatrachus* as well as describing its larval morphology and reproductive mode. Likewise, we provide a more complete definition of *A. leopardus* and formally describe *Anomaloglossus* sp. "Mitaraka" of Vacher *et al*. (2017), which is closely related to these two taxa.

## Material and methods

We undertook fieldwork across several localities in French Guiana, Suriname and Amapá (Brazil) during the last decade and collected specimens and tissue samples, recorded calls and ecological data of *Anomaloglossus baeobatrachus*, *A. leopardus* and *A*. sp. "Mitaraka" (Fig. 1). Frogs were collected by hand and euthanized by intraperitoneal injection of Xylocaine® (lidocaine hydrochloride). Tissue samples (a piece of liver) were removed and stored in 95 % ethanol for molecular analyses, before preservation of the specimens. All specimens were tagged and fixed in 10 % formalin before being transferred to a solution of 70 % ethanol for permanent storage. Specimens were deposited in the Museum National d'Histoire Naturelle (Paris, France) (MNHN 2018.31–77) and the National Zoological collection of Suriname (NZCS A249–51).
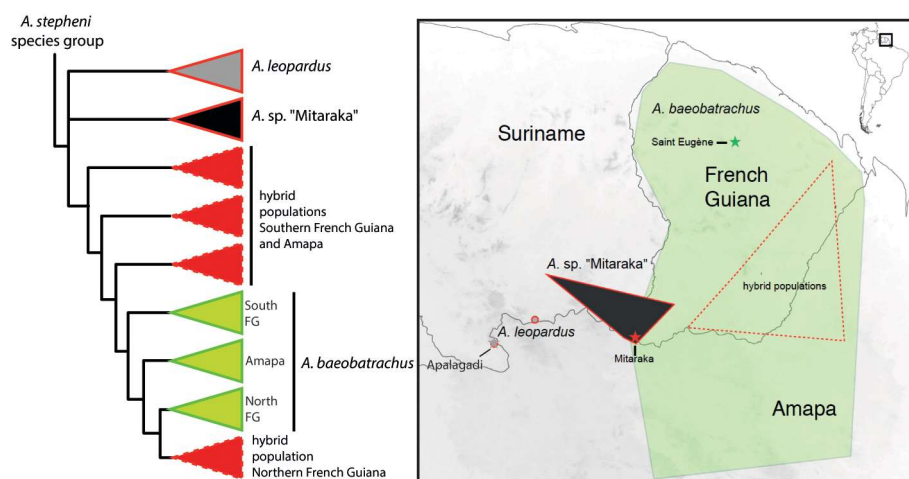


**FIGURE 1**. Phylogenetic tree adapted from Fouquet *et al.* (2018) and respective distributions of the species in the *Anomaloglossus stepheni* species group. Red contours of collapsed branches in the tree indicate groups with exotrophic tadpoles, while green contours indicate groups with endotrophic Tadpoles. The same colors correspond to geographic distributions of these groups in the map.

**Morphometric analysis**. The sex of 20 adult specimens (16 males, 4 females) of *A. baeobatrachus*, 11 specimens (7 males, 4 females) of *A. leopardus* and 11 specimens (8 males, 3 females) of *A*. sp. "Mitaraka" was determined either in the field via calling activity, or in the laboratory by checking the condition of vocal slits and/or gonads. We measured 17 variables: 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 edge of eye to tip of snout (SL); eye to naris distance from anterior edge of eye to center of naris (EN); internarial distance (IN); horizontal eye diameter (ED); interorbital distance (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); tibia length from outer edge of flexed knee to heel (TL); foot length from proximal edge of inner metatarsal tubercle to tip of toe IV (FL); width of disc on Toe IV (WTD); thigh length from vent opening to flexed knee (ThL); length of Finger I from inner edge of thenar tubercle to tip of disc (1FiL), following Fouquet *et al*. (2015). Webbing formula followed Savage & Heyer (1967) and Lescure (1975) with modifications suggested by Myers & Duellman (1982) and Savage & Heyer (1997).

**Larval morphology**. Three jelly nests of *Anomaloglossus baeobatrachus* were found in French Guiana: (1) at Mitaraka, where a clutch of four eggs at early developmental stage was collected; tadpoles were raised until they reached Gosner stage 24 (AF2876C), 30 (AF2876A), 32 (AF2876B) and 45 (AF2876D) and fixed in formalin 10 %; (2) at Saut Maripa, where four tadpoles were collected including two fixed in ethanol and two at stage 33

(PG743A) and at stage 34 (PG743B) fixed in formalin, and (3) at Saint Eugene AF2592 with three froglets fixed in formalin.

One nest of *Anomaloglossus* sp. "Mitaraka" with one tadpole at stage 28 (AF2732), and two males with, respectively, five (AF2751) and nine (AF2878) tadpoles at stage 27 on their backs were collected and fixed in formalin 10 %. Additionally, two groups of tadpoles found in small puddles nearby calling males were raised until one tadpole reached stage 28 (AF2817A) ) and another tadpole reached stage 30 (AF2875A). The two tadpoles were fixed in formalin 10 %. An additional tadpole (AF2875B) was raised until metamorphosis.

The following 16 measurements were taken on four formalin-fixed tadpoles of *A. baeobatrachus* at stages 30–34 and five tadpoles of *A.* sp. "Mitaraka" at stages 26–30 by the same person (AF) according to McDiarmid & Altig (1999) using a Stemi 2000C Zeiss stereomicroscope connected to an Axiocam ERC 5S: TL, Total Length (from tip of the snout to tip of the tail); BL, Body Length (from tip of snout to junction of posterior body and tail musculature); TAL, Tail Length (from junction of posterior body and tail musculature to tip of tail); BW, Body Width (maximum width of body); BH, Body Height (maximum height of body); HW, Head Width (at level of eyes); TMH, Tail Muscle Height (at base of tail); UTF, Upper Tail Fin Height (maximum height of upper fin, from upper margin of tail musculature to upper margin of upper fin); LTF, Lower Tail Fin Height (maximum height of lower fin, from lower margin of lower fin to lower margin of tail musculature); TMW, Tail Muscle Width (at base of tail); MTH, Maximum Height of Tail; END, Eye-Naris Distance (from anterior corner of eye to posterior margin of nostril); NSD, Naris-Snout Distance (from anterior margin of naris to tip of snout); IND, Internarial Distance (distance between the median margins of nares); IOD, Interorbital Distance; ED, Eye Diameter (greatest length of orbit from anterior margin to posterior margin of eye). In tadpoles of *A. baeobatrachus*, the mouth is bare and labial teeth definition was thus not applicable. Seven additional nests were observed in French Guiana near Saint Laurent du Maroni and at Trésor Natural Reserve by Deschamps (2005) who provided data on the reproductive ecology as well.

We compared these data with those of the larva of *A. stepheni* (Juncá *et al.* 1994), the only other species in this clade with described tadpoles (which are nidicolous and endotrophic) and *A. degranvillei* (Lescure 1984), which are also endotrophic but distantly related.

**Bioacoustics**. The call of nine males of *A. baeobatrachus*: MNHN2018.38 (field n°AF0821) recorded by A. Fouquet, 31 December 2012, Chutes Voltaire, French Guiana, 5.03122° N 54.08778° W, ~60 m elevation; field n°AF1120 recorded by Antoine Fouquet, 04 April 2013, Mana River, French Guiana, 5.09949° N 53.80057° W, ~60 m elevation; MNHN2018.39-40 (field n°AF1839, 1841) recorded by Antoine Fouquet, 24 March 2014, RN2 corridor 3, French Guiana, 4.10583° N 52.05096° W, ~50 m elevation; MNHN2018.41-42 (field n°AF2098-2099) recorded by Andy Lorenzini, 01 April 2014, RN2 corridor 5, French Guiana, 4.03322° N 51.99078° W, ~50 m elevation; MNHN2018.31 (field n°AF2589) recorded by Jean-Pierre Vacher, 21 February 2015, Saint Eugène, French Guiana, 4.82167° N 53.06766° W, ~60 m elevation; and two uncollected specimens by Philippe Gaucher, 21 December 2000, Pic Matecho, French Guiana, 3.75° N 53.033333° W, ~300 m elevation; and 01 January 1996, Kaw mountain, French Guiana 4.516105° N 52.10053° W, 200 m elevation, four males of *A. leopardus* MNHN2018.58-59 (field n°AF2035, 2038) recorded by A. Fouquet, 19 April 2014, Apalagadi, Suriname, 2.16977° N 56.08083° W, ~100 m elevation and two uncollected specimens by Paul Ouboter, 15 August 1989, 2.16977° N 56.08083° W at the same locality; and six males of *A.* sp. "Mitaraka": MNHN2018.65-66, 69 (field n°AF2732, 2750) MNHN2018.69 (field n°AF2808) MNHN2018.64 (AF2814) and one uncollected individual recorded by A. Fouquet, 24 February 2015, Mitaraka, French Guiana, 2.23577° N 54.44928° W, ~150 m elevation and one uncollected individual by Michel Blanc, 01 February 2013, Pic Coudreau du Sud, French Guiana, 2.2534° N 54.3534° W, ~150 m elevation; were recorded in the field using either an Olympus LS11 digital recorder or a Zoom H4N digital recorder attached to a Sennheiser ME-66 supercardioid microphone powered by a K6P module at 44.1 kHz sampling rate. We measured six call variables from the train of pulsed notes emitted by these species in the software Audacity v.2.1.1. Variables follow those standardized in Kok & Kalamandeen (2008): call rate (number of calls divided by the duration of the recording window), call length, note length, inter-note interval, note repetition rate (note rate: call duration divided by the number of notes in the call). We also measured the dominant (emphasized) frequency from a spectral slice taken through the portion of the note with the highest amplitude (using Blackman function; frequency resolution 43 Hz) in Audacity. For each variable per individual, we used the mean value calculated across four different calls. Illustrations of spectrograms and oscillograms were produced using the package Seewave (Sueur *et al.* 2008) implemented in R (R Development Core Team 2016). We

compared these data to four recordings of *A. stepheni* (AF2043 recorded by Antoine Fouquet, 19 April 2014, Apalagadi, Suriname, 2.17965° N 56.09078° W; AF2221 recorded by Antoine Fouquet, 25 April 2014, Sipaliwini, Suriname, 2.03253° N 56.11449° W; AF3450 recorded by Antoine Fouquet, 02 May 2015, Spari Creek, Suriname, 5.23285° N 55.80462° W; an uncollected specimen recorded by Antoine Fouquet, 16 December 2014, Nassau, Suriname, 4.80412° N 54.5555° W), the only other described species of the group that emits a train of <mark>pulsed</mark> notes.

## Results

Hereafter we redescribe *A. baeobatrachus* and designate a neotype as well as describing its larval morphology and reproductive mode. We also provide a more complete definition of *A. leopardus* and formally describe *Anomaloglossus* sp. "Mitaraka" of Vacher *et al.* (2017). The three species belong to the genus *Anomaloglossus* and are allocated to the *A. stepheni* group based on previous studies (Grant *et al.* 2006; Vacher *et al.* 2017) which included some of the voucher specimens examined herein and the presence of a median lingual process.

### *Anomaloglossus baeobatrachus* (Boistel & de Massary, 1999)
Figs. 2–5

**Neotype.** MNHN2018.31 (field n°AF2589), an adult male, collected by Jean-Pierre Vacher, 21 February 2015, Saint Eugène, French Guiana, 4.82167° N 53.06766° W, ~60 m elevation (Figs. 2, 3).

**Additional specimens examined.** Twenty-one specimens: MNHN2018.34–36 (field n°AF0207–8, 0214) two adult males and one female, collected by A. Fouquet and Régis Gallais, 08 April 2007, Angoulème, French Guiana, 5.383333° N 53.650000° W, ~20 m elevation. MNHN2018.37 (field n°AF0244) an adult female, collected by A. Fouquet, 10 May 2007, Nouragues field station, French Guiana, 4.083333° N 52.683333° W, ~100 m elevation. MNHN2018.38 (field n°AF0821) an adult male, collected by A. Fouquet, 31 December 2012, Chutes Voltaire, French Guiana, 5.031222° N 54.087778° W, ~60 m elevation. MNHN2018.39–40 (field n°AF1839, 1841) two adult males, collected by A. Fouquet and Jean-Pierre Vacher, 24 March 2014, RN2 corridor 3, French Guiana, 4.10583° N 52.05096° W, ~50 m elevation. MNHN2018.41–44 (field n°AF2098-9, 2101-2) four adult males, collected by A. Lorenzini, 01 April 2014, RN2 corridor 5, French Guiana, 4.03297° N 51.99078° W, ~50 m elevation. MNHN2018.32–33 (field n°AF2590-1) two adult males with same data as neotype. MNHN2018.45–48,50 (field n°AF2667, 2704-6, 2709) four adult males and MNHN2018.49 (field n°AF2707) and adult female, collected by Jean-Pierre Vacher, 18 February 2015, Alikéné, French Guiana, 3.21153° N 52.39981° W, ~280 m elevation. MNHN2018.51–52 (field n°AF2942, 2963) an adult female and an adult male, collected by Antoine Fouquet and Pedro S. Nunes, 15 March 2015, Mémora, French Guiana, 3.31774° N 52.19329° W, ~50 m elevation.

**Definition.** (1) A small-sized *Anomaloglossus* (average male SVL 16.2 mm [14.8–17.1, *n* = 16], female SVL 18.4 mm [17.3–19.4, *n* = 4]) (Table 1); (2) body robust; (3) skin tuberculate on dorsum (particularly the posterior half) and legs, with a large tubercle on each eyelid, ventral skin smooth; (4) diffuse supratympanic fold; (5) tympanic annulus distinct anteroventrally; (6) snout short and protruding in lateral view; (7) nares oriented ventrolaterally, situated near tip of snout; (8) Finger II same length as Finger I when fingers adpressed; (9) tip of Finger IV reaching distal subarticular tubercle on Finger III when fingers adpressed; (10) distal subarticular tubercle distinct on Finger III but absent on the other fingers; (11) Finger III swollen dorsally and preaxially extending largely on dorsal surface of hand in males, with well-developed lateral fringe in females; (12) Fingers II with preaxial fringes in both sexes; (13) toes basally webbed, with fringes on all toes more developed preaxially on Toe II and pre- and postaxially on Toes III and IV (*sensu* Grant *et al.* 2006; keel-like lateral folds *sensu* Myers & Donnelly 2008); (14) tarsal keel well-defined, curved; (15) black arm gland at the junction of distal forearm with wrist in males (*sensu* Grant & Castro 1998, see also Grant *et al.* 2006); (16) cloacal tubercles present; (17) paracloacal mark present (orangish in life, cream in preservative); (18) dorsolateral stripe present, discontinuous (bluish to yellowish particularly posteriorly in life, white in preservative), flanks and dorsum dark brown in males paler in females; (19) ventrolateral stripe absent; (20) sexual dichromatism in throat color present, in life sometimes anteriorly and laterally yellow in males, evenly yellow in females, with sparse black melanophores; (21)

sexual dichromatism in ventral color present, in life abdomen mostly cream with flanks often yellow in males, abdomen entirely and uniformly bright yellow in females in life; (22) iris with metallic pigmentation and pupil ring interrupted ventrally and dorsally by transversal black pigmentation; (23) median lingual process as long as wide, tapered, bluntly pointed, smooth (non-papillate), reclined in pit; (24) call 0.84–1.33 s long, consisting of a train of 13–28 pulsed notes 0.018–0.021 s long spaced by intervals of 0.043–0.047 s, dominant frequency at 4.960–5.591 kHz ($n$ = 9); (25) tadpole of type 2 (Orton 1953), endotrophic, with bare mouth and prominent trophic reserves (Fig. 4; Table 2).

**Morphological comparisons with other *Anomaloglossus*.** The only other species group co-occurring with the *Anomaloglossus stepheni* group is the *A. degranvillei* group, currently represented by *A. blanci* Fouquet, Vacher, Courtois, Villette, Reizine, Gaucher, Jairam, Ouboter & Kok, 2018, *A. degranvillei* Lescure, 1975, *A. dewynteri* Fouquet, Vacher, Courtois, Villette, Reizine, Gaucher, Jairam, Ouboter & Kok, 2018, and *A. surinamensis* Ouboter & Jairam, 2012, which are readily distinguishable by their moderate webbing (basal in *A. baeobatrachus*) and well-developed fringes on all toes (smaller and more developed on Toe II, III, IV) and the absence of a dorsolateral stripe (present). Outside these two groups all the other described *Anomaloglossus* species exclusively occur in Pantepui (i.e., the Guiana Shield highlands, see Kok *et al.* 2018) and have moderate to extensive toe webbing except *A. meansi* Kok, Nicolaï, Lathrop & MacCulloch, 2018*, A. kaiei* (Kok, Sambhu, Roopsind, Lenglet & Bourne, 2006), *A. rufulus* (Gorzula, 1990) and *A. roraima* (La Marca, 1997). However, unlike *A. baeobatrachus*, these last four species lack developed fringes on toes.

Within the *Anomaloglossus stepheni* group, *A. baeobatrachus* can be distinguished from *A. stepheni* (Figs. 2–3, Table 1) by (1) a smaller body size (mean = 16.2; range 14.8–17.15 mm in males [$n$ = 16] and mean = 18.4; range 17.3–19.4 mm in females [$n$ = 4] in *A. baeobatrachus* vs. mean = 17.15, range 16.5–18.0 mm in males [$n$ = 10] and mean = 17.3, range 17.0–18.0 mm in females [$n$ = 5] (from Martins 1989) in *A. stepheni*); (2) skin of dorsum irregularly tuberculate in *A. baeobatrachus* vs. evenly tuberculate in *A. stepheni*; (3) ventral coloration with yellow shades, at least posteriorly in males in *A. baeobatrachus* vs. entirely translucent white in *A. stepheni*; (4) dorsolateral line thin and interrupted in *A. baeobatrachus* vs. thick and ill-defined margins dorsally in *A. stepheni*; (5) call much longer (mean = 1.12, range 0.84–1.33 s) in *A. baeobatrachus* [$n$ = 9] vs. mean = 0.25, range 0.18–0.29 s in *A. stepheni* [$n$ = 4]) emitted at a slower pace (call rate mean = 0.33, range 0.18–0.48 calls/s in *A. baeobatrachus* [$n$ = 11] vs. mean = 1.40, range 1.10–1.89 calls/s in *A. stepheni* [$n$ = 4]), with a higher dominant frequency (mean = 5.39, range 4.96–5.59 kHz in *A. baeobatrachus* [$n$ = 6] vs. mean = 4.48 kHZ, range 4.30–4.85 kHz in *A. stepheni* [$n$ = 4]).

*Anomaloglossus baeobatrachus* can be distinguished from *A. leopardus* (Figs. 2–3, Table 1) by (1) a smaller body size (mean = 16.2; range 14.8–17.1 mm in males [$n$ = 16] and mean = 18.4; range 17.3–19.4 mm in females [$n$ = 4] in *A. baeobatrachus* vs. mean = 18.8, range 18.5–19.2 mm in males [$n$ = 10] and mean = 21.1, range 20.5–21.5 mm in females [$n$ = 4] in *A. leopardus*); (2) dorsal coloration uniformly dark brown with inconspicuous dark transverse bars on legs in *A. baeobatrachus* vs dorsal coloration with large dark blotches, particularly visible in preservative and conspicuous dark transverse bars on legs in *A. leopardus*; (3) ventral coloration with yellow restricted to the posterior part in males in *A. baeobatrachus* vs. generally entirely yellow in *A. leopardus*; (4) dorsolateral line thin and discontinuous in *A. baeobatrachus* vs. thick and continuous in *A. leopardus*; (5) call with a faster note rate (mean = 16.1, range 15.7–16.8 note/s in *A. baeobatrachus* [$n$ = 9] vs. mean = 13.4, range 12.9–13.6 notes/s in *A. leopardus* [$n$ = 4]) with a higher dominant frequency (mean = 5.39, range 4.96–5.59 kHz in *A. baeobatrachus* [$n$ = 6] vs. mean=4.49 kHZ, range 4.40–4.57 kHz in *A. leopardus* [$n$ = 4], Table 2).

**Description of the neotype.** An adult male, 15.9 mm SVL; body robust; head wider than long, HL 94 % of HW; HL 32 % of SVL; dorsal skin irregularly tuberculate, one enlarged tubercle on each eyelid, snout long (SL 55 % of HL), rounded to nearly truncate in dorsal view, protruding in lateral view, extending past lower jaw. Nares located anterolaterally; canthus rostralis rounded, loreal region concave; IN 44 % of HW; EN 31 % of HL, 70 % of ED. Tympanum distinct anteroventrally; supratympanic fold diffuse; choanae small, circular, located anterolaterally to palatine (Fig. 3).

Forelimb slender, skin dorsally tuberculate; metacarpal ridge present; HAND 24 % of SVL; Finger I longer than Finger II when fingers adpressed; fingers large and flattened without webbing, lateral fringes present on preaxial edges of Fingers II; Finger III distinctly swollen dorsally and preaxially; tip of Finger IV not reaching distal subarticular tubercle on Finger III when fingers adpressed; finger discs expanded, wider than long, about 1.5X width of digit; width of disc on Finger III 0.5 mm; discs with distinct dorsal scutes. Relative lengths of

adpressed fingers III > IV > I > II; palmar tubercle large, heart-shaped, 0.7 mm in diameter (larger than Finger III disc), thenar tubercle small (equal to Finger III disc), elliptic, half the size of palmar tubercle, well separated from palmar tubercle. Only basal subarticular tubercles on Fingers I, II and IV are conspicuous; Subarticular tubercle of Finger I larger than Finger II and IV subarticular tubercles.

Hind limb robust, skin dorsally tuberculate; TL 47 % of SVL; heels not in contact when hind limbs are flexed at right angle to sagittal plane of body; FL 42 % of SVL; relative length of adpressed toes IV > III > V > II > I; Toe I very short, its tip reaching the base of subarticular tubercle on Toe II when toes adpressed; toe discs larger than width of toes; disc on Toe I only slightly larger than width of digit. Width of disc on Toe IV 0.7 mm. Feet poorly webbed; lateral fringes present on all toes. Toe webbing formula **I**$1^+$–$1^-$**II**$1^+$–$1^-$**III**$1^{1/2}$–$1^{1/2}$**IV**$0$–$1^+$**V**. One to three subarticular tubercles on toes as follows: one on Toes I and II, two on Toes III and V, three on Toe IV. Inner metatarsal tubercle protuberant elliptical, 0.5 mm in length, outer metatarsal tubercle round, protuberant, 0.3 mm in diameter. Tarsal keel well defined, tubercle-like and strongly curved at proximal end. Metatarsal fold conspicuous and strongly curved.

**Color of neotype in life.** Dorsal color uniformly dark brown. Discontinuous pale dorsolateral stripes consisting of irregular bluish, white, orangish and yellow (near groin) small blotches (Fig. 2). Dark brown lateral band extending from tip of snout to the groin and containing the indistinct dorsal part of tympanum. Upper lip with small iridescent light blue blotches. Lower flanks pale yellow with small iridescent white blotches. Throat anteriorly yellow, centrally white and posteriorly pinkish, covered with melanophores more densely anterolaterally; belly centrally white and laterally and posteriorly yellow, ventral surface of thighs and arms pale orange. Iris with copper metallic pigmentation and pupil ring interrupted dorsally and ventrally by transversal dark pigmentation (Fig. 2).

Upper arm pale orange dorsally with a conspicuous proximal white spot, anteriorly and posteriorly light brown with small bluish spots. Lower arm light brown with ill-defined dark brown blotches and small bluish spots. Dorsal surfaces of thigh, shank and tarsus dark brown with ill-defined darker blotches. Paracloacal marks orangish, elongated anteroposteriorly. Toes and digits with small light blue dots. Palms and soles dark brown.

**Color of neotype in preservative.** After three years in 70 % ethanol, some colors of the specimen faded and the dorsal coloration now varies from brown to grey and the yellow ventral coloration disappeared. All bluish freckles and orange and reddish marks turned cream (Fig. 3).

**Variation.** Measurements (range, mean, and standard deviation) are provided in Table 1. Adult dorsal coloration varies from brown to reddish brown in males, females being paler and with more conspicuous darker dorsal blotches. The dorsolateral line varies from almost continuous to continuous; bluish flecks may be numerous or absent. Additionally, overall coloration and tuberculation may vary with light intensity, time of the day and probably reproductive activity as males carrying tadpoles apparently display overall lighter colors, smoother skin and sharper contrasts while calling males are very dark and highly tuberculate. Ventral coloration of female is entirely yellow while the yellow parts are limited in various extent to the posterior region and throat in males. Vocal sac, slits and small dark melanophores on throat only observed in males as well as swelling on the Finger III.

**Advertisement call.** Nine specimens (two not collected) calling from the leaf litter were recorded from a distance of about 1 m and at temperatures ranging from 23 to 26°C. Descriptive statistics of call parameters are presented in Table 2. *Anomaloglossus baeobatrachus* emits trains (call length mean = 1.12 s; range 0.84–1.33 s) of short pulsed notes (note length mean = 0.019 s; range 0.018–0.022 s; inter-note interval mean = 0.045 s; range 0.043–0.046 s) (Fig. 4). The spectral structure of the note has a developed harmonic structure and the dominant frequency is 5.39 kHz on average (range 4.96–5.59 kHz) with a slight upward modulation (ca. 0.2 kHz) (Fig. 4, Table 2).

**Larval morphology.** The following description is based on four tadpoles at stage 30, 32, 33 and 34 (Fig. 5). Measurements are presented in Table 3. Tadpoles correspond to Type 2 tadpoles of Orton (1953) although an external spiracle is absent; tadpoles endotrophic; body skin smooth; TL 10.86–12.92 mm; BL 3.97–4.62 mm, 36–37 % of TL, 141–159 % of BW, 212–241 % of BH; BW 137–171 % of BH (Table 2); body inflated from trophic reserves until stage 33 when it becomes ovoid; round snout in dorsal and lateral view; eyes positioned and directed laterally (Fig. 5); ED 0.46–0.68 mm, 65–81 % of IOD; IOD more than IND; nares positioned frontally and directed laterodorsally; narial opening reniform in lateral view; END 0.28–0.40 mm. Spiracular tube absent. Lateral-line system inconspicuous. Caudal musculature highest at its base, tapering posteriorly, terminating at tail tip; tail tip rounded; upper fin originating at junction of body and tail, gradually increasing in height to about 3/4 of

tail; UTF 39–50 % of TMH; LTF 26–42 % of TMH; MTH 15–18 % of TL. Mouth small and bare (without marginal papillae, labial teeth nor sheaths), directed ventrally, oral disc width 0.5 mm (from edges of jaws) (Fig. 5, Table 3).

In life, until stage 32 the entire body is light grey except the tail fins that are translucent and the abdomen that is yellowish. From stage 33 the body becomes dark grey with golden speckles, and the tail and fin become translucent posteriorly (Fig. 5).

Tadpoles of *Anomaloglossus baeobatrachus* can be distinguished from those of any other *Anomaloglossus* of the *stepheni* group (except *A. apiau* and *A. stepheni*) by the absence of functional mouth and the prominent trophic reserves.

Only two other *Anomaloglossus* with an endotrophic tadpole have been described, *A. stepheni* (Juncá *et al.* 1994) and *A. degranvillei* (Lescure 1984); although the latter may in fact correspond to *A. surinamensis* or *A. blanci* (Fouquet *et al.* 2019). Tadpoles of *A. baeobatrachus* can be distinguished from those of *Anomaloglossus stepheni* by the absence of a spiracle (present in *A. stepheni*), a mouth located anteriorly to the eyes (at the level of the eyes in *A. stepheni*), eyes located dorsolaterally (laterally in *A. stepheni*), a proportionally shorter tail – BL 36–37 % of TL (vs. 33 %) (Juncá *et al.* 1994). They can be distinguish from tadpoles of *A. degranvillei* by the presence of an oral disc (absent in *A. degranvillei*), presence of a vent tube (absent in *A. degranvillei*), eyes located dorsolaterally (laterally in *A. degranvillei*) and by their development, which is not completed on the back of the male parent.

**Distribution and natural history.** Populations of *Anomaloglossus baeobatrachus* have been documented throughout French Guiana the state of Amapá, in Brazil (Fig. 1). However, southern FG and Amapá populations form genetic clusters distinct from the ones from northern FG, where lies the type locality (Fouquet *et al.* 2019). These three clusters remain indistinguishable based on call and morphology and display similar larval development modes (Fouquet *et al.* 2019). The species is absent west of the Maroni River where it is replaced by *A. stepheni*, a species that seems to have a similar niche. A similar situation may occur on the eastern margin of the Jari River (state of Pará, Brazil) but too few surveys are available to confirm that hypothesis. Several still undescribed species with exotrophic larvae have been confused with *A. baeobatrachus* (Vacher *et al.* 2017) in Suriname (Ouboter & Jairam 2012) and in Pará state (Avila-Pires *et al.* 2011). Populations with exotrophic larvae have also been documented in French Guiana and Amapá but are assumed to have undergone historical admixture and their status remains ambiguous (Fouquet *et al.* 2019).

*Anomaloglossus baeobatrachus* is a diurnal species inhabiting the leaf litter in primary and secondary terra-firme forest at low to mid elevations (from 10 to 800 m elevation). It can be found alongside or far from any water bodies. Males call all day long when the weather is rainy, with two apparent peaks of daily activity, a minor one in the morning (08:00–11:00h a.m.) and a major one at the end of the day (15:00–18:00h). The species seems to be more abundant on slopes and plateaus. Males aggregate in groups of two to several dozen individuals. Breeding occurs mainly at the beginning of the rainy season (December to April). Males respond to playback of intraspecific advertisement calls with shorter and more rapidly emitted trills and also emit a different vocalization during courtship. They are territorial and defend, sometimes engaging in physical contact, territories of approximately 13 m² (Deschamps 2005), which are separated by a few meters only. Males usually call slightly above the leaf litter, exposed on a branch or a leaf. Males generally use the same calling and oviposition sites throughout the season (Deschamps 2005). Eggs are usually deposited in the fold of a dead leaf. Breeding behaviours are very similar to those observed in *A. stepheni* in central Amazonia (Juncá 1998), although these species are not each other's sister group (Vacher *et al.* 2017). When a female approaches a calling male, the male emits shorter and more rapid trills and then directs the female to an oviposition site that seems to have been previously chosen (Deschamps 2005). If the female is receptive, the mating will last approximately 5–6 h, consisting of two phases between which the male leaves the nest. While the pair is inside the nest a soft irregular vocalisation is emitted. Because of the amount of trophic reserve required for the endotrophic development of embryos, the eggs are large and limited in number (from 3 to 5). It has been observed that the female lays beforehand (shortly before the eggs) a series (from 14 to 39) of small gelatinous spheres on which the eggs will be secondarily deposited and fertilized. These spheres inflate and fuse after 48 hours to form a single gelatinous mass in which the eggs bathe, probably serving as protection (Deschamps 2005). Eggs usually take nine days to hatch and several successive clutches can be pooled on the same leaf (Deschamps 2005). We do not know if successive clutches are deposited by the same female and if the reproduction system polygamous. It will take another twenty days for the tadpoles to metamorphose.

### *Anomaloglossus leopardus* Ouboter & Jairam, 2012
Figures 2–3

**Amended definition.** We here provide an amended definition of *A. leopardus* based on the examination of 11 additional specimens (MNHN2018.53–63) collected in 2014 by two of us (AF, JPV) at Apalagadi, Suriname, the species type locality, as well as by the re-examination of the type series deposited in the NZCS (NZCS A249–51) (Paramaribo, Suriname).

(1) Medium-sized *Anomaloglossus* (mean = 18.8 mm [18.4–19.2, $n$ = 7] in males, mean = 21.1 mm [20.5–21.5, $n$ = 4] in females) (Table 1); (2) body robust; (3) skin slightly tuberculate on dorsum (more tuberculated posteriorly) and legs, with a larger tubercle on each eyelid, ventral skin smooth; (4) diffuse supratympanic fold; (5) tympanic annulus distinct anteroventrally; (6) snout short and protruding in lateral view; (7) nares oriented ventrolaterally, situated near tip of snout; (8) Finger II slightly shorter than Finger I when fingers adpressed; (9) tip of Finger IV hardly reaching distal subarticular tubercle on Finger III when fingers adpressed; (10) distal subarticular tubercle distinct on Finger III and absent on the other fingers; (11) Finger III swollen dorsally and preaxially in males extending largely on dorsal surface of hand, with well-developed fringes in females; (12) fringes on all fingers particularly developed preaxially on Fingers II, in both sexes; (13) toes poorly webbed (Toe webbing formula $I2^{-}–1^{-}II1^{+}–1^{-}III1^{+}–1^{+}IV0–1^{+}V$ (MNHN2018.58, AF2035), with well-developed fringes on all toes but more developed preaxially on Toe II, and pre- and postaxially on Toes III and IV (*sensu* Grant *et al.* 2006; keel-like lateral folds *sensu* Myers & Donnelly 2008); (14) tarsal keel well-defined, curved; (15) black arm gland at the junction of forearm with wrist in males (*sensu* Grant & Castro 1998, see also Grant *et al.* 2006); (16) cloacal tubercles present; (17) paracloacal mark present (orangish in life, cream in preservative); (18) dorsolateral stripe present, thick and continuous (cream and yellowish posteriorly in life, white in preservative), flanks and dorsum dark brown in males, paler with dark brown blotches in females; (19) ventrolateral stripe absent; (20) sexual dichromatism in throat color pattern present, in life sometimes anteriorly yellow with uniformly distributed sparse black melanophores in males, evenly yellow in females; (21) sexual dichromatism in ventral color pattern present, abdomen entirely or only posteriorly and laterally orange, centrally cream in males in life, abdomen uniformly orange in females in life; (22) iris with metallic pigmentation and pupil ring interrupted ventrally and dorsally by transversal black pigmentation; (23) median lingual process as long as wide, tapered, bluntly pointed, smooth (non-papillate), reclined in pit; (24) call 1.08–2.00 s long consisting of a train of 14–28 ==pulsed== notes 0.024–0.029 s long and spaced by intervals of 0.051–0.055 s, dominant frequency at 4.20–4.61 kHz ($n$ = 9) (Fig. 4; Table 2).

**Distribution and natural history.** *Anomaloglossus leopardus* is only known from two streams at its type locality Apalagadi above 400 m elevation, and from the southern border of Suriname with Brazil (2.4788N, 55.63161W). The species also likely occurs between these two localities and maybe throughout the massif extending northwest in Suriname and southeast in Brazil. The tadpole is unknown, but since the species is associated with streams and has a more extensive webbing than the endotrophic *A. baeobatrachus*, and because all closely-related species (except *A. baeobatrachus*) are associated to streams and have exotrophic tadpoles transported to the water, we assume this is likely also the case for *A. leopardus*. It co-occurs with *A. stepheni*, which is endotrophic, throughout its range.

### *Anomaloglossus mitaraka* sp. nov.

*Anomaloglossus* sp. "Mitaraka" Vacher *et al.* 2017

**Holotype.** MNHN2018.64 (field n°AF2814), an adult male, collected by A. Fouquet and M. Dewynter, 24 February 2015, Mitaraka, French Guiana, 2.23577° N 54.44928° W, ~150 m elevation (Figs. 2–3).

**Paratopotypes.** Nine specimens: MNHN2018.65–70 (field n°AF2732, 2750-1, 2754, 2808, 2878) six adult males and MNHN2018.71–73 (field n°AF2724, 2731, 2824) three females collected with the holotype by A. Fouquet and M. Dewynter.

**Etymology.** The specific epithet is a noun in apposition and refers to the type locality (Mitaraka, French Guiana).

**Definition.** (1) Medium-sized *Anomaloglossus* (average male SVL 18.6 mm [18.2–19.3, $n$ = 7], female SVL

20.1 mm [19.2–21.0, *n* = 3]) (Table 1); (2) body robust; (3) skin on dorsum with irregularly scattered tubercles becoming denser on the posterior half and legs, with a larger tubercle on each eyelid, ventral skin smooth; (4) inconspicuous supratympanic fold; (5) tympanum distinct anteroventrally; (6) snout short and protruding in lateral view; (7) nares oriented ventrolaterally, situated near tip of snout; (8) Finger II equal to Finger I when fingers adpressed; (9) tip of Finger IV not reaching distal subarticular tubercle on Finger III when fingers adpressed; (10) distal subarticular tubercle distinct on Finger III, absent on the other fingers; (11) Finger III swollen dorsally and preaxially, extending largely towards dorsal surface of hand in males; (12) fringes present on all fingers particularly developed preaxially on Finger II in males and females; (13) toes basally webbed, with well-developed fringes on all toes, more developed preaxially on Toe II, and pre- and postaxially on toes III and IV (*sensu* Grant *et al.* 2006; keel-like lateral folds *sensu* Myers & Donnelly 2008); (14) tarsal keel well-defined, curved; (15) black arm gland at the junction with wrist in males (*sensu* Grant & Castro 1998, see also Grant *et al.* 2006); (16) cloacal tubercles present; (17) paracloacal mark present (orangish in life, cream in preservative); (18) pale dorsolateral stripe present, solid (white to orangish anteriorly, yellow posteriorly in life, white in preservative), flanks and dorsum uniformly dark brown in males, reddish brown with dark brown blotches in females in life; (19) ventrolateral stripe absent; (20) sexual dichromatism in throat color pattern present in life, sometimes anteriorly yellow in males with sparse black melanophores, evenly and entirely yellow in females; (21) sexual dichromatism in ventral color pattern present, abdomen mostly cream, posteriorly and laterally yellow in males, uniformly bright yellow in females in life; (22) iris with metallic pigmentation and pupil ring interrupted ventrally and dorsally by transversal black pigmentation; (23) median lingual process as long as wide, tapered, bluntly pointed, smooth (non-papillate), reclined in pit; (24) a 0.74–1.23 s length call consisting of a train of 8–16 notes of 0.028–0.036 s in length and spaced by intervals of 0.051–0.068 s and of dominant frequency at 4.13–4.76 kHz (*n* = 6); (25) tadpole of type 4 (Orton 1953), exotrophic, with a functional mouth with marginal papillae and labial teeth (Fig. 4; Table 2).

**Morphological comparisons with other *Anomaloglossus*.** The only other species group co-occurring with the *Anomaloglossus stepheni* group is the *A. degranvillei* group, represented by *A. blanci, A. degranvillei, A. dewynteri* and *A. surinamensis*, which are readily distinguishable by their moderate webbing (basal in *A. mitaraka*) and well-developed fringes on all toes (smaller and more developed on Toe II, III, IV) and the absence of a dorsolateral stripe (present). Outside these two groups all the other described *Anomaloglossus* species exclusively occur in Pantepui (i.e., the Guiana Shield highlands, see Kok *et al.* 2018) and have moderate to extensive toe webbing except *A. meansi* Kok, Nicolaï, Lathrop & MacCulloch, 2018*, A. kaiei* (Kok, Sambhu, Roopsind, Lenglet & Bourne, 2006), *A. rufulus* (Gorzula, 1990) and *A. roraima* (La Marca, 1997). However, unlike *A. mitaraka*, *A. meansi* lacks a conspicuous dorsolateral stripe, Finger III in males of *A. kaei* is not distinctly swollen, *A. rufulus* has as an extensively spotted ventral face, and *A. roraima* lacks well-developed fringes.

Within the *Anomaloglossus stepheni* group, *A. mitaraka* can be distinguished from can be distinguished from its probable sister species (Fouquet *et al.* 2019) *A. leopardus* (Figs. 2–3) by (1) narrower dark brown bars on legs vs large and more conspicuous dark transverse bars on legs in *A. leopardus*; (3) ventral coloration with orange restricted to the posterior part in males in *A. mitaraka* vs. generally entirely yellow in *A. leopardus*; (4) dorsolateral line thin in *A. mitaraka* vs. thick and well defined in *A. leopardus*; (5) advertisement call with a slower note rate (mean = 11.43, range 10.8–12.3 note/s in *A. mitaraka* [*n* = 6] vs. mean = 13.4, range 12.9–13.6 notes/s in *A. leopardus* [*n* = 4]) (Table 2).

*Anomaloglossus mitaraka* can be distinguished from *A. stepheni* (Figs. 2–3, Table 1) by (1) a larger body size (mean = 18.6; range 18.2–19.3 mm in males [*n* = 7] and mean = 20.1; range 19.2–21.0 mm in females [*n* = 3] in *A. mitaraka*, mean = 17.15, range 16.5–18.0 mm in males [*n* = 10] and mean = 17.3, range 17.0–18.0 mm in females [*n* = 5] [from Martins 1989] in *A. stepheni*); (2) skin of dorsum with scattered tubercules in *A. mitaraka*, evenly tuberculate in *A. stepheni*; (3) orange ventral coloration posteriorly and laterally in males of *A. mitaraka*,. entirely translucent white in *A. stepheni*; (4) dorsolateral line thin but well defined and continuous in *A. mitaraka* vs. thick and ill-defined dorsally in *A. stepheni*; (5) advertisement call much longer (mean = 1.04 s, range 0.74–1.23 s in *A. mitaraka* [*n* = 6] vs. mean= 0.25 s, range 0.18–0.29 s in *A. stepheni* [*n* = 4]), emitted at a slower pace (call rate mean = 0.43, range 0.32–0.52 calls/s in *A. mitaraka* [*n* = 6] vs. mean = 1.40, range 1.10–1.89 calls/s in *A. stepheni* [*n* = 4]) (Table 2).

*Anomaloglossus mitaraka* can be distinguished from *A. baeobatrachus* by (1) a larger body size (mean = 18.6; range 18.2–19.3 mm in males [*n* = 7] and mean = 20.1; range 19.2–21.0 mm in females [*n* = 3] in *A. mitaraka*, mean = 16.2; range 14.8–17.1 mm in males [*n* = 16] and mean = 18.4; range 17.3–19.4 mm in females [*n* = 4] in *A.*

*baeobatrachus*); (2) ventral coloration posteriorly and laterally in males in *A. mitaraka*, yellow and less extensive in *A. baeobatrachus*; (3) dorsolateral line thin but well defined and solid in *A. mitaraka*, narrower and interrupted in *A. baeobatrachus*; (4) call with lower note rate (mean = 11.43 notes/s, range 10.83–12.28 in *A. mitaraka* [$n = 6$], mean = 16.10, range 15.62–16.85 s in *A. baeobatrachus* [$n = 9$]) lower dominant frequency (mean= 4.44, range 4.13–4.76 kHz in *A. mitaraka* [$n = 6$] vs. mean = 5.39, range 4.96–5.59 kHz in *A. baeobatrachus* [$n = 9$]) (Table 2).

**Description of the holotype.** An adult male, 18.6 mm SVL; body robust; head wider than long, HL 94 % of HW; HL 33 % of SVL; dorsal skin tuberculate, one enlarged tubercle on each eyelid, snout long (SL 52 % of HL), rounded to nearly truncate in dorsal view, protruding in lateral view, extending past lower jaw. Nares located anterolaterally; canthus rostralis rounded, loreal region concave; IN 39 % of HW; EN 29 % of HL, 75 % of ED. Tympanum distinct anteroventrally; supratympanic fold absent; choanae small, circular, located anterolaterally (Figs. 2–3).

Forelimb slender, skin tuberculate; metacarpal ridge present; HAND 24 % of SVL; Finger I longer than Finger II when fingers adpressed; fingers large and flattened; webbings absent on fingers; lateral fringes present on preaxial edges of Finger II; Finger III distinctly swollen dorsally and preaxially; tip of Finger IV not reaching distal subarticular tubercle on Finger III when fingers adpressed; finger discs expanded, wider than long, about 1.5 times width of digit; width of disc on Finger III 0.6 mm; discs with distinct dorsal scutes. Relative lengths of adpressed fingers III > IV > I > II; palmar tubercle large, heart-shaped, 0.8 mm in diameter (larger than Finger's III disc), thenar tubercle elliptic, small (equal to Finger III's disc in maximum diameter), elliptic, half the size of palmar tubercle, well separated from palmar tubercle. Only basal subarticular tubercles on Fingers are conspicuous; subarticular tubercles on fingers I and II the largest, followed by Finger IV's subarticular tubercles and basal subarticular tubercle on Finger III.

Hind limb robust, skin tuberculate; TL 47 % of SVL; heels in contact when hind limbs are flexed at right angles to the sagittal plane of body; FL 42 % of SVL; relative length of adpressed toes IV > III > V > II > I; Toe I very short, its tip reaching the base of subarticular tubercle on Toe II when toes adpressed; toe discs larger than width of toes. Width of disc on Toe IV 0.7 mm. Foot basally webbed; lateral fringes present on all toes. Toe webbing formula $\mathbf{I}1^{+}$–$1^{-}\mathbf{II}1^{+}$–$1^{-}\mathbf{III}1^{+}$–$1^{+}\mathbf{IV}0$–$1^{+}\mathbf{V}$. One to three subarticular tubercles on toes as follows: one on Toes I and II, two on Toes III and V, three on Toe IV. Inner metatarsal tubercle protuberant elliptical, 0.5 mm in length, outer metatarsal tubercle round, protuberant, 0.3 mm in diameter. Tarsal keel well defined, tubercle-like and strongly curved at proximal end. Metatarsal fold strong.

**Color of holotype in life.** Dorsal color uniformly dark brown. Dorsolateral stripe thin, continuous, bluish white (yellow near groin) (Fig. 2). Dark brown lateral band extending from tip of snout to the groin and containing the indistinct dorsal part of tympanum, tapering posteriorly. Upper lip with small white blotches. Lower flanks pale white anteriorly and orange posteriorly with small white blotches. Throat white covered with melanophores, more densely anterolaterally; belly anteriorly white, white laterally, orange posteriorly, ventral surfaces of thighs and arms orange. Iris with coper metallic pigmentation and pupil ring interrupted dorsally and ventrally by transversal pigmentation (Fig. 2).

Upper and lower arm pale red dorsally, light brown with small dark brown spots elsewhere. Dorsal surfaces of thigh, shank and tarsus brown with dark brown transverse bars and ill-defined blotches. Paracloacal marks orangish, elongated anteroposteriorly. Toes and digits with small light blue dots dorsally and laterally. Palms and soles dark brown.

**Color of holotype in preservative.** After three years in 70 % ethanol, some colors of the specimen faded and the dorsal coloration now varies from brown to grey with interorbital, mid-dorsal and sacral dark brown blotches and the orangish ventral coloration disappeared (Fig. 3). Bluish freckles and orange and reddish marks turned cream.

**Variation among type specimens.** Measurements (range, mean, and standard deviation) of the type series are provided in Table 1. Coloration of limbs varies from brown to reddish brown, females being paler and with more conspicuous dark dorsal blotches. Colour of dorsolateral line varies from white to orangish. Overall dorsal and lateral coloration and tuberculation may vary with light intensity, time of the day and probably reproductive activity as males carrying tadpoles apparently display overall lighter colors, smoother skin and sharper contrasts, whereas calling males are very dark and highly tuberculate. Ventral coloration of female is entirely orangish while the orangish parts are limited in various extent to the posterior region and throat in males. Vocal sac, slits and small dark melanophores on throat only observed in males as well as swelling on the Finger III.
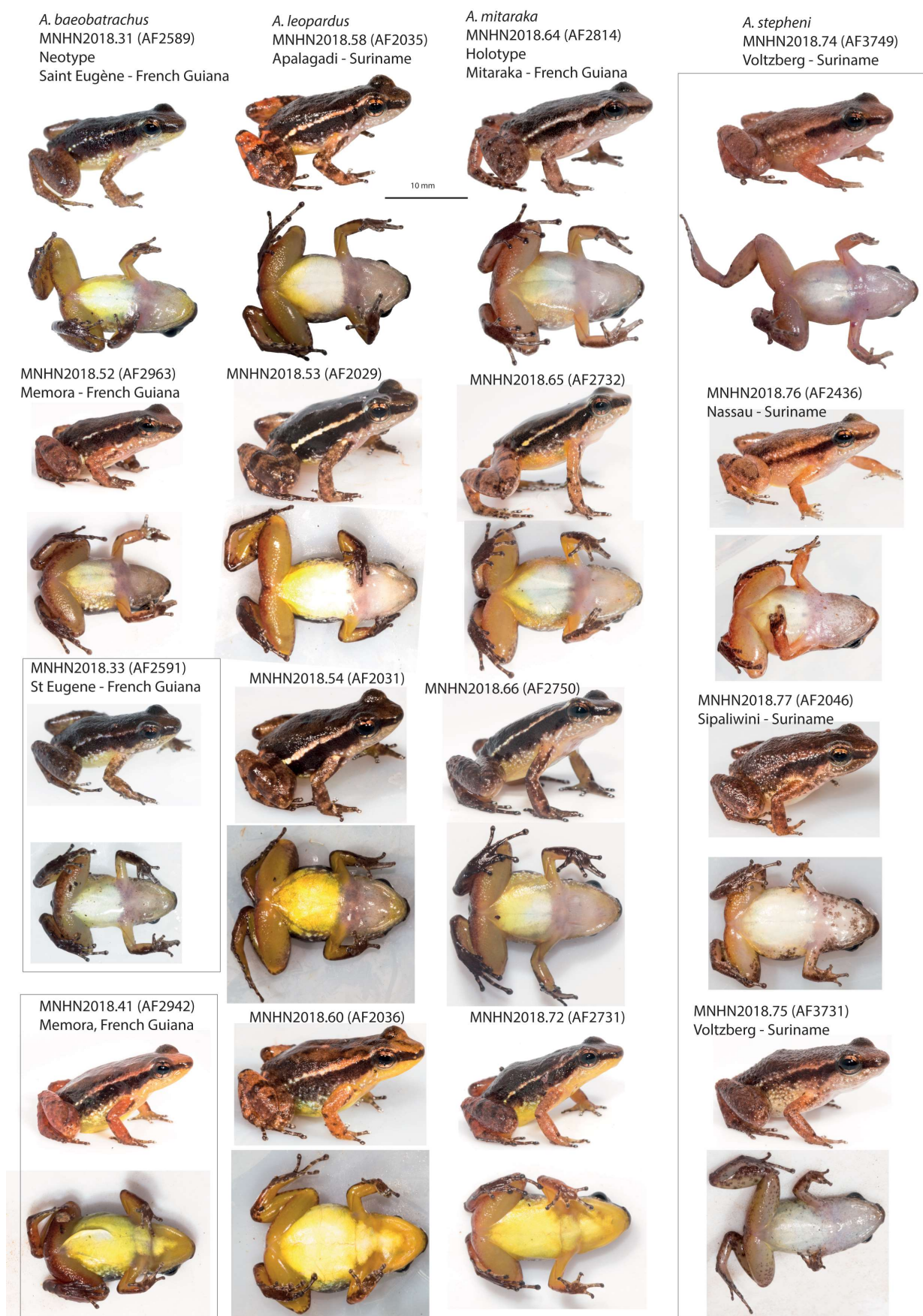
A. baeobatrachus
MNHN2018.31 (AF2589)
Neotype
Saint Eugène - French Guiana

A. leopardus
MNHN2018.58 (AF2035)
Apalagadi - Suriname

A. mitaraka
MNHN2018.64 (AF2814)
Holotype
Mitaraka - French Guiana

A. stepheni
MNHN2018.74 (AF3749)
Voltzberg - Suriname

10 mm

MNHN2018.52 (AF2963)
Memora - French Guiana

MNHN2018.53 (AF2029)

MNHN2018.65 (AF2732)

MNHN2018.76 (AF2436)
Nassau - Suriname

MNHN2018.33 (AF2591)
St Eugene - French Guiana

MNHN2018.54 (AF2031)

MNHN2018.66 (AF2750)

MNHN2018.77 (AF2046)
Sipaliwini - Suriname

MNHN2018.41 (AF2942)
Memora, French Guiana

MNHN2018.60 (AF2036)

MNHN2018.72 (AF2731)

MNHN2018.75 (AF3731)
Voltzberg - Suriname

**FIGURE 2**. Three males (top) and one female (bottom) of four species of the *Anomaloglossus stepheni* group. Size of the specimens within black contour is not scaled.
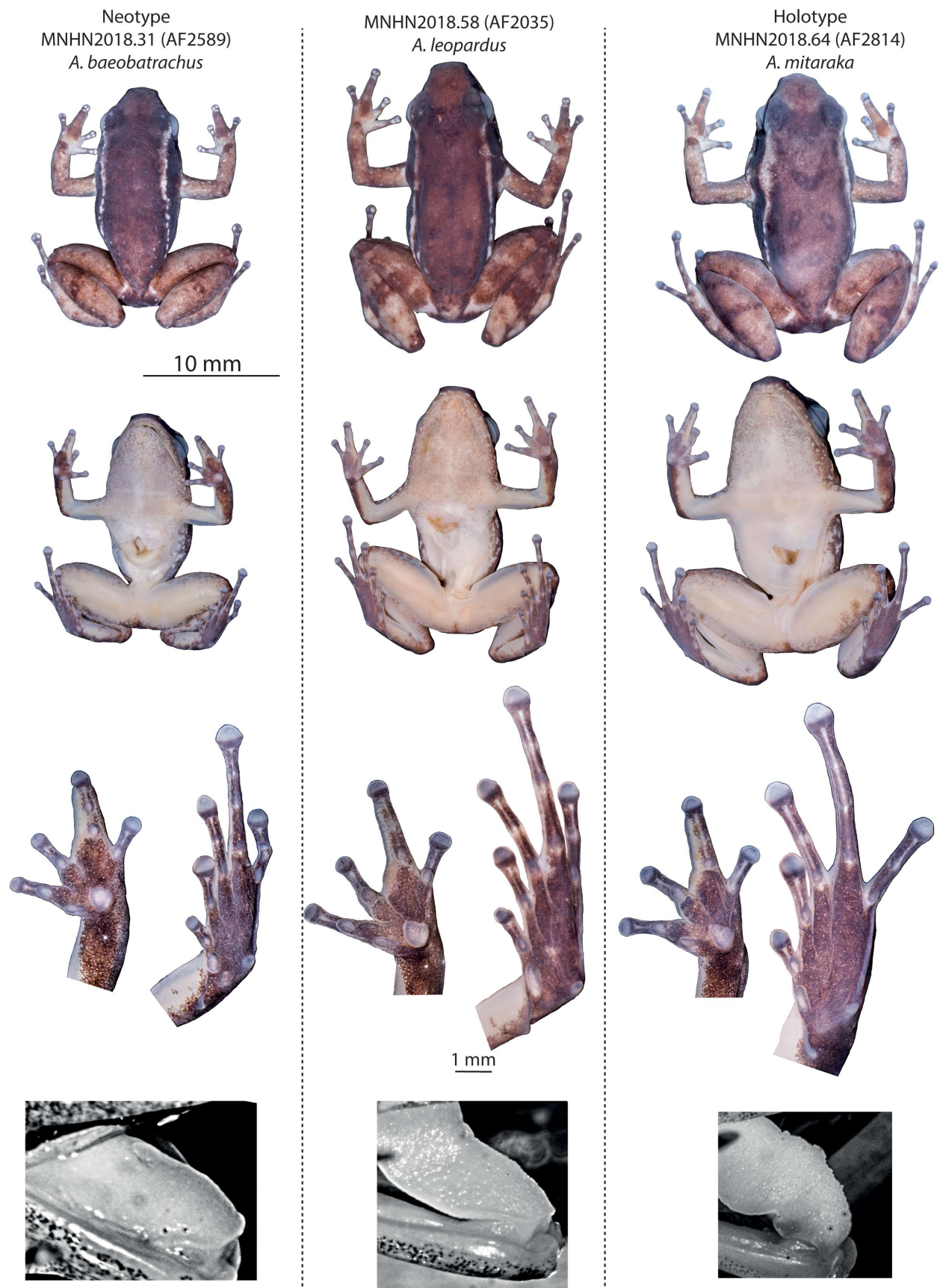
**FIGURE 3**. Views of dorsum, venter, left hand, left foot and Median Lingual Process of the neotype of *A. baeobatrachus* (left column), of a topotypical specimen of *A. leopardus* (central column) and of the holotype of *A. mitaraka* sp. nov. (right column).

**Advertisement call.** Six specimens (one uncollected) calling from the leaf litter were recorded from a distance of about 1 m and at temperatures ranging from 23 to 26°C. Descriptive statistics of call parameters are presented in Table 2. *Anomaloglossus mitaraka* emits trains (call length mean = 1.04 s; range 0.74–1.23 s) of short pulsed notes (note length mean = 0.030 s; range 0.028–0.036 s; inter-note interval mean = 0.060 s; range 0.051–0.068 s). The spectral structure of the note has a developed harmonic structure and the dominant frequency is 4.44 kHz on average (range 4.13–4.76 kHz) with a slight upward modulation (ca. 0.2 kHz) (Fig. 4, Table 2).

**Larval morphology**. The following description is based on three tadpoles at stage 26, 28 and 30 (Fig. 6). Tadpoles correspond to a Type 4 tadpole of Orton (1953); exotrophic; body skin smooth; TL 12.21–19.43 mm; BL 4.41–7.14 mm, 35–37 % of TL, 164–181 % of BW, 221–256 % of BH; BW 131–143 % of BH (Table 3); body ovoid, snout round in dorsal and lateral view; eyes positioned and directed laterally; ED 0.48–0.63 mm, 45–98 % of IOD; IOD equal to IND; nares frontally positioned and directed laterodorsally; narial opening reniform in lateral view; END 0.34–0.73 mm. Spiracular tube sinistral, conical, projecting posterodorsally, its tip located at 60–63 % of BL posteriorly to snout. Lateral-line system inconspicuous. Caudal musculature highest at its base, tapering posteriorly, terminating at tail tip; tail tip rounded; upper fin originating at junction of body and tail, gradually increasing in height to about 3/4 of tail; UTF 28–53 % of TMH; LTF 38–55 % of TMH; MTH 14–17 % of TL (Fig. 6, Table 3).

Mouth ventral, oral disc strongly emarginated, width 1.90 mm. Labial teeth long, in single rows, LTRF 2(2)/3. A-2 consisting of two short rows, separated by a large and deep gap; P-1 not interrupted. Marginal papillae long, of equal size on each labium, tapered, blunt-tipped, in a single row, evenly distributed; median gap on upper labium approximately 2/3 the length of A-1; jaw sheaths large, serrated, lower jaw sheath broadly V-shaped.

In life, the entire body is dark grey with abundant golden flecks, particularly on dorsum. Golden flecks become scarce ventrally. Posteriorly, dark grey coloration fades and tail becomes translucent.
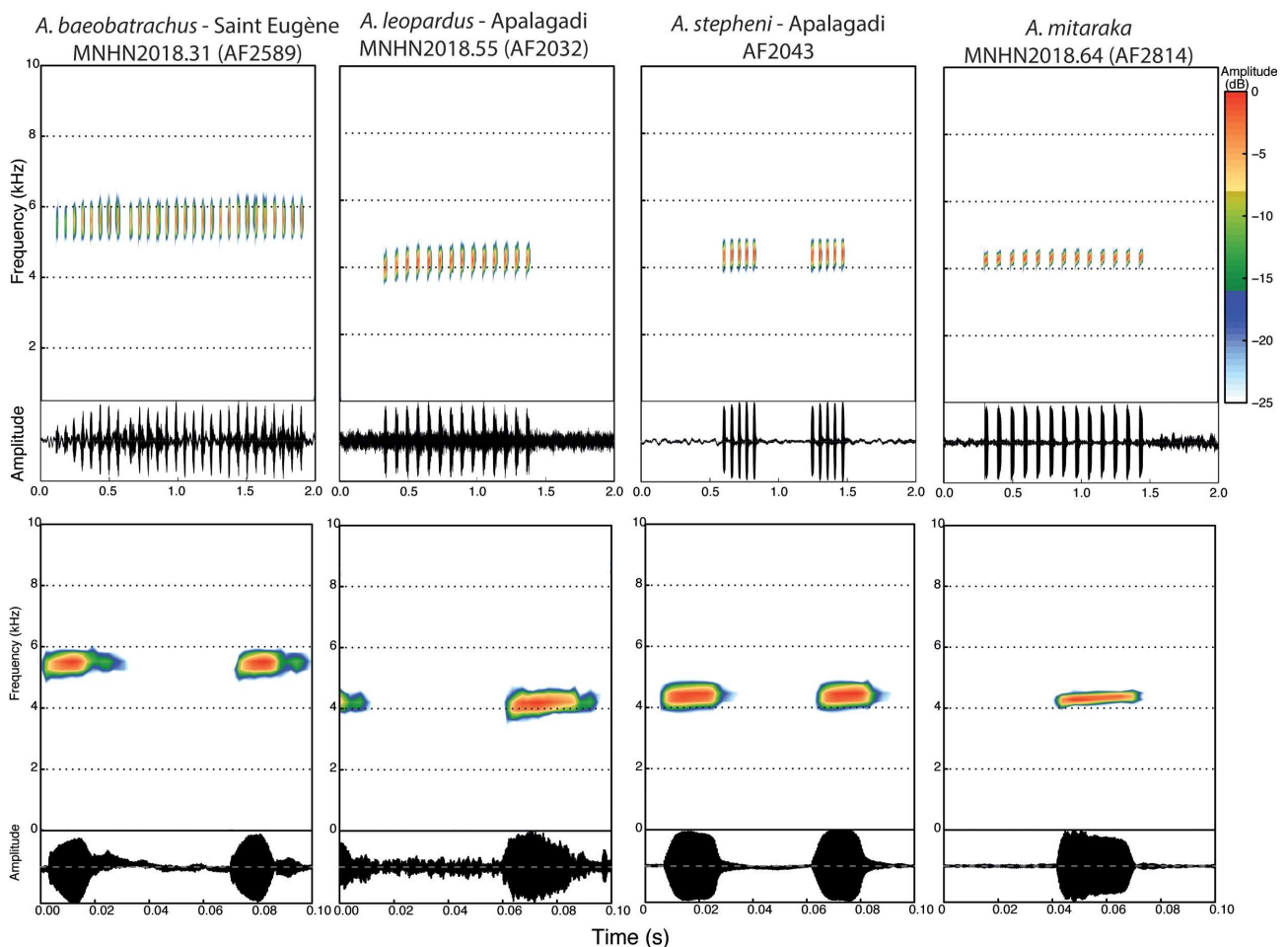


**FIGURE 4**. Spectrograms and oscillograms of typical call of four species of the *Anomaloglossus stepheni* group in a 2 s time window.

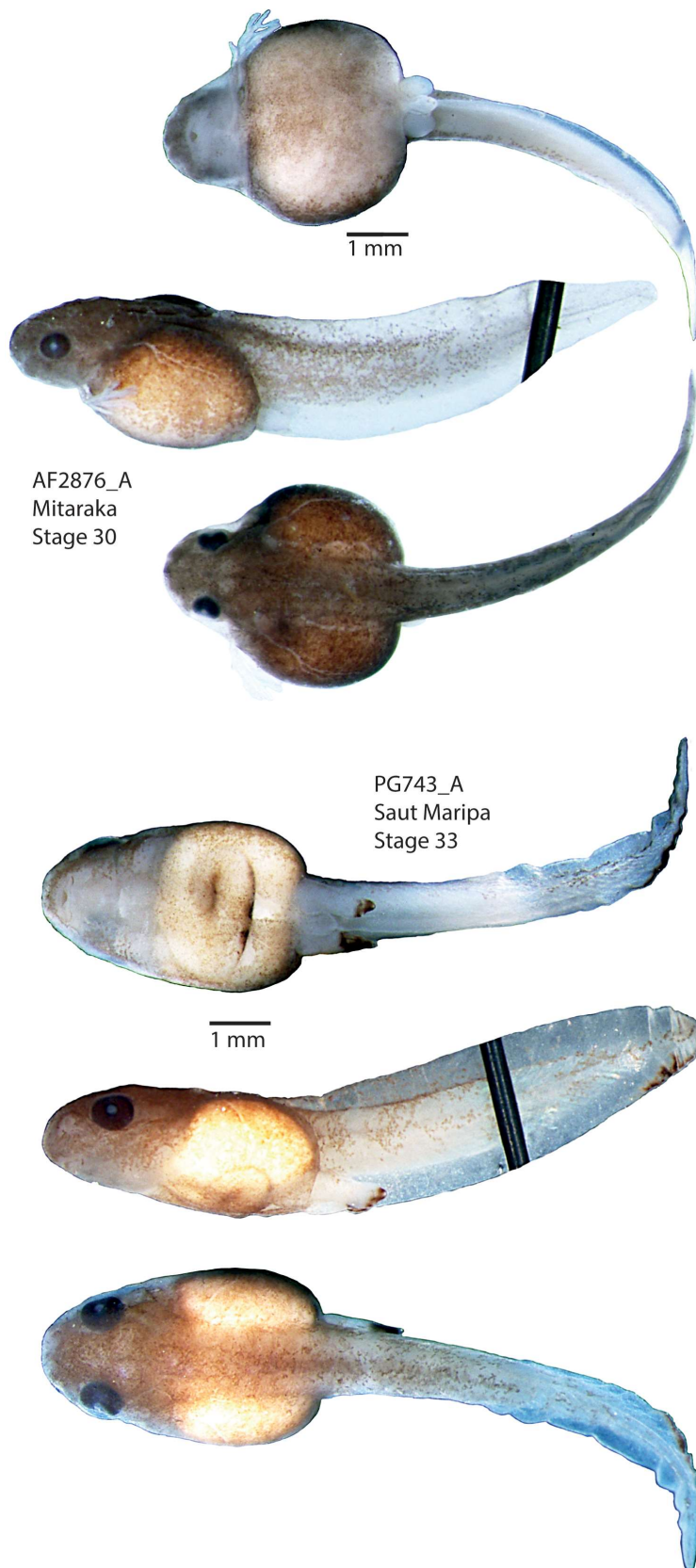**FIGURE 5**. Tadpoles of *Anomaloglossus baeobatrachus*: on the left ventral, lateral and dorsal pictures of AF2876_A at Gosner stage 30 (top) and ventral, lateral and dorsal pictures of PG743_A at Gosner stage 33 (bottom), the black bars on the specimens tails are not part of the specimens; on the right two clutches AF2876 and AF2877 photographed at different stages from egg (top) to froglet (bottom).
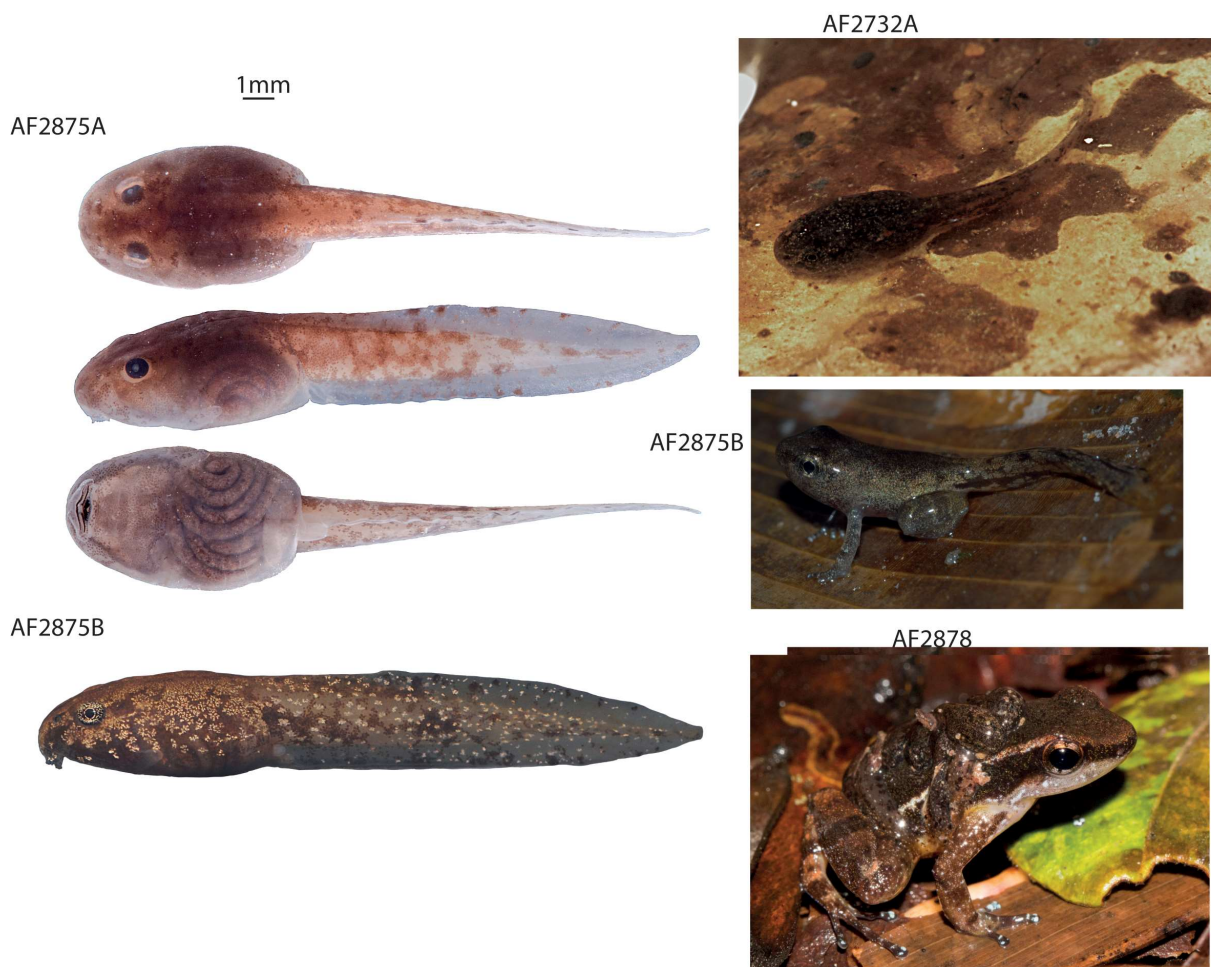
**FIGURE 6**. Tadpoles of *Anomaloglossus mitaraka*: on the left dorsal, lateral and ventral pictures of AF2875A preserved (top) and lateral picture of AF2875B in life (bottom); on the right picture of AF2732A in the nest (top), froglet AF2875B (middle), male AF2878 carrying tadpoles to the water (bottom).

Tadpoles of *Anomaloglossus mitaraka* can be distinguished from those of any other described *Anomaloglossus* of the *stepheni* group (*A. stepheni* and *A. baeobatrachus* - this study) by the presence of a functional mouth with marginal papillae and labial teeth.

**Distribution and natural history.** *Anomaloglossus mitaraka* is a diurnal species inhabiting the leaf litter in primary forest at low to mid elevations (from 150 to 500 m a.s.l.). The species is usually found close to streams next to which it deposits its exotrophic tadpoles into puddles, but some specimens can be found more than 50 m from water bodies.

Males call all day long when the weather is rainy. Breeding occurs during the rainy season, between January and May. The males respond to intraspecific playbacks with shorter and more rapidly emitted note trills. Males are territorial, their small territories being spaced at least a few meters apart. Males usually call slightly above the leaf litter, exposed on a branch or a dead leaf. Eggs are deposited in the fold of a dead leaf (a single observation). This clutch was raised (Fig. 6) and some tadpoles were genotyped.

Populations have been documented in southwestern French Guiana and adjacent Suriname (Mitaraka massif, Pic Coudreau, Haute Marwini, upper Tapanahony; Fig. 1). It also likely occurs in adjacent Brazil and may occupy similar habitats in other regions of Suriname.


## Discussion

During the last decade, several works have highlighted the hidden diversity in *Anomaloglossus* (Fouquet *et al.*

2012; 2015; 2018; Kok *et al.* 2018, Vacher *et al.* 2017). Vacher *et al.* (2017), in particular, demonstrated the existence of at least six putative unnamed species within the *A. stepheni* group only. Taxonomic uncertainty of nominal taxa (*A. baeobatrachus* and *A. leopardus*) prevented the description of these undescribed species, an issue that is solved in the present study, thus already allowing the description of other new species restricted to a few massifs in the interior of the Eastern Guiana Shield (Brownsberg, Bakhuis, Acari, Parú). This clade occurs in the lowlands of the Eastern Guiana Shield and displays a variety of reproductive modes (endotrophic vs. exotrophic tadpoles; phoresy vs. nidicoly). Species with exotrophic tadpoles in the *A. stepheni* group seem to have narrow distributions, probably associated with mid-elevation areas of these rocky massifs. This is likely due to the requirements of their reproductive modes, i.e., the occurrence of clear-water streams for larval development. Therefore, some additional still undocumented species likely occur in hardly accessible massifs of the Guiana Shield. On the other hand, the endotrophic *A. stepheni* and *A. baeobatrachus* have strikingly wider distribution ranges, likely because their endotrophic/nidicolous larval development allows them to occur far from any water bodies and, thus, colonize a wider range of terrestrial habitats within the rainforest.

**TABLE 1.** Adult body measurements (in millimeters).

| Species | A. baeobatrachus | | | | A. leopardus | | | | A. mitaraka | | | | A. stepheni | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sex | M (16) | | F (4) | | M (7) | | F (4) | | M (7) | | F (3) | | M (10) | | F (0) | |
| | X | sd | X | sd | X | sd | X | sd | X | sd | X | sd | X | sd | X | sd |
| SVL | 16.20 | 0.68 | 18.40 | 0.88 | 18.80 | 0.29 | 21.10 | 0.48 | 18.60 | 0.44 | 20.10 | 0.87 | 17.20 | 0.49 | NA | NA |
| HL | 5.37 | 0.24 | 5.92 | 0.29 | 6.31 | 0.18 | 6.98 | 0.17 | 6.23 | 0.21 | 6.8 | 0.10 | 5.33 | 0.23 | NA | NA |
| HW | 5.51 | 0.27 | 6.15 | 0.09 | 6.6 | 0.17 | 7.55 | 0.37 | 6.51 | 0.17 | 6.90 | 0.13 | 5.82 | 0.20 | NA | NA |
| SL | 2.72 | 0.16 | 2.81 | 0.26 | 3.24 | 0.08 | 3.45 | 0.06 | 3.21 | 0.13 | 3.32 | 0.02 | 2.85 | 0.08 | NA | NA |
| EN | 1.67 | 0.12 | 1.83 | 0.08 | 1.93 | 0.08 | 2.03 | 0.05 | 1.89 | 0.09 | 1.91 | 0.04 | 1.66 | 0.07 | NA | NA |
| IN | 2.27 | 0.11 | 2.42 | 0.11 | 2.61 | 0.11 | 2.88 | 0.05 | 2.66 | 0.11 | 2.72 | 0.12 | 2.36 | 0.10 | NA | NA |
| ED | 2.18 | 0.14 | 2.57 | 0.54 | 2.44 | 0.05 | 2.55 | 0.06 | 2.37 | 0.05 | 2.47 | 0.13 | 2.13 | 0.08 | NA | NA |
| IO | 1.80 | 0.13 | 1.77 | 0.09 | 2.21 | 0.09 | 2.43 | 0.05 | 2.06 | 0.10 | 2.21 | 0.10 | 1.94 | 0.11 | NA | NA |
| TYM | 1.00 | 0.12 | 1.07 | 0.14 | 1.29 | 0.07 | 1.4 | 0.00 | 1.16 | 0.08 | 1.22 | 0.07 | 1.17 | 0.09 | NA | NA |
| FAL | 3.45 | 0.18 | 3.67 | 0.23 | 3.96 | 0.13 | 4.48 | 0.05 | 4.10 | 0.13 | 4.16 | 0.17 | 3.70 | 0.20 | NA | NA |
| HAND | 3.59 | 0.31 | 3.62 | 0.61 | 4.64 | 0.20 | 5.03 | 0.13 | 4.59 | 0.24 | 4.73 | 0.28 | 3.91 | 0.15 | NA | NA |
| WFD | 0.52 | 0.04 | 0.54 | 0.04 | 0.66 | 0.05 | 0.70 | 0.08 | 0.6 | 0.06 | 0.60 | 0.07 | 0.50 | 0.00 | NA | NA |
| TL | 7.43 | 0.24 | 8.01 | 0.35 | 8.91 | 0.27 | 9.80 | 0.41 | 8.8 | 0.24 | 9.03 | 0.12 | 7.65 | 0.37 | NA | NA |
| FL | 6.48 | 0.38 | 6.97 | 0.69 | 8.19 | 0.37 | 8.93 | 0.43 | 8.04 | 0.31 | 8.34 | 0.22 | 6.96 | 0.30 | NA | NA |
| WTD | 0.98 | 1.50 | 0.67 | 0.12 | 0.77 | 0.05 | 0.83 | 0.05 | 0.73 | 0.05 | 0.72 | 0.03 | 0.59 | 0.06 | NA | NA |
| ThL | 7.82 | 0.21 | 8.26 | 0.62 | 9.16 | 0.28 | 10.1 | 0.47 | 9.00 | 0.42 | 9.52 | 0.10 | 7.81 | 0.40 | NA | NA |
| 1FiL | 2.10 | 0.24 | 3.64 | 3.27 | 2.74 | 0.14 | 3.05 | 0.13 | 2.77 | 0.11 | 2.73 | 0.12 | 2.39 | 0.12 | NA | NA |

**TABLE 2.** Summary variables of the calls of four species of the *Anomaloglossus stepheni* group.

| | A. baeobatrachus (n = 9) | | A. leopardus (n = 4) | | A. mitaraka (n = 6) | | A. stepheni (n = 4) | |
|---|---|---|---|---|---|---|---|---|
| | X | sd | X | sd | X | sd | X | sd |
| Call rate | 0.33 | 0.10 | 0.19 | 0.08 | 0.43 | 0.07 | 1.40 | 0.34 |
| Call length | 1.12 | 0.16 | 1.52 | 0.39 | 1.04 | 0.17 | 0.25 | 0.05 |
| Note length | 0.02 | 0.00 | 0.03 | 0.00 | 0.03 | 0.00 | 0.02 | 0.00 |
| Inter-note interval | 0.05 | 0.00 | 0.05 | 0.00 | 0.06 | 0.01 | 0.03 | 0.00 |
| Note rate | 16.10 | 0.44 | 13.36 | 0.33 | 11.43 | 0.51 | 21.28 | 1.18 |
| Dom freq. | 5.390 | 0.180 | 4.487 | 0.070 | 4.435 | 0.231 | 4.480 | 0.273 |

*Anomaloglossus stepheni* and *A. baeobatrachus* seem to have non-overlapping distributions. Known geographic boundaries between these two species include the Maroni River, between Suriname and French Guiana, and possibly the Jari River, between the Brazilian states of Amapá and Pará. This distribution pattern could result from competitive exclusion and/or historical factors followed by dispersion limitations across rivers. The similarity between their ecology (terra-firme inhabitants) and their breeding systems (mating, endotrophic tadpole, number of eggs, etc.) is striking. Even the deposition of a jelly mattress before oviposition is common to both species (Juncá pers. com.). The production of this structure may also occur in other dendrobatids like *Oophaga speciosa* (Lötters *et al.* 2007) and deserves more investigation given that it may represent a yet unregistered ovipositional mode (Altig & Mc Darmid 2007). However, these two species are distantly related and endotrophy has most likely been acquired independently (Vacher *et al.* 2017). The evolution of endotrophy in the *Anomaloglossus stepheni* species group is intriguing as its acquisition in *Anomaloglossus baeobatrachus* seems to represent a recent event given the close relatives of *A. baeobatrachus* are all exotrophic, denoting a convergent evolution with *A. stepheni*. As these two species are more widely distributed than the exotrophic species, this trait, associated with nidicoly, might be advantageous for dispersal and colonization of new habitats during warm and wet climatic phases such as the current one (Fouquet *et al.* 2019).

The external morphological differences among species of the *stepheni* group remain subtle. Exotrophic species are larger than endotrophic ones. However, the calls are clearly distinct across all detected species (Vacher *et al.* 2017; Fouquet *et al.* 2019). In the case of *A. baeobatrachus*, Fouquet *et al.* (2019) demonstrated that past hybridizations have occurred in exotrophic populations (Borne 4, Itoupé, Serra do Navio, Lourenço, RN2). Therefore, the taxonomic status of these populations remains contentious and deserves more investigation.

The fact that the populations of the exotrophic species may be circumscribed to small mountain ranges implies conservation concerns. *Anomaloglossus leopardus* and *A. mitaraka* are only known from only two and three localities, respectively. They are likely more extensively distributed but given the concerns raised for other *Anomaloglossus* species (Fouquet *et al.* 2015, 2019), their populations should be monitored, their potential range should be explored, and the remaining undescribed species in Suriname (Brownsberg, Bakhuis) and in Brazil (Pará: Parú, Acari) should be urgently described.

**TABLE 3.** Tadpole measurements (in millimeters).

| Species | *A. baeobatrachus* | | | | *A. mitaraka* | | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Specimen | AF2876_A | AF2876_B | PG743_A | PG743_B | AF2875A | AF2817 | AF2751 |
| Gosner stage | 30 | 32 | 33 | 34 | 30 | 28 | 27 |
| TL | 10.86 | 12.4 | 12.57 | 12.92 | 19.43 | 16.12 | 12.21 |
| BL | 3.97 | 4.65 | 4.55 | 4.62 | 7.14 | 5.64 | 4.41 |
| TAL | 6.89 | 7.75 | 8.06 | 8.30 | 12.27 | 10.65 | 7.93 |
| BW | 2.56 | 3.30 | 2.94 | 2.91 | 4.35 | 3.36 | 2.44 |
| BH | 1.87 | 1.93 | 1.95 | 2.10 | 3.04 | 2.55 | 1.72 |
| HW | 1.61 | 2.00 | 2.07 | 2.14 | 3.79 | 2.88 | 2.00 |
| TMH | 1.10 | 1.20 | 1.13 | 1.15 | 1.63 | 1.54 | 1.20 |
| UTF | 0.43 | 0.60 | 0.56 | 0.50 | 0.87 | 0.64 | 0.34 |
| LTF | 0.29 | 0.50 | 0.40 | 0.32 | 0.90 | 0.77 | 0.45 |
| TMW | 0.85 | 1.07 | 1.10 | 1.10 | 1.73 | 1.39 | 1.19 |
| MTH | 1.76 | 2.26 | 2.14 | 1.90 | 2.70 | 2.61 | 2.08 |
| END | 0.28 | 0.30 | 0.34 | 0.40 | 0.73 | 0.57 | 0.34 |
| NSD | 0.35 | 0.40 | 0.49 | 0.38 | 0.79 | 0.67 | 0.52 |
| SSD | na | na | na | na | 4.51 | 3.57 | 2.66 |
| IND | 0.60 | 0.63 | 0.80 | 0.70 | 1.28 | 1.04 | 0.80 |
| IOD | 0.71 | 0.87 | 0.84 | 0.88 | 1.23 | 1.07 | 0.85 |
| ED | 0.46 | 0.60 | 0.68 | 0.65 | 0.63 | 0.48 | 0.58 |

**TABLE 4.** Material examined

| Museum Voucher | Type Mat. | Genus | Species | Field number | Locality | Country | Latitude | Longitude | Sex | Collectors | Date |
|---|---|---|---|---|---|---|---|---|---|---|---|
| MNHN2018.34 | Paratype | *Anomaloglossus* | *baeobatrachus* | AF0207 | Mana | Fr. Guiana | 5.383333 | -53.65 | M | A. Fouquet - R. Gallais | 2007_04_08 |
| MNHN2018.35 | Paratype | *Anomaloglossus* | *baeobatrachus* | AF0208 | Mana | Fr. Guiana | 5.383333 | -53.65 | M | A. Fouquet - R. Gallais | 2007_04_08 |
| MNHN2018.36 | Paratype | *Anomaloglossus* | *baeobatrachus* | AF0214 | Mana | Fr. Guiana | 5.383333 | -53.65 | F | A. Fouquet - R. Gallais | 2007_04_08 |
| MNHN2018.37 | Paratype | *Anomaloglossus* | *baeobatrachus* | AF0244 | Nouragues | Fr. Guiana | 4.08333 | -52.68333 | F | A. Fouquet | 2007_05_10 |
| MNHN2018.38 | Paratype | *Anomaloglossus* | *baeobatrachus* | AF0821 | Chutes Voltaire | Fr. Guiana | 5.03122 | -54.08778 | M | A. Fouquet - V. Rufray - O. Chaline | 2012_12_31 |
| MNHN2018.39 | Paratype | *Anomaloglossus* | *baeobatrachus* | AF1839 | RN2 cor. 3 | Fr. Guiana | 4.10583 | -52.05096 | M | A. Fouquet - J.P. Vacher | 2014_03_24 |
| MNHN2018.40 | Paratype | *Anomaloglossus* | *baeobatrachus* | AF1841 | RN2 cor. 3 | Fr. Guiana | 4.10583 | -52.05096 | M | A. Fouquet - J.P. Vacher | 2014_03_24 |
| MNHN2018.41 | Paratype | *Anomaloglossus* | *baeobatrachus* | AF2098 | RN2 cor. 5 | Fr. Guiana | 4.03297 | -51.99078 | M | A. Lorenzini | 2014_04_01 |
| MNHN2018.42 | Paratype | *Anomaloglossus* | *baeobatrachus* | AF2099 | RN2 cor. 5 | Fr. Guiana | 4.03297 | -51.99078 | M | A. Lorenzini | 2014_04_01 |
| MNHN2018.43 | Paratype | *Anomaloglossus* | *baeobatrachus* | AF2101 | RN2 cor. 5 | Fr. Guiana | 4.03297 | -51.99078 | M | A. Lorenzini | 2014_03_26 |
| MNHN2018.44 | Paratype | *Anomaloglossus* | *baeobatrachus* | AF2102 | RN2 cor. 5 | Fr. Guiana | 4.03297 | -51.99078 | M | A. Lorenzini | 2014_03_26 |
| **MNHN2018.31** | **Neotype** | ***Anomaloglossus*** | ***baeobatrachus*** | AF2589 | Saint-Eugêne | Fr. Guiana | 4.82167 | -53.06766 | **M** | **J.P. Vacher - B. Villette - S. Cally - J.F. Szpigel** | **2015_02_21** |
| MNHN2018.32 | Paratype | *Anomaloglossus* | *baeobatrachus* | AF2590 | Saint-Eugêne | Fr. Guiana | 4.82167 | -53.06766 | M | J.P. Vacher - B. Villette - S. Cally - J.F. Szpigel | 2015_02_21 |
| MNHN2018.33 | Paratype | *Anomaloglossus* | *baeobatrachus* | AF2591 | Saint-Eugêne | Fr. Guiana | 4.82167 | -53.06766 | M | J.P. Vacher - B. Villette - S. Cally - J.F. Szpigel | 2015_02_21 |
| MNHN2018.45 | Paratype | *Anomaloglossus* | *baeobatrachus* | APA-973-23-AF2667 | Alikéné | Fr. Guiana | 3.21153 | -52.39981 | M | J.P. Vacher - S. Cally | 2015_02_13 |
| MNHN2018.46 | Paratype | *Anomaloglossus* | *baeobatrachus* | APA-973-23-AF2704 | Alikéné | Fr. Guiana | 3.21153 | -52.39981 | M | J.P. Vacher - S. Cally | 2015_02_18 |
| MNHN2018.47 | Paratype | *Anomaloglossus* | *baeobatrachus* | APA-973-23-AF2705 | Alikéné | Fr. Guiana | 3.21153 | -52.39981 | M | J.P. Vacher - S. Cally | 2015_02_18 |
| MNHN2018.48 | Paratype | *Anomaloglossus* | *baeobatrachus* | APA-973-23-AF2706 | Alikéné | Fr. Guiana | 3.21153 | -52.39981 | M | J.P. Vacher - S. Cally | 2015_02_18 |
| MNHN2018.50 | Paratype | *Anomaloglossus* | *baeobatrachus* | APA-973-23-AF2709 | Alikéné | Fr. Guiana | 3.21153 | -52.39981 | M | J.P. Vacher - S. Cally | 2015_02_17 |
| MNHN2018.49 | Paratype | *Anomaloglossus* | *baeobatrachus* | APA-973-23-AF2707 | Alikéné | Fr. Guiana | 3.21153 | -52.39981 | F | J.P. Vacher - S. Cally | 2015_02_18 |
| MNHN2018.51 | Paratype | *Anomaloglossus* | *baeobatrachus* | APA-973-23-AF2942 | Mémora G | Fr. Guiana | 3.31774 | -52.19329 | F | A. Fouquet - P. Nunes | 2015_03_15 |
| MNHN2018.52 | Paratype | *Anomaloglossus* | *baeobatrachus* | APA-973-23-AF2963 | Mémora G | Fr. Guiana | 3.31774 | -52.19329 | M | A. Fouquet - P. Nunes | 2015_03_15 |
| **NZCS A249** | **Holotype** | ***Anomaloglossus*** | ***leopardus*** | NA | Sipaliwini | Suriname | 2.16977 | -56.08083 | **M** | **P. Ouboter - J. Mol - J. Toto** | **1989_08_15** |
| NZCS A250 | Paratype | *Anomaloglossus* | *leopardus* | NA | Sipaliwini | Suriname | 2.16977 | -56.08083 | F | P. Ouboter - J. Mol - J. Toto | 1989_08_15 |

**TABLE 4.** (Continued)

| Museum Voucher | Type Mat. | Genus | Species | Field number | Locality | Country | Latitude | Longitude | Sex | Collectors | Date |
|---|---|---|---|---|---|---|---|---|---|---|---|
| MNHN2018.53 | NA | *Anomaloglossus* | *leopardus* | AF2029 | Sipaliwini | Suriname | 2.16977 | -56.08083 | M | A. Fouquet - J.P. Vacher | 2014_04_19 |
| MNHN2018.54 | NA | *Anomaloglossus* | *leopardus* | AF2031 | Sipaliwini | Suriname | 2.16977 | -56.08083 | M | A. Fouquet - J.P. Vacher | 2014_04_19 |
| MNHN2018.55 | NA | *Anomaloglossus* | *leopardus* | AF2032 | Sipaliwini | Suriname | 2.16977 | -56.08083 | M | A. Fouquet - J.P. Vacher | 2014_04_19 |
| MNHN2018.56 | NA | *Anomaloglossus* | *leopardus* | AF2033 | Sipaliwini | Suriname | 2.16977 | -56.08083 | M | A. Fouquet - J.P. Vacher | 2014_04_19 |
| MNHN2018.57 | NA | *Anomaloglossus* | *leopardus* | AF2034 | Sipaliwini | Suriname | 2.16977 | -56.08083 | M | A. Fouquet - J.P. Vacher | 2014_04_19 |
| MNHN2018.58 | NA | *Anomaloglossus* | *leopardus* | AF2035 | Sipaliwini | Suriname | 2.16977 | -56.08083 | M | A. Fouquet - J.P. Vacher | 2014_04_19 |
| MNHN2018.59 | NA | *Anomaloglossus* | *leopardus* | AF2038 | Sipaliwini | Suriname | 2.16977 | -56.08083 | M | A. Fouquet - J.P. Vacher | 2014_04_19 |
| MNHN2018.60 | NA | *Anomaloglossus* | *leopardus* | AF2036 | Sipaliwini | Suriname | 2.16977 | -56.08083 | M | A. Fouquet - J.P. Vacher | 2014_04_19 |
| MNHN2018.61 | NA | *Anomaloglossus* | *leopardus* | AF2039 | Sipaliwini | Suriname | 2.16977 | -56.08083 | F | A. Fouquet - J.P. Vacher | 2014_04_19 |
| MNHN2018.62 | NA | *Anomaloglossus* | *leopardus* | AF2041 | Sipaliwini | Suriname | 2.16977 | -56.08083 | F | A. Fouquet - J.P. Vacher | 2014_04_19 |
| MNHN2018.63 | NA | *Anomaloglossus* | *leopardus* | AF2042 | Sipaliwini | Suriname | 2.16977 | -56.08083 | F | A. Fouquet - J.P. Vacher | 2014_04_19 |
| MNHN2018.65 | Paratype | *Anomaloglossus* | *mitaraka* | APA-973-1-AF2732 | Mitaraka | Fr. Guiana | 2.23577 | -54.44928 | M | A. Fouquet - M. Dewynter | 2015_02_24 |
| MNHN2018.66 | Paratype | *Anomaloglossus* | *mitaraka* | APA-973-1-AF2750 | Mitaraka | Fr. Guiana | 2.23577 | -54.44928 | M | A. Fouquet - M. Dewynter | 2015_02_24 |
| MNHN2018.67 | Paratype | *Anomaloglossus* | *mitaraka* | APA-973-1-AF2751 | Mitaraka | Fr. Guiana | 2.23577 | -54.44928 | M | A. Fouquet - M. Dewynter | 2015_02_24 |
| MNHN2018.68 | Paratype | *Anomaloglossus* | *mitaraka* | APA-973-1-AF2754 | Mitaraka | Fr. Guiana | 2.23577 | -54.44928 | M | A. Fouquet - M. Dewynter | 2015_02_24 |
| MNHN2018.69 | Paratype | *Anomaloglossus* | *mitaraka* | APA-973-1-AF2808 | Mitaraka | Fr. Guiana | 2.23577 | -54.44928 | M | A. Fouquet - M. Dewynter | 2015_02_24 |
| **MNHN2018.64** | **Holotype** | ***Anomaloglossus*** | ***mitaraka*** | APA-973-1-AF2814 | Mitaraka | Fr. Guiana | 2.23577 | -54.44928 | **M** | **A. Fouquet - M. Dewynter** | **2015_02_24** |
| MNHN2018.70 | Paratype | *Anomaloglossus* | *mitaraka* | APA-973-1-AF2878 | Mitaraka | Fr. Guiana | 2.23577 | -54.44928 | M | A. Fouquet - M. Dewynter | 2015_02_24 |
| MNHN2018.71 | Paratype | *Anomaloglossus* | *mitaraka* | APA-973-1-AF2724 | Mitaraka | Fr. Guiana | 2.23577 | -54.44928 | F | A. Fouquet - M. Dewynter | 2015_02_24 |
| MNHN2018.72 | Paratype | *Anomaloglossus* | *mitaraka* | APA-973-1-AF2731 | Mitaraka | Fr. Guiana | 2.23577 | -54.44928 | F | A. Fouquet - M. Dewynter | 2015_02_24 |
| MNHN2018.73 | Paratype | *Anomaloglossus* | *mitaraka* | APA-973-1-AF2824 | Mitaraka | Fr. Guiana | 2.23577 | -54.44928 | F | A. Fouquet - M. Dewynter | 2015_02_24 |
| MNHN2018.74 | NA | *Anomaloglossus* | *stepheni* | AF3749 | Voltzberg | Suriname | 4.68169 | -56.18568 | M | A. Fouquet - R. Jairam | 2016_01_27 |
| MNHN2018.76 | NA | *Anomaloglossus* | *stepheni* | AF2536 | Nassau | Suriname | 4.80412 | -54.5555 | M | A. Fouquet - R. Jairam | 2014_12_16 |
| MNHN2018.77 | NA | *Anomaloglossus* | *stepheni* | AF2046 | Sipaliwini | Suriname | 2.16977 | -56.08083 | M | A. Fouquet - J.P. Vacher | 2014_04_19 |
| MNHN2018.75 | NA | *Anomaloglossus* | *stepheni* | AF3731 | Voltzberg | Suriname | 4.68169 | -56.18568 | F | A. Fouquet - R. Jairam | 2016_01_27 |

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