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On the brink of extinction: two new species of *Anomaloglossus* from French Guiana and amended definitions of *Anomaloglossus degranvillei* and *A. surinamensis* (Anura: Aromobatidae)

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Abstract

A large portion of the amphibian species occurring in Amazonia remains undescribed. A recent study on species delineation in *Anomaloglossus*, a genus endemic to the Guiana Shield, demonstrated the existence of two undescribed species previously identified as *A. degranvillei*, which we describe herein. In addition to divergence at the molecular level, these two new taxa are also distinguished by subtle morphological characters and substantial differences in the advertisement calls (note length, dominant frequency, note structure). One species occurs in the hilly lowlands of north-eastern French Guiana and is mainly distinguished from its closest relatives by a small body size (15.9–18.8 mm in males) and by vocalisations characterized by the emission of short notes of 0.09 s on average. The other species is only known from the Itoupé Massif in southern French Guiana and is mainly distinguished from its closest relatives by a moderate body size (19.4–20.4 mm in males) and by vocalisations characterized by the emission of long notes of 0.23 s on average. We also provide amended definitions for two previously described species in the *A. degranvillei* species group: *A. degranvillei*, which is endemic to a few massifs in central French Guiana, and *A. surinamensis*, which is distributed throughout Suriname and French Guiana. The new species described here and *A. degranvillei* have very narrow ranges within French Guiana and seem to have rapidly declined during the last decade. Therefore, we suggest *A. degranvillei* and *A. dewynteri* to be considered as "Critically Endangered" and *A. blanci* as "Vulnerable" according to the IUCN standards.

Key words: Amazonia, conservation, decline, endemism, Guiana Shield, taxonomy

Introduction

Despite a striking boost in amphibian species descriptions during the last decades (Köhler *et al.* 2005; Giam *et al.* 2012), many tropical regions such as Amazonia still harbour a vast number of undescribed species (Fouquet *et al.* 2007, 2012; Funk *et al.* 2012). This is partly due to challenging delineation among closely related anuran species often displaying subtle interspecific morphological differentiation. Nevertheless, many recent studies combining morphology with other lines of evidence, particularly bioacoustics and molecular data, have been successful in delineating species that form vast complexes in Amazonia (e.g. Caminer *et al.* 2017; Rojas *et al.* 2016).

The Guiana Shield endemic genus *Anomaloglossus* (Grant *et al.* 2017) is one of these morphologically cryptic groups of frogs hiding undescribed species. They are all terrestrial, and most of the 26 nominal species are associated with streams. This is the case of the two described species forming the *Anomaloglossus degranvillei* group: *A. degranvillei* Lescure, 1975 and *A. surinamensis* Ouboter & Jairam, 2012. *Anomaloglossus degranvillei*

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was described by Lescure (1975), who designated a specimen from Atachi Bakka, a remote mountain range in the west-central part of French Guiana, as the holotype. Paratypes are from dispersed localities throughout French Guiana. The species was subsequently reported from Suriname (Lescure & Marty 2001) and Guyana (Grant *et al.* 2006), although it was later demonstrated by Kok *et al.* (2006) that the records from Guyana belong to a morphologically roughly similar species named *Anomaloglossus kaiei* Kok, Sambhu, Roopsind, Lenglet & Bourne, 2006. Likewise, the populations from Suriname, although morphologically similar to *A. degranvillei*, also correspond to a distinct species that was described as *A. surinamensis* by Ouboter and Jairam (2012). Molecular evidence revealed that *A. surinamensis* occurs in French Guiana (Fouquet *et al.* 2012), where its distribution overlaps with that of *A. degranvillei*. The type material of *A. degranvillei* might therefore include more than one species. This hypothesis is strengthened by molecular data showing the existence of several deeply divergent mtDNA linages within *A. degranvillei* and *A. surinamensis* (Vences *et al.* 2003; Grant *et al.* 2006; Fouquet *et al.* 2007, 2012).

More recently, Vacher *et al.* (2017) using molecular, morphological, bioacoustical, and natural history data investigated species boundaries among *Anomaloglossus* from the Guiana Shield lowlands including topotypical material of *A. degranvillei* and *A. surinamensis*. Their study revealed a contrasted pattern of phenotypic evolution between *A. degranvillei* and *A. surinamensis*. *Anomaloglossus surinamensis* was shown to harbour five highly divergent mtDNA lineages, but little phenotypic differentiation among populations. In contrast, and despite less divergent mtDNA lineages, a clear differentiation was detected, both in calls and body size, among the populations harbouring the three mtDNA lineages forming *A. degranvillei*. That study implied that *A. degranvillei* sensu stricto is endemic to a few massifs of central French Guiana, and that other populations previously assigned to this species in northern French Guiana and on the Itoupé massif belong to two undescribed species.

We here provide a formal description of these two species as well as amended definitions for *Anomaloglossus degranvillei* and *A. surinamensis*. We also discuss the conservation status of these species as our field observations raise concerns about possible declines.

Material and methods

Fieldwork. We undertook fieldwork in many localities in French Guiana during the last decade and collected specimens and tissue samples, recorded calls and ecological data of *Anomaloglossus degranvillei* sensu lato in 14 of these localities (Figure 1). However, these animals remain geographically very localised, secretive and usually not abundant. Therefore, only limited material is currently available. The sampling locations were: (1) the type locality of *A. degranvillei* (Atachi Bakka), explored by one of us (PG) in 2009, while a second expedition (by JPV & BV) in 2015 failed to find any individual; (2) at the foot of Mont Galbao where two specimens of *A. degranvillei* were found in 2009 (by AF), but a second attempt by three of us (AF, BV, EC) failed to detect any specimen in 2013; (3) on Mont Itoupé, where a preliminary exploration was undertaken in 2010 during which many individuals were observed along streams, and two individuals collected, but unfortunately badly preserved. A second expedition in 2016 succeeded in detecting the species, but in very low density with only four individuals observed (three collected). A last expedition in 2017 (EC) detected two calling males and two juveniles at that locality; and (4) in north-eastern French Guiana where well-preserved specimens were collected from three localities. Eight localities in this area were surveyed in 2010 and 2016, and only five of them (Patawa, Coq de Roche, Réserve Trésor, RN2 Corridor 5, RN2 Corridor 7) still seemed to harbour large populations according to our most recent surveys, whereas the three other historical populations seem to have gone extinct (Montagne Favard, Cacao, Tibourou) (Reizine 2016).

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 before preservation of the individuals. All specimens were tagged and fixed in 10% formalin before being transferred in a solution of 70% ethanol for permanent storage. Type specimens were deposited at the Museum national d'Histoire naturelle (Paris, France) (MNHN2017.0103–114) and the Royal Belgian Institute of Natural Sciences (Brussels, Belgium) (IRNSB4198–200).

Molecular analysis. The phylogenetic relationships among delineated species of the *A. degranvillei* species group remained poorly supported in Vacher *et al.* (2017) due to the small size of the DNA locus used (400 bp).

Therefore, we selected one representative of each species of the *A. degranvillei* species group (except *A. surinamensis*, for which three representatives were included) and acquired additional genomic data in order to determine these relationships.

DNA was isolated from liver tissue using the Wizard Genomic extraction protocol (Promega; Madison, WI, USA). Mitogenomes were sequenced and assembled following the method described in Vacher *et al.* (2016). We used 200 ng of DNA to create a DNA sequencing library that was hybridized and sequenced on a 1/24th of lane of an Illumina HiSeq 2500 flow cell (Illumina Inc., San Diego, CA). The mitochondrial genomes were assembled using the python-based organelle assembler Org.Asm (Coissac 2016). The resulting genomes were verified and completed when necessary with an iterative mapping strategy implemented in the software Geneious v.9 (Kearse *et al.* 2012). The mitogenomes were annotated with the MITOS web annotator (Bernt *et al.* 2013), and all gene annotations were subsequently verified and corrected when necessary in Geneious v.9 (Kearse *et al.* 2012). All six new mitogenomes have been deposited in GenBank (Appendix 3).

We then used MAFFT v.7 (Katoh *et al.* 2013) with default parameters to align the six mitogenomes together with 32 additional 16S DNA sequences of the *A. degranvillei* clade used by Vacher *et al.* (2017) and the already available mitogenome of *A. baeobatrachus* (Vacher *et al.* 2016) as outgroup, excluding the control region, resulting in an alignment of 15,406 base pairs (bp). We conducted a Maximum Likelihood phylogenetic analysis on this alignment using RAxML Next Generation (Flouri *et al.* 2014; Stamatakis 2014). We considered a single partition applying a GTR+I+G model and 500 bootstrap replicates.

Distribution data. Twenty-two adult specimens of *Anomaloglossus degranvillei* sensu lato were collected during daytime in French Guiana (see above). Occurrence data from 16 additional localities are based on available molecular data, direct field observations and the type series of *A. degranvillei*. In total, *A. degranvillei* sensu lato is reported from 21 localities in French Guiana (Appendix 1; Figure 1). This material was compared with 12 adult specimens of the parapatric *A. surinamensis* from three localities in French Guiana and one in Suriname (see Appendix 2).

Morphometric analysis. Sex of adult specimens was determined either in the field via calling activity, or in the laboratory by checking the condition of vocal slits and gonads. We followed the terminology of diagnostic characters and measurements (rounded to the nearest 0.1 mm using electronic digital callipers under a stereomicroscope) provided in Caldwell *et al.* (2002), with modifications from Grant and Rodríguez (2001) to facilitate congeneric comparison. We measured 16 variables: snout-vent length (SVL); head length from angle of jaw 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); 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 outer 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). Diameter of tympanum was not measured, as it is inconspicuous in species of the *A. degranvillei* species group. Webbing formula follows Savage and Heyer (1967) and Lescure (1975) with modifications suggested by Myers and Duellman (1982) and Savage and Heyer (1997).

Acoustic analysis. We recorded the advertisement call of 11 specimens of *Anomaloglossus degranvillei* sensu lato and of 20 specimens of *A. surinamensis* during various field trips in French Guiana and Suriname. The material used for call recording included Olympus LS11 and Zoom H4N digital recorders, attached to a Sennheiser ME-66 supercardioid microphone powered by a K6P module. Species of the *A. degranvillei* clade (sensu Vacher *et al.* 2017) regularly emit single-note calls, and we considered three variables for our analyses: note length, inter-note interval, and dominant frequency, following Kok and Kalamandeen (2008) and Köhler *et al.* (2017). We 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) using 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 R package Seewave (Sueur *et al.* 2008).

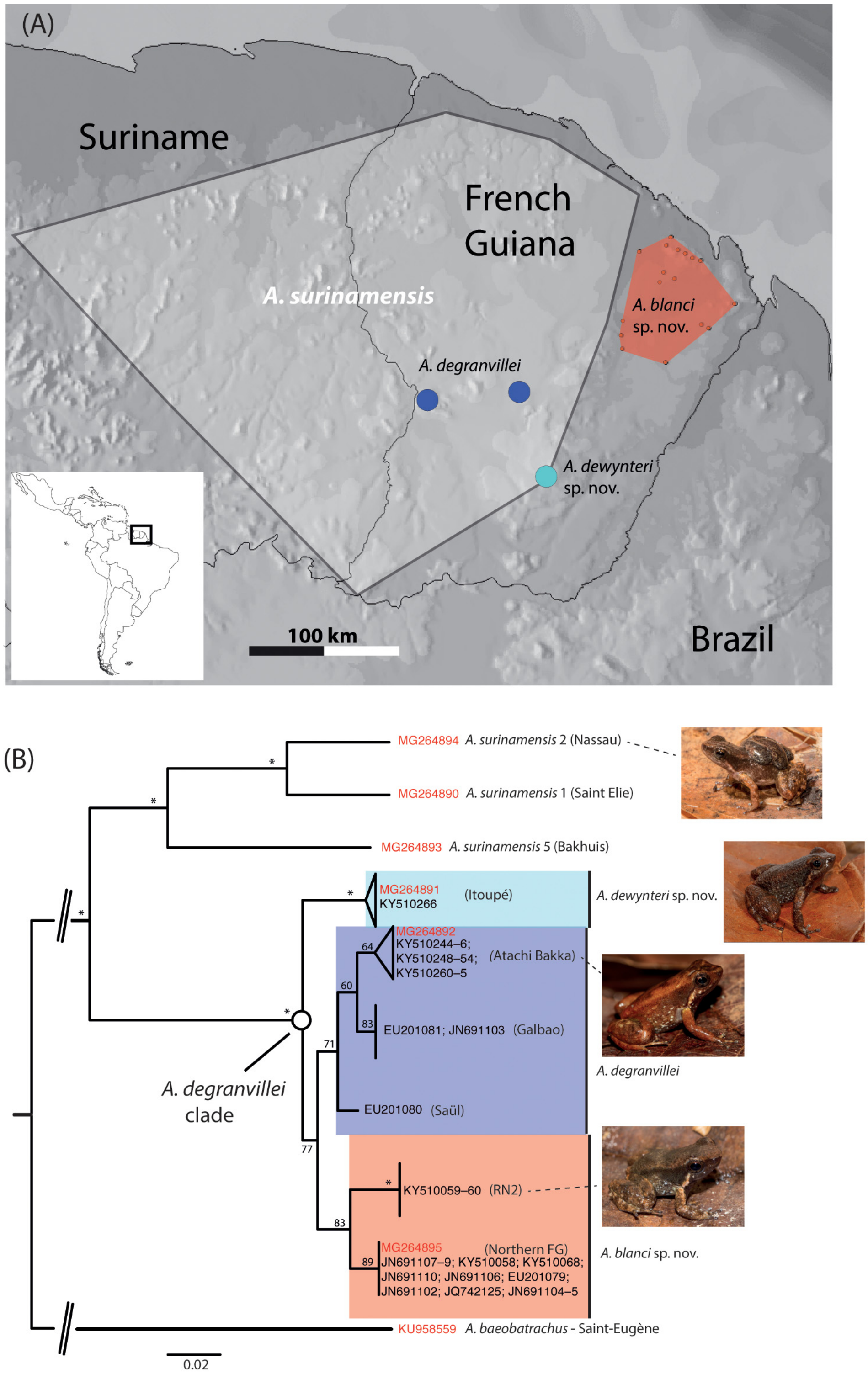

FIGURE 1. (A) Map of occurrences of the four species of the *A. degranvillei* species group. The range of *A. surinamensis* is depicted by a grey convex polygon. (B) Best ML tree obtained from RAxML NG using >15kb of mtDNA for six terminals (accession numbers in red) and 418 bp of 16S for 32 terminals (accession numbers in black). The tree is rooted on *Anomaloglossus baeobatrachus*. Bootstrap values are given in % for each node (*=99 or 100%).

Results

Phylogenetic results. Previous analysis of Vacher *et al.* (2017) using 418 bp of 16S rDNA included 37 terminals of the *A. degranvillei* clade (20 terminals of *A. degranvillei*, two of *A.* sp. "Itoupé" and 15 of *A.* sp. "North FG") and demonstrated the existence of three main lineages within the clade, but obtained low support for their interrelationships. The new phylogenetic analysis using >15 kb of mtDNA for selected terminals strongly supports (bootstrap=77%) *Anomaloglossus* sp. *"*Itoupé" as the sister species of a clade formed by *A. degranvillei* and *A.* sp. "North FG" (Figure 1B). *Anomaloglossus* sp. *"*Itoupé" is described below as *A. dewynteri* sp. nov. and *A.* sp. "North FG" as *A. blanci* sp. nov. Along with *A. degranvillei* these three taxa form the clade (bootstrap=100%) sister to *A. surinamensis*.

Species description

***Anomaloglossus blanci* sp. nov.**

Colostethus degranvillei — Lescure 1975 (in part): 414; Lescure & Marty 2001 (in part): 86
Anomaloglossus degranvillei — Fouquet *et al.* 2007 (in part): Fig. S2; Fouquet *et al.* 2012 (in part): 469
Anomaloglossus sp. "north FG" — Vacher *et al.* (2017)

Holotype. MNHN2017.0103 (field no. AF0953), an adult male, collected by Michel Blanc and Maël Dewynter, 10 August 2014, corridor 7 on Route Nationale 2, French Guiana, 4.0639 N 52.0416 W, ~100 m elevation (Figure 2).
Paratypes. Ten specimens: MNHN2017.0110 (field no. AF0952), an adult male, collected with the holotype (carrying two froglets on its back). MNHN2017.0105 (field no. AF0293), an adult male collected by Antoine Fouquet, 25 May 2007, crique Diamant near Patawa Camp, French Guiana, 4.5161 N 52.1005 W, ~200 m elevation. MNHN2017.0106–8 (field no. AF0878, AF0932, AF0933), three adult males collected by Antoine Fouquet, 01 February 2013, crique Diamant near Patawa Camp, French Guiana, 4.5161 N 52.1005 W, ~200 m elevation. MNHN2017.0104 (field no. AF0292), an adult female collected by Antoine Fouquet, 25 May 2007, crique Diamant near Patawa Camp, French Guiana, 4.5161 N 52.1005 W, ~200 m elevation. MNHN2017.0109 (field no. AF1332), an adult male collected by Maël Dewynter, 16 December 2013, Saut Grand Machicou, French Guiana, 3.8974 N 52.5836 W, ~150 m elevation. IRSNB4198 (field no. PK3287), an adult male collected by Philippe J. R. Kok, 18 April 2010, near Patawa Camp, French Guiana, ca. 4.5161 N 52.1005 W, ~200 m elevation. IRSNB4199, 4200 (field no. PK3284, 3286), two juvenile females collected by Philippe J. R. Kok, 18 April 2010, near Patawa Camp, French Guiana, ca. 4.5161 N 52.1005 W, ~200 m elevation.

Etymology. This species is dedicated to our friend Michel Blanc, in honour of his invaluable contribution to field herpetology in French Guiana, notably the discovery of many previously undocumented species and crucial natural history observations.

Definition and diagnosis. We assigned the new species to the genus *Anomaloglossus* based on previous studies (Fouquet *et al.* 2012; Vacher *et al.* 2017) and the presence of a median lingual process. The new species belongs to the *A. degranvillei* clade (Vacher *et al.* 2017).

(1) Small-sized *Anomaloglossus* (average male SVL=16.9 mm [15.9–18.8, n=8], female SVL=17.9 mm [n=1]) (Table 1); (2) body robust; (3) skin tuberculate on dorsum (particularly the posterior half) and legs, with a larger tubercle on each eyelid, ventral skin smooth; (4) conspicuous dark brown to black glandulous supratympanic fold anteroventrally bordered by a light stripe (orange in life, cream in preservative) extending from the ventroposterior edge of the eye onto the upper arm to the anterior cubital region; (5) tympanum indistinct; (6) snout short and protruding in lateral view; (7) nares oriented ventrolaterally, situated near tip of snout; (8) Finger II shorter than Finger I when fingers adpressed; (9) tip of Finger IV almost reaching distal subarticular tubercle on Finger III when fingers adpressed; (10) distal subarticular tubercle on Finger III and IV indistinct; (11) Finger III not distinctly swollen in males; (12) Fingers II and III with preaxial fringes particularly developed in males, inconspicuous in females; (13) toes moderately webbed, with well-developed fringes on Toes II, III and IV (*sensu* Grant *et al.* 2006; keel-like lateral folds *sensu* Myers & Donnelly 2008); (14) tarsal keel well-defined, curved; (15) no black arm gland in males (*sensu* Grant & Castro 1998, see also Grant *et al.* 2006); (16) cloacal tubercles present; (17) paracloacal mark ill-defined but present (reddish in life, cream speckled with melanophores in preservative); (18) dorsolateral stripe present, faint, upper part of flanks much darker than dorsum, a thin middorsal raphe going from the tip of snout to behind the head and more rarely to the vent sometimes present; (19) ventrolateral stripe absent but ventral part of flanks lighter with white or bluish flecks (in life); (20) sexual dichromatism in throat colour pattern present, throat black in reproductive males, evenly grey with small ill-defined white dots in females; (21)

no sexual dichromatism in ventral colour pattern, abdomen mostly pale grey with small ill-defined white dots in both sexes, lower abdomen and ventral surface of legs yellowish in life and cream in preservative; (22) iris with metallic pigmentation and pupil ring interrupted ventrally and dorsally by transversal black pigmentation; (23) median lingual process longer than wide, tapered, bluntly pointed, smooth (non-papillate), reclined in pit; (24) single note call of 0.090–0.103 s length and dominant frequency at 4.48–5.41 kHz (n=6) (Figure 3; Table 2).

Morphological comparisons with other lowland *Anomaloglossus*. The only other species group co-occurring with the *Anomaloglossus degranvillei* group is the *A. stepheni* group, represented in French Guiana by *A. baeobatrachus*, which is readily distinguishable by conspicuous dorsolateral stripes, swollen third finger in males and absence of webbing and fringes on toes.

Within the *Anomaloglossus degranvillei* group, *A. blanci* can be distinguished from *A. surinamensis* (Figure 4) by (1) a shorter snout, protruding in lateral view (vs. rounded in *A. surinamensis*); (2) a larger body size ($\bar{X}$=16.9; range 15.9–18.8 mm in males [n=8] and one adult female measuring 17.9 mm in *A. blanci* vs. $\bar{X}$=14.75, range 14.0–15.3 mm in males [n=8] and $\bar{X}$=16.5, range 16.0–17.1 mm in females [n=4] in *A. surinamensis*); (3) large fringes on fingers and toes in males (narrow in *A. surinamensis*); (4) presence of a large tubercle on the top of the eyelid (inconspicuous in *A. surinamensis*); (5) ventral colouration entirely grey with small ill-defined white dots (vs. grey throat and cream belly, the latter with irregular grey blotches less abundant posteriorly in *A. surinamensis*); (6) yellowish ventral surface of thigh (vs. light grey and more heavily spotted with black in *A. surinamensis*); (7) large MLP (>0.5 mm vs. <0.5 mm in *A. surinamensis*); (8) call characterized by longer pulsed notes ($\bar{X}$=0.094, range 0.090–0.103 s in *A. blanci* [n=6] vs. tonal note $\bar{X}$=0.032, range 0.028–0.037 s in *A. surinamensis* [n=20]) emitted between longer intervals ($\bar{X}$=1.414, range 1.200–1.906 s in *A. blanci* [n=6] vs. $\bar{X}$=0.573, range 0.372–0.825 s in *A. surinamensis* [n=20]), but both species have a similar dominant frequency ($\bar{X}$=4.75, range 4.48–5.41 kHz in *A. blanci* [n=6] vs. $\bar{X}$=4.89 kHZ, range 4.55–5.35 kHz in *A. surinamensis* [n=20]).

Anomaloglossus blanci can be distinguished from *A. degranvillei* (Figure 5) by (1) a smaller size ($\bar{X}$=16.9; range 15.9–18.8 mm in males [n=8] and one female measuring 17.9 mm in *A. blanci* vs. $\bar{X}$=20.17; range 19.60–20.50 mm in males [n=3] and $\bar{X}$=23.40, range 22.4–23.9 mm in females [n=5] of *A. degranvillei*); (2) belly pale grey with small ill-defined white dots (from solid black to dark grey with abundant small conspicuous white spots in *A. degranvillei*); (3) ventral surface of thighs yellowish in life and cream in preservative (dark grey in *A. degranvillei*); (4) call with shorter notes (0.090–0.103 s in *A. blanci* [n=6] vs. 0.157–0.160 s in *A. degranvillei* [n=2]) and higher dominant frequency (4.48–5.41 kHz in *A. blanci* [n=6] vs. 3.60–3.62 s in *A. degranvillei* [n=2]).

Description of the holotype (Figure 2). An adult male, 17.1 mm SVL; body robust; head wider than long, HL 89% of HW; HL 33% of SVL; dorsal skin tuberculate, one enlarged tubercle on each eyelid, snout long (SL 53% 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 28% of HL, 70% of ED. Tympanum indistinct; supratympanic fold present extending from posteroventral corner of the eye onto the upper arm; choanae small, circular, located anterolaterally.

Forelimb slender, skin tuberculate; metacarpal ridge absent; 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 and III; Finger III not distinctly swollen; 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 0.6 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 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 III and IV are conspicuous; Finger I subarticular tubercle largest followed by Finger II subarticular tubercle, basal subarticular tubercle on Finger III and IV smaller, subequal.

Hind limb robust, skin tuberculate; TL 46 % 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 0.8 mm. Feet moderately webbed, webbing present between Toes I–IV, webbing without melanophores; lateral fringes present on all toes. Toe webbing formula **I**$1^{1/2}$-1^{-}**II**$1^{1/2}$-2^{-}**III**1^{-}-3**IV**3^{-}-2^{+}**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, extending distally to the fringe on preaxial edge of Toe I. Metatarsal fold strong.

TABLE 1. Morphometric measurements summary statistics for the four species of the *Anomaloglossus degranvillei* clade

			SVL	HL	HW	SL	EN	IN	EL	IO	FAL	HAND	WFD	TL	FL	WTD	ThL	1FiL
A. blanci sp. nov.	M (N=8)	X	16.88	5.54	6.25	2.88	1.54	2.46	2.28	2.10	3.64	3.99	0.59	7.85	7.05	0.77	8.48	2.35
		sd	0.90	0.20	0.30	0.09	0.11	0.15	0.28	0.12	0.21	0.26	0.06	0.48	0.4	0.06	0.58	0.35
	F (N=1)	X	17.90	5.42	7.24	2.23	1.42	2.40	2.60	1.80	3.23	3.19	0.64	7.60	6.21	0.77	8.13	1.60
		sd	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
A. dewynteri sp. nov.	M (N=3)	X	19.90	6.43	7.50	3.63	2.00	3.03	2.60	2.60	4.37	5.05	0.80	9.27	8.60	1.00	10.43	2.73
		sd	0.50	0.15	0.10	0.15	0.00	0.06	0.00	0.10	0.06	0.21	0.00	0.15	0.35	0.00	0.45	0.06
	F (N=0)	X	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		sd	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
A. degranvillei	M (N=3)	X	20.17	6.73	7.53	3.53	1.93	3.03	2.63	2.60	4.53	4.93	0.80	9.63	8.40	1.00	10.13	2.80
		sd	0.49	0.15	0.40	0.06	0.06	0.12	0.06	0.10	0.15	0.25	0.00	0.35	0.40	0.00	0.40	0.10
	F (N=5)	X	23.40	6.90	8.91	3.02	2.03	3.16	3.14	2.80	4.88	4.17	0.77	10.26	8.41	0.95	11.30	2.40
		sd	0.56	0.48	0.34	0.30	0.13	0.17	0.26	0.19	0.40	0.44	0.09	0.37	0.45	0.10	0.55	0.23
A. surinamensis	M (N=8)	X	14.75	4.68	5.11	2.43	1.43	2.19	1.99	1.81	3.28	3.54	0.50	7.16	6.40	0.60	7.43	2.00
		sd	0.42	0.13	0.15	0.09	0.05	0.08	0.06	0.06	0.12	0.14	0.00	0.29	0.19	0.00	0.29	0.08
	F (N=4)	X	16.50	5.60	5.83	2.60	1.58	2.45	2.35	2.00	3.25	3.78	0.53	7.65	7.15	0.60	8.23	1.38
		sd	0.45	0.16	0.15	0.22	0.13	0.17	0.17	0.18	0.17	0.19	0.05	0.26	0.24	0.12	0.34	0.10

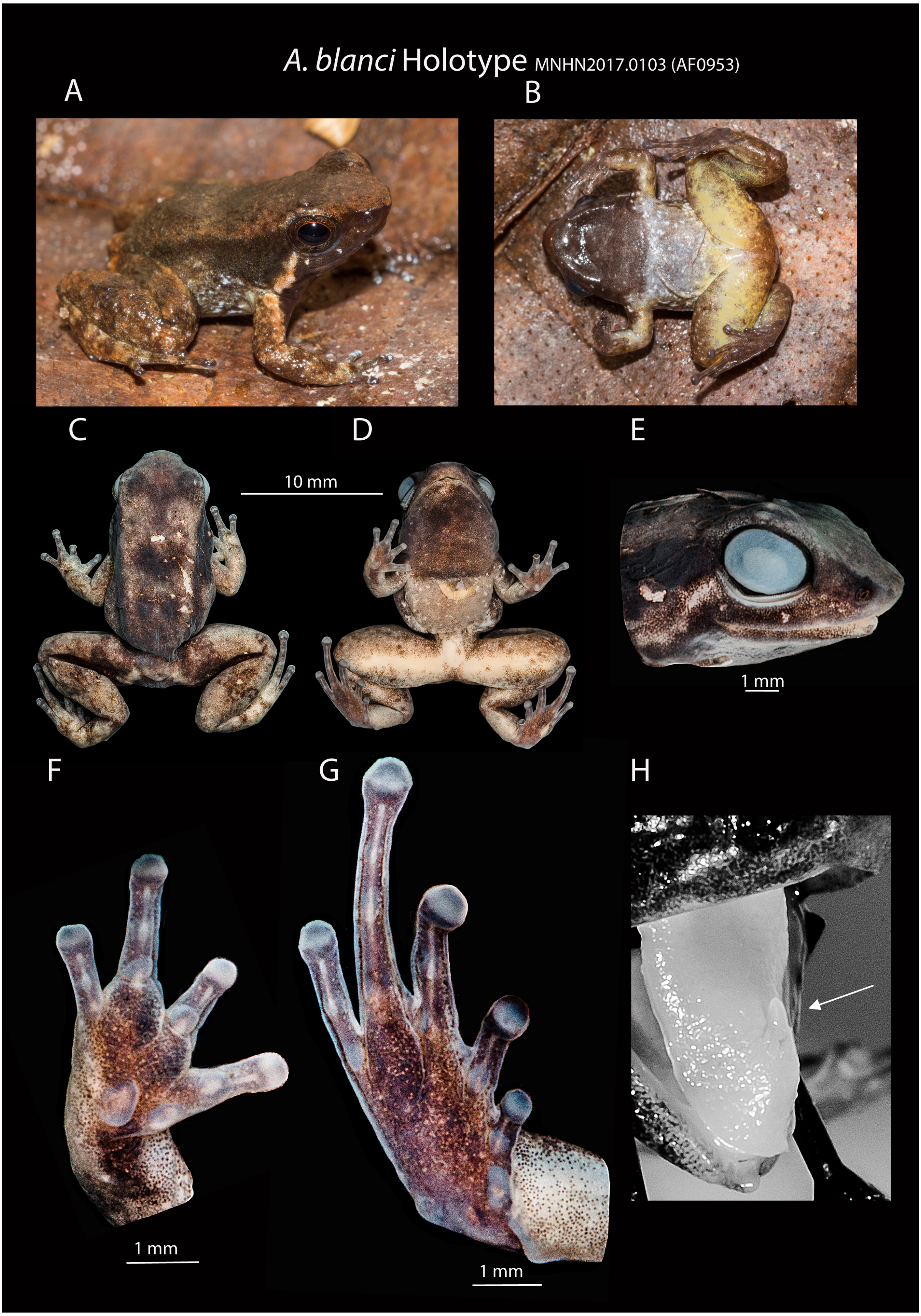

FIGURE 2. Holotype of *Anomaloglossus blanci* sp. nov MNHN2017.0103 (AF0953): (A) in life dorsolateral view; (B) in life ventral view; (C) in preservative dorsal view; (D) in preservative ventral view; (E) in preservative head lateral view; (F) right hand; (G) right foot; (H) median lingual process.

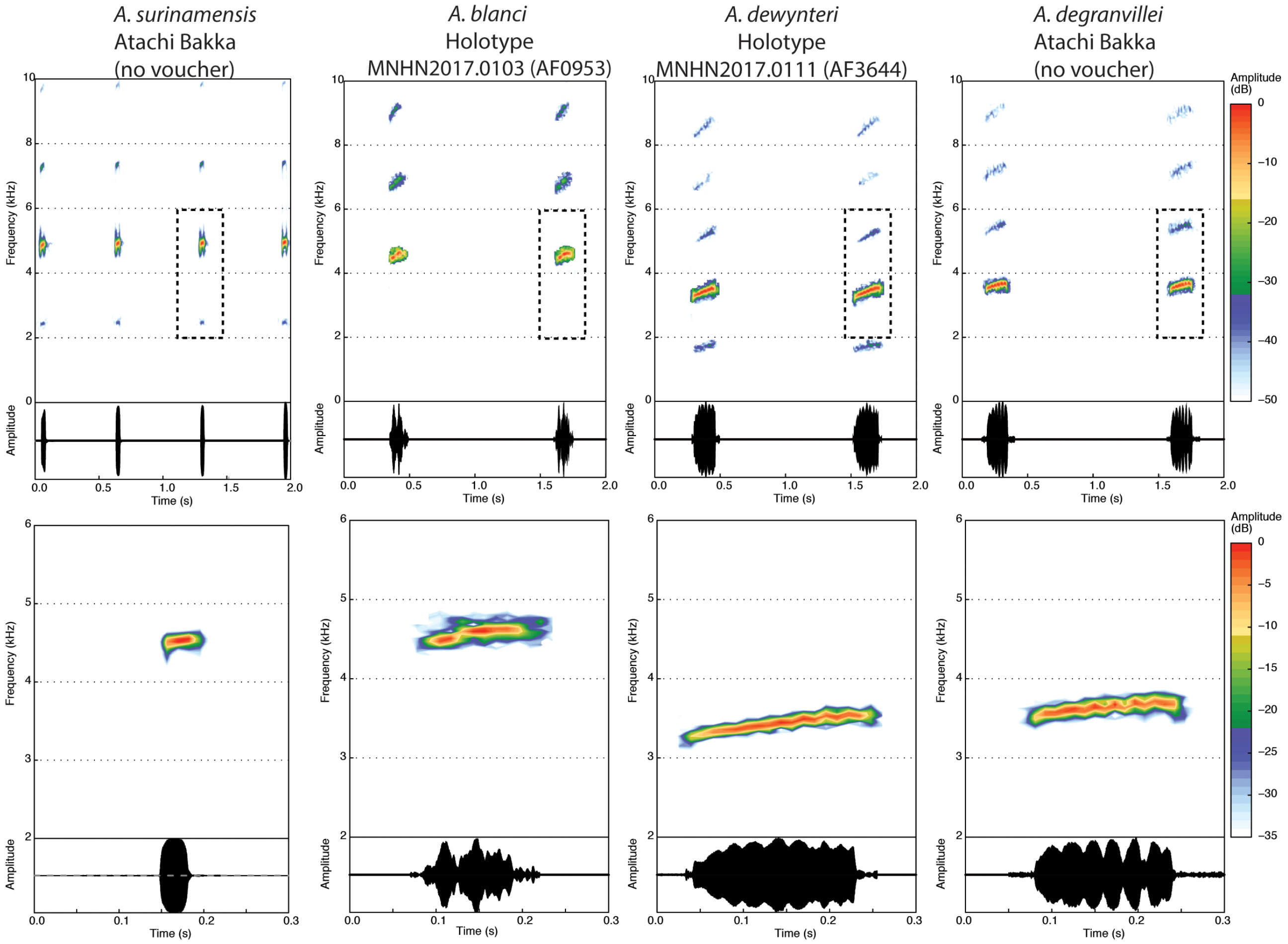

FIGURE 3. Spectrograms and oscillograms of typical call of the four species of the *Anomaloglossus degranvillei* clade with two time windows; 2 s and 0.3 s. For *A. blanci* and *A. degranvillei* the background noises masked the fundamental frequency.

Colour of holotype in life (Figure 2). Dorsal colour chestnut brown, with a diffuse dark brown hourglass pattern extending from the interorbital region to middorsum immediately followed by a diffuse dark brown patch over the sacrum. Faint dorsolateral stripes. Black lateral mask extending from tip of snout to the upper part of flanks, tapering to groin and containing most of the indistinct tympanum and supratympanic fold, only interrupted by a large postocular orange stripe extending from eye onto the upper arm down to the anterior cubital region. Upper lip with 2–3 small light blue blotches. Posteroventral part of flanks pale brown with a few small white-blue and dark brown blotches. Throat solid black becoming paler posteriorly; belly grey with ill-defined light blue and white spots, lower part of belly and ventral surface of thighs and arms orange with a few ill-defined grey spots. Iris with reddish metallic pigmentation and pupil ring interrupted dorsally and ventrally by transversal pigmentation.

Upper arm pale orange dorsally, black on its anterior part (same colour as throat), and dark brown with ill-defined orange marbling on its posterior part. Lower arm light brown with two ill-defined dark brown cross bands. Dorsal surfaces of thigh, shank and tarsus with diffuse combination of orange, pale brown and a wide ill-defined dark brown cross band; more cross bands on tarsus. Reddish paracloacal marks. Toes and digits with small light blue dots. Palms and soles dark grey.

Colour of holotype in preservative. After three years in preservative (70% ethanol), the specimen faded and the dorsal colouration now varies from brown to grey. The bluish freckles turned cream as did the orange and reddish marks.

Variation among type specimens. Measurements (range, mean, and standard deviation) of the type series are provided in Table 1. Intraspecific variation is high and adult dorsal colouration varies from brown to reddish brown. Most specimens have dark brown blotches on dorsum. One male (MNHN2017.0108/AF0933) has a middorsal raphe running from the tip of the snout to the vent; in four males (MNHN2017.0105–7/AF0293, 0878, 0932 and MNHN2017.0109/AF1332; Figure 6) that raphe is inconspicuous and extends only from the tip of the snout to the interorbital region. Flanks can be dark brown to light grey rendering the lateral black band more or less conspicuous. Additionally, overall colouration and tuberculation may vary with light intensity, time of the day and probably reproductive activity as males carrying tadpole apparently display overall lighter colours, smoother skin and sharper contrasts while calling males are very dark and highly tuberculate.

Advertisement call (Figure 3). Six specimens (three uncollected) calling from the leaf litter 1–3 meters away from a stream were recorded from a distance of about 1 m and at temperatures ranging from 23 to 26°C. They emitted single short pulsed notes (note length $\bar{X}$=0.094 s; range 0.090–0.103 s) at a regular pace (inter-note interval $\bar{X}$=1.414 s; range 1.200–1.906 s). The spectral structure of the note has a developed harmonic structure and the dominant frequency is 4.75 kHz on average (range 4.48–5.41 kHz) with a slight upward modulation (ca. 0.1 kHz).

Distribution and ecology. *Anomaloglossus blanci* inhabits small sandy or rocky streams at low elevations (from 50 to 200 m elevation) often close to larger tributaries (e.g. Crique Diamant, Approuague). Males call from stream banks during the day with peak in intensity at dawn (6–7 am) and late afternoon (4–5 pm) during the rainy season, but also during humid days of the dry season.

Eighteen populations have been documented in north-eastern French Guiana (Figure 1), but despite intensive surveys of these populations in 2016, no individual could be found in three of them. No noticeable degradation of the habitat has been observed. Interestingly, this species does not co-occur with *A. surinamensis*, whose populations seem stable.

No tadpole before Gosner stage 41 has been observed, either in the water or carried by males. However, two observations have been made of adults carrying tadpoles at a late development stage (> stage 41) (Figure 6). The tadpoles are endotrophic and lack functional mouth. If they are detached from the back of their father, they die within a few hours despite humid and ideal thermal conditions (pers. obs.). These observations suggest that the tadpoles may undergo a phase of nidicolous development after hatching and only complete their development on the back of the adult from an advanced stage.

Only 1–4 tadpoles of the same stage were observed at a time carried by adults. This reduced clutch size is likely linked to the fact that large eggs are needed to complete endotrophic development. However, adults were often observed carrying tadpoles at two different stages, demonstrating that they can keep mating while already attending a clutch. This is likely linked to the extended time needed for the tadpoles to develop until complete metamorphosis.

***Anomaloglossus dewynteri* sp. nov.**

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

Holotype. MNHN2017.0111 (field no. AF3644/APA-973-23-2), an adult male, collected by Antoine Fouquet, 11 January 2016, near base camp on Mont Itoupé, French Guiana, 3.0230 N 53.0955 W, elevation ca. ~600 m (Figure 7).

Paratopotypes. Three specimens: MNHN2017.0112 (field no. AF0574; not measured because badly preserved), an adult male, collected by Maël Dewynter, 05 April 2010, near base camp on Mont Itoupé, French Guiana, 3.0230 N 53.0955 W, ~600 m elevation. MNHN2017.0113–4 (field no. AF3686/APA-973-23-1, AF3645/APA-973-23-3), two adult males, collected by Antoine Fouquet, with the holotype.

Etymology. This species is dedicated to our friend Maël Dewynter for his invaluable contribution to the herpetology of French Guiana.

Adult definition and diagnosis. We assigned the new species to the genus *Anomaloglossus* based on previous studies (Fouquet *et al.* 2012; Vacher *et al.* 2017) and the presence of a median lingual process. The new species belongs to the *A. degranvillei* clade according to Vacher *et al.* (2017).

(1) Medium-sized *Anomaloglossus* (average male SVL=19.9 mm [19.4–20.4, n=3], female unknown) (Table 1); (2) body robust; (3) skin tuberculate on dorsum (particularly the posterior half) and legs, with a larger tubercle on each eyelid, ventral skin smooth; (4) conspicuous dark brown to black glandulous supratympanic fold flanked anteroventrally by a discontinuous stripe (orange in life, cream in preservative) running from the ventroposterior edge of the eye and extending onto the upper arm; (5) tympanum indistinct; (6) snout short and acute in lateral

view; (7) nares oriented ventrolaterally, situated near tip of snout; (8) Finger II shorter than 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 on Finger III and IV indistinct; (11) Finger III not distinctly swollen in males; (12) fingers with fringes particularly developed on preaxial edges of Fingers II and III; (13) toes moderately webbed, with well-developed fringes (*sensu* Grant *et al.* 2006; keel-like lateral folds *sensu* Myers & Donnelly 2008); (14) tarsal keel well-defined, curved, slightly tuberclelike; (15) no black arm gland in males (*sensu* Grant & Castro 1998. see also Grant *et al.* 2006); (16) cloacal tubercles present; (17) paracloacal mark inconspicuous; (18) dorsolateral stripe absent or inconspicuous, dorsal part of flanks darker than dorsum; (19) ventrolateral stripe sometimes present as a broken, poorly defined pale brown blotch, ventral part of flanks with flecks white or bluish (in life); (20) sexual dichromatism in throat colour pattern unknown (although likely because present in other species of the clade), throat solid black in reproductive males; (21) abdomen and ventral side of legs dark grey with small ill-defined white dots; (22) iris with metallic pigmentation and pupil ring interrupted ventrally by transversal black pigmentation; (23) median lingual process longer than wide, tapered, bluntly pointed, smooth (non-papillate), reclined in pit; (24) single note call of 0.221–0.237 s length and dominant frequency at 3.45–3.59 kHz (n=3) (Table 2; Figure 3).

TABLE 2. Acoustic measurements summary statistics for the four species of the *Anomaloglossus degranvillei* clade.

		Note length (s)	Internote length (s)	Dominant Frequency (kHz)
A. blanci sp. nov. (N=6)	X	0.09	1.41	4.75
	sd	0.01	0.27	0.37
A. dewynteri sp. nov. (N=3)	X	0.23	0.76	3.52
	sd	0.01	0.15	0.07
A. degranvillei (N=2)	X	0.16	1.44	3.61
	sd	0.00	0.07	0.01
A. surinamensis (N=20)	X	0.03	0.57	4.89
	sd	0.00	0.10	0.20

Morphological comparisons with other lowland *Anomaloglossus*. The only other species group co-occurring with the *Anomaloglossus degranvillei* species group is the *A. stepheni* species group, represented by *A. baeobatrachus* in French Guiana, which is readily distinguishable by conspicuous dorsolateral stripes, swollen third fingers in males and absence of webbing and fringes on toes.

Within the *Anomaloglossus degranvillei* group, *A. dewynteri* can be distinguished from *A. surinamensis* (Figure 4) by (1) a shorter snout, acute in lateral view (vs. rounded in *A. surinamensis*); (2) a larger body size in males ($\bar{X}$=19.9 mm, range 19.4–20.4 mm in *A. dewynteri* [n=3] vs. $\bar{X}$=14.75, range 14.0–15.3 mm in *A. surinamensis* [n=8]); (3) more developed fringes on fingers and toes; (4) presence of a large tubercle on the top of the eyelid (inconspicuous in *A. surinamensis*); (5) belly dark grey with small white spots (vs. cream with irregular grey blotches less abundant posteriorly in *A. surinamensis*); (6) ventral surface of thigh dark grey (vs. cream with dark spots on the edges in *A. surinamensis*); (7) larger MLP (>0.5 mm vs <0.5 mm in *A. surinamensis*; (8) call characterized by much longer pulsed notes (pulsed note $\bar{X}$=0.228, range 0.221–0.237 s [n=3] in *A. dewynteri* vs. tonal note $\bar{X}$=0.032, range 0.028–0.037 s in *A. surinamensis* [n=20]) emitted between longer intervals ($\bar{X}$=0.76, range 0.60–0.88 s in *A. dewynteri* [n=3] vs. $\bar{X}$=0.573, range 0.372–0.825 s in *A. surinamensis* [n=20]) and with lower dominant frequency ($\bar{X}$=3.52, range 3.45–3.59 kHz in *A. dewynteri* [n=4] vs. $\bar{X}$=4.89 kHZ, range 4.55–5.35 kHz in *A. surinamensis* [n=20]).

Anomaloglossus dewynteri can be distinguished from *A. blanci* (Figure 2) by (1) its larger size in males (X=19.9 mm, range 19.4–20.4 mm in *A. dewynteri* [n=3] vs. $\bar{X}$=16.9, range 15.9–18.8 mm in *A. blanci* [n=8]); (2) belly from solid black to dark grey with abundant small conspicuous white spots (pale grey with small white ill-defined spots in *A. blanci*); (3) ventral surface of thighs dark grey (yellowish in life and cream in preservative in *A. blanci*); (4) strong metacarpal ridge (inconspicuous in *A. blanci*, Figures 2F, 7F); (5) call with longer notes (X=0.228, range 0.221–0.237 s [n=3] in *A. dewynteri* vs. $\bar{X}$=0.094, range 0.090–0.103 s in *A. blanci* [n=6]) and higher dominant frequency ($\bar{X}$=3.52, range 3.45–3.59 kHz in *A. dewynteri* [n=4] vs. $\bar{X}$=4.75, range 4.48–5.41 kHz in *A. blanci* [n=6]).

Anomaloglossus dewynteri can only be distinguished from the most similar *A. degranvillei* (Figure 5) by its call consisting of longer notes ($\bar{X}$=0.228, range 0.221–0.237 s [n=3] in *A. dewynteri* [n=4] vs. $\bar{X}$=0.158, range 0.157–0.160 s in *A. degranvillei* [n=2]) (Figure 3; Table 2). Molecular data provided by Vacher *et al.* (2017) demonstrated that these two species harbour well-differentiated mtDNA lineages (2.3% on 16S) and our phylogenetic analysis indicates that *A. dewynteri* is not the sister species of *A. degranvillei* (see below). *Anomaloglossus dewynteri* could possibly be distinguished from *A. degranvillei* by its more tuberculate skin and by its darker dorsal and lateral colouration. However, these two features should be taken with caution given the small number of specimens available and the paucity of available data from living specimens.

Description of the holotype (Figure 7). An adult male 19.9 mm SVL; body robust; head wider than long, HL 85% of HW; HL 32% of SVL; dorsal skin tuberculate, large tubercle on eyelids, snout large, rounded to nearly truncate in dorsal view, acute in lateral view, extending past lower jaw, SL 56% of HL. Nares located anterolaterally; canthus rostralis rounded but well defined, loreal region concave; IN 40% of HW; EN 31% of HL, 77% of ED. Tympanum indistinct; supratympanic fold present, extending from ventrodorsal corner of the eye onto the upper arm; choanae round, small, located anterolaterally.

Forelimb slender, skin tuberculate; metacarpal ridge present; HAND 25% 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 and III; Finger III not distinctly swollen; tip of Finger IV not reaching distal subarticular tubercle on Finger III when fingers appressed; finger discs expanded, wider than long, about 1.5X width of digit; width of disc on Finger III 0.8 mm. Relative lengths of adpressed fingers III > IV > I > II; palmar tubercle large, quadrangular. 1.0 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 of Fingers III and IV are conspicuous; Finger I subarticular tubercle largest followed by Finger II subarticular tubercle, basal subarticular tubercle on Finger III and IV smaller, subequal. The holotype has a missing left hand (all the individuals collected in 2016 had some atrophied or missing fingers/toes).

Hind limb robust, skin 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; discs on toes larger than width of toes; disc on Toe I only slightly larger than width of digit. Size of disc on Toe IV 1.0 mm. Feet moderately webbed, webbing present between Toes I–IV, webbing without melanophores; lateral fringes present on all toes. Toe webbing formula **I**0$^-$-1$^-$**II**1½-2$^-$**III**1$^-$-3**IV**3$^-$-2$^+$**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, 0.7 mm in length, outer metatarsal tubercle round, protuberant, 0.5 mm in diameter. Tarsal keel well defined, tubercle-like and strongly curved at proximal end, extending distally to the fringe on preaxial edge of Toe I. Metatarsal fold strong.

Colour of holotype in life (Figure 7). Dorsal colour dark brown, faint dorsolateral stripe, upper flanks black becoming slightly lighter ventrally with a few white-blue freckles. Supratympanic fold black bordered by a discontinuous orange postocular stripe. Upper lip brown, loreal and internarial region black. Throat solid black becoming slightly paler posteriorly, belly and ventral parts of legs dark grey with light blue freckles. Iris with reddish metallic pigmentation and pupil ring interrupted ventrally by transversal pigmentation.

Upper and posterior surfaces of arm pale orange, black anteriorly (same colour as throat). Dorsal surfaces of thigh, shank and tarsus with diffuse combination of orange, pale brown and two wide poorly defined dark brown cross bands; more cross bands on tarsus. Paracloacal marks inconspicuous. Toes and digits with small light blue dots. Palms and soles black.

Colour of holotype in preservative. After one year in preservative (70% ethanol), the specimen faded and he dorsal colouration now varies from brown to grey. The bluish freckles turned cream as well as the orange and reddish marks.

Variation among type specimens. Measurements (range, mean, and standard deviation) of the type series are provided in Table 1. There is only slight variation among specimens of the type series. However, specimens photographed in 2010 displayed a dorsal colouration going from brown with black blotches to uniform brick; flank colouration black with various pattern of brown ventroposterior marks as well as white and bluish dots (Figure 6).

Advertisement call (Figure 3). Three specimens (one uncollected) calling from the leaf litter near a stream were recorded from a distance of about 1 m and at temperatures ranging from 21 to 24°C. They emitted single pulsed notes (note length $\bar{X}$=0.228, range 0.221–0.237 s [n=3]) at a regular pace (inter-note interval $\bar{X}$=0.761, range

0.600–0.883 s). The spectral structure of the note has a developed harmonic structure and the dominant frequency is 3.52 kHz on average (range 3.45–3.59 kHz) with a slight upward modulation (ca. 0.2 kHz).

Distribution and ecology. *Anomaloglossus dewynteri* is only known from two rocky streams close to each other at 600 m elevation, on the slope of the Itoupé massif, an isolated mountain reaching 800 m elevation in the south-eastern part of French Guiana. Males call from the banks of these streams during the day and their activity seems fostered by rainfall. Many individuals were observed during the first exploration of the massif in 2010. However, only four individuals were detected in 2016 despite eight days of searching by four herpetologists, and despite any obvious perturbation of the habitat. This species co-occurs with *A. surinamensis* on the massif, but the two species were not found together along the same streams.

Anomaloglossus dewynteri has the same reproductive mode as *A. blanci* and *A. degranvillei*, with endotrophic tadpoles carried by the male until metamorphosis. In 2010, one individual carrying six metamorphs at similar stages (Gosner stages 42–43) was observed. We cannot exclude that these metamorphs are not from two different clutches of smaller size.

Comparison with the type series of *Anomaloglossus degranvillei*. Our examination of the original type series used by Lescure (1975) to describe *Anomaloglossus degranvillei* shows that it included three distinct species of the *A. degranvillei* clade occurring in French Guiana. Based on the original description and according to the characters observed in the holotype, we restrict the type series to the holotype and three of the original paratypes (MNHNP1973-1656–58) from Atachi Bakka (3.5455 N 53.9068 W).

Paratypes MNHNP1659–63 and MNHNP1667–70 from Eaux Clément (4.6556 N 52.2480 W) and MNHNP1665-66 from Cacao (4.5610 N 52.4629 W) correspond to *A. blanci* based on the following combination of characters: (1) body size comprised between 15.9–18.8 mm in males; (2) belly pale grey with small white freckles; and (3) protruding snout in lateral view.

Paratype MNHNP1973-1672 from Galbao (3.600 N 53.2833 W), MNHNP1664 from Saül (3.62556 N 53.2072 W) and MNHNP1676 from Crique Grégoire (5.0975 N 53.0506 W) correspond to *A. surinamensis* as inferred from the following combination of characters: (1) small body size (between 14.0–15.3 mm in males 16.0–17.1 mm in females); (2) snout short and rounded in lateral view; (3) toes moderately webbed, with fringes (4) abdomen and ventral side of legs cream with brown freckles.

Unfortunately, we could not examine LACM44211-12 from Crique Ipoussing (4.1307 N 52.5760 W), LG870–873 from Eaux Clément (4.6556 N 52.2480 W) and LACM44213–23 from Montagne Tortue (4.300 N 52.3667 W), but these localities lie within the range of *Anomaloglossus blanci* and, to our knowledge, no other species of the group occur there. These paratypes are thus excluded from the type series of *A. degranvillei*.

Amended definition of *Anomaloglossus degranvillei* (Figure 5)

Given the inclusion of three closely related species of *Anomaloglossus* in the original description of *A. degranvillei*, we here provide an amended definition of *A. degranvillei* improved by the examination of eight additional specimens collected in 2010 by one of us (PG) at the type locality as well as the re-examination of the type series deposited at the MNHN (Paris, France).

(1) Medium-sized *Anomaloglossus* ($\bar{X}$=20.17, range 19.60–20.50 mm in males [n=3] and $\bar{X}$=22.68, range 20.1–23.9 mm in females [n=6; including holotype]); (2) body robust; (3) skin tuberculate on dorsum (particularly the posterior half) and legs, with a larger tubercle on each eyelid, ventral skin smooth; (4) conspicuous black to dark brown glandulous supratympanic fold flanked by a discontinuous stripe (orange in life, cream in preservative) running from the ventroposterior edge of the eye and extending onto the upper arm; (5) tympanum indistinct; (6) snout short acute in lateral view; (7) nares oriented ventrolaterally, situated near tip of snout; (8) Finger I longer than II when fingers adpressed, relative finger lengths III > IV > I > II; (9) tip of Finger IV not reaching distal subarticular tubercle on Finger III when fingers adpressed; (10) distal subarticular tubercle on Finger III and IV indistinct; (11) Finger III not distinctly swollen in males; (12) fingers with fringes particularly developed on preaxial edges of Fingers II and III, inconspicuous in females; (13) toes moderately webbed, with well-developed fringes (*sensu* Grant *et al.* 2006; keel-like lateral folds *sensu* Myers & Donnelly 2008); (14) tarsal keel well-defined, curved, slightly tuberclelike; (15) no black arm gland in males (*sensu* Grant & Castro 1998; see also Grant *et al.* 2006); (16) cloacal tubercles present; (17) paracloacal mark inconspicuous; (18) dorsolateral stripe absent, dorsal part of flanks darker than dorsum; (19) ventrolateral stripe usually absent, but sometimes present as a broken, poorly defined pale brown blotch, ventral part of flanks with white or bluish flecks (in life); (20) sexual dichromatism in throat colour pattern, solid black in reproductive males, grey with cream speckles in females; (21)

abdomen and ventral side of legs dark grey with white freckles; (22) iris with metallic pigmentation and pupil ring interrupted ventrally by transversal black pigmentation; (23) median lingual process longer than wide, tapered, bluntly pointed, smooth (non-papillate), reclined in pit; (24) single note call of $\bar{X}$=0.158 s length, range 0.1572–0.156 s (n=2), and dominant frequency of 3.61 kHz (n=2) on average (range 3.60–3.62 kHz).

One male has been photographed in 2010 by one of us (PG), carrying four tadpoles. This species has the same reproductive mode as *Anomaloglossus blanci* and *A. dewynteri* with endotrophic tadpoles carried by the male from a late stage of development until complete metamorphosis.

Anomaloglossus degranvillei is only known from the type locality at >400 m elevation and from the foot of Mont Galbao near Saül >300 m elevation. The species thus also likely occurs between these two localities in the Inini massif that reaches >800 m elevation. However, *A. degranvillei* has not been observed since 2009, despite targeted searches at the two known localities.

Amended definition of *Anomaloglossus surinamensis* (Figure 4)

Given the confusion regarding the identification of specimens in the *A. degranvillei* clade and the recent finding that *A. surinamensis* spatially overlaps with two distinct species of Anomaloglossus of the *A. degranvillei* clade (and allopatric with *A. blanci*), we provide herein an amended definition of *A. surinamensis*. This new definition is based on the holotype (female) and 12 specimens collected from the type locality (Nassau) in Suriname and two localities in French Guiana.

(1) Small-sized *Anomaloglossus* ($\bar{X}$=14.75, range 14.0–15.3 mm in males [n=8] and $\bar{X}$=16.5, range 16.0–17.1 mm in females [n=4]; Table 1); (2) body robust; (3) skin tuberculate on dorsum (particularly the posterior half) and legs, with an inconspicuous tubercle on each eyelid, ventral skin smooth; (4) conspicuous black to dark brown glandulous supratympanic fold flanked by a continuous cream stripe running from the ventroposterior edge of the eye and extending onto the upper arm where it turns orange in life; (5) tympanum indistinct; (6) snout short and rounded in lateral view; (7) nares oriented ventrolaterally, situated near tip of snout; (8) Finger I longer than II when fingers adpressed; (9) tip of Finger IV not reaching distal subarticular tubercle on Finger III when fingers appressed; (10) distal subarticular tubercle on Finger III and IV indistinct; (11) Finger III not distinctly swollen in males; (12) fingers with narrow fringes on preaxial edges of Fingers II and III, inconspicuous in females; (13) toes moderately webbed, with fringes (*sensu* Grant *et al.* 2006; keel-like lateral folds *sensu* Myers & Donnelly 2008); (14) tarsal keel well-defined, curved, tuberclelike; (15) no black arm gland in males (*sensu* Grant & Castro 1998; see also Grant *et al.* 2006); (16) cloacal tubercles present; (17) paracloacal mark conspicuous; (18) dorsal colour light to dark brown, a dark brown lateral band from snout continuing dorsolaterally behind the eye, dorsolateral stripe absent, middorsal raphe often present; (19) ventrolateral stripe usually absent, ventral part of flanks with flecks white or bluish (in life); (20) sexual dichromatism in throat colour pattern, darker in reproductive males; (21) dorsal surface of legs light brown with indistinct dark brown bands; (22) abdomen and ventral side of legs cream with brown freckles; (23) iris with metallic pigmentation and pupil ring interrupted ventrally by transversal black pigmentation; (24) median lingual process small, as long as wide, tapered, bluntly pointed, smooth (non-papillate), reclined in pit; (25) single tonal note call of $\bar{X}$=0.032 s length, range 0.028–0.037 s (n=20), and dominant frequency of $\bar{X}$=4.89 kHZ, range 4.55–5.35 kHz (n=20).

Like the species of the *degranvillei* clade (sensu Vacher *et al.* 2017), *Anomaloglossus surinamensis* has an endotrophic tadpole carried by the male. However, unlike in the other species of the degranvillei clade, tadpoles carried by males were always at an early stage of development (<34 Gosner stage). The clutches (1–3 eggs, n=9), are deposited in the leaf litter about 2 m maximum from the stream; it takes 13–14 days before the male starts carrying the tadpoles. During this time, the males do not call and attend only one single clutch. Four males carrying tadpoles were collected and kept in captivity, all the tadpoles detached from the back of their father after six days maximum and continued their development in water until metamorphosis without any apparent problem (Brouquisse, unpublished data).

Anomaloglossus surinamensis is distributed in Suriname (Nassau, Brownsberg, Bakhuis, Tafelberg) and French Guiana. However, it seems absent east of the Approuague River, where *Anomaloglossus blanci* occurs, and is absent further east in the Amapá State (Brazil). It occurs sympatrically with *A. degranvillei* on Atachi Bakka and around Saül, and with *A. dewynteri* on Itoupé. However, these species never occur along the same streams. *Anomaloglossus surinamensis* seems to be associated with very small, sandy stream, often simple water films coming out from the ground in small talwegs.

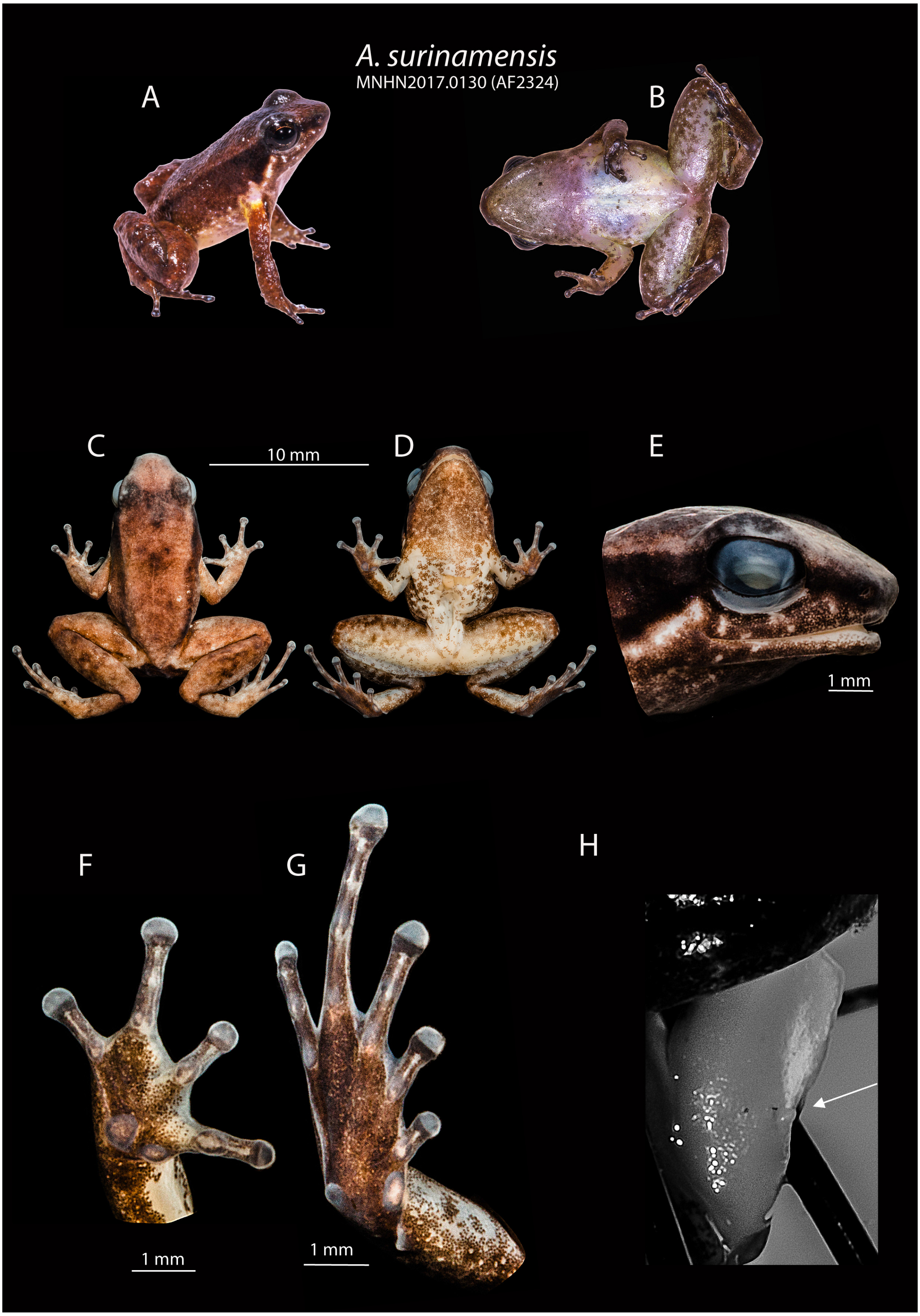

FIGURE 4. Male specimen MNHN2017.0130 (AF2324) of *Anomaloglossus surinamensis* from Chutes Voltaire, French Guiana: (A) in life dorsolateral view; (B) in life ventral view; (C) in preservative dorsal view; (D) in preservative ventral view; (E) in preservative head lateral view; (F) Right hand; (G) right foot; (H) median lingual process.

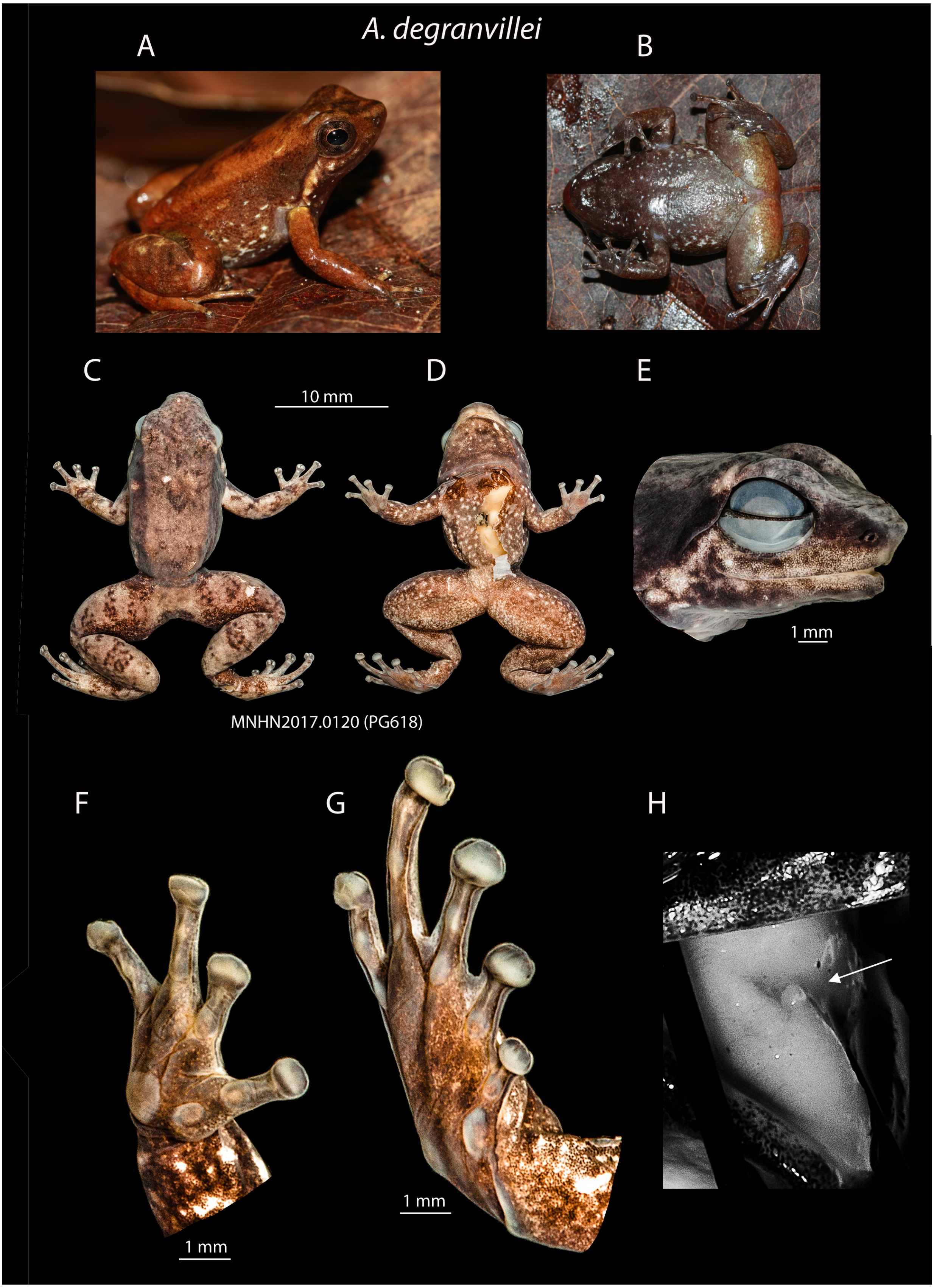

FIGURE 5. Specimens of *Anomaloglossus degranvillei* from Atachi Bakka, French Guiana: (A) unvouchered female specimen in life dorsolateral view; (B) unvouchered female specimen in life ventral view; (C) MNHN2017.0120 (PG618) male specimen in preservative dorsal view; (D) in preservative ventral view; (E) in preservative head lateral view; (F) Right hand; (G) right foot; (H) median lingual process.

FIGURE 6. Living specimens and habitats of the four species of the *Anomaloglossus degranvillei* clade; (A) *A. blanci* including two males carrying tadpoles MNHN2017.0110 (AF0952) was carrying two metamorphs but one was removed, a mark left by the missing tadpole is visible on the skin; an unvouchered male with three tadpoles at different stages probably from two different clutches); (B) *A. dewynteri* including one uncollected male carrying six tadpoles; (C) *A. degranvillei* uncollected male carrying four tadpoles; (D) *A. surinamensis* male from the type locality in Suriname carrying three tadpoles.

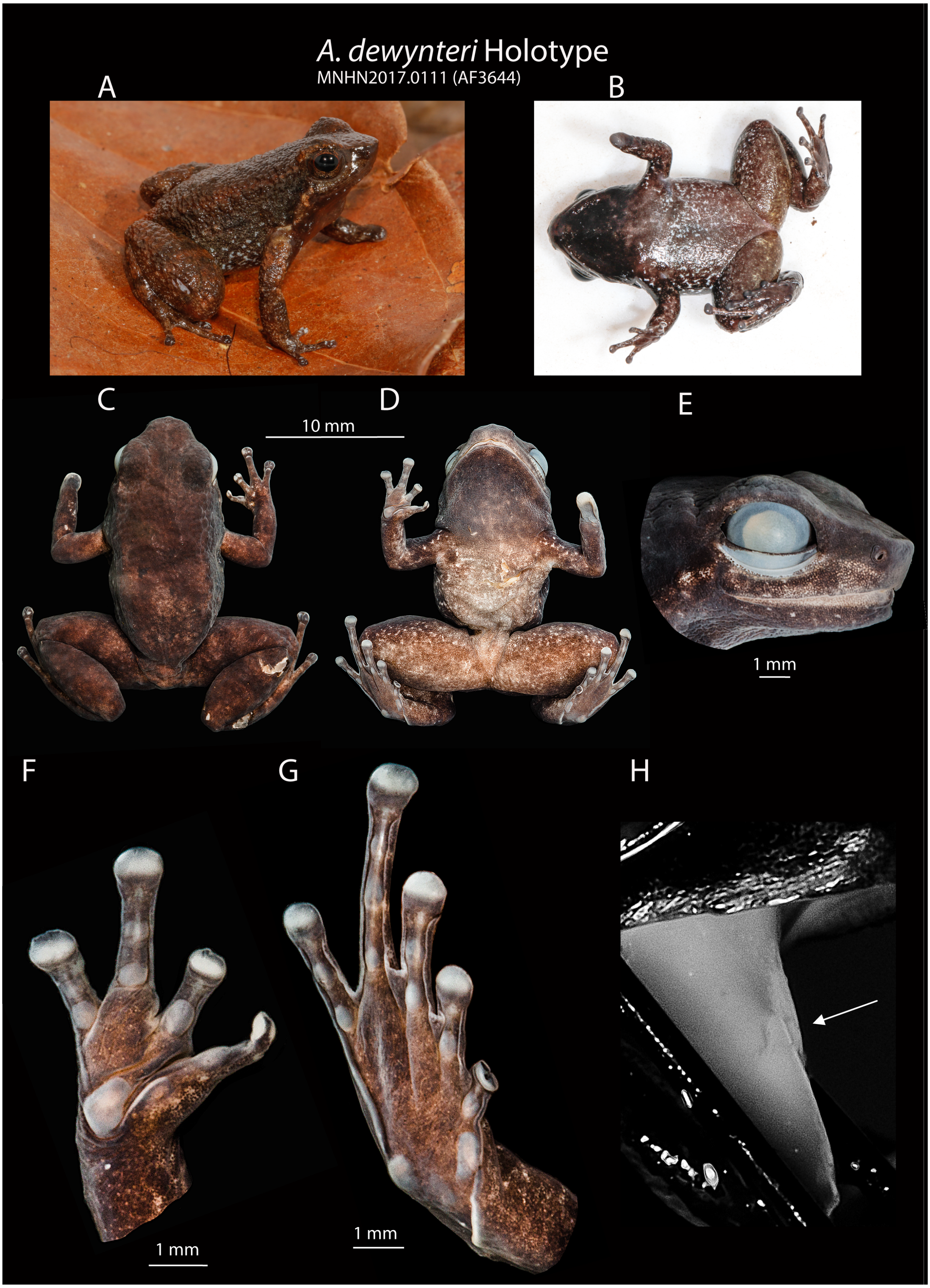

FIGURE 7. Holotype of *Anomaloglossus dewynteri* sp. nov MNHN2017.0111 (AF3644): (A) in life dorsolateral view; (B) in life ventral view; (C) in preservative dorsal view; (D) in preservative ventral view; (E) in preservative head lateral view; (F) Right hand; (G) right foot; (H) median lingual process.

Discussion

The recent study by Vacher *et al.* (2017) revealed an intriguing example of contrasted degree of divergence between phenotypic and molecular (mtDNA) data in the *Anomaloglossus degranvillei* clade. *Anomaloglossus surinamensis* displays highly divergent populations on mtDNA in western Suriname and French Guiana, but very little morphological and acoustical differentiation among them. In contrast, the lineages forming the *A. degranvillei* clade, which is restricted to French Guiana, display less-pronounced mtDNA divergence than *A. surinamensis*, but clear morphological and acoustical differences. Our mitogenomic analysis confirms this pattern with longer branches within *A. surinamensis* than among the three species of the *A. degranvillei* clade (Figure 1B).

The case of the *Anomaloglossus degranvillei* clade represents an additional example of our misperception of the actual magnitude of the diversity existing in Amazonia, and strengthens the view that regional endemism in Amazonia is largely underestimated (e.g. Fouquet *et al.* 2007, 2016). Many recent studies demonstrated that supposedly widespread Amazonian species are in fact mosaics of regional endemics (e.g. Caminer & Ron 2014; Caminer *et al.* 2017; Fouquet *et al.* 2014, 2015b; Gehara *et al.* 2014; Rojas *et al.* 2016). However, examples of so narrowly distributed cryptic species are rare in Amazonia. In this respect, *Anomaloglossus* represents a challenging group to study, as several additional species certainly remain undocumented in the Guiana Shield.

Interestingly, the only species previously assigned to *Anomaloglossus degranvillei* (described as *A. blanci* in the present work) that is allopatric with *A. surinamensis* shares similar body size and call dominant frequency. On the opposite, the two species that occur sympatrically with *A. surinamensis* (*A. degranvillei* and *A. dewynteri*) display larger body size and lower call dominant frequency. Moreover, the interrelationships among *A. surinamensis* mtDNA lineages suggest a western (Suriname) origin of the French Guiana populations. Therefore, Vacher *et al.* (2017) hypothesised that the historical contact between *A. surinamensis* and *A. degranville*i in central and southern French Guiana fostered character displacement in *A. degranvillei* towards larger body size, and maybe also niche displacement towards higher elevations. Moreover, although *A. degranvillei* is morphologically very similar to *A. dewynteri*, it is more closely related to *A. blanci*. This additional discrepancy strengthens not only the independent taxonomic status of *A. dewynteri* but also the idea that the contrasted phenotypes of *A. blanci* vs. *A. dewynteri* and *A. degranvillei* resulted from recent ecological processes.

In recent decades, amphibian declines have become a major concern (Stuart *et al.* 2004; Wake & Vredenburg 2008). The main causes of this decline are habitat destruction (Laurance *et al.* 2012), worldwide epidemic disease (Pounds *et al.* 2006), and climate change (Foden *et al.* 2013). Some taxonomic groups seem more exposed to these declines, particularly the stream-associated frogs in the Andes and Central America (e.g., *Atelopus*: Coloma *et al.* 2010), Australian wet tropics (e.g., *Rheobatrachus* and *Taudactylus*: Schloegel *et al.* 2006) or the Atlantic Forest (e.g., *Cycloramphus*: Verdade *et al.* 2011). Occurrence in highland areas and association with streams are two conditions known to increase extinction risk (Gillespie & Hines 1999; Woodhams & Alford 2005). Many species in the genus *Anomaloglossus* seem to be microendemic associated to mountain streams (Kok *et al.* 2006), with one species, *A. tepequem*, having been described after it probably went extinct during the last decade (Fouquet *et al.* 2015a). The species of the *A. degranvillei* clade share these ecological characteristics and two microendemic species are associated with >400 m elevations. Field observations since 2010 strongly suggest that these uplands populations, but also *A. blanci* in the lowlands, are severely declining. The causes of this decline remain speculative, but habitat modifications can be eliminated. Therefore, climate change and epidemic diseases are the most likely causes. Indeed, higher elevation populations of amphibians (>400 m) have been shown to be more severely affected by chytridiomycosis (Pounds *et al.* 2006). The presence of *Batrachochytrium dendrobatidis* (*Bd*) in French Guiana has been shown by Courtois *et al.* (2012). Although infection by *Bd* is not always directly linked with declines and no obvious case of chytridiomycosis outbreak has been reported in French Guiana yet, the prevalence of the pathogen in Dendrobatoidea is particularly high in the country (Courtois *et al.* 2015). In addition, the observation of many atrophied fingers, hands and feet as well as skin lesions in many individuals may suggest the existence of other kinds of pathogens (Gray *et al.* 2009).

Currently *Anomaloglossus degranvillei* is considered as "Least Concern" by the IUCN (2014) and its range is encompassing the cumulative range of the four species of the clade. Therefore, the status of the four species should be assessed separately. Given the relatively widespread distribution throughout Suriname and French Guiana and the apparently stable populations, we suggest that *A. surinamensis* should be considered as "Least Concern". However, *A. degranvillei* and *A. dewynteri* should be considered as "Critically Endangered" considering criterion

A2b (observation of population reduction and potential decline by 80% during the last decade) and B, i.e., an entire geographic range (area of occurrence) smaller than 100 km^2, an area of occupancy smaller than 10 km^2 ("B2"), a single known isolated population ("B2(a)") and projected decline ("B2(b)"). Finally, *A. blanci* should be considered as "Vulnerable" considering its range being <20.000 km^2 ("B1"), and that signs of decline are unambiguous ("B1(b)"). Moreover, the populations are severely fragmented ("B1(a)") and probably small. As suggested previously by Fouquet *et al.* (2015a), the entire genus should be the subject of conservation programs and monitoring schemes.

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APPENDIX 1. Occurrences of *Anomaloglossus blanci*, *A. degranvillei*, and *A. dewynteri* in French Guiana.

Species	Locality	Data type	Lat	Lon
A. blanci	Armontabo	Specimen/Molecular	3.804444	-52.288056
A. blanci	Crique Diamant	Specimen/Molecular	4.516105	-52.100530
A. blanci	RN2 corridor 7	Specimen/Molecular	4.063933	-52.041607
A. blanci	Saut Grand Machicou	Specimen/Molecular	3.897416	-52.583565
A. blanci	Mont. Petite Tortue	Specimen/Molecular	4.374737	-52.223434
A. blanci	Tibourou	Specimen/Molecular	4.416667	-52.300000
A. blanci	Eaux Clement	Type series *degranvillei*	4.655600	-52.248000
A. blanci	Cacao	Type series *degranvillei*	4.561000	-52.462900
A. blanci	Crique Ipoussing	Type series *degranvillei*	4.130700	-52.576000
A. blanci	Mont. Grande Tortue	Type series *degranvillei*	4.300000	-52.366700
A. blanci	Coq de roche	field obs.	4.573944	-52.200806
A. blanci	Trésor	field obs.	4.603250	-52.278639
A. blanci	Route Nationale 2 corridor 5	field obs.	4.035722	-51.988694
A. blanci	Trois Pitons	field obs.	4.202400	-51.815200
A. blanci	Camp Asarco	field obs.	4.548056	-52.151944
A. blanci	Armontabo	Molecular	3.804444	-52.288056
A. blanci	Camp Arataye	field obs.	3.990900	-52.590200
A. blanci	Montagne Favard	field obs.	4.498611	-52.046917
A. degranvillei	Saül Galbao	Molecular	3.600000	-53.283333
A. degranvillei	Atachi Bakka	Specimen/Molecular	3.545461	-53.906851
A. dewynteri	Itoupé	Specimen/Molecular	3.023020	-53.095470

APPENDIX 2. Additional material examined.

Anomaloglossus surinamensis: SURINAME: Nassau: MNHN2017.0131–4 (AF2429, 2456, 2458, 2490) (males), NZCS A2175 (Holotype female); FRENCH GUIANA: Voltaire: MNHN2017.0127 (AF1746), MNHN2017.0129–30 (AF2322, 2324) (males), MNHN2017.0126 (AF1736), MNHN2017.0128 (AF1747) (females); Nouragues: MNHN2017.0123 (AF0259) (male). Trinite: MNHN2017.0124–5 (AF1147–8) (females).
Anomaloglossus degranvillei: Males, FRENCH GUIANA: Atachi Bakka: MNHN2017.0115 (PG601), MNHN2017.0118 (PG610), MNHN2017.0120 (PG618) (males), MNHN1973-1655 (Holotype female), MNHN2017.0116–7 (PG608–9), MNHN2017.0119 (PG611), MNHN2017.0121 (PG619), MNHN2017.0122 (PG627) (females).

APPENDIX 3. Accession numbers. Field numbers are between parentheses and museum vouchers are indicated for deposited specimens.

Anomaloglossus surinamensis: (AF0585)-MG264890; MNHN2017.0132 (AF2456)-MG264894; (AF3340)-MG264893; *A. dewynteri*: (PG660)-MG264891; *A. degranvillei*: MNHN2017.0115 (PG601)-MG264892; *A. blanci*: MNHN2017.0107 (AF0932)-MG264895