



HAL
open science

Two new species of *Anomaloglossus* (Anura: Aromobatidae) of the stepheni group from Suriname

Antoine Fouquet, Rawien Jairam, Paul Ouboter, Philippe Kok

► To cite this version:

Antoine Fouquet, Rawien Jairam, Paul Ouboter, Philippe Kok. Two new species of *Anomaloglossus* (Anura: Aromobatidae) of the stepheni group from Suriname. *Zootaxa*, 2020, 4820 (1), pp.147-164. 10.11646/zootaxa.4820.1.7 . hal-03006030

HAL Id: hal-03006030

<https://hal.science/hal-03006030v1>

Submitted on 18 Nov 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Two new species of *Anomaloglossus* (Anura: Aromobatidae) of the *stepheni* group from Suriname

ANTOINE FOUQUET^{1*}, RAWIEN JAIRAM², PAUL OUBOTER³ & PHILIPPE J. R. KOK⁴

¹Laboratoire Evolution et Diversité Biologique (EDB), UMR5174, Toulouse, France.

✉ fouquet.antoine@gmail.com; <https://orcid.org/0000-0003-4060-0281>

²National Zoological Collection Suriname (NZCS), Anton de Kom University of Suriname, Paramaribo, Suriname.

✉ rawien_2000@yahoo.com; <https://orcid.org/0000-0002-6310-8321>

³Institute for Neotropical Wildlife and Environmental Studies (NeoWild), Paramaribo, Suriname

✉ p.ouboter@uvs.edu; <https://orcid.org/0000-0003-3114-8676>

⁴Department of Life Sciences, The Natural History Museum, London, United Kingdom

✉ pjrkok@gmail.com; <https://orcid.org/0000-0001-9743-9738>

*Corresponding author

Abstract

Anomaloglossus is a species-rich genus of frogs endemic to the Guiana Shield that still harbours several unnamed species. According to a recent integrative taxonomic survey, the *A. stepheni* species group includes five valid nominal species and at least four putatively unnamed species, two in Brazil and two in Suriname. In this paper, we describe the two species from Suriname based on adult and tadpole morphology as well as calls and natural history. Both have exotrophic tadpoles transported by the male to small water bodies.

- These two new species differ from each other and from other congeners in body size, colouration pattern, call characteristics and breeding sites. Both have narrow distributions and should be considered Endangered according to IUCN criteria.

Key words: Amazonia, Conservation, Endemism, Guiana Shield, Taxonomy

Introduction

Anomaloglossus Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel, & Wheeler, 2006 currently contains 30 valid nominal species from the Guiana Shield (Frost 2019). Nine of these species occur in the lowlands of the Guiana Shield and are structured in two species groups, the *A. stepheni* and the *A. degranvillei* groups (Vacher *et al.* 2017). Using molecular, morphometric and bioacoustic data, Vacher *et al.* 2017 detected the presence of several unnamed species belonging to these two species groups. Two species of the *degranvillei* group have been subsequently described (Fouquet *et al.* 2018) as well as one of the *stepheni* group (Fouquet *et al.* 2019a). The *stepheni* group therefore contains five described species: *A. stepheni* (Martins, 1989), *A. baeobatrachus* (Boistel & de Massary, 1999), *A. leopardus* Ouboter & Jairam, 2012, *A. apiau* Fouquet, Souza, Nunes, Kok, Curcio, Carvalho, Grant & Rodrigues, 2015 and *A. mitaraka* Fouquet, Vacher, Courtois, Deschamps, Ouboter, Jairam, Gaucher, Dubois, & Kok, 2019 and four species remain undescribed (Vacher *et al.* 2017). Two of these species occur in Suriname (*A. sp.* “Bakhuis”, *A. sp.* “Brownsberg”) and two occur in northern Par. Brazil (*A. sp.* “Paru”, *A. sp.* “Acari”).

The reproductive biology of the species of the *stepheni* species group is particularly interesting. While some species have a “classical” dendrobatoid exotrophic tadpole transported to a water body, other species display nidiolous and endotrophic tadpoles (*A. stepheni* Junca *et al.* 1994; *A. baeobatrachus* Fouquet *et al.* 2019a) or even phoretic and endotrophic tadpoles (*A. apiau* Vacher *et al.* 2017).

Previous works raised concerns about the conservation status of many *Anomaloglossus* spp. because most species are microendemics and some are declining (Fouquet *et al.* 2018) or have not been seen for decades such as *A. tepequem* (Fouquet *et al.* 2015). Today, out of the 30 described species of *Anomaloglossus*, three are considered as

Least Concern and nine have not been evaluated, while seven are considered as threatened by the IUCN (Vulnerable - VU, Endangered - EN, or Critically Endangered—CR status) and 14 are considered as Data Deficient (DD) (IUCN 2019). It is therefore crucial to describe the yet unnamed species of *Anomaloglossus* and assess their conservation status.

Herein we describe two additional species of the *stepheni* group from Suriname and evaluate their conservation status. Description of these new species are based on differences in adult and tadpole morphology as well as calls, and reproductive behaviour.

Material and methods

We undertook fieldwork across three localities in Suriname in 2015 (Bakhuis Mountains, a hilly massif reaching 300–400 m elevation covered by rainforest) and 2016 (Voltzberg, lowland forest 100 m elevation along the Coppename River with a nearby inselberg, and Brownsberg, a bauxitic plateau reaching 500 m elevation covered by rainforest) and collected specimens and tissue samples, recorded calls and ecological data of *Anomaloglossus* spp. (Fig. 1). Frogs were collected by hand and sacrificed by intraperitoneal injection of Xylocaine (lidocaine hydrochloride). 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_RA_2019.0009–29) and the National Zoological collection of Suriname (NZCS A1206–09).

Morphometric analysis. The sex of 18 adult specimens (10 males, 8 females) of *Anomaloglossus* sp. “Brownsberg” and 9 specimens (8 males, 1 female) of *A.* sp. “Bakhuis” was determined either in the field via calling activity, or in the laboratory by examining the condition of vocal slits and Finger III. 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 centre 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) with modifications suggested by Myers & Duellman (1982) and Savage & Heyer (1997).

Larval morphology. Two males (MNHN_RA_2019.0028–29) of *Anomaloglossus* sp. “Brownsberg” carrying three and nine tadpoles, respectively (Gosner stages 27–28), were found in Brownsberg, Suriname. These 12 tadpoles were fixed in 10 % formalin. Thirteen additional tadpoles at stages 28–29 were found in one small (1 m²) puddle adjacent to a temporary stream; three of these tadpoles were fixed in ethanol while the remaining 10 were fixed in formalin. These tadpoles were morphologically similar to the ones found on the back of the males and readily distinguished from the one of *Allobates granti*, the only co-occurring aromobatid with exotrophic tadpoles.

Four tadpoles at stages 28–30 were found in two puddles (two in each puddle) close to calling males of *A.* sp. “Bakhuis” in Bakhuis, Suriname. These tadpoles were fixed in 10% formalin but for one tadpole of each pair, tail-clips were previously taken and fixed in 95 % ethanol. One of these tail clips (AF3422) was previously used to obtain DNA and a 16S sequence (KY510162). Moreover, these tadpoles are readily distinguished from the tadpoles of co-occurring aromobatids *Allobates granti* and *Allobates femoralis*.

The following 16 measurements were taken on the six best-preserved formalin-fixed tadpoles of *A.* sp. “Brownsberg” at stages 28–29 and two best-preserved tadpoles (not tail-clipped) of *A.* sp. “Bakhuis” at stages 28–30 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).

We compared these data with those of the larva of *A. mitaraka* (Fouquet *et al.* 2019a), the only other species of the *A. stepheni* group with described exotrophic tadpole.

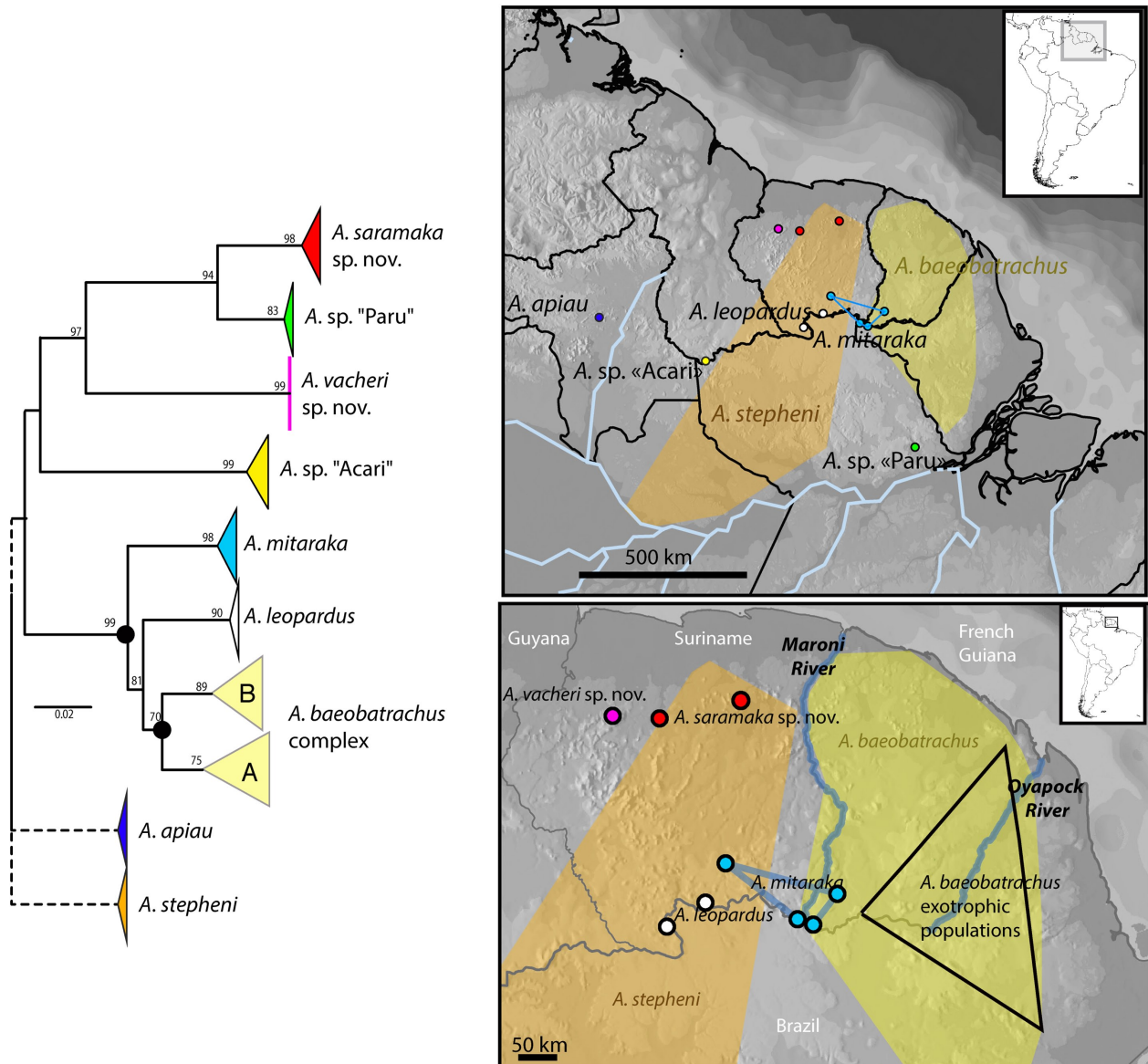


FIGURE 1. Phylogenetic tree adapted from Fouquet *et al.* (2019) and Vacher *et al.* (2017) and maps of the distribution of the species of *Anomaloglossus* of the *stepheni* group. The phylogenetic positions of *A. stepheni* and *A. apiau* remain ambiguous and corresponding branches are depicted with dashed lines. The ranges of the two species with endotrophic tadpoles (*A. baeobatrachus* and *A. stepheni*) are illustrated with a solid yellow and an orange polygon, respectively. The known populations of the species with exotrophic tadpoles are depicted by coloured dots except the range of the putatively introgressed populations related to *A. baeobatrachus* that is illustrated with a black-contoured triangle (Fouquet *et al.* 2019b).

Bioacoustics. The call of seven males of *A. sp.* “Brownsberg” were included in the call analysis: MNHN_RA_2019.0017 (field n AF3774) recorded by A. Fouquet, 25 January 2016 between 17h and 18h (22–24°C 100% RH), Voltzberg, Suriname, 4.68169 N 56.18568 W, ~100 m elevation; MNHN_RA_2019.0018–21, 16 (field n AF3840–3845) recorded by A. Fouquet, 01 February 2016, Brownsberg, Suriname, 4.936527 N 55.194826 W, ~500 m elevation. The call of five males of *A. sp.* “Bakhuis” were used : MNHN_RA_2019.0010, 11, 13–15 (field n AF3412,

3424, 3426, 3430, 3434) recorded by A. Fouquet, 30 April 2015 between 10h and 11h (25–26°C 98% RH), Bakhuis, Suriname, 4.72462 N 56.7638 W, ~200 m elevation. All calls were recorded in the field using an Olympus LS14 digital recorder attached to a Sony ECM MS907 at 44.1 kHz sampling rate. We measured six call variables from the train of notes emitted by these specimens with the software Audacity v.2.1.1. Variables follow Köhler *et al.* (2017): call rate (number of calls within a 10s recording window), call length, note length, inter-note interval, note repetition 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 the calls of *A. stephensi*, *A. mitaraka*, *A. leopardus* and *A. baeobatrachus* from Fouquet *et al.* (2019a).

Results

We hereafter formally describe *Anomaloglossus* sp. “Brownsberg” and *Anomaloglossus* sp. “Bakhuis” of Vacher *et al.* (2017) and Fouquet *et al.* (2019) (Fig. 1). The two species belong to the genus *Anomaloglossus* and are allocated to the *A. stephensi* group based on previous studies (Grant *et al.* 2006; Vacher *et al.* 2017; Fouquet *et al.* 2019), which included some of the voucher specimens examined.

Anomaloglossus saramaka sp. nov.

Anomaloglossus sp. “Brownsberg” Grant *et al.* 2006

Anomaloglossus sp. Fouquet *et al.* 2007

Anomaloglossus sp. Fouquet *et al.* 2012

Anomaloglossus baeobatrachus Ouboter and Jairam 2012

Anomaloglossus sp. “Brownsberg” Grant *et al.* 2017

Anomaloglossus sp. Brownsberg Vacher *et al.* 2017

Holotype. MNHN_RA_2019.0016 (field n°AF3845), an adult male, collected by A. Fouquet, S. Cally and R. Jairam on 01 February 2016 at Brownsberg, Suriname (4.936527 N 55.194826 W, ~500 m elevation; Figs. 2–3; Appendix 1).

Paratypes. Fifteen specimens: MNHN_RA_2019.0018–21, 27, 28, 29 (field n°AF3840–43, 3884, 3889, 3897) and NZCS-A1206 (field n°AF3844) eight adult males and MNHN_RA_2019.0022–26 (field n°AF3848, 3876, 3877, 3881, 3882) and NZCS-A1207 (field n°AF3847) six females collected with the holotype by A. Fouquet, S. Cally and R. Jairam, and MNHN_RA_2019.0017 (field n°AF3774) an adult male collected by A. Fouquet, S. Cally and R. Jairam on 25 January 2016 at Voltzberg, Suriname (4.68169 N 56.18568 W, ~100 m elevation).

Etymology. The specific epithet is a noun in apposition and refers to the Saramaka people who live nearby the type locality and are one of the Maroon communities living in Suriname.

Definition. (1) Medium-sized *Anomaloglossus* (average male SVL 19.3 mm [18.6–19.9, $n = 10$], female SVL 20.3 mm [19.9–21.6, $n = 6$]) (Table 1); (2) body robust; (3) skin on dorsum finely granular with larger scattered tubercles becoming denser on the posterior half and legs, with a larger tubercle on each eyelid; (4) ventral skin smooth except under thighs where it is finely granular; (5) inconspicuous supratympanic fold; (6) tympanum distinct anteroventrally; (7) snout long and protruding in lateral view; (8) nares oriented ventrolaterally, situated near tip of snout; (9) Finger II smaller than Finger I when fingers adpressed; (10) tip of Finger IV reaching distal edge of distal subarticular tubercle on Finger III when fingers adpressed; (11) distal subarticular tubercle distinct on Finger III and IV, not visible on the other fingers; (12) Finger III swollen dorsally and preaxially in males, extending largely towards dorsal surface of hand forming a cream-coloured gland basally; (13) fringes present on all fingers, particularly developed postaxially on Finger I and preaxially on Fingers II and III, in males and females; (14) toes basally webbed, with well-developed fringes on all toes, more developed preaxially on Toes II, III and IV; (15) tarsal keel well-defined, slightly curved; (16) glandular supracarpal pad present in both sexes (larger and more glandular in males); (17) cloacal tubercles present; (18) paracloacal mark present (orangish to light brown in life, cream to

grey in preservative); (19) dorsolateral stripe absent; (20) oblique lateral stripe present, solid, undulating (cream but sometimes white anteriorly, yellow at groin level in life, white in preservative), lateral band in life uniformly dark brown/black in males, brown in females, lower flank grey with white speckles, more or less extensively yellowish orange in the axillary and the groin regions; (21) ventrolateral stripe absent; (22) sexual dichromatism in throat colour pattern present, in life light grey in males with sparse minute black melanophores, evenly and entirely yellow in females; (23) sexual dichromatism in ventral colour pattern present, in life abdomen entirely or only posteriorly yellowish orange in males, uniformly bright yellowish orange in females; (24) iris with metallic pigmentation and pupil ring interrupted ventrally and dorsally by transversal black pigmentation; (25) median lingual process as long as wide, tapered, bluntly pointed, smooth (non-papillate), reclined in pit; (26) call 0.44–0.69 s in length, consisting of a train of 5–11 notes ranging 0.028–0.036 s in length and spaced by intervals of 0.024–0.030 s with a dominant frequency at 4.55–5.02 kHz ($n = 7$) (Table 2); (27) type 4 tadpole (Orton 1953), exotrophic, with a functional mouth with marginal papillae and labial teeth (Fig. 5; Table 3).

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* Fouquet, Vacher, Courtois, Villette, Reizine, Gaucher, Jairam, Ouboter, and Kok, 2018, *A. degranvillei* (Lescure, 1975), *A. dewynteri* Fouquet, Vacher, Courtois, Villette, Reizine, Gaucher, Jairam, Ouboter, and Kok, 2018 and *A. surinamensis* Ouboter and Jairam, 2012. *Anomaloglossus saramaka* **sp. nov.** can be distinguished from species of the *A. degranvillei* group by its basal webbing (moderate in species of the *A. degranvillei* group), smaller fringes that are more developed on Toes II-IV (well-developed fringes on all toes) and the presence of a solid oblique lateral stripe (absence) and from all the other described *Anomaloglossus* species by the presence of an oblique lateral stripe. Besides 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 (Barrio-Amorós 2006; Barrio-Amorós & Brewer-Carías 2008; Barrio-Amorós *et al.* 2004, 2010; Fouquet *et al.* 2015; Kok *et al.* 2010; La Marca 1997; Meinhardt & Parmalee 1996; Noble 1923; Rivero 1961) except *A. meansi* Kok, Nicola, Lathrop & MacCulloch, 2018, *A. kaiei* (Kok, Sambhu, Roopsind, Lenglet & Bourne, 2006), *A. rufulus* (Gorzula, 1990) and *A. roraima* (La Marca, 1997). However, unlike *A. saramaka*, all these species lack an oblique lateral stripe.

Within the *Anomaloglossus stepheni* group (comparisons follow below), *Anomaloglossus saramaka* **sp. nov.** is morphologically most similar to *A. baeobatrachus*, *A. leopardus*, *A. mitaraka* and *A. sp.* “Bakhuis” (see below) and can easily be confused with these species.

Anomaloglossus saramaka **sp. nov.** can mainly be distinguished from *A. baeobatrachus* by (1) larger body size (mean = 19.3; range 18.6–19.9 mm in males [$n = 10$] and mean = 20.3; range 19.9–21.6 mm in females [$n = 6$] in *A. saramaka* **sp. nov.** vs 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) venter mostly yellowish orange in males in *A. saramaka* **sp. nov.** (presence of a cream/white central patch in *A. baeobatrachus*); (3) call with lower note rate (mean = 14.6, range 14.0–15.3 notes/s in *A. saramaka* **sp. nov.** [$n = 7$] vs mean = 16.2, range 15.6–16.8 notes/s in *A. baeobatrachus* [$n = 9$]) (Table 2).

Anomaloglossus saramaka **sp. nov.** can mainly be distinguished from *A. leopardus* by (1) narrow, poorly defined dark brown bars on legs (broad and conspicuous in *A. leopardus*); (2) venter mostly yellowish-orange in males in *A. saramaka* **sp. nov.** (presence of a more or less extensive cream/white central patch in *A. leopardus*); (3) shorter advertisement call (mean = 0.51, range 0.38–0.69 s in *A. saramaka* **sp. nov.** [$n = 7$] vs mean = 1.52, range 1.08–2.00 s in *A. leopardus* [$n = 4$]); (4) fewer notes in calls (6–11 in *A. saramaka* **sp. nov.** [$n = 7$] vs 14–28 in *A. leopardus* [$n = 4$]) (Table 2).

Anomaloglossus saramaka **sp. nov.** can mainly be distinguished from *A. mitaraka* by (1) venter mostly yellowish orange in males in *A. saramaka* **sp. nov.** (presence of a more or less extensive cream/white central patch in *A. mitaraka*); (2) shorter advertisement call (mean = 0.51, range 0.38–0.69 s in *A. saramaka* **sp. nov.** [$n = 7$] vs mean = 1.04, range 0.74–1.23 s in *A. mitaraka* **sp. nov.** [$n = 6$]); (3) higher note rate call (mean = 14.6, range 14.0–15.3 note/s in *A. saramaka* **sp. nov.** [$n = 7$] vs mean = 11.43 note/s, range 10.8–12.3 in *A. mitaraka* [$n = 6$]) (Table 2).

Anomaloglossus saramaka **sp. nov.** can mainly be distinguished from *A. apiau* by (1) solid oblique lateral stripe in *A. saramaka* **sp. nov.** (partial, only present as a series of conspicuous white dots extending from groin midway along flank in *A. apiau*); (2) shorter advertisement call (mean = 0.51, range 0.38–0.69 s in *A. saramaka* **sp. nov.** [$n = 7$] vs mean = 19.6, range 7.0–39.4 s in *A. apiau* [$n = 10$]).

Anomaloglossus saramaka **sp. nov.** can mainly be distinguished from *A. stepheni* (Figs. 2–3, Table 1) by (1)

larger body size (mean = 19.3; range 18.6–19.9 mm in males [$n = 10$] and mean = 20.3; range 19.9–21.6 mm in females [$n = 6$] in *A. saramaka* **sp. nov.** vs mean = 17.2, 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. stephensi*); (2) skin on dorsum finely granular in *A. saramaka* **sp. nov.** (evenly tuberculate in *A. stephensi*); (3) ventral colouration mostly yellowish orange in males in *A. saramaka* **sp. nov.** (uniformly cream or white in *A. stephensi*); (4) longer advertisement call (mean = 0.51, range 0.38–0.69 s in *A. saramaka* **sp. nov.** [$n = 7$] vs mean = 0.25 s, range 0.18–0.29 s in *A. stephensi* [$n = 4$]); (5) lower note rate call (mean = 14.6, range 14.0–15.3 note/s in *A. saramaka* **sp. nov.** [$n = 7$] vs mean = 21.3, range 20.2–22.6 note/s in *A. stephensi* [$n = 4$]) (Table 2).

Description of the holotype. An adult male, 18.9 mm SVL; body robust; head wider than long, HL 95 % of HW; HL 33 % of SVL; dorsal skin finely granular, 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 42 % of HW; EN 29 % of HL, 75 % of ED. Tympanum distinct anteroventrally; supratympanic fold inconspicuous; choanae small, drop shaped, located anterolaterally.

Forelimb slender, skin tuberculate; HAND 24 % of SVL; Finger I longer than Finger II when fingers adpressed; fingers large and flattened; webbing absent on fingers; lateral fringes present on all fingers, particularly developed on postaxial edge of Finger I and on preaxial edges of Finger II and III; Finger III distinctly swollen dorsally and preaxially, swelling largely extending towards dorsal surface of hand; tip of Finger IV reaching distal edge of 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 > II > I; palmar tubercle large, heart-shaped, 0.8 mm in diameter (larger than disc on Finger III), thenar tubercle elliptic, small (equal to disc on Finger III in maximum diameter), half the size of palmar tubercle, well separated from palmar tubercle; only basal subarticular tubercles on fingers are conspicuous; distal subarticular tubercle of Finger III and IV are almost inconspicuous, basal subarticular tubercles on Fingers I and II the largest, followed by subarticular tubercle and basal subarticular tubercle on Finger III.

Hind limb robust, skin tuberculate; TL 48 % of SVL; heels in contact when hind limbs are flexed at right angles to the sagittal plane of body; FL 43 % 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, more developed preaxially on Toes II, III and IV. Toe webbing formula $I^{1+1}II^{1+1}III^{1+1}IV^{0-1}V$. 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 slightly curved at proximal end. Metatarsal fold strong.

Colour of holotype in life. Dorsal colour uniformly dark brown. Oblique lateral stripe solid, continuous, undulating, anteriorly brownish white, cream in the middle and yellow near groin (Fig. 2). Black lateral band below oblique lateral stripe, tapering posteriorly, extending from tip of snout to groin and containing the indistinct dorsal part of tympanum. Upper lip brownish white with a few small white speckles. Lower flank (below black lateral band) grey with white speckles with yellowish orange extensions from the axillary and the groin region. Throat grey covered with minute melanophores, more densely laterally; belly anteriorly greyish white, yellowish orange laterally and posteriorly, ventral surfaces of thighs and arms yellowish orange. Iris with copper metallic pigmentation and pupil ring interrupted dorsally and ventrally by transversal pigmentation (Fig. 2).

Upper and lower arm reddish brown dorsally with brown ill-defined spots and white speckles. Bright yellow spot at junction of upper arm with body, and anterior part of upper arm with a black band. Black glandular spot at junction between lower arm and hand, followed by a cream coloured part of the swollen gland extending on Finger III. Dorsal surfaces of thigh, shank and tarsus dark brown with ill-defined dark brown, almost black transverse bars, and ill-defined dark brown blotches. Paracloacal marks light brown, elongate. Toes and digits with small light blueish speckles dorsally and laterally. Palms and soles dark brown.

Colour of holotype in preservative. After four years in 70 % ethanol, colours of the specimen faded, and the dorsal colouration now varies from pale brown to grey with a brown interorbital bar; yellowish orange ventral colouration faded to white (Fig. 3). Bluish speckles and orange/reddish marks turned white as well.

Variation among type specimens. Measurements (range, mean, and standard deviation) of the type series are provided in Table 1. Colouration of limbs varies from brown to reddish brown, females being more reddish. Colour

of dorsum varies from light brown to dark brown and some specimens (e.g., NZCS-A1206, field n°AF3844) display diffuse dark brown blotches, more frequently on the interorbital region. Colour of oblique lateral stripe varies from white to orangish. Overall dorsal and lateral colouration and tuberculation may vary with light intensity, time of the day and probably reproductive activity as males carrying tadpoles apparently display overall lighter colours, smoother skin and sharper contrasts, whereas calling males are very dark coloured and highly tuberculate. Ventral colouration of female is entirely yellowish orange while the yellowish orange parts are always limited to the posterior region of throat in males. Vocal sac, slits and minute black melanophores on throat only observed in males as well as swelling of Finger III.

Advertisement call. Seven collected specimens calling from the leaf litter were recorded from a distance of about 2 m and at temperatures ranging from 22 to 24°C. Descriptive statistics of call parameters are presented in Table 2. *Anomaloglossus saramaka* **sp. nov.** emits trains (call length mean = 0.51, range 0.38–0.69 s) of 6–11 short notes (note length mean = 0.028 s; range 0.024–0.031 s; inter-note interval mean = 0.05 s; range 0.04–0.05 s). The spectral structure of the note has a developed harmonic structure and the dominant frequency is 4.84 kHz on average (range 4.55–5.02 kHz) with a slight upward modulation (ca. 0.3 kHz) (Fig. 4, Table 2).

Larval morphology. The following description is based on six tadpoles at stage 27, 28 and 29 (Fig. 5, Table 3). Tadpoles correspond to a type 4 tadpole of Orton (1953); exotrophic; body skin smooth; TL 12.95–17.19 mm; BL 4.33–5.89 mm, 33–36 % of TL, 146–165 % of BW, 191–238 % of BH; BW 123–149 % of BH (Table 3); body ovoid, snout round in dorsal and lateral view; eyes positioned and directed laterally; ED 0.45–0.60 mm, 53–64 % of IOD; IOD larger than IND; nares frontally positioned and directed laterodorsally; narial opening circular in lateral view; END 0.45–0.56 mm. Spiracular tube sinistral, conical, projecting posterodorsally, its tip located at 60–65 % 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 40–53 % of TMH; LTF 33–47 % of TMH; MTH 13–15 % of TL (Fig. 5, Table 3).

Mouth ventral, oral disc strongly emarginated, width 1.40–1.50 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.

The tadpole of *Anomaloglossus saramaka* **sp. nov.** can be distinguished from those of *Anomaloglossus* of the *stepheni* group that are endotrophic (*A. stepheni* and *A. baeobatrachus*) by the presence of a functional mouth with marginal papillae and labial teeth. However, it virtually cannot be distinguished from the tadpole of *A. mitaraka* based on morphological evidence.

Distribution and natural history. *Anomaloglossus saramaka* **sp. nov.** is a diurnal species inhabiting the leaf litter in primary forest at low to mid elevations (from 100 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 were found more than 50 m away from water bodies.

Males call all day long when the weather is rainy but otherwise calling activity is limited to sunset and sunrise. Breeding occurs during the rainy season, from December to July. The rainfall between December and April being highly variable, the reproduction seems to be concentrated in the second half (May–July) of this period. The males respond to intraspecific playbacks with shorter and more rapidly emitted note trills. Males are territorial, their small territories being spaced at least two metres apart. They usually call slightly above the leaf litter, exposed on a branch or a dead leaf. Eggs are probably deposited under or in the fold of a dead leaf. After hatching, the male carries the tadpoles (up to 9) to a small water body. We observed what appears to be shedding skin with the tadpoles being carried, which could represent food provisioning during transportation, although this remains very speculative.

Only two populations are known to date, one in Brownsberg and one in Voltzberg, both in Suriname. The species might occur between these two localities and probably in surrounding areas. However, it is unlikely that the species extends much further since other species occur nearby (*A. sp.* “Bakhuis”, *A. mitaraka*, *A. leopardus*), and that other species of this group with exotrophic tadpoles display a strong allopatric pattern of distribution. Goldmining activities in northeastern Suriname have been increasing during the last decade (Dezecache *et al.* 2017) and likely threaten a large part of the range of the new species even within protected areas such as Brownsberg Nature Park.



FIGURE 2. Two males (top) and one female (bottom) of the two species described herein, *Anomaloglossus saramaka* **sp. nov.** and *A. vacheri* **sp. nov.**, along with one male of the three additional species of the *A. stepheni* group occurring in Suriname.

Anomaloglossus saramaka sp. nov.
MNHN_RA_2019.0016 (AF3845)
Holotype male
Brownsberg, Suriname

Anomaloglossus vacheri sp. nov.
MNHN_RA_2019.0009 (AF3413)
Holotype male
Bakhuis, Suriname

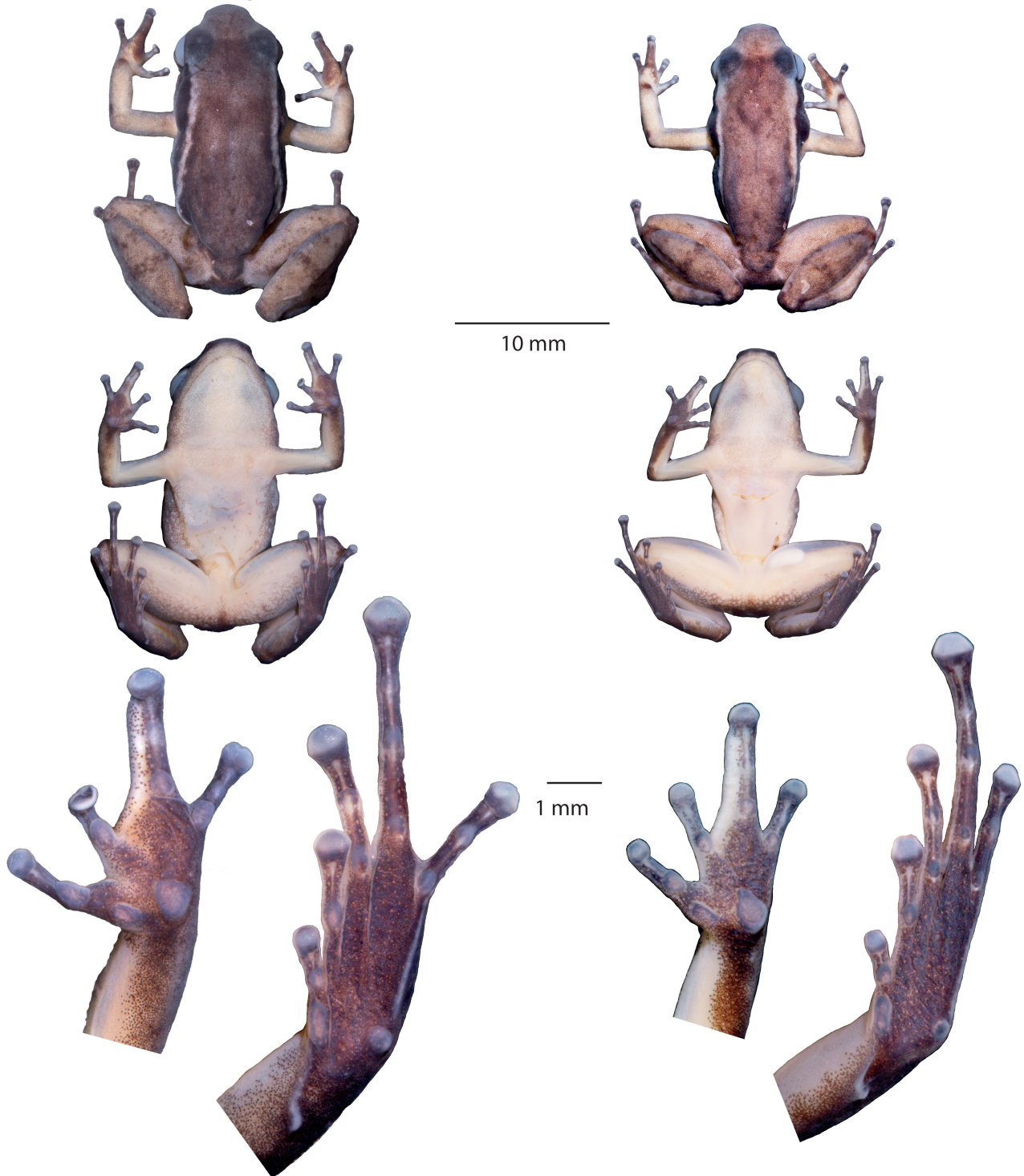


FIGURE 3. Views of dorsum, venter, left hand, left foot of the holotype of *A. saramaka* sp. nov. (left) and of the holotype of *A. vacheri* sp. nov. (right).

Anomaloglossus vacheri sp. nov.

Anomaloglossus baeobatrachus Ouboter & Jairam 2012

Anomaloglossus sp. Bakhuis Vacher *et al.* 2017

Holotype. MNHN_RA_2019.0009 (field n°AF3413), an adult male, collected by A. Fouquet, S. Cally and R. Jairam on 30 April 2015 at Bakhuis Mountains, Suriname (4.72462 N 56.7638 W, ~200 m elevation; Figs. 2–3; Appendix 1).

Paratopotypes. Eight specimens: MNHN_RA_2019.0009–11, 13–15 (field n°AF3412, 3424, 3426, 3430, 3434) and NZCS-A1208–9 (field n°AF3433, 3441) seven adult males and MNHN_RA_2019.0012 (field n°AF3425) one female collected with the holotype by A. Fouquet, S. Cally and R. Jairam.

Etymology. This species is dedicated to Jean-Pierre Vacher, in honour of his strong contribution to the understanding of the diversity and the evolution of the genus *Anomaloglossus*.

Definition. (1) Small-sized *Anomaloglossus* (average male SVL 17.4 mm [17.0–17.8, $n = 8$], female SVL 19.7 mm [$n = 1$]) (Table 1); (2) body robust; (3) skin on dorsum finely granular with larger scattered tubercles becoming denser on the posterior half and legs, with a larger tubercle on each eyelid; (4) ventral skin smooth except under thighs, where it is finely granular; (5) inconspicuous supratympanic fold; (6) tympanum distinct anteroventrally; (7) snout long and protruding in lateral view; (8) nares oriented ventrolaterally, situated near tip of snout; (9) Finger II equal to Finger I when fingers adpressed; (10) tip of Finger IV not reaching distal subarticular tubercle on Finger III when fingers adpressed; (11) distal subarticular tubercle distinct on Finger III and IV, inconspicuous on the other fingers; (12) Finger III swollen dorsally and preaxially in males, extending largely towards dorsal surface of hand; (13) fringes present on all fingers, particularly developed post- and preaxially on Finger II and preaxially on Finger III, almost inconspicuous on Finger IV, in males and females; (14) toes basally webbed, with well-developed fringes on all toes, more developed preaxially on Toes II and III; (15) tarsal keel well-defined, strongly curved; (16) glandular supracarpal pad present in both sexes (larger and more glandular in males); (17) cloacal tubercles present; (18) paracloacal mark present (orangish in life, cream to grey in preservative); (19) dorsolateral stripe absent; (20) oblique lateral stripe present, diffuse (composed of yellow and white speckles), particularly diffuse anteriorly, extending along upper eyelid into a diffuse canthal stripe, lateral band uniformly dark brown/black in males and females in life, lower flank yellowish orange to grey with white speckles; (21) ventrolateral stripe absent; (22) dorsal surface of arms barely blotched in males, orange; (23) sexual dichromatism in throat colour pattern present, in life light grey in males with sparse minute black melanophores (chin often yellow), evenly and entirely yellow in females; (24) sexual dichromatism in ventral colour pattern present, in life abdomen entirely yellowish orange in males, uniformly yellowish orange in females; (25) iris with metallic pigmentation and pupil ring inconspicuously interrupted ventrally by transversal black pigmentation; (26) median lingual process as long as wide, tapered, bluntly pointed, smooth (non-papillate), reclined in pit; (27) call 0.47–0.91 s in length, consisting of a train of 8–18 notes of 0.019–0.021 s in length and spaced by intervals of 0.042 s with a dominant frequency at 5.11–5.35 kHz ($n = 5$; Table 2); (28) type 4 tadpole (Orton 1953), exotrophic, with a functional mouth with marginal papillae and labial teeth (Fig. 5; Table 3).

Morphological comparisons with other *Anomaloglossus*. Like *Anomaloglossus saramaka* sp. nov., *A. vacheri* sp. nov. can be distinguished from species of the *A. degranvillei* group by its basal webbing (moderate in species of the *A. degranvillei* group), smaller fringes that are more developed on Toes II–IV (well-developed fringes on all toes) and the presence of a solid oblique lateral stripe (absence) and from all the other described *Anomaloglossus* species by the presence of an oblique lateral stripe.

Within the *Anomaloglossus stepheni* group (comparisons follow below), *A. vacheri* sp. nov. is morphologically most similar to *A. baeobatrachus*, *A. leopardus*, *A. mitaraka* and *A. saramaka* and can easily be confused with these species.

Anomaloglossus vacheri sp. nov. can mainly be distinguished from *A. baeobatrachus* by (1) oblique lateral stripe extending along upper eyelid into a canthal stripe in *A. vacheri* sp. nov. (oblique lateral stripe not extending along upper eyelid into a canthal stripe in *A. baeobatrachus*); (2) dorsal surface of arms barely blotched and orange in males of *A. vacheri* sp. nov. (with dark brown blotches and light brown in *A. baeobatrachus*); (3) ventral coloration yellowish orange in males in *A. vacheri* sp. nov. (white or only posteriorly yellow in *A. baeobatrachus*); (4) call with higher note rate (mean = 18.2, range 17.3–19.2 note/s in *A. vacheri* sp. nov. [$n = 8$] vs mean = 16.2, range 15.6–16.8 note/s in *A. baeobatrachus* [$n = 9$]) (Table 2).

Anomaloglossus vacheri can mainly be distinguished from *A. leopardus* by (1) narrow, poorly defined dark brown bars on legs (broad and conspicuous dark brown in *A. leopardus*); (2) dorsal surface of arms barely blotched and orange in males of *A. vacheri* (light brown with dark brown blotches in *A. leopardus*); (3) oblique lateral stripe extending along upper eyelid into a canthal stripe in *A. vacheri* **sp. nov.** (not extending along upper eyelid into a canthal stripe in *A. leopardus*); (4) advertisement call shorter (mean = 0.63, range 0.47–0.91 s in *A. vacheri* **sp. nov.** [$n = 5$] vs mean = 1.52, range 1.08–2.00 s in *A. leopardus* [$n = 4$]) and higher in frequency (mean = 5.25, range 5.11–5.35 kHz in *A. vacheri* **sp. nov.** [$n = 5$] vs mean = 4.45, range 4.40–4.57 kHz in *A. leopardus* [$n = 4$]) (Table 2).

Anomaloglossus vacheri **sp. nov.** can mainly be distinguished from *A. mitaraka* by (1) smaller male body size (mean = 17.4; range 17.0–17.8 mm in males [$n = 8$] in *A. vacheri* **sp. nov.** vs mean = 18.6; range 18.2–19.3 mm in males [$n = 7$] in *A. mitaraka*); (2) dorsal surface of arms barely blotched and orange in males of *A. vacheri* (with dark blotches and light brown in *A. mitaraka*); (3) oblique lateral stripe extending along upper eyelid into a canthal stripe *A. vacheri* **sp. nov.** (not extending along upper eyelid into a canthal stripe in *A. mitaraka*); (4) advertisement with a higher note rate (mean = 18.2, range 17.3–19.1 note/s in *A. vacheri* **sp. nov.** [$n = 8$] vs mean = 11.4 note/s, range 10.8–12.3 in *A. mitaraka* [$n = 6$]) and higher in frequency (mean = 5.25, range 5.11–5.35 kHz in *A. vacheri* **sp. nov.** [$n = 5$] vs mean = 4.43, range 4.12–4.76 kHz in *A. mitaraka* [$n = 6$]) (Table 2).

Anomaloglossus vacheri **sp. nov.** can mainly be distinguished from *A. saramaka* by (1) smaller male body size (mean = 17.4; range 17.0–17.8 mm in males [$n = 8$] in *A. vacheri* **sp. nov.** vs mean = 19.3; range 18.6–19.9 mm in males [$n = 10$] in *A. saramaka*); (2) dorsal surface of arms barely blotched and orange in males of *A. vacheri* (with dark blotches and light brown in *A. saramaka*); (3) oblique lateral stripe extending along upper eyelid into a canthal stripe in *A. vacheri* **sp. nov.** (not extending along upper eyelid into a canthal stripe in *A. saramaka*); (4) advertisement with a higher note rate (mean = 18.2, range 17.3–19.2 note/s in *A. vacheri* **sp. nov.** [$n = 8$] vs mean = 14.5 note/s, range 14.0–15.3 in *A. saramaka* [$n = 6$]) and higher in frequency (mean = 5.25, range 5.11–5.35 kHz in *A. vacheri* **sp. nov.** [$n = 5$] vs mean = 4.84, range 4.55–5.02 kHz in *A. saramaka* [$n = 6$]) (Table 2).

Anomaloglossus vacheri **sp. nov.** can be mainly distinguished from *A. apiau* by (1) solid oblique lateral stripe in *A. vacheri* **sp. nov.** (present as a series of conspicuous white dots extending from groin midway along flank in *A. apiau*); (2) by its shorter call (mean = 0.63, range 0.47–0.91 s in *A. vacheri* **sp. nov.** [$n = 5$] vs mean = 19.6, range 7.0–39.4 s in *A. apiau* [$n = 10$]).

Anomaloglossus vacheri **sp. nov.** can mainly be distinguished from *A. stepheni* (Figs. 2–3) by (1) skin on dorsum finely granular in *A. vacheri* **sp. nov.** vs evenly tuberculate in *A. stepheni*; (2) ventral colouration mostly yellowish orange in males in *A. vacheri* vs uniformly white in *A. stepheni*; (3) oblique lateral stripe extending along upper eyelid into a canthal stripe in *A. vacheri* **sp. nov.** vs oblique lateral stripe not extending along upper eyelid into a canthal stripe in *A. stepheni*; (4) advertisement call longer (mean = 0.63, range 0.47–0.91 s in *A. vacheri* **sp. nov.** [$n = 5$] vs mean = 0.25 s, range 0.18–0.29 s in *A. stepheni* [$n = 4$]), and higher in frequency (mean = 5.25, range 5.11–5.35 kHz in *A. vacheri* **sp. nov.** [$n = 5$] vs mean = 4.48, range 4.25–4.85 kHz in *A. stepheni* [$n = 4$]) (Table 2).

Description of the holotype. An adult male, 17.5 mm SVL; body robust; head wider than long, HL 98 % of HW; HL 33 % of SVL; dorsal skin finely tuberculate with larger tubercles posteriorly, one enlarged tubercle on each eyelid, snout long (SL 51 % 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 41 % of HW; EN 30 % of HL, 77 % of ED. Tympanum distinct anteroventrally; supratympanic fold inconspicuous; choanae small, circular, located anterolaterally.

Forelimb slender, skin tuberculate; HAND 23 % of SVL; Finger I as long as Finger II when fingers adpressed; fingers large and flattened; webbing absent on fingers; lateral fringes present, particularly developed post and preaxially on Finger II and preaxially on Finger III; Finger III distinctly swollen dorsally and preaxially, swelling largely extending towards dorsal surface of hand; 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 > II > I; palmar tubercle large, heart-shaped, 0.75 mm in diameter (larger than disc on Finger III), thenar tubercle elliptic, small (equal to disc on Finger III in maximum diameter), half the size of palmar tubercle, well separated from palmar tubercle; basal subarticular tubercles on fingers and distal subarticular tubercle of Finger III and IV conspicuous; subarticular tubercles on Fingers I and II the largest, followed by subarticular tubercles and basal subarticular tubercle on Finger III.

TABLE 1. Adult body measurements (in mm).




Species	<i>A. saramaka</i> sp. nov.								<i>A. vacheri</i> sp. nov.					
	M (10)				F (6)				M (8)				F (1)	
	X	sd	Min	Max	X	sd	Min	Max	X	sd			X	sd
SVL	19.25	0.44	18.6	19.9	20.33	0.63	19.90	21.60	17.41	0.31	17.00	17.80	19.70	NA
HL	6.24	0.08	6.10	6.30	6.73	0.15	6.60	7.00	5.76	0.17	5.50	6.00	6.00	NA
HW	6.51	0.20	6.08	6.70	7.02	0.21	6.70	7.30	5.93	0.17	5.06	6.10	6.30	NA
SL	3.25	0.19	3.00	3.50	3.48	0.12	3.30	3.60	2.99	0.11	2.80	3.10	3.20	NA
EN	1.89	0.07	1.80	2.00	2.10	0.14	1.90	2.30	1.78	0.05	1.70	1.80	1.90	NA
IN	2.73	0.12	2.06	2.90	2.77	0.15	2.50	2.90	2.41	0.06	2.30	2.50	2.60	NA
EL	2.39	0.09	2.20	2.05	2.50	0.14	2.30	2.70	2.24	0.05	2.20	2.30	2.30	NA
IO	2.12	0.09	2.00	2.30	2.27	0.08	2.20	2.40	2.03	0.05	2.00	2.10	2.10	NA
TYM	1.36	0.07	1.27	1.50	1.50	0.00	1.50	1.50	1.23	0.10	1.10	1.40	1.40	NA
FAL	4.19	0.13	4.06	4.40	4.40	0.14	1.50	4.60	3.80	0.08	3.70	3.90	4.00	NA
HAND	4.68	0.13	4.50	4.90	4.77	0.16	4.60	5.00	4.21	0.12	4.10	4.40	4.30	NA
WFD	0.67	0.04	0.60	0.70	0.68	0.04	0.60	0.70	0.61	0.04	0.60	0.70	0.50	NA
TL	9.06	0.24	8.80	9.60	9.50	0.28	9.20	10.00	8.30	0.15	8.10	8.50	8.80	NA
FL	8.24	0.31	7.70	8.70	8.50	0.28	8.20	8.90	7.43	0.09	7.30	7.50	7.50	NA
WTD	0.83	0.06	0.70	0.90	0.83	0.05	0.80	0.90	0.79	0.04	0.70	0.80	0.70	NA
ThL	9.34	0.21	9.10	9.80	9.83	0.29	9.40	10.30	8.49	0.15	8.30	8.70	9.00	NA
IFiL	2.69	0.12	2.50	2.90	2.80	0.06	2.70	2.90	2.31	0.08	2.20	2.50	2.40	NA

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

Species	<i>A. saramaka</i> sp. nov. (n = 7)				<i>A. vacheri</i> sp. nov. (n = 5)			
	X	sd	Min	Max	X	sd	Min	Max
Call rate (calls/s)	0.914	0.177	0.700	1.100	0.985	0.242	0.711	1.270
Call length (s)	0.509	0.108	0.381	0.695	0.629	0.205	0.470	0.912
Note length (s)	0.028	0.002	0.024	0.031	0.02	0.001	0.019	0.021
Inter-note interval (s)	0.047	0.003	0.042	0.052	0.039	0.003	0.035	0.042
Note rate (notes/s)	14.58	0.396	14.0	15.3	18.21	0.765	17.3	19.2
Number of notes	7.500	0.901	5	11	6.35	0.137	8	20
Dominant frequency (kHz)	4.837	0.152	4.55	5.02	5.255	0.103	5.11	5.35

Hind limb robust, skin tuberculate; TL 48 % 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 0.8 mm. Foot basally webbed; lateral fringes present on all toes, more developed preaxially on Toes II and III. Toe webbing formula $I^{+,-1} \cdot II^{+,-1} \cdot III^{+,-1} \cdot IV^{0,-1} \cdot V$. 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.

Colour of holotype in life. Dorsal colour light brown with dark brown blotches occurring on the interorbital region and at mid-body forming an hourglass pattern. Blotches of the same colour also occur laterally along the oblique lateral stripe. Oblique lateral stripe thin, diffuse (particularly anteriorly), formed by white and yellow speckles, extending along the upper eyelid into a diffuse canthal stripe (Fig. 2). Dark brown lateral band below oblique lateral stripe, tapering posteriorly, extending from tip of snout to groin and containing the indistinct dorsal part of tympanum, tapering posteriorly. Upper lip grey with a few small white speckles. Lower flank (below dark brown lateral band) grey with white speckles. Throat light grey, chin yellowish orange, throat and chin covered with minute

melanophores, more densely laterally; belly bright yellowish orange, ventral surfaces of thighs and arms yellowish orange. Iris with copper metallic pigmentation and pupil ring uninterrupted by transversal pigmentation (Fig. 2).

Upper and lower arm light orange dorsally with a few white speckles. Black glandular spot at junction between lower arm and hand, followed by a grey coloured part of the swollen gland extending on Finger III. Dorsal surfaces of thigh, shank and tarsus light brown with ill-defined dark brown transverse bars and ill-defined dark brown blotches. Paracloacal marks light brown, elongate. Toes and digits with small light blueish speckles dorsally and laterally. Palms and soles dark brown.

Colour of holotype in preservative. After four years in 70 % ethanol, colours of the specimen faded and the dorsal colouration now varies from pale brown to grey with darker blotches, the yellowish orange ventral colouration faded to white (Fig. 3). Bluish speckles and orange marks turned white as well.

Variation among type specimens. Measurements (range, mean, and standard deviation) of the type series are provided in Table 1. Colour of oblique lateral stripe varies in its proportion of white and yellow. Overall dorsal and lateral coloration and tuberculation may vary with light intensity, time of the day and probably reproductive activity as calling males are dark coloured and highly tuberculate. Dorsal dark brown hourglass pattern may be absent (MNHN_RA_2019.0013, field n°AF3426; NZCS-A1208, field n°AF3433). Paracloacal marks sometimes inconspicuous. Throat colouration of female is entirely yellowish orange while the yellowish orange parts are often limited to the chin in males (extent of coloured part of chin varies). Vocal sac, slits and minute black melanophores on throat only observed in males as well as swelling of Finger III.

Advertisement call. Five collected specimens calling from the leaf litter were recorded from a distance of about 2 m and at temperatures between 25–26°C and 98% relative humidity. Descriptive statistics of call parameters are presented in Table 2. *Anomaloglossus vacheri* emits trains (call length mean = 0.63, range 0.47–0.91 s) of 8–18 short notes (note length mean = 0.020 s; range 0.019–0.021 s; inter-note interval mean = 0.039 s; range 0.036–0.042 s). The spectral structure of the note has a developed harmonic structure and the dominant frequency is 5.25 kHz on average (range 5.11–5.35 kHz) with a slight upward modulation (ca. 0.4 kHz) (Fig. 4, Table 2).

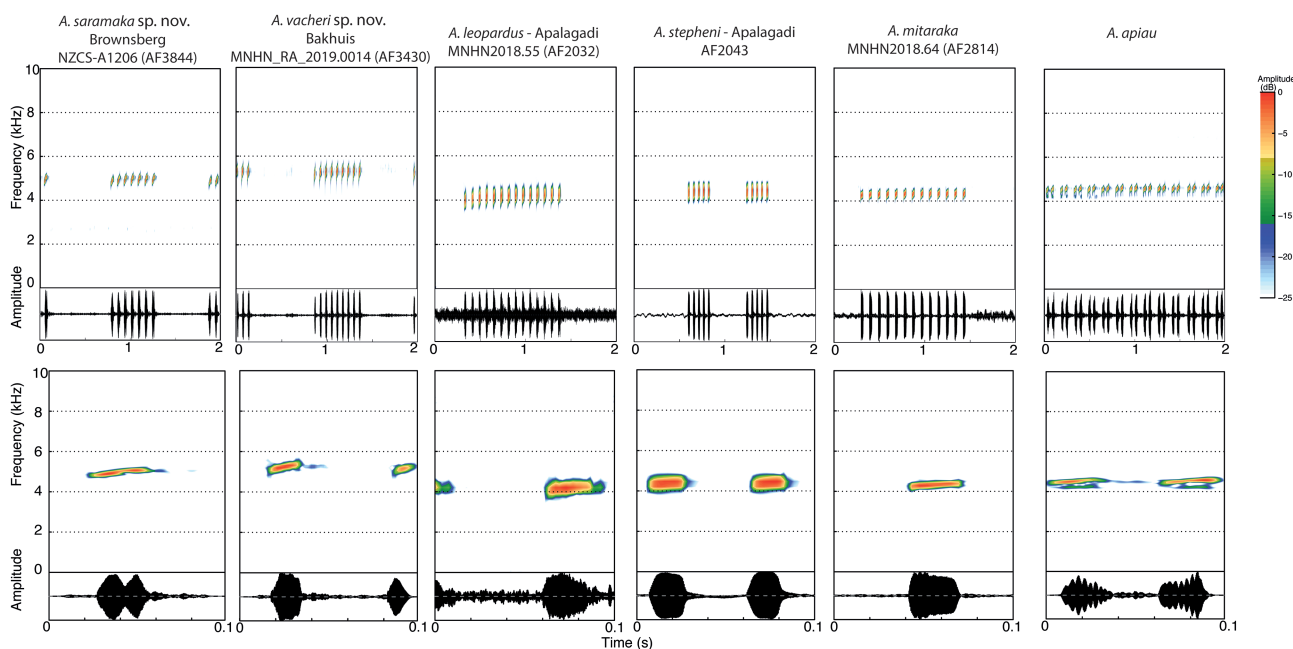


FIGURE 4. Spectrograms and oscillograms of the advertisement calls of the two species described herein, *Anomaloglossus saramaka* sp. nov. and *A. vacheri* sp. nov., along with the calls of four additional described species of the *A. stepheni* group; in a 2 s time window (top) and a close-up in a 0.1 s time window (bottom).

Larval morphology. The following description is based on two tadpoles at stage 28 and 30 (Fig. 5). Tadpoles correspond to a type 4 tadpole of Orton (1953); exotrophic; body skin smooth; TL 15.00–19.06 mm; BL 5.27–6.46 mm, 34–35 % of TL, 151–160 % of BW, 261–267 % of BH; BW 135–144 % of BH (Table 3); body ovoid, snout round in dorsal and lateral view; eyes positioned and directed laterally; ED 0.49–0.61 mm, 55–58 % of IOD; IOD smaller than IND; nares frontally positioned and directed laterodorsally; narial opening circular in lateral view; END 0.55–0.71 mm. Spiracular tube sinistral, conical, projecting posterodorsally, its tip located at 57–59 % 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 47–48 % of TMH; LTF 46–49 % of TMH; MTH 13–16 % of TL (Fig. 5, Table 3).

TABLE 3. Tadpole measurements (in mm).

Species	<i>A. saramaka</i> sp. nov.						<i>A. vacheri</i> sp. nov.	
	AF3865A	AF3865B	AF3865C	AF3897A	AF3897B	AF3897C	AF3442A	AF3422A
Gosner stage	28	29	28	28	28	27	28	30
TL	14.48	17.19	15.46	13.32	13.72	12.95	15.00	19.06
BL	4.73	5.89	5.49	4.43	4.53	4.33	5.27	6.46
TAL	9.84	11.24	10.24	9.07	9.13	9.01	9.53	12.64
BW	3.24	3.60	3.33	2.92	2.84	2.73	3.50	4.05
BH	2.48	2.82	2.70	2.02	1.90	2.04	2.43	2.99
HW	2.74	3.35	2.97	2.48	2.47	2.41	2.82	3.68
TMH	1.23	1.36	1.25	1.25	1.38	1.41	1.30	1.50
UTF	0.64	0.67	0.66	0.64	0.59	0.56	0.63	0.71
LTF	0.53	0.60	0.59	0.47	0.46	0.49	0.64	0.69
TMW	1.39	1.42	1.21	1.24	1.10	1.24	1.24	1.52
MTH	2.12	2.20	2.20	1.98	2.00	1.87	2.35	2.55
END	0.46	0.53	0.50	0.49	0.56	0.45	0.55	0.71
NSD	0.70	0.78	0.62	0.59	0.59	0.49	0.67	0.58
IND	0.73	0.83	0.80	0.75	0.80	0.78	0.95	1.15
IOD	0.84	0.93	0.90	0.87	0.87	0.89	0.84	1.11
ED	0.45	0.60	0.51	0.46	0.47	0.48	0.49	0.61

Mouth ventral, oral disc strongly emarginated, width 1.27–1.89 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.

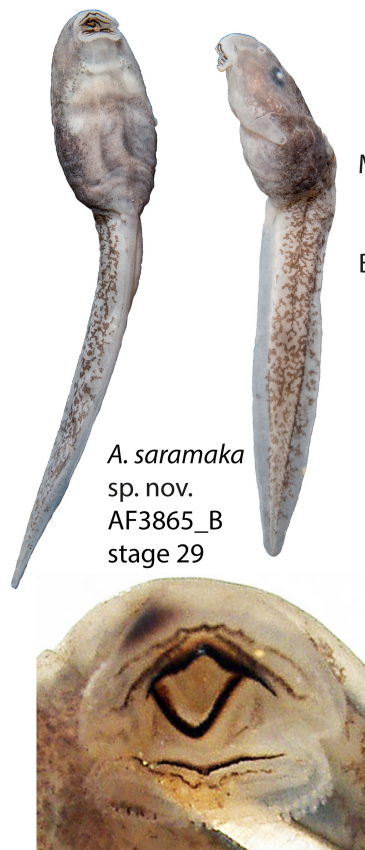
In life, the body is dark grey with abundant golden flecks, particularly on dorsum, except the loreal and post-ocular regions that are pink. Golden flecks become scarce ventrally. Posteriorly, dark grey coloration fades and tail becomes translucent.

The tadpole of *Anomaloglossus vacheri* can be distinguished from those of *Anomaloglossus* of the *stepheni* group that are endotrophic (*A. stepheni* and *A. baeobatrachus*) by the presence of a functional mouth with marginal papillae and labial teeth. It can be distinguished from the tadpole of *A. mitaraka* and *A. saramaka* by its less dense pigmentation particularly ventrally and by a spiracle located more anteriorly.

Distribution and natural history. *Anomaloglossus vacheri* is a diurnal species inhabiting the leaf litter in primary forest at low elevation (200 m a.s.l.). The species has only been found in *terra firme* forest on lateritic crust distant from streams.

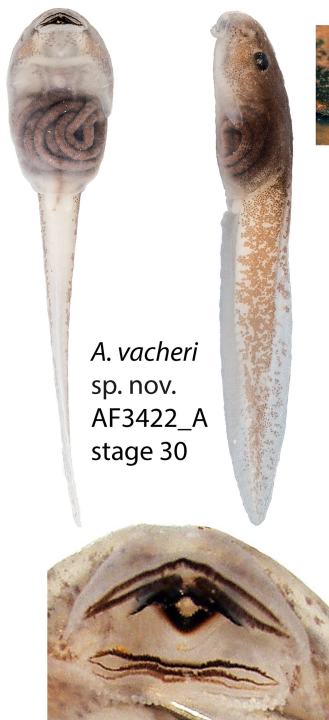
Males call after rainfall. Breeding apparently occurs during the rainy season, probably extending between December and July, depending on rainfall. The males respond to intraspecific playbacks with shorter and more rapidly emitted note trills. Males are spaced by at least five metres apart. They usually call slightly above the leaf litter, exposed on a branch or a dead leaf. Eggs are probably deposited under or in the fold of a dead leaf. After they hatch the male probably carries the tadpoles to small water bodies formed in the lateritic crust where tadpoles were found (Fig. 5).

A single population is known to date, in Bakhuis Mountains, Suriname. The species likely occurs throughout the massif, but it unlikely extends much further since other species occur nearby (*A. leopardus*, *A. mitaraka*, *A. saramaka*), and that other species of this group with exotrophic tadpole display a strong allopatric pattern of distribution.



A. saramaka
sp. nov.
AF3865_B
stage 29

A. saramaka
sp. nov.
MNHN_RA_2019.0029
(AF3897)
Paratype male
Brownsberg, Suriname



A. vacheri
sp. nov.
AF3422_A
stage 30



FIGURE 5. The tadpole of *Anomaloglossus saramaka* **sp. nov.** and *A. vacheri* **sp. nov.**, and pictures of habitat and males in situ. Top: ventral and lateral view of AF3865_B at Gosner stage 29, a close-up of the mouth, a male (MNHN_RA_2019.0029, field n°AF3897) carrying 9 tadpoles (note the shedding skin), and habitat where males deposit tadpoles during the wet season (here dry). Bottom: ventral and lateral view of AF3422_A at Gosner stage 30, a close-up of the mouth, a picture of the specimen in situ within a small cavity in the lateritic crust indicated by an arrow, and the calling male nearby on lateritic crust.

Discussion

Vacher *et al.* (2017) demonstrated the existence of at least eight putatively unnamed species in the Guiana Shield lowlands, six in the *A. stepheni* group and two in the *A. degranvillei* group. Since 2017, one species has been described (*A. mitaraka*) in the *A. stepheni* group and two (*A. dewynteri*, *A. blanci*) in the *A. degranvillei* group. With the two additional species described herein the number of *Anomaloglossus* taxa in this region reaches eleven species and has nearly quadrupled since 2012.

Two candidate species identified by Vacher *et al.* (2017), restricted to massifs in the interior of the Eastern Guiana Shield (Acari, Pará), remain to be described. The species with exotrophic tadpoles in the *A. stepheni* group seem to have narrow distributions, associated with mid-elevation 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 such as the Kanuku mountains in Guyana, central massifs in Suriname and the numerous massifs in lowland Roraima, Northern Amazonas and Northern Pará states in Brazil.

The fact that the populations of the exotrophic species may be circumscribed to small mountain ranges raises conservation concerns. *Anomaloglossus leopardus*, *A. mitaraka*, *A. saramaka* **sp. nov.**, and *A. vacheri* **sp. nov.** are only known from a handful of localities. As a matter of fact, the distribution pattern of the species in the entire genus is similarly microendemic with the exception of the two species with endotrophic and nidicolous tadpoles (*A. baeobatrachus* and *A. stepheni*), which comparatively have large distributions. Moreover, rapid declines have been documented in several *Anomaloglossus* species (Fouquet *et al.* 2015, 2018).

Some ecological groups seem more prone to decline in anurans. The stream-associated frogs throughout the tropics are particularly hit by declines (Gillespie & Hines 1999; Woodhams & Alford 2005), and climate change and epidemic diseases are the most likely causes. Finally, gold mining activities in northeastern Suriname have been increasing in the last decade (Dezecache *et al.* 2017) and likely threaten part of the range of the new species even within protected area such as Brownsberg Nature Park. Therefore, the populations of these two new species should be monitored with care.

These two new *Anomaloglossus* species should be considered as Endangered (EN) according to IUCN criteria: ranges are likely <5,000 km² with less than five known population that are likely severely fragmented and probably small (“B1(a)”), and decline caused by human activities is likely (“B1(b)”). As suggested previously by Fouquet *et al.* (2015; 2018), the entire genus should be included in conservation programs.

Acknowledgements

This work has benefited from an “Investissement d’Avenir grant managed by the Agence Nationale de la Recherche (CEBA, ref. ANR-10-LABX-25-01). PJRK’s work was supported by postdoctoral fellowships from the Fonds voor Wetenschappelijk Onderzoek Vlaanderen (FWO12A7614N/FWO12A7617N). We thank the Nature Conservation Division and the STINASU for collecting permits in Suriname. We are grateful to Jason Brown and one anonymous reviewer for helpful comments on the manuscript, to Sébastien Cally for his help in the field, and to Annemarie Ohler for accepting deposition of the specimens at MNHN.

References

- Barrio-Amorós, C.L. (2006) A new dendrobatid frog (Anura: Dendrobatidae: *Colostethus*) from Aprada tepui, southern Venezuela. *Zootaxa*, 1110 (1), 59–68.
<https://doi.org/10.11646/zootaxa.1110.1.6>
- Barrio-Amorós, C.L. & Brewer-Carías, C. (2008) Herpetological results of the 2002 expedition to Sarisariñama, a tepui in Venezuelan Guayana, with the description of five new species. *Zootaxa*, 1942 (1), 1–68.
<https://doi.org/10.11646/zootaxa.1942.1.1>
- Barrio-Amorós, C.L., Fuentes-Ramos, O. & Rivas-Fuenmayor, G.A. (2004) Two new species of *Colostethus* (Anura: Dendrobatidae) from the Venezuelan Guayana. *Salamandra*, 40, 183–200.
- Barrio-Amorós, C.L., Santos, J.C. & Jovanovic, O. (2010) A new dendrobatid frog (Anura: Dendrobatidae: *Anomaloglossus*) from the Orinoquian rainforest, southern Venezuela. *Zootaxa*, 2413 (1), 37–50.

<https://doi.org/10.11646/zootaxa.2413.1.3>

- Boistel, R. & de Massary, J.-C. (1999) Les amphibiens vénéneux de la famille des dendrobatidés. *Le Courrier de la Nature*, 176, 34–39.
- Dezécache, C., Faure, E., Gond, V., Salles, J.M., Vieilledent, G. & Hérault, B. (2017) Gold-rush in a forested El Dorado: deforestation leakages and the need for regional cooperation. *Environmental Research Letters*, 12, 034013. <https://doi.org/10.1088/1748-9326/aa6082>
- Fouquet, A., Ferrier, B., Salmona, J., Tirera, S., Vacher, J.-P., Courtois, E.A., Gaucher, P., Dias Lima, J., Nunes, P.M.S., de Souza, S.M., Rodrigues, M.T., Noonan, B. & de Thoisy, B. (2019b) Phenotypic and life-history diversification in Amazonian frogs despite past introgressions. *Molecular Phylogenetics and Evolution*, 130, 169–180. <https://doi.org/10.1016/j.ympev.2018.09.010>
- Fouquet, A., Gilles, A., Vences, M., Marty, C., Blanc, M. & Gemmell, N.J. (2007) Underestimation of species richness in Neotropical frogs revealed by mtDNA analyses. *PLoS One*, 2, e1109. <https://doi.org/10.1371/journal.pone.0001109>
- Fouquet, A., Noonan, B.P., Rodrigues, M.T., Pech, N., Gilles, A. & Gemmell, N.J. (2012) Multiple quaternary refugia in the eastern Guiana Shield revealed by comparative phylogeography of 12 frog species. *Systematic Biology*, 61, 461–489. <https://doi.org/10.1093/sysbio/syr130>
- Fouquet, A., Souza, S.M., Nunes, P.M.S., Kok, P.J.R., Curcio, F.F., de Carvalho, C.M., Grant, T. & Rodrigues, M.T. (2015) Two new endangered species of *Anomaloglossus* (Anura: Aromobatidae) from Roraima State, northern Brazil. *Zootaxa*, 3926 (2), 191–210. <https://doi.org/10.11646/zootaxa.3926.2.2>
- Fouquet, A., Vacher, J.-P., Courtois, E.A., Deschamps, C., Ouboter, P.E., Jairam, R., Gaucher, P., Dubois, A. & Kok, P.J.R. (2019a) A new species of *Anomaloglossus* (Anura: Aromobatidae) of the *stephensi* group with the redescription of *A. baeobatrachus* (Boistel and de Massary, 1999), and an amended definition of *A. leopardus* Ouboter and Jairam, 2012. *Zootaxa*, 4576 (3), 439–460. <https://doi.org/10.11646/zootaxa.4576.3.2>
- Fouquet, A., Vacher, J.-P., Courtois, E.A., Villette, B., Reizine, H., Gaucher, P., Jairam, R., Ouboter, P. & Kok, P.J.R. (2018) On the brink of extinction: two new species of *Anomaloglossus* from French Guiana and amended definition of *Anomaloglossus degranvillei* and *A. surinamensis* (Anura: Aromobatidae). *Zootaxa*, 4379 (1), 001–023. <https://doi.org/10.11646/zootaxa.4379.1.1>
- Frost, D.R. (2019) *Amphibian Species of the World: an Online Reference*. Version 6.0. American Museum of Natural History, New York. Electronic Database accessible. Available from: <http://research.amnh.org/herpetology/amphibia/index.html>.
- Gillespie, G. & Hines, H. (1999) Status of temperate riverine frogs in south-eastern Australia. In: Campbell, A. (Ed.), *Declines and disappearances of Australian frogs*. Biodiversity Group, Environment Australia, Canberra, pp. 109–130.
- Gorzula, S.J. (1990 “1988”) Una nueva especie de *Dendrobates* (Amphibia: Dendrobatidae) del Macizo del Chimantà, Estado Bolívar, Venezuela. *Memoria Sociedad de Ciencias Naturales La Salle*, 48, 143–149.
- Grant, T., Frost, D.R., Caldwell, J.P., Gagliardo, R., Haddad, C.F., Kok, P.J.R., Means, D.B., Noonan, B.P., Schargel, W.E. & Wheeler, W.C. (2006) Phylogenetic systematics of dart-poison frogs and their relatives (Amphibia: Athesphatanura: Dendrobatidae). *Bulletin of the American Museum of Natural History*, 299, 1–262. [https://doi.org/10.1206/0003-0090\(2006\)299\[1:PSODFA\]2.0.CO;2](https://doi.org/10.1206/0003-0090(2006)299[1:PSODFA]2.0.CO;2)
- Grant, T. & Castro, F. (1998) The cloud forest *Colostethus* (Anura, Dendrobatidae) of a region of the Cordillera Occidental of Colombia. *Journal of Herpetology*, 32, 378–392. <https://doi.org/10.2307/1565452>
- IUCN (2019) The IUCN Red List of Threatened Species. Version 2019-3. <http://www.iucnredlist.org> (accessed 10 December 2019)
- Juncá, F.A., Altig, R. & Gascon, C. (1994) Breeding biology of *Colostethus stephensi*, a dendrobatid frog with a nontransported nidicolous tadpole. *Copeia*, 1994, 747–750. <https://doi.org/10.2307/1447191>
- Köhler, J., Jansen, M., Rodríguez, A., Kok, P.J.R., Toledo, L.F., Emmrich, M., Glaw, F., Haddad, C., Rödel, M.-O. & Vences, M. (2017) The use of bioacoustics in anuran taxonomy: theory, terminology, methods and recommendations for best practice. *Zootaxa*, 4251 (1), 1–124. <https://doi.org/10.11646/zootaxa.4251.1.1>
- Kok, P.J.R., Nicolai, M.P.J., Lathrop, A. & MacCulloch, R.D. (2018) *Anomaloglossus meansi* sp. n., a new Pantepui species of the *Anomaloglossus beebei* group (Anura, Aromobatidae). *ZooKeys*, 759, 99–116. <https://doi.org/10.3897/zookeys.759.24742>
- Kok, P.J.R., Sambhu, H., Roopsind, I., Lenglet, G.L. & Bourne, G.R. (2006) A new species of *Colostethus* (Anura: Dendrobatidae) with maternal care from Kaieteur National Park, Guyana. *Zootaxa*, 1238 (1), 35–61. <https://doi.org/10.11646/zootaxa.1238.1.3>
- Kok, P.J.R., MacCulloch, R.D., Lathrop, A., Willaert, B. & Bossuyt, F. (2010) A new species of *Anomaloglossus* (Anura: Aromobatidae) from the Pakaraima Mountains of Guyana. *Zootaxa*, 2660, 18–32.
- La Marca, E. (1997 1996) Ranas del genero *Colostethus* (Amphibia: Anura: Dendrobatidae) de la Guayana Venezolana con la descripción de siete especies nuevas. *Publicaciones de la Asociación de Amigos de DonPana*, 9, 1–64.
- Lescure, J. (1975) Contribution à l'étude des amphibiens de Guyane Française. III. Une nouvelle espèce de *Colostethus* (Dendro-

- batidae): *Colostethus degranvillei* n. sp. *Bulletin du Museum National d'Histoire Naturelle. Paris, Serie 3, Zoologie*, 293, 413–420.
- McDiarmid, R.W. & Altig, R. (1999) *Tadpoles: The Biology of Anuran Larvae*. University of Chicago Press, Chicago & London, 458 pp.
- Martins, M. (1989) Nova especie de *Colostethus* da Amazonia central (Amphibia: Dendrobatidae). *Revista Brasileira de Biologia*, 49, 1009–1012.
- Meinhardt, D.J. & Parmelee, J.R. (1996) A new species of *Colostethus* (Anura: Dendrobatidae) from Venezuela. *Herpetologica*, 52, 70–77.
- Myers, C.W. & Donnelly, M.A. (2008) The summit herpetofauna of Auyantepui, Venezuela: report from the Robert G. Goelet American Museum-Terramar Expedition. *Bulletin of the American Museum of Natural History*, 308, 1–147.
<https://doi.org/10.1206/308.1>
- Myers, C.W. & Duellman, W.E. (1982) A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. *American Museum Novitates*, 2752, 1–32.
- Noble, G.K. (1923) New batrachians from the Tropical Research Station British Guiana. *Zoologica*, 3, 289–299.
- Orton, G.L. (1953) The systematics of vertebrate larvae. *Systematic Zoology*, 2, 63–75.
<https://doi.org/10.2307/2411661>
- Ouboter, P.E. & Jairam, R. (2012) *Amphibians of Suriname*. Brill, Leiden, 376 pp.
<https://doi.org/10.1163/9789004208001>
- R Development Core Team (2016) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. [program]
- Rivero, J.A. (1961) Salientia of Venezuela. *Bulletin of the Museum of Comparative Zoology. Cambridge, Massachusetts*, 126, 1–207.
- Savage, J.M. & Heyer, W.R. (1967) Variation and distribution in the tree-frog genus *Phyllomedusa* in Costa Rica, central America. *Studies on Neotropical Fauna and Environment*, 5, 111–131.
<https://doi.org/10.1080/01650526709360400>
- Savage, J.M. & Heyer, W. (1997) Digital webbing formulae for anurans: a refinement. *Herpetological Review*, 28, 131.
- Sueur, J., Aubin, T. & Simonis, C. (2008) Seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics*, 18, 213–226.
<https://doi.org/10.1080/09524622.2008.9753600>
- Vacher, J.-P., Kok, P.J.R., Rodrigues, M.T., Dias Lima, J., Lorenzini, A., Martinez, Q., Fallet, M., Courtois, E.A., Blanc, M., Gaucher, P., Dewynter, M., Jairam, R., Ouboter, P., Thébaud, C. & Fouquet, A. (2017) Cryptic diversity in Amazonian frogs: integrative taxonomy of the genus *Anomaloglossus* (Amphibia: Anura: Aromobatidae) reveals a unique case of diversification within the Guiana Shield. *Molecular Phylogenetics and Evolution*, 112, 158–173.
<https://doi.org/10.1016/j.ympev.2017.04.017>
- Woodhams, D.C. & Alford, R.A. (2005) Ecology of chytridiomycosis in rainforest stream frog assemblages of tropical Queensland. *Conservation Biology*, 19, 1449–1459.
<https://doi.org/10.1111/j.1523-1739.2005.004403.x>