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A NEW DIAGNOSIS AND DESCRIPTION OF
ANOMALOGLOSSUS RORAIMA (LA MARCA, 1998)
(ANURA: AROMOBATIDAE: ANOMALOGLOSSINAE),
WITH DESCRIPTION OF ITS TADPOLE AND CALL

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Abstract

The frog *Anomaloglossus roraima* was originally described as *Colostethus roraima* by E. La Marca in 1998 on the basis of a single immature female collected at 2700 m elevation on the upper slopes of Mount Roraima, a tepui (table mountain) located in southeastern Venezuela. We herein provide a redescription of the species on the basis of new material from Wei-Assipu-tepui and Maringma-tepui in Guyana. The redescription includes the first descriptions of the tadpole and vocalisation. *Anomaloglossus roraima* is a small-sized species mainly distinguished from its known congeners in having Finger I < II; fingers with narrow pre- and postaxial unfolded fringes; toes unwebbed (although rudimentary webbing is sometimes present between Toe III and IV) with narrow pre- and postaxial unfolded fringes; symmetrical cloacal tubercles present; dorsolateral stripe usually present, often inconspicuous; ventrolateral stripe absent; oblique lateral stripe absent; no obvious sexual dichromatism in throat, chest and ventral colour patterns. The tadpole is large, black, exotrophic, arboreal, LTRF 2(2)/3. The advertisement call consists of a single note repeated at a rate of 8.5–17 notes/min with a dominant frequency ranging from 4107 to 4362 Hz. The species is restricted to a small area in the Eastern Tepui Chain in southeastern Venezuela and western Guyana and mainly inhabits large bromeliads in tepui scrub and high-tepui meadows at elevations between 1860–2700 m above sea level. The discovery on different tepui summits and upper slopes of a species previously reported as having a highly restricted range is important for the understanding of the biogeography of the Pantepui region.

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INTRODUCTION

The genus *Anomaloglossus* was erected by Grant *et al.* (2006) to accommodate all the species formerly included in *Colostethus* that have a median lingual process (MLP), an unusual anatomic structure also known in some Asian and African ranoid frogs (Grant *et al.*, 1997). According to Grant *et al.* (2006) *Anomaloglossus* is sister to *Rheobates*, a genus reported from the Cordillera Central and the Cordillera Oriental in Colombia. Twenty-nine *Anomaloglossus* species are currently recognized (Kok, 2010; Kok *et al.*, 2010; Ouboter and Jairam, 2012; Myers *et al.*, 2012), 18 of which being reported as endemic to Pantepui (Frost, 2013). The genus *Anomaloglossus* includes several species having very restricted distributions in the Guiana Shield, sometimes reported from the summit of a single tepui only, whereas the genus is reported to have some representatives in the Andes, in Panama, and a single species in the Amazonian lowlands (Frost, 2013). Grant *et al.* (2006) pointed out that more taxon sampling is needed to clarify relationships between *cis*-Andean species and those occurring west of the Andes (= *trans*-Andean) and that the *trans*-Andean species having a median lingual process must be included in phylogenetic analyses to corroborate their placement in *Anomaloglossus*. Grant *et al.* (2012) and Myers *et al.* (2012) recently suggested that the Panamian and *trans*-Andean *Anomaloglossus* form a clade phylogenetically distant from the *cis*-Andean *Anomaloglossus* and should be reallocated to a different genus. This would leave *Anomaloglossus* with 25 species, all restricted to the Guiana Shield and peripheral lowland areas.

Anomaloglossus species have a biphasic life cycle, eggs are usually laid on the ground, and the tadpoles are carried by the male to a suitable body of water (*e.g.* streams, puddles). Phytotelm-breeding species have specific ecological niche preferences. In those species, eggs are laid on bromeliad leaves and tadpoles slide into the bromeliad tank.

As already pointed out by Kok (2010) and Kok *et al.* (2010) several *Anomaloglossus* descriptions overlook and/or erroneously describe important diagnostic characters. Most are poorly illustrated (photographs of many *Anomaloglossus* species in life are not available) and are based on very few specimens. This is a significant obstacle to accurate comparisons between species, but also with possible new taxa. Redescriptions of those poorly known species and a more complete understanding of their morphology are thus of primary importance.

The distribution of many tepui taxa is very poorly known and the discovery of the occurrence of a same *Anomaloglossus* species on several tepui summits/upper slopes is central to understanding the biogeography of the area.

Anomaloglossus roraima was originally described in 1998 by Enrique La Marca (see Myers & Donnelly, 2008: 143 for comment on date of publication) in his revision of the genus *Colostethus* from the Venezuelan Guayana. The description was solely based on the holotype, an immature female collected in 1996 at 2700 m elevation on “La Rampa” just below the summit of Mount Roraima, Estado Bolívar, Venezuela. As for many *Anomaloglossus* species known only from the type series, the species’ name rarely appeared in the literature since the original description (*e.g.* Barrio-Amorós, 1998, 2004; McDiarmid & Donnelly, 2005; Grant *et al.*, 2006, MacCulloch *et al.*, 2007), except in the diagnoses of new congeneric taxa. Besides the few data provided in the original description, no information is available about the species, which is considered as highly restricted (*i.e.* restricted to a single tepui) by McDiarmid & Donnelly (2005).

Grant *et al.* (2006) included *Anomaloglossus roraima* in their phylogenetic study on the basis of DNA samples from two specimens and a tadpole collected by DBM between 1860–2350 m elevation on the north slopes of Mount Roraima, Cuyuni-Mazaruni District, Guyana. The authors indicated that *A. roraima* breeds in phytotelmata and suggested a sister-species relationship with *A. beebei* (Noble, 1923) (the only other known phytotelm-breeding *Anomaloglossus* species) based on molecular evidence. The purpose of Grant *et al.* (2006) was not to redefine the species and they did not examine the type specimen of *A. roraima*, however they concluded that their additional specimens—all from close to the type locality—sufficiently agreed with the original description to be considered conspecific.

As already pointed out by Kok (2010) and Kok *et al.* (2010) several *Anomaloglossus* descriptions overlook and/or erroneously describe important diagnostic characters. Most are poorly illustrated (photographs of many *Anomaloglossus* species in life are not available) and are based on very few specimens. This is a significant obstacle to accurate comparisons between species, but also with possible new taxa. Redescriptions of those poorly known species and a more complete understanding of their morphology are thus of primary importance. The distribution of many tepui taxa is very poorly known and the discovery of the occurrence of a same *Anomaloglossus* species on several tepui summits/upper slopes is central to understanding the biogeography of the area.

Thirty additional specimens of *Anomaloglossus roraima*, as well as 24 tadpoles, were collected at two different localities in the Eastern Tepui Chain in Guyana, and the vocalization of the species was recorded at both sites. On the basis of this new material (listed in the Appendix), and direct comparison with the holotype of *A. roraima*, we provide below a redescription of the taxon based on morphology and call as well as the first description of its tadpole. An updated diagnosis is provided and the IUCN Red List Category of *A. roraima* is discussed.

MATERIAL AND METHODS

The newly collected specimens of *Anomaloglossus roraima* are from the summit of Maringma-tepui (05° 12' 57"N, 060° 35' 07"W, between 2000–2100 m elevation, Fig. 1), Cuyuni-Mazaruni District, Guyana, where 13 adult individuals (six males, seven females), one sub-adult female, six juveniles, and seven tadpoles were secured, and from the summit of Wei-Assipu-tepui, at the border between Guyana and Brazil (05° 13' 05"N, 060° 42' 23"W, between 2200–2300 m elevation, Fig. 1) where seven adult individuals (two males, five females), two sub-adult females, one juvenile, and 17 tadpoles were collected. Additional specimens and tadpoles were collected at the base of the ultimate cliffs of the "Prow" of Mount Roraima in Guyana by DBM, but these specimens could not be recovered and are therefore not included in the morphological analyses.

Specimens were euthanized by immersion in a 2% Xylocaine solution, fixed in 10% formalin for several days and transferred to 70% ethanol (adults and juveniles) or preserved in 10% formalin (20 tadpoles) for permanent storage. A piece of liver and/or thigh muscle was taken from 15 specimens prior to fixation and preserved in 95% ethanol for later molecular analyses. Four tadpoles were preserved in 95% ethanol for the same purpose. Specimens were deposited in the collections of the Institut Royal des Sciences Naturelles

de Belgique (IRSNB) and tissue samples were deposited in the Amphibian Evolution Lab, Biology Department, Vrije Universiteit Brussel (see Appendix for material examined).

Color in life is described from digital photographs and field notes. Sex and maturity were determined by the presence/absence of vocal slit(s) and by dissection when sex determination was doubtful. Internal soft anatomy was examined by dissection of preserved specimens. All morphometric data were taken from the preserved specimens by the same person (BW during his master internship at the IRSNB), to the nearest 0.01 mm and rounded to the nearest 0.1 mm, under a Leica stereo dissecting microscope using an electronic digital calliper or an ocular micrometer.

Abbreviations and standard measurements for adults are as follows: (1) snout-vent length (SVL); (2) head length from corner of mouth to tip of snout (HL); (3) head width at level of angle of jaws (HW); (4) snout length from anterior corner of eye to tip of snout (SL); (5) eye to naris distance from anterior corner of eye to posterior margin of naris (EN); (6) internarial distance (IN); (7) eye length (EL); (8) interorbital distance (IO); (9) greatest length of tympanum from its anterior margin to its posterior margin (TYM); (10) forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow (FAL); (11) length of Finger I from proximal edge of palmar tubercle to tip of finger (HAND I); (12) length of Finger II from proximal edge of palmar tubercle to tip of finger (HAND II); (13) length of Finger III from proximal edge of palmar tubercle to tip of finger (HAND III, also equivalent to hand length); (14) length of Finger IV from proximal edge of palmar tubercle to tip of finger (HAND IV); (15) width of disc on Finger III (WFD); (16) foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV (FL); (17) width of disc on Toe IV (WTD); (18) tibia length from outer edge of flexed knee to heel (TIL); (19) upper arm length from anterior insertion with the body to outer edge of flexed elbow (AL). Relative lengths of fingers were compared according to Kaplan (1997), using the distance from the proximal edge of the palmar tubercle to the tip of each finger.

Three lots of tadpoles were collected, all from terrestrial tank bromeliads (*Brocchinia tatei*, Bromeliaceae). Developmental stages of tadpoles follow Gosner (1960); terminology and oral disc characters follow Altig & McDiarmid (1999). Color in life is described from field notes and color photographs. Abbreviations and standard measurements for tadpoles are as follows: (1) total length from tip of snout to tip of tail (TL); (2) body length from tip of snout to junction of posterior body and tail musculature (BL); (3) tail length from junction of posterior body and tail musculature to tip of tail (TAL); (4) greatest body width (BW); (5) highest body height (BH); (6) head width at level of eyes (HW); (7) tail muscle height at base of tail (TMH); (8) tail muscle width at base of tail (TMW); (9) maximum height of tail (MTH); (10) eye-naris distance (END); (11) naris-snout distance (NSD); (12) internarial distance (IND); (13) interorbital distance (IOD); (14) eye diameter (ED). The oral disc of a 28.7 mm long, stage-27 formalin preserved tadpole was dissected, critical-point dried, and coated with gold following the usual protocol (Echeverría, 1997; Kok & Kalamandeen, 2008) for scanning electron microscopy (SEM). Observations and photomicrographs were made with a FEI Quanta-200 environmental scanning electron microscope (ESEM). Ethanol-preserved tadpoles were not included in Table 2 because ethanol caused soft tissue desiccation and body deformation.

Advertisement calls were recorded (1.5 to 3 minutes) at a distance of less than 1 m from one calling male collected on Maringma-tepui and one uncollected male on Wei-Assiputepui using a Sony ECM-MS907 microphone attached to a DAT Sony TCD-D100 recorder

using Maxell DM60 digital audiotape. The calls were analysed at a sampling rate of 44100 Hz using Raven version 1.4 software (Charif *et al.*, 2010). Temporal variables measured included: call duration (= note duration); inter-call interval (beginning of one call to beginning of the next); and call rate (= number of calls per minute) (Kok & Kalamandeen, 2008). The dominant (emphasized) frequency of the note was measured from a spectral slice taken through the portion of the note with the highest amplitude (using the Blackman window function at a 3 dB filter bandwidth of 120 Hz) (Kok & Kalamandeen, 2008). Air temperature at the call sites was measured with a Hanna digital pH/thermometer and was 17°C at both sites.

Taxonomy follows Grant *et al.* (2006). Institutional acronyms follow Frost (2013).

RESULTS

Redescription of *Anomaloglossus roraima* (La Marca, 1998)

(Figs. 2–8)

Adult definition and diagnosis. (1) Small-sized *Anomaloglossus* (males 16.5–19.0 mm SVL, females 16.5–19.3 mm SVL); (2) body robust; (3) skin on dorsum fairly variable, rarely smooth, usually shagreen to finely granular, more granular posteriorly, skin on venter smooth to shagreen; (4) Finger I < II; (5) tip of Finger IV reaching or surpassing the base of the distal subarticular tubercle on Finger III when fingers adpressed (when the distal subarticular tubercle on Finger III is visible, see below); (6) distal tubercle on Finger IV present, although often barely distinguishable; (7) Finger III faintly swollen in some males (preaxial and postaxial keeling weakly more developed than in females, only visible under magnification); (8) fingers with narrow pre- and postaxial unfolded fringes (best visible under magnification); (9) toes unwebbed—although rudimentary webbing is sometimes present between Toes III–IV—with narrow pre- and postaxial unfolded fringes (best visible under magnification); (10) tarsal keel weakly curved, slightly tuberclelike, not extending from metatarsal tubercle; (11) black arm gland absent in male (*sensu* Grant & Castro-Herrera, 1998, see also Grant *et al.*, 2006); (12) symmetrical cloacal tubercles present; (13) pale paracloacal mark usually absent; (14) thin pale dorsolateral stripe present or absent in both sexes, when present it extends from the anterior or posterior corner of eye to the level of anterior thigh insertion (dorsolateral stripe less conspicuous in preserved specimens); (15) ventrolateral stripe absent; (16) oblique lateral stripe absent; (17) no obvious sexual dichromatism in throat color; (18) no obvious sexual dichromatism in ventral coloration; (19) iris with metallic pigmentation and pupil ring; (20) large intestine extensively pigmented; (21) testes cream, unpigmented; (22) mature oocytes darkly pigmented; (23) median lingual process short, tapered; (24) maxillary teeth present, small.

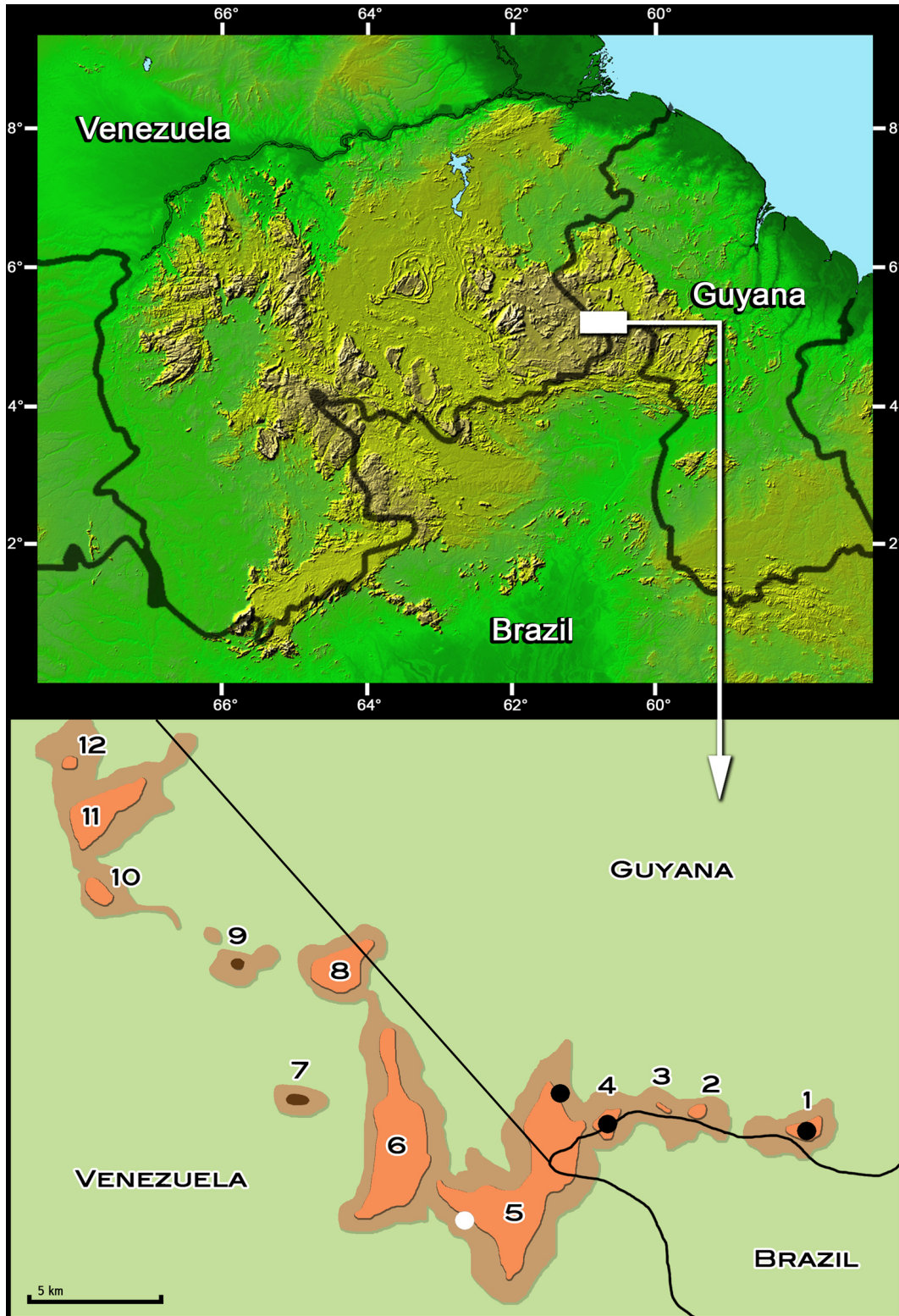


Figure 1. Map of the Pantepui region, with enlarged white rectangle corresponding to the Eastern Tepui Chain: 1 = Maringma-tepui, 2 = Yakontipu-tepui, 3 = Appokailang-tepui, 4 = Wei-Assipu-tepui, 5 = Mount Roraima, 6 = Kukenan-tepui, 7 = Achipo-tepui, 8 = Yuruani-tepui, 9 = Guadacapiapu-tepui, 10 = Karaurin-tepui, 11 = Ilu-tepui, 12 = Tramen-tepui. Areas in orange indicate summits higher than 2000 m elevation; areas in dark brown indicate summits lower than 2000 m; areas in light brown indicate tepui slopes above 1500 m elevation. Dots show collecting localities of *Anomaloglossus roraima* (white dot = type locality, black dots = new localities).

Comparison with other species. Twenty-nine species of *Anomaloglossus* are currently recognized (Frost, 2013), many of which apparently have restricted ranges. Eleven *Anomaloglossus* species are known to occur in the Eastern Pantepui District in the Guiana highlands of Venezuela and Guyana (*i.e.* east of the Rio Caroní, which likely acts as a biogeographic barrier for *Anomaloglossus* species since no species has been reported to occur on both sides of the river): *A. beebei*, *A. breweri* (Barrio-Amorós, 2006), *A. kaiei* (Kok, Sambhu, Roopsind, Lenglet and Bourne, 2006), *A. megacephalus* Kok, MacCulloch, Lathrop, Willaert and Bossuyt, 2010, *A. moffetti* Barrio-Amorós and Brewer-Carías, 2008, *A. parkerae* (Meinhardt and Parmelee, 1996), *A. praderioi* (La Marca, 1998), *A. murisipanensis* (La Marca, 1998), *A. rufulus* (Gorzula, 1990), *A. tepuyensis* (La Marca, 1998), and *A. triunfo* (Barrio-Amorós, Fuentes-Ramos and Rivas, 2004). *Anomaloglossus roraima* is readily distinguished from these species in having adult females reaching less than 20 mm SVL [adult females of all other known *Anomaloglossus* species from the area exceed 20 mm SVL, except in *A. beebei*, *A. kaiei* (Kok, Sambhu, Roopsind, Lenglet & Bourne, 2006), and *A. triunfo*¹ (Barrio-Amorós, Fuentes-Ramos & Rivas, 2004)] and by lacking toe webbing (webbing basal to extensive in all other known *Anomaloglossus* species from the area).

Adult description. Major differences from the original description are italicized between brackets; see Table 1 for morphometric data of the holotype of *Anomaloglossus roraima* (ULABG 4197, illustrated in Fig. 2) compared to new material (partly illustrated in Figs. 3–7). Adult males 16.5–19.0 mm SVL (n = 8), adult females 16.5–19.3 mm SVL (n = 12). Dorsal skin texture fairly variable, from smooth (uncommon) to finely granular, becoming more granular posteriorly and on hind limbs; ventral skin smooth to shagreen. Dorsal surface of hind limbs granular, with two distinct symmetrical enlarged tubercles located laterally between urostyle and vent in 23 specimens (77% of our sample); these tubercles are less easily distinguishable in the other specimens, possibly due to an artefact of preservation.

Head wider than long, greatest width 36% of SVL in males, 35% in females. Snout rounded in lateral view, extending past lower jaw, broadly rounded in ventral and dorsal views. Nares located close to tip of snout, directed posterolaterally; nares visible from front, barely visible from above and not visible from below; internarial distance 33% of greatest head width in both sexes. Canthus rostralis barely defined, rounded; loreal region concave, sloping outward to lip. Interorbital distance slightly shorter than eye length, shorter than upper eyelid. Snout length 104% of eye length in both sexes, 45% (in males) to 46% (in females) of head length; distance from anterior corner of eye to posterior margin of naris 60% (in males) to 62% (in females) of eye length. Postrictal tubercles usually few and inconspicuous. Tympanic membrane poorly recessed, inconspicuous, round, much smaller than eye, concealed posterodorsally by a more or less prominent supratympanic swelling; tympanic annulus usually detectable anteroventrally.

¹ Barrio-Amorós *et al.* (2004) reported one of the paratypes of *Anomaloglossus triunfo* to be an adult female. Upon re-examination by PJRK that specimen (EBRG 4758) proved to be a subadult individual. Therefore none of the specimens examined by Barrio-Amorós *et al.* (2004) is an adult female, and the correct female size is still unknown in that species. We believe that *Anomaloglossus triunfo* is likely a synonym of *A. tepuyensis* La Marca, 1998.

Forearm subequal to upper arm length, no distinct ulnar fold, but sometimes a row of low tubercles instead. Hand moderate, its length 27% (in males) to 28% (in females) of SVL; hand length 77% (in males) to 79% (in females) of greatest head width. Relative length of fingers III > IV > II > I. Fingers unwebbed. Discs of fingers expanded, disc on Finger IV slightly widest. Fingers with narrow pre- and postaxial unfolded fringes (*sensu* Myers & Donnelly, 2008), Finger III faintly swollen in some males (preaxial and postaxial keeling weakly more developed than in females, only visible under magnification; Fig. 3 A–B).

Palmar tubercle large, rounded to ovoid; thenar tubercle smaller, elliptical; one, rarely two round to ovoid subarticular tubercles (one each on Fingers I and II, usually one–rarely two–each on Fingers III and IV, with distal tubercle on these fingers usually barely detectable). No distinct outer metacarpal fringe. Tip of Finger IV reaching or surpassing the base of the distal subarticular tubercle on Finger III when fingers adpressed (when the distal subarticular tubercle on Finger III is visible, which is rarely the case; Fig. 3 A–B) [*although the distal subarticular tubercle on Finger III is well visible on fig. 9 in the original description, it is in fact barely detectable on the holotype; the opposite is true for the basal subarticular tubercle on Finger III, which is not seen on fig. 9 in the original description although it is well visible on the holotype*]. No fleshy supracarpal fold atop wrist.

Hind limbs moderately robust, moderately long, with heel of adpressed leg reaching posterior to anterior corner of eye; tibia 51% (in males) to 52% (in females) of SVL. Relative lengths of adpressed toes IV > III > V > II > I; first toe short, usually, but not always reaching the base of subarticular tubercle of second toe. Toe discs moderately expanded, subequal or slightly larger than finger discs. Feet unwebbed, although rudimentary webbing is sometimes present between Finger III and IV; toes with narrow pre- and postaxial unfolded fringes (*sensu* Myers & Donnelly, 2008) that are best visible under magnification.

Inner metatarsal tubercle small, elliptical; outer metatarsal tubercle small, round, between half and two-third the size of the inner. One to three round to ovoid subarticular tubercles (one each on Toes I and II, two each on Toes III and V, and three on Toe IV, with distal tubercle on Toe IV the smallest and least conspicuous). A medial metatarsal tubercle is detectable at least on one side in 50% of the specimens examined. Outer metatarsal fold absent. A straight or weakly curved tuberclelike tarsal keel not extending from metatarsal tubercle (Fig. 3 A–B).

Maxillary teeth present, small. Tongue longer than wide, free posteriorly, with rounded margin; median lingual process short, tapered. Vocal slits bilateral, large, extending from edge of tongue to angle of jaw.

Color in life.– Dorsal ground color varies from tan to shades of light brown, sometimes monochromatic (Figs. 4B, 5A, 5C) but often with dark brown pigment arranged as limited (Figs. 4C, 4D, 5D) to heavy (Figs. 4A, 5B) mottling, the mottles having no particular shape. Upper surface of arm and forearm slightly lighter than ground color, sometimes reddish, the upper arm with tiny, faint white dots and the forearm with 1–3 transverse dark brown bands. Upper surface of thigh, shank, and heel identical with dorsal ground color and having 1–3 transverse dark brown mottles often forming poorly distinct bands. Dorsal ground color set off from flanks by the same quality of dark brown pigment as dorsal mottles, forming along the contact a poorly defined, slightly lighter, narrow dorsolateral stripe. Dark flank pigment runs posterior from the naris through the middle of the eye and

expands to the top of the shoulder arching over the tympanum. Posterior to the shoulder, the flank pigment sometimes is continuously dark brown but in other examples breaks up into the same kinds of mottles mixed with dorsal ground color as on the back. Upper lip under the naris posterior to the shoulder the same uniformly tan to light brown dorsal ground color, but sometimes invaded partially by dark flank pigment. Belly yellowish (Fig. 4A') to light rusty colour in both sexes (Figs. 4B', 4C', 4D', 5C', 5D'), but sometimes heavily suffused with dark brown, uniform (Fig 5A') or mottled (Fig. 5B') pigment in some males. Chin undersurface slightly lighter in tone, sometimes with a few dark brown mottles or completely suffused with dark pigment (Figs. 5A', 5B'). Undersurfaces of front and hind legs darker in tone than the belly and often mottled (Figs. 5B', 5D') or completely suffused with dark brown pigment (Figs. 5A', 5C'). Undersurfaces of hands, feet, and toes uniformly dark brown. Toe tips of manus and pes dorsally dark brown set off prominently from the lighter coloured dorsal ground colour of the rest of the toes by a sky blue narrow transverse band. Iris light rusty brown above, dark brown pigment through the middle of the eye, light rusty brown below.

Colour of juvenile.- In one juvenile, the dorsal ground colour was light gray with dark mottling between the eyes and upper back. Flanks were similarly gray with no darker pigment but a narrow, tan, faint dorsolateral stripe was present from the naris to the urostyle. A narrow zone of dark pigment ran posterior to the naris through the iris and ends on the cheek and shoulder as in the adult, but somewhat less prominently. Dorsal surface of upper arms and forearms were reddish brown with about ten round white to light gray spots on each part of the arm. Ground color of dorsal surfaces of the thigh, shank, and heel were light gray-brown with one or two darker crossbands. Undersurfaces of arms and legs were reddish-yellow in color with a light suffusion of dark pigment over the legs. Belly and throat were yellowish but peppered with light gray specks that double in size on the chin that is blackish anteriorly. Toes of both manus and pes are dark brown to black with light gray speckles and a prominent light blue band across the base of the ultimate phalange. Iris as in the adult.

Color in preservative.- After 12 years in preservative, the yellow and red pigments of the holotype have disappeared leaving only dark gray to brown pigments uniformly suffused over the dorsum and prominent as transverse bands across the forearm (1 band), thigh (2), shank (2), heel (1), and foot (1). Brown pigment also is present on the toe tips, undersurfaces of the manus, pes, forearm, heel, anterior and posterior surfaces of the forearm, and lightly suffused over the dorsal surfaces of the legs between the darker crossbands. The belly, chin, and undersurfaces of the upper arm, leg, and shank were pigmentless (Fig. 2). After about four years in preservative, five males and eight females displayed a similar loss of yellow and red color as in the holotype. Dark gray to brown pigments remained as a dorsal suffusion with varying degrees of darker mottling (Fig. 6) on the belly and undersurfaces of the arms and legs. In all cases, the dark pigments were retained as they were present in life, but the yellow and red pigments presumably were dissolved out of the skin in preservatives. Limited dark mottling may occur on the otherwise colorless undersurfaces of the chin, belly, and legs and a suffusion of dark pigment may increase posteriorly (Fig. 6).

Character	Subadult female holotype (ULABG 4197)	Adult males from Wei-Assipu-tepui (n=2)	Adult females from Wei-Assipu-tepui (n=5)	Adult males from Maringma-tepui (n=6)	Adult females from Maringma-tepui (n=7)
SVL	15.4	17.8 ± 1.2 (16.6–18.9)	17.5 ± 0.8 (16.5–18.8)	17.9 ± 0.8 (16.5–19.0)	18.6 ± 0.8 (17.4–19.3)
HL	4.3	5.6 ± 0.3 (5.3–5.8)	5.6 ± 0.3 (5.3–6.2)	5.4 ± 0.3 (5.0–5.8)	5.8 ± 0.3 (5.2–6.0)
HW	5.1	6.4 ± 0.5 (5.9–6.8)	6.1 ± 0.2 (5.9–6.3)	6.3 ± 0.3 (5.9–6.7)	6.5 ± 0.3 (6.1–7.0)
SL	2.6	2.5 ± 0.2 (2.3–2.6)	2.5 ± 0.1 (2.3–2.6)	2.5 ± 0.2 (2.3–2.8)	2.6 ± 0.2 (2.3–2.8)
EN	1.2	1.5 ± 0.1 (1.4–1.5)	1.5 ± 0.1 (1.3–1.5)	1.5 ± 0.1 (1.3–1.6)	1.5 ± 0.1 (1.4–1.6)
IN	1.7	2.1 ± 0.2 (1.9–2.2)	2.0	2.0 ± 0.1 (1.9–2.1)	2.2 ± 0.1 (2.1–2.4)
EL	2.2	2.4 ± 0.1 (2.3–2.5)	2.5 ± 0.1 (2.4–2.6)	2.4 ± 0.1 (2.2–2.6)	2.5 ± 0.1 (2.3–2.6)
IO	2.0	2.0 ± 0.2 (1.8–2.2)	1.9 ± 0.1 (1.8–2.1)	2.0 ± 0.1 (1.8–2.1)	2.1 ± 0.1 (2.0–2.2)
TYM	-	0.8 ± 0.1 (0.7–0.8)	0.8 ± 0.1 (0.6–0.9)	0.9 ± 0.1 (0.8–1.1)	0.9 ± 0.1 (0.8–1.2)
FAL	3.9	4.1	4.2 ± 0.2 (4.0–4.4)	4.2 ± 0.1 (4.1–4.4)	4.2 ± 0.3 (3.7–4.5)
HAND I	2.8	3.1 ± 0.2 (2.9–3.2)	3.1 ± 0.1 (3.0–3.4)	3.2 ± 0.2 (3.0–3.5)	3.2 ± 0.2 (2.9–3.4)
HAND II	3.2	3.5 ± 0.1 (3.4–3.5)	3.6 ± 0.1 (3.4–3.8)	3.6 ± 0.2 (3.4–3.9)	3.6 ± 0.2 (3.2–3.8)
HAND III	4.4	4.8 ± 0.1 (4.7–4.8)	4.9 ± 0.0 (4.9–5.0)	5.0 ± 0.1 (4.8–5.2)	5.0 ± 0.3 (4.4–5.3)
HAND IV	3.3	4.0 ± 0.1 (3.9–4.0)	3.8 ± 0.1 (3.6–3.9)	3.8 ± 0.2 (3.6–4.1)	3.9 ± 0.3 (3.5–4.3)
WFD	0.6	0.6 ± 0.1 (0.6–0.7)	0.7 ± 0.1 (0.6–0.8)	0.7 ± 0.1 (0.6–0.8)	0.7 ± 0.1 (0.5–0.9)
FL	7.0	8.1 ± 0.2 (7.9–8.3)	8.0 ± 0.1 (7.8–8.2)	8.2 ± 0.3 (7.9–8.7)	8.4 ± 0.4 (7.7–8.8)
WTD	0.5	0.8 ± 0.1 (0.7–0.8)	0.6 ± 0.1 (0.5–0.7)	0.7 ± 0.1 (0.6–0.8)	0.8 ± 0.0 (0.7–0.8)
TIL	8.3	9.4 ± 0.1 (9.3–9.4)	9.3 ± 0.1 (9.0–9.4)	9.2 ± 0.4 (8.6–9.8)	9.2 ± 0.4 (8.7–10.0)
AL	3.4	4.5 ± 0.1 (4.4–4.5)	4.1 ± 0.1 (4.0–4.3)	4.4 ± 0.3 (4.1–4.9)	4.5 ± 0.2 (4.1–4.8)

Table 1. Measurements (in mm) of the holotype (ULABG 4197) of *Anomaloglossus roraimae* and new material from Maringma-tepui and Wei-Assipu-tepui, Guyana. Abbreviations are defined in the text. Mean ± SD are followed by the range in parentheses.

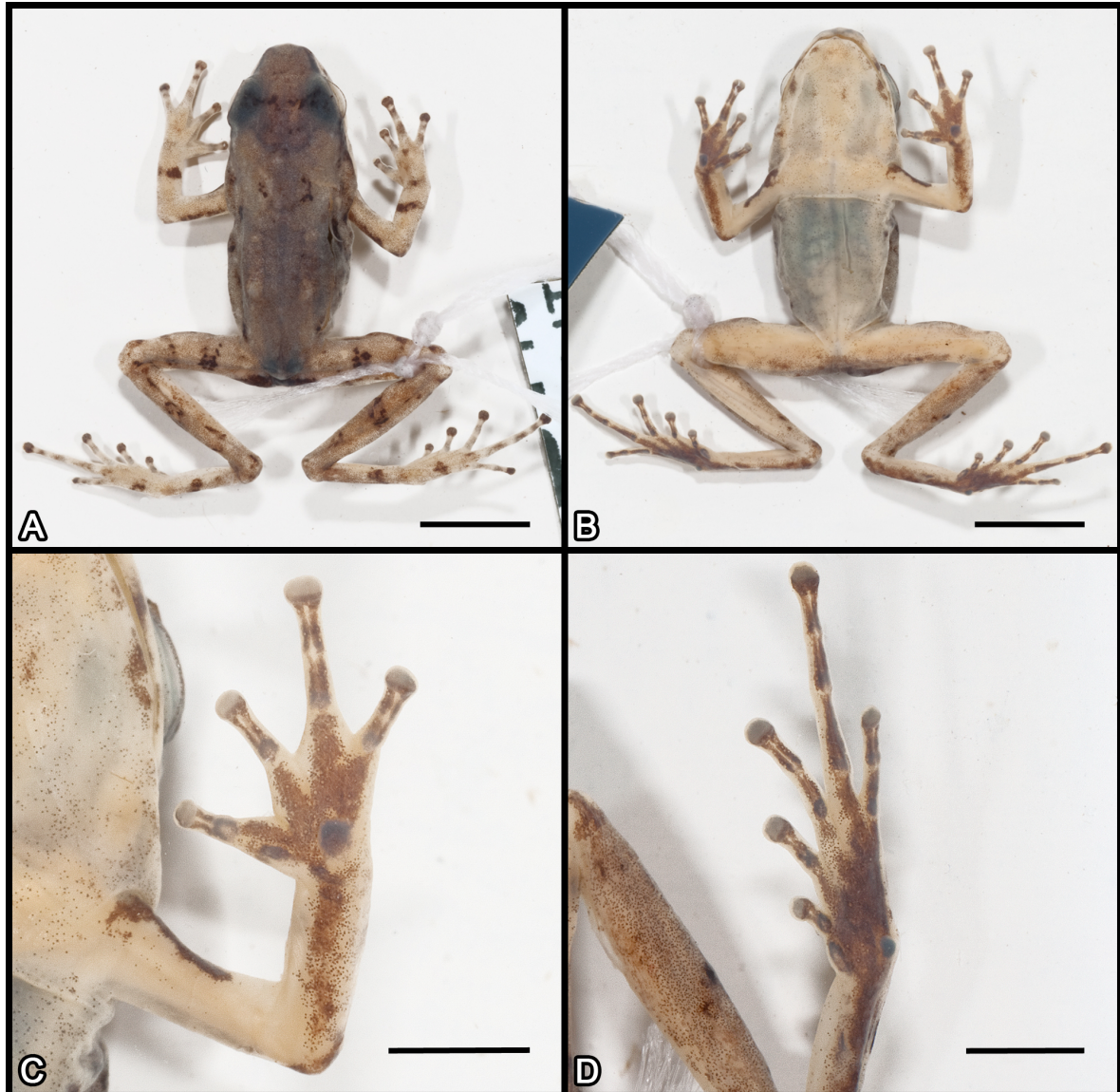


Figure 2. *Anomaloglossus roraima*, preserved subadult female holotype (ULABG 4197). **A:** Dorsal view. **B:** Ventral view. Scale bars are 5 mm. **C:** Left hand. **D:** Left foot. Scale bars are 2 mm. Photos by Philippe J.R. Kok.

Undersurfaces of forearms, hands, and feet dark brown. Undersurfaces of the chin, belly, and rear legs white (or pigmentless as in the holotype) with varying degrees of dark brown pigment suffused in increasing intensity posteriorward, often appearing in mottled patches (especially under the chin) and culminating in two males (IRSNB 15898, IRSNB 15864) with all ventral surfaces very dark brown (Fig. 6).

Tadpole description.— The following description—except oral disc—is based on an *Anomaloglossus roraima* tadpole in stage 28 (IRSNB 15903-e, Fig. 8 A) collected in the phytotelma of a *Brocchinia tatei* (Bromeliaceae) on Wei-Assipu-tepui. All values are in millimetres. See Table 2 for additional measurements and descriptive statistics for 14 meristic characters based on 19 tadpoles of stages 25–44.

Type 4 tadpole (Orton, 1953), exotrophic, arboreal Type 2 (Lannoo *et al.*, 1987; Altig & Johnson, 1989). Total length 26.1; body length 10.2 (39% of total length); tail length 15.9

(61% of total length). Body ovoid and depressed; greatest body width 6.4, highest body height 4.2; snout bluntly rounded in dorsal and lateral views. Naris very small, circular, directed anterodorsally, opening 1.5 from tip of snout; distance from naris to anterior margin of eye 0.9; internarial distance 1.4, 26% of head width at level of eyes. Eyes dorsal and directed dorsolaterally; eye diameter 1.0; interorbital distance 2.6, 49% of head width at level of eyes. Spiracle sinistral, tube free, opening directed posterodorsally; tube length 0.9; tube transverse width 1.0; distance from tip of snout to spiracular opening 5.7, 56% of body length. Vent tube 0.8, dextrally attached to ventral fin, opening directed dextrally. Developing hind limb bud 0.4 in length, 0.3 in width. Caudal musculature robust, highest at mid-length between body and tail tip, deeper than fins, tapering to tail terminus, terminating slightly anterior to tail tip; tail muscle width at base of tail 2.0; tail muscle height at base of tail 2.5. Upper fin originates posterior to junction of body and tail (Fig. 8 A), mostly equal in height to lower fin; upper fin gradually increasing in height to slightly before tip; upper tail fin height 0.9, lower tail fin height 1.1, at midtail. Lateral-line system with an infraorbital branch originating near upper labium and terminating just behind the eye; a longitudinal branch originating near lower labium and meeting the angular branch; an angular branch originating below eye and terminating onto the ventral surface; a lateroventral branch originating near lower labium, in contact with the longitudinal branch and the angular branch at its extremities; a short middle body branch curving above spiracle, dropping posteroventrally and terminating before mid-body length.



Figure 3. *Anomaloglossus roraima*, showing ventral views of hand and foot. **A:** Left hand (left) and left foot (right) of a male specimen (IRSNB 15888, 17.3 mm SVL). **B:** Left hand (left) and left foot (right) of a female specimen (IRSNB 15885, 17.4 mm SVL). Scale bars are 2 mm. Photos by Philippe J.R. Kok.

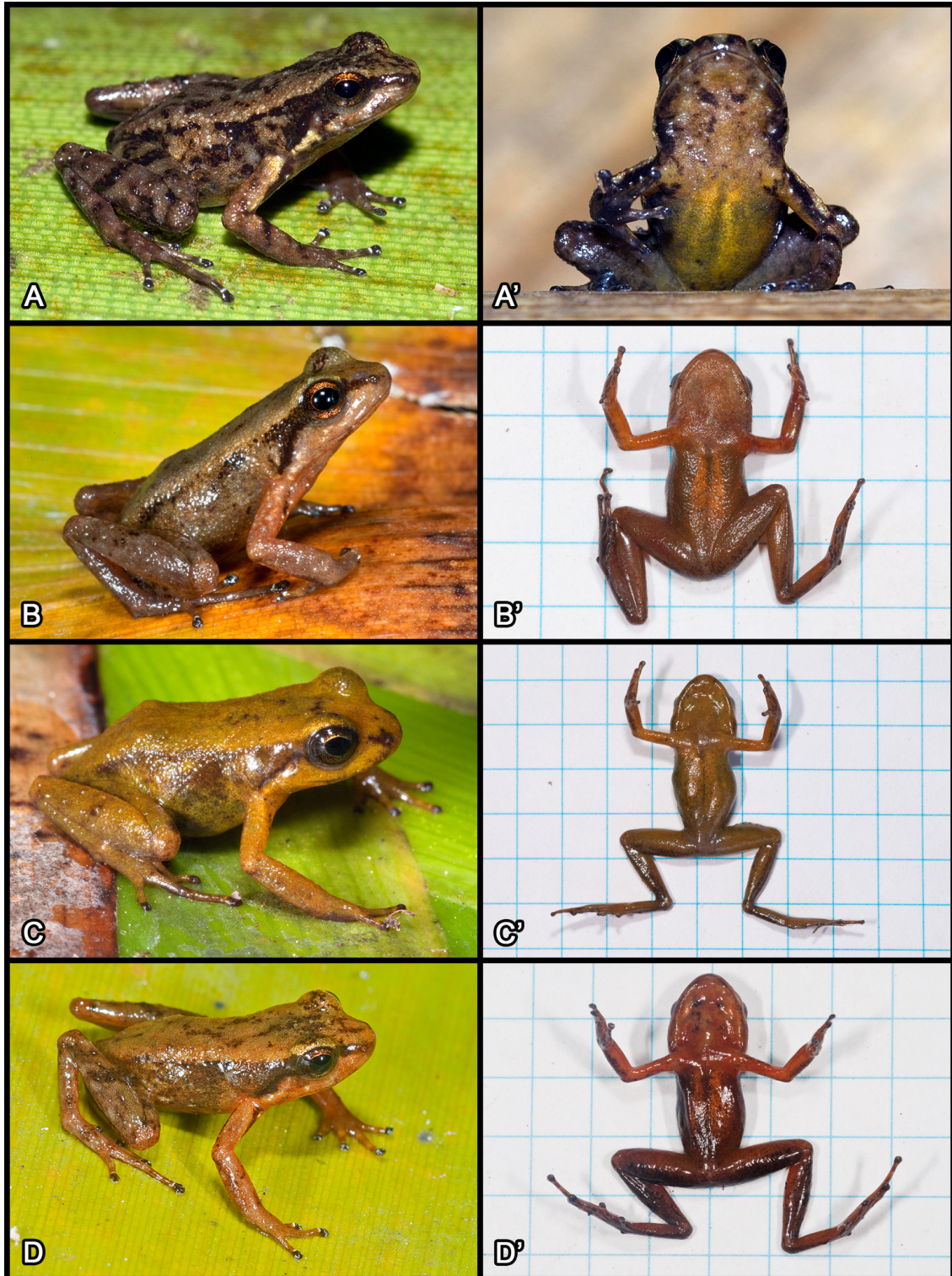


Figure 4. *Anomaloglossus roraima*, showing inter- and intrapopulation variation in color in life. **A**: Dorsolateral view of CPI-10212 (sex and SVL unknown) from Mount Roraima. **A'**: Ventral view of the same specimen. **B**: Dorsolateral view of IRSNB 15905, male 16.6 mm SVL from Wei-Assipu-tepui. **B'**: Ventral view of the same specimen. **C**: Dorsolateral view of IRSNB 15865, male 18.9 mm SVL from Wei-Assipu-tepui. **C'**: Ventral view of the same specimen. **D**: Dorsolateral view of IRSNB 15909, female 16.5 mm SVL from Wei-Assipu-tepui. **D'**: Ventral view of the same specimen. Grid squares = 5 mm. Photos A-A' by D. Bruce Means, B-D' by Philippe J.R. Kok.

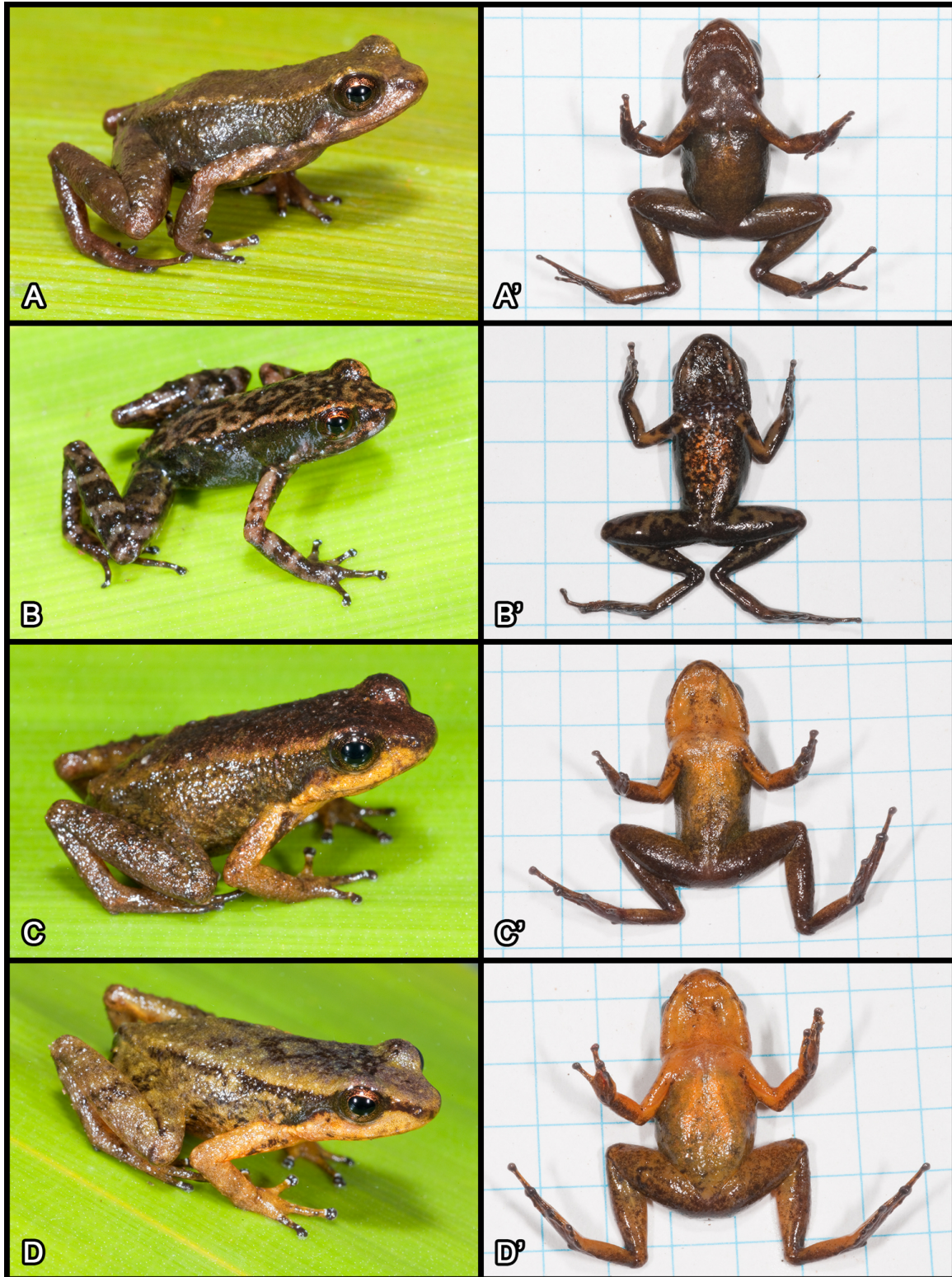


Figure 5. *Anomaloglossus roraima*, showing intrapopulation variation in color in life. **A**: Dorsolateral view of IRSNB 15901, male 18.1 mm SVL from Maringma-tepui. **A'**: Ventral view of the same specimen. **B**: Dorsolateral view of IRSNB 15864, male 16.5 mm SVL from Maringma-tepui. **B'**: Ventral view of the same specimen. **C**: Dorsolateral view of IRSNB 15887, female 19.3 mm SVL from Maringma-tepui. **C'**: Ventral view of the same specimen. **D**: Dorsolateral view of IRSNB 15883, female 18.9 mm SVL from Maringma-tepui. **D'**: Ventral view of the same specimen. Grid squares = 5 mm. Photos by Philippe J.R. Kok.

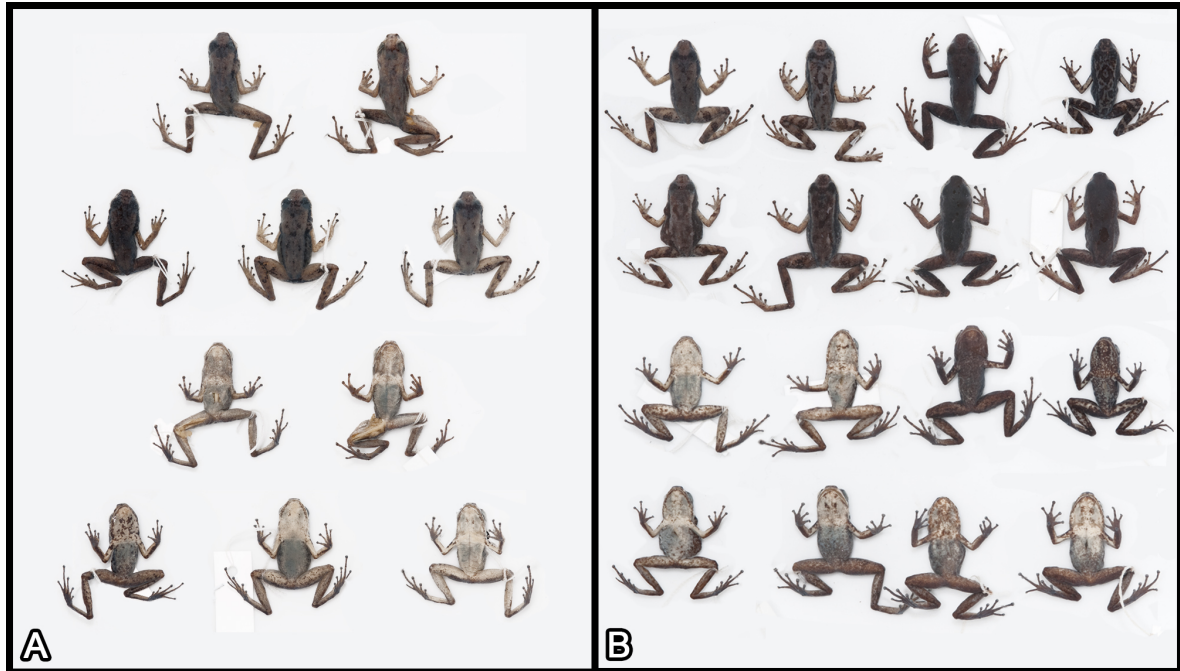


Figure 6. *Anomaloglossus roraima*, showing inter- and intrapopulation variation in dorsal and ventral pattern in preservative. **A:** specimens from Wei-Assipu-tepui, first row, dorsal pattern in males, from left to right: IRSNB 15905, 18.9 mm SVL, IRSNB 15865, 16.6 mm SVL; second row, dorsal pattern in females, from left to right: IRSNB 15904, 17.1 mm SVL, IRSNB 15908, 19.2 mm SVL, IRSNB 15906, 17.2 mm SVL; third and fourth row, ventral patterns of the same specimens. **B:** specimens from Maringma-tepui, first row, dorsal pattern in males, from left to right: IRSNB 15888 17.3 mm SVL, IRSNB 15886, 18.4 mm SVL, IRSNB 15898, 19.0 mm SVL, IRSNB 15864, 16.5 mm SVL; second row, dorsal pattern in females, from left to right: IRSNB 15885, 17.4 mm SVL, IRSNB 15891, 19.1 mm SVL, IRSNB 15893, 18.6 mm SVL, IRSNB 15887, 19.3 mm SVL; third and fourth row, ventral patterns of the same specimens. Photos by Philippe J.R. Kok.

Oral disc description is based on a tadpole in stage 27 (IRSNB 15902-f, Fig. 8 B). Oral disc located anteroventrally, laterally emarginated; transverse width 2.9; border of disc surrounded with *ca.* 60 marginal papillae, *ca.* 16 on posterolateral margins of anterior labium, *ca.* 44 on entire posterior labium; gap in papillae on anterior labium *ca.* 0.4; all papillae small, tapered, blunt-tipped, subequal; a few submarginal papillae present on posterior labium, where papillae are mostly arranged in a weak double row; lower jaw sheath slightly V-shaped, slightly higher than upper jaw sheath; each side of upper sheath slightly curved, not sigmoid; both upper and lower sheaths serrated; medial serrations blunt-tipped, lateral ones pointed; serrations extend entire length of sheaths, but do not include lateral processes (Fig. 8 B). Labial tooth row formula 2(2)/3; labial teeth numerous, moderately long, strongly curved, bearing *ca.* 15–20 cusps; tooth row A-1 complete, slightly longer than A-2; tooth row A-2 interrupted medially; lower tooth rows complete, shorter than A-1; tooth row P-2 slightly longer than P-1 and P-3, which are subequal.

Color of tadpole in life.- Black with few scattered lighter flecks on sides; caudal musculature and fins with scattered light gray flecks (Fig. 7 B).

Color of tadpole in preservative.- Background color, including venter, dark brown. Caudal musculature brown with scattered light gray flecks, fins translucent with scattered dark brown flecks (Fig. 8 A).

Ontogenetic changes.- Changes in body size are summarized in Table 2. There is no remarkable ontogenetic change, the lateral-line system is well detectable in stages 25-40, with an infraorbital branch originating near upper labium and terminating below or just behind the eye; a longitudinal branch originating near lower labium and meeting the angular branch; an angular branch originating below eye and terminating onto the ventral surface; a lateroventral branch originating near lower labium, often in contact with the longitudinal branch and the angular branch; in one stage-40 specimen a short supraorbital branch originating near upper labium and terminating just before the nostril; a middle body branch curving above spiracle, dropping posteroventrally and usually terminating near the end of the body. Lateral line system less developed after stage 42, absent in one stage-44 specimen; only a short angular branch detectable in another stage-44 specimen. From stage 39 onward, larvae have marginal papillae on posterior labium arranged in a double row, while smaller tadpoles have a weakly doubled row of papillae, sometimes with a single row retained on lateral edges of posterior labium.

Comparison with other known Anomaloglossus tadpoles occurring in the Eastern Pantepui District.- The tadpole of *A. roraima* is immediately distinguished from all known *Anomaloglossus* tadpoles (except that of *A. beebei*, see Kok *et al.*, 2006b for comparison) in being arboreal and exotrophic (other known *Anomaloglossus* tadpoles are either lentic or lotic and exotrophic, or nidicolous and/or endotrophic). The tadpole of *A. beebei* (the only known species that also breeds exclusively in bromeliad phytotelmata) is pale yellow to golden and has a higher upper fin originating from tail-body junction (vs. black with a low upper fin originating posterior to junction of body and tail in *A. roraima*). Although most benthic *Anomaloglossus* tadpoles are roughly similar and sometimes difficult to distinguish, especially in preservative, the tadpoles of *A. kaiei* and *A. praderioi* (La Marca, 1998) are immediately distinguished from the tadpole of *A. roraima* by their smaller size at equal stage (range of total length in stage-27 tadpoles is 12.6–16.4 in *A. kaiei*, 17.5–22.4 in *A. praderioi* vs. 24.0–27.8 in *A. roraima*, see Kok *et al.*, 2006a and Kok, 2010 for comparison). The tadpole of *A. roraima* mainly differs from the tadpoles of *A. parkerae* (Meinhardt & Parmelee, 1996) and *A. tepuyensis* (La Marca, 1998) in having a lower upper fin originating posterior to junction of body and tail (vs. higher upper fin originating from tail-body junction, see illustrations in Duellman, 1997 and in Myers & Donnelly, 2008 for comparison).

Advertisement call.- The following description is based on two advertisement calls from two different males: IRSNB 15901 from Maringma-tepui (recorded on 29/11/2007 at 9h00) and an unvouchered specimen from Wei-Assipu-tepui (recorded on 19/11/2009 at 9h30), both individuals were calling at 17°C air temperature, in bromeliads. Measurements of acoustic parameters for each individual recorded are provided in Table 3. The data presented below are inferred from the calls of both individuals.

Temporal structure.- The advertisement call of *Anomaloglossus roraima* consists in a single note repeated at a rate of 8.5–17 calls/min. A weak amplitude modulation is present and is most visible in the male from Maringma-tepui. Mean call duration is 0.143s ± 0.027 (range: 0.113–0.201s). The inter-call interval is not uniform and has a mean of 4.391s ± 2.130 and a range of 2.689–13.659s (Fig. 9).

Spectral structure.- Five to six harmonics are developed with the dominant frequency located in the second harmonic (mean: 4229 Hz ± 130; range: 3939–4362 Hz), although this is not always obvious. Frequency modulation is not detectable (Fig. 9).

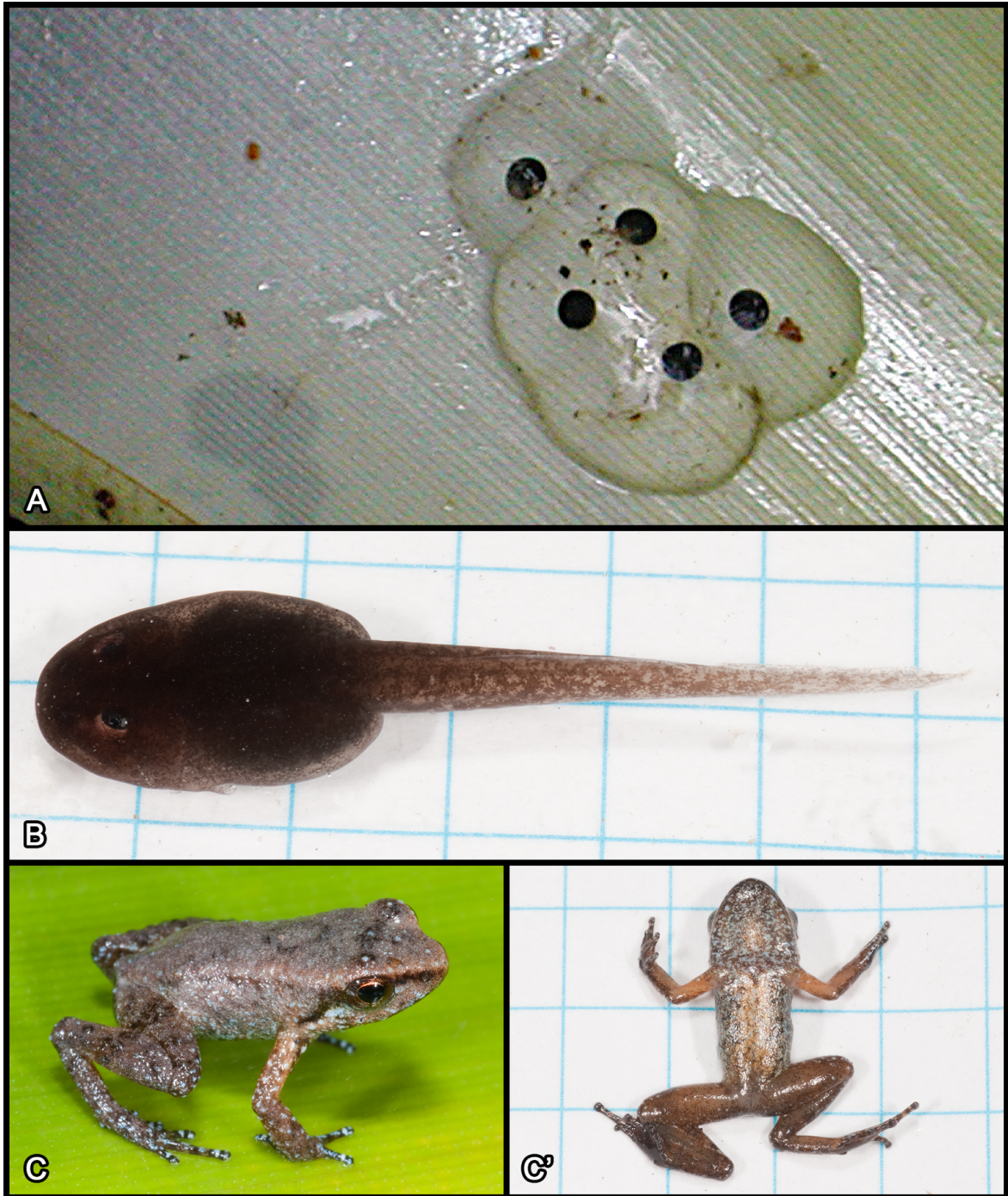


Figure 7. Egg clutch, tadpole, and juvenile of *Anomaloglossus roraima* in life. **A:** Egg clutch deposited on a leaf of a terrestrial tank bromeliad *Brocchinia tatei*. **B:** IRSNB 15902-c, a stage-27 tadpole. **C:** Dorsolateral view of IRSNB 15884, 11.3 mm SVL, a juvenile of *A. roraima* collected on Maringma-tepui. **C':** Ventral view of the same specimen. Grid squares = 5 mm. Photo A by D. Bruce Means, B-C' by Philippe J.R. Kok.

Character	Stage 25 (n=1)	Stage 26 (n=2)	Stage 27 (n=3)	Stage 28 (n=2)	Stage 38 (n=1)	Stage 39 (n=2)	Stage 40 (n=2)	Stage 41 (n=1)	Stage 42 (n=3)	Stage 44 (n=2)
TL	18.9	25.1 ± 0.3 (24.8–25.3)	25.8 ± 1.6 (24.0–27.8)	27.8 ± 1.7 (26.1–29.5)	31.6	28.1 ± 1.4 (26.7–29.5)	30.4 ± 0.2 (30.2–30.6)	32.0	32.6 (n=1)	22.9 (n=1)
BL	7.0	9.6 ± 0.1 (9.5–9.7)	9.6 ± 0.6 (9.1–10.5)	10.0 ± 0.3 (9.7–10.2)	11.1	9.4 ± 0.1 (9.2–9.5)	9.9 ± 0.5 (9.4–10.3)	10.2	9.8 ± 1.0 (8.4–10.5)	10.1 ± 0.1 (10.0–10.2)
TAL	11.9	15.5 ± 0.2 (15.3–15.6)	16.2 ± 1.1 (14.8–17.3)	17.9 ± 2.0 (15.9–19.8)	20.5	18.8 ± 1.6 (17.2–20.3)	20.6 ± 0.3 (20.3–20.8)	21.8	22.1 (n=1)	12.7 (n=1)
BW	4.5	6.6 ± 0.2 (6.4–6.7)	6.2 ± 0.3 (5.9–6.7)	6.7 ± 0.3 (6.4–7.0)	7.2	7.1 ± 0.2 (6.9–7.3)	7.3 ± 0.0 (7.2–7.3)	7.0	5.2 ± 0.7 (4.4–6.1)	4.5 ± 0.3 (4.2–4.8)
BH	2.8	4.0 ± 0.5 (3.8–4.1)	3.7 ± 0.3 (3.3–3.9)	4.5 ± 0.3 (4.2–4.7)	4.7	4.6 ± 0.1 (4.4–4.7)	4.6 ± 0.2 (4.4–4.8)	4.8	4.4 ± 0.4 (3.9–5.0)	3.9 ± 0.2 (3.8–4.1)
HW	4.1	5.5	5.3 ± 0.2 (5.2–5.6)	5.6 ± 0.3 (5.3–5.8)	6.1	5.7 ± 0.1 (5.6–5.8)	5.6	5.5	5.0 ± 0.5 (4.4–5.6)	3.7 ± 0.2 (3.4–3.9)
TMH	1.4	2.7 ± 0.2 (2.5–2.8)	2.3 ± 0.4 (1.9–2.8)	2.3 ± 0.3 (2.5–2.8)	2.7	2.5	2.5	2.3	2.1 ± 0.2 (1.9–2.3)	1.5 ± 0.2 (1.4–1.7)
TMW	1.3	2.3	2.3 ± 0.2 (2.0–2.5)	2.2 ± 0.1 (2.0–2.3)	2.7	2.5 ± 0.2 (2.3–2.7)	2.7	2.5	2.4 ± 0.3 (2.0–2.7)	2.1 ± 0.2 (1.9–2.2)
MTH	2.7	3.8	3.6 ± 0.2 (3.3–3.9)	4.0 ± 0.2 (3.8–4.1)	4.4	4.0 ± 0.1 (3.9–4.1)	4.2 ± 0.0 (4.1–4.2)	3.9	3.5 ± 0.5 (3.0–4.1)	2.2 ± 0.5 (1.7–2.7)
END	0.6	0.8 ± 0.1 (0.7–0.8)	0.8 ± 0.0 (0.8–0.9)	0.9	1.1	1.0 ± 0.1 (0.9–1.1)	1.0 ± 0.2 (0.8–1.2)	0.8	1.2 ± 0.0 (1.1–1.2)	0.9 ± 0.2 (0.7–1.1)
NSD	0.8	0.9 ± 0.1 (0.8–0.9)	1.1	1.1 ± 0.0 (1.0–1.1)	1.5	1.2 ± 0.1 (1.1–1.3)	1.2 ± 0.2 (1.0–1.3)	1.1	1.0 ± 0.2 (0.8–1.3)	0.8 ± 0.1 (0.7–0.8)
IND	1.1	1.5 ± 0.1 (1.4–1.6)	1.4 ± 0.0 (1.3–1.4)	1.5 ± 0.1 (1.4–1.6)	1.8	1.6	1.7	1.6	1.4 ± 0.0 (1.4–1.5)	1.5 ± 0.1 (1.4–1.6)
IOD	1.6	2.1 ± 0.1 (2.0–2.1)	2.1 ± 0.1 (2.0–2.3)	2.5 ± 0.1 (2.3–2.6)	1.6	1.2 ± 0.1 (1.1–1.3)	1.5 ± 0.1 (1.4–1.6)	1.2	1.6 ± 0.2 (1.4–1.8)	1.5 ± 0.1 (1.4–1.6)
ED	0.7	1.0	1.0 ± 0.1 (0.8–1.1)	1.0	1.1	1.3 ± 0.1 (1.1–1.4)	1.3 ± 0.1 (1.2–1.4)	1.2	1.4 ± 0.0 (1.4–1.5)	1.4

Table 2. Measurements (in mm) of tadpoles of *Anomaloglossus roraima*. Abbreviations are defined in the text. Mean ± SD are followed by the range in parentheses.

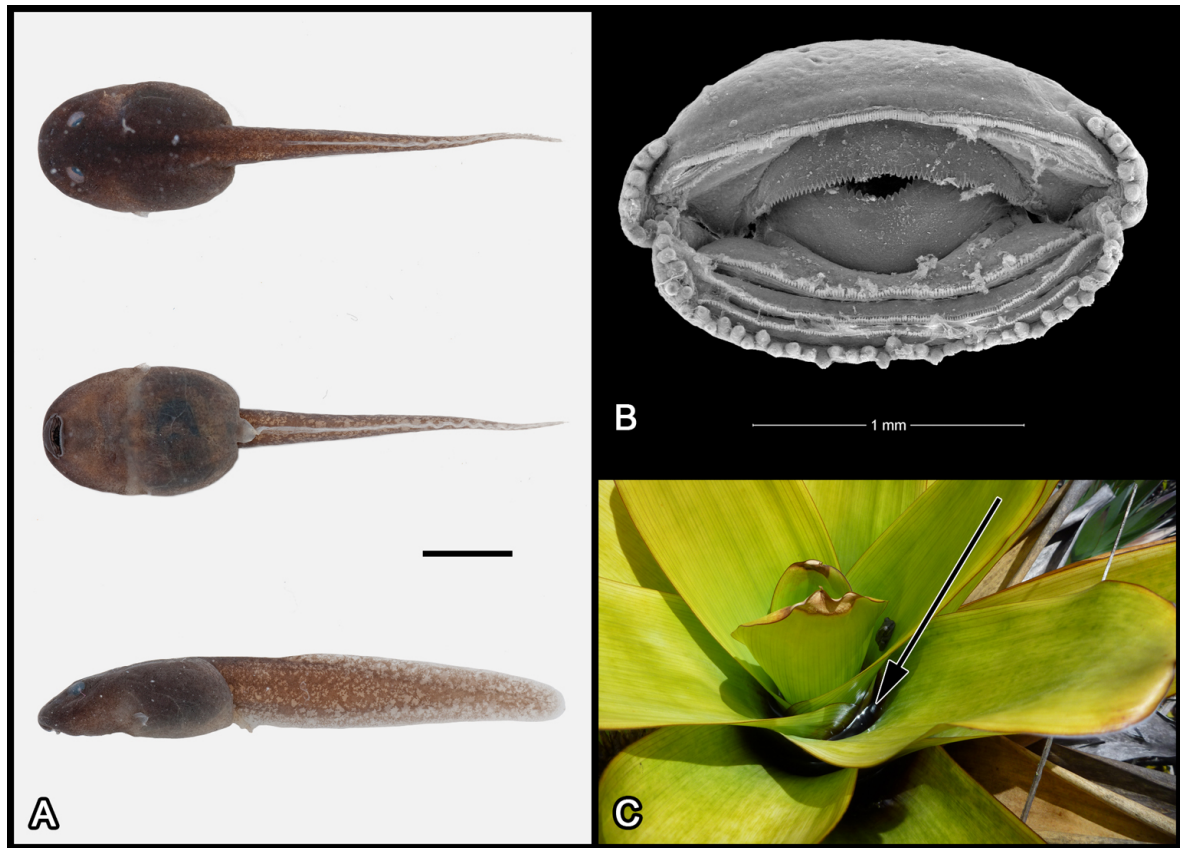


Figure 8. Tadpole of *Anomaloglossus roraima* in preservative, and larvae microhabitat. **A:** Dorsal, ventral and lateral views of IRSNB 15903-e, a stage-28 tadpole. Scale bar is 5 mm. **B:** Photomicrograph of the oral disc of IRSNB 15902-f, a stage-27 tadpole (140x magnification). **C:** A terrestrial tank bromeliad *Brocchinia tatei* with black arrow showing tadpole microhabitat (the frog seen above the arrow is a *Tepuihyla* sp.). Photos by Philippe J.R. Kok.

Individual	Call rate (calls/min)	Note duration (s)	Inter-call interval (s)	Dominant frequency (Hz)
IRSNB 15901, Maringma-tepui	8.5	0.186 ± 0.006 (0.178–0.201)	6.835 ± 2.465 (4.432–13.659)	4034 ± 81.098 (3939–4132)
Unvouchered specimen, Wei-Assipu-tepui	17	0.127 ± 0.004 (0.113–0.136)	3.560 ± 1.162 (2.689–10.665)	4299 ± 49.473 (4107–4362)

Table 3. Measurements of acoustic parameters for two *Anomaloglossus roraima* males from two different tepui summits. Mean ± SD are followed by the range in parentheses. Temperature was 17°C at both sites.

Intraspecific (interpopulational) variation.- Some variation is present between the calls of the male from Maringma-tepui and the male from Wei-Assipu-tepui. Call duration in the Maringma male is slightly longer, dominant frequency lower, and inter-call interval longer (Table 3). Furthermore the amplitude in notes in the Maringma male's call is more obviously modulated (Fig. 10) and the first harmonic more difficult to detect. It should be noted that although air temperature was the same during both recordings, the hygrometry was much higher during the recording of the Maringma male (*ca.* 90% during a cloudy misty day) than during the recording of the Wei-Assipu male (*ca.* 30% during a dry sunny day). It is unknown whether the differences between the calls were related to the

hygrometry level or whether they merely reflect intraspecific variation, but in any case they were not substantial.

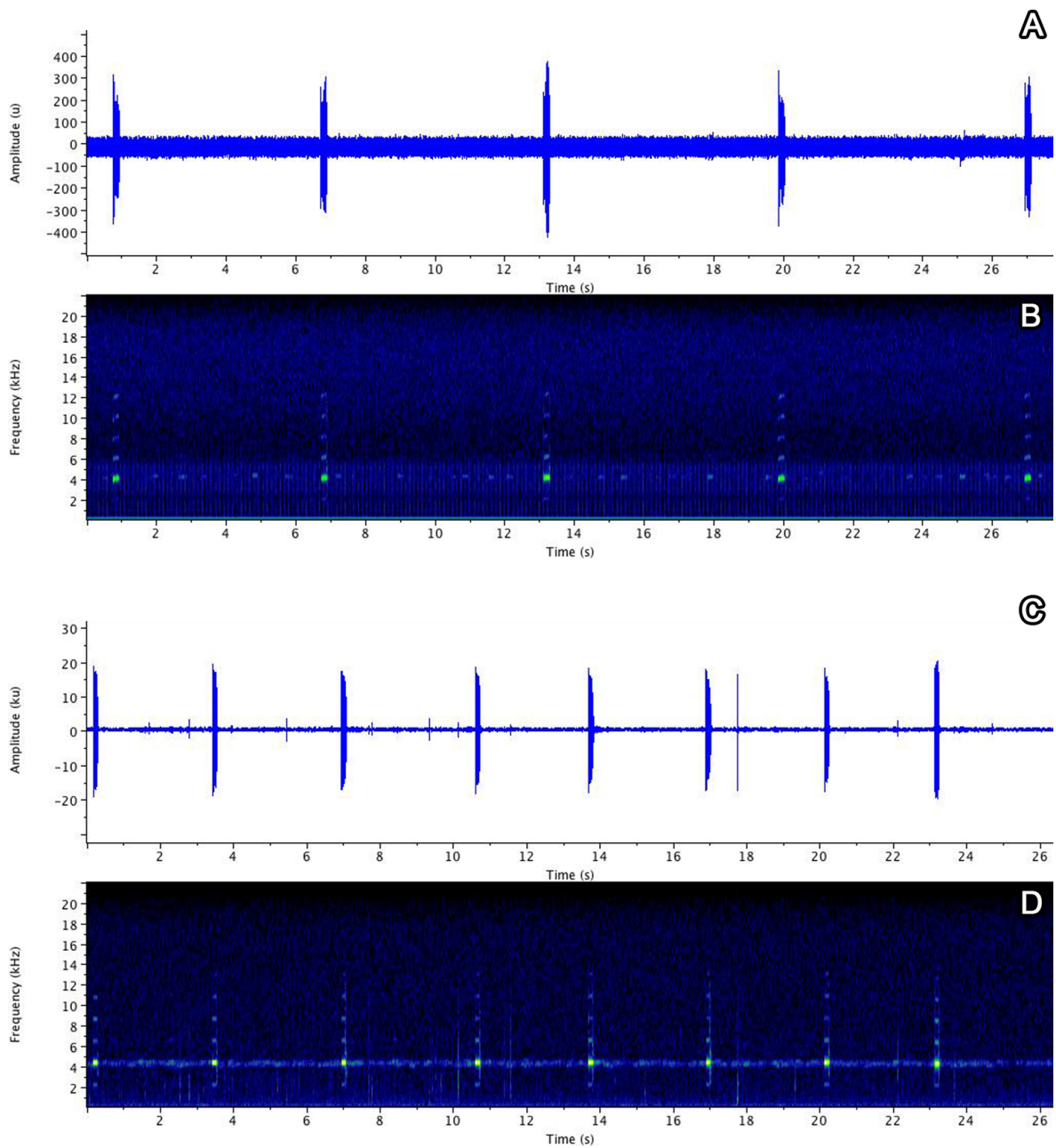


Figure 9. Vocalization of *Anomaloglossus roraima*. **A:** Oscillogram. **B:** Spectrogram (recording of IRSNB 15901 from Maringma-tepui). **C:** Oscillogram. **D:** Spectrogram (recording of an unvouchered specimen from Wei-Assipu-tepui). Temperature was 17°C in both cases.

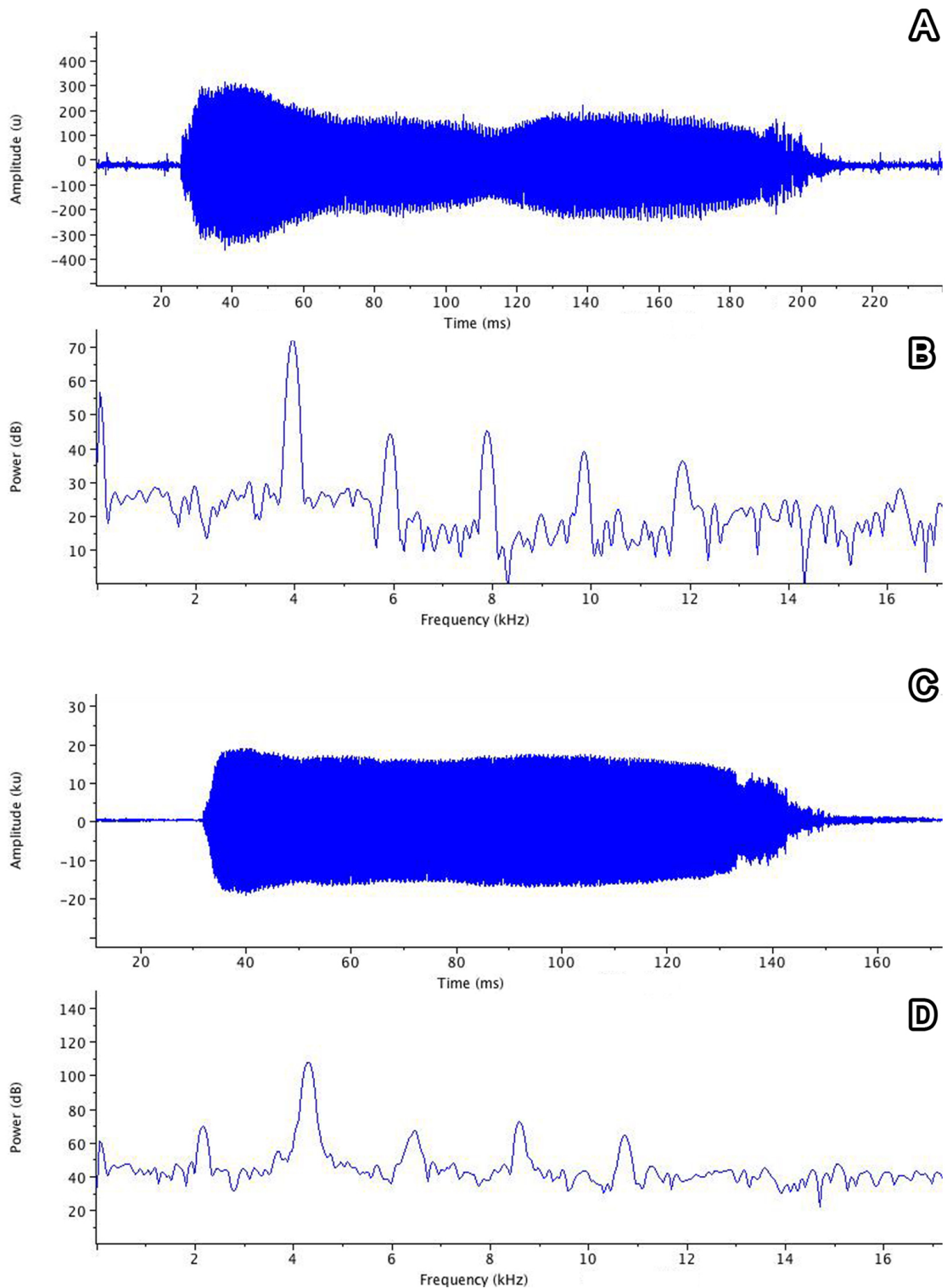


Figure 10. Vocalization of *Anomaloglossus roraima*. **A-B**: Expanded oscillogram of the first note in Fig. 9 A-B showing slight amplitude modulation (A) and spectral slice of the same note showing poorly defined fundamental frequency at *ca.* 2 kHz (B). **C-D**: Expanded oscillogram of the first note in Fig. 9 C-D showing absence of significant amplitude modulation (C) and spectral slice of the same note showing a well detectable fundamental frequency at *ca.* 2 kHz (D). Temperature was 17°C in both cases.

Comparison with other Anomaloglossus calls.- Only three *cis*-Andean *Anomaloglossus* species for which calls are known produce a single note per call: *A. degranvillei* (Lescure, 1975), a riparian species that does not occur in the Pantepui region but in French Guiana and Suriname and likely in adjacent Brazil (Frost, 2013), and *A. praderioi*, which is sympatric with *A. roraima* on the upper slopes of Mount Roraima (Kok, 2010), and *A. surinamensis* Ouboter and Jairam, 2012, a riparian species that does not occur in the Pantepui region but in eastern Suriname. The call of *A. degranvillei* (see Lescure and Marty, 2001 for comparison) is the most similar to that of *A. roraima*, having a similar dominant frequency (4280–4640 vs. 3939–4362 in *A. roraima*) located in the second harmonic. It is however easily distinguished by the higher call rate (42 vs. 8.5–17 in *A. roraima*). In *A. praderioi* the call rate is much higher (61–76), the dominant frequency is slightly lower (3562–3856), and is located in the fundamental harmonic (vs. 3939–4362 with dominant frequency located in the second harmonic in *A. roraima*, even if this is not always obvious). Furthermore, in *A. praderioi* the dominant frequency is slightly modulated upwards, while there is no such frequency modulation detectable in *A. roraima*. Comparison with the call of *A. surinamensis* is made difficult by the brevity of the description, but in *A. surinamensis* (see Ouboter and Jairam, 2012 for comparison) the dominant frequency is reported to be 4550–4950Hz (vs. 3939–4362Hz in *A. roraima*) and the call rate faster than in *A. degranvillei* (therefore much faster than in *A. roraima*, see above).

Distribution and natural history.- *Anomaloglossus roraima* is currently known only from the upper slopes and summits of three tepuis in southeastern Venezuela and western Guyana: between 1860–2700 m elevation on the slopes of Mount Roraima (type locality, currently the westernmost known locality), between 2200–2300 m elevation on the summit of Wei-Assipu-tepui, and between 2000–2100 m elevation on the summit of Maringma-tepui (currently the easternmost known locality; Fig. 1). *Anomaloglossus roraima* seems restricted to tepui scrub and high-tepui meadow at elevations between 1860–2700 m and is probably restricted to the eastern part of the Eastern Pantepui District. It is expected to be discovered in suitable habitat between Mount Roraima and Maringma-tepui in Guyana (e.g. on Yakontipu-tepui and on Appokailang-tepui, both still unexplored herpetologically), and likely between Mount Roraima and Kukenan-tepui in Venezuela.

Anomaloglossus roraima breeds in the large terrestrial bromeliad *Brocchinia tatei* (Fig. 11). The species is locally common and was found sympatric with *A. praderioi* on the upper slopes of Mount Roraima only. All specimens were collected during the day, in large terrestrial tank bromeliads or on the ground close to these bromeliads, usually along rivulets and small puddles. A very small juvenile (IRSNB 15884, 11.3 mm SVL, Fig. 7 C-C') was collected moving on the ground close to bromeliads, another one (lost) was found during patch sampling (5 x 5 m patch) among plant rootlets under the ground. Males emitted vocalizations the entire day, but significantly more males were calling during misty days. Courtship was not observed. Eggs are deposited in low number (ca. five) on the leaves of terrestrial tank bromeliads (Fig. 7A). No male was found carrying tadpoles on his back, and we hypothesize that reproduction in this species is similar to that in its sister species *Anomaloglossus beebei* (see Kok et al., 2005, 2006b for details). We found up to 29 tadpoles in a same bromeliad phytotelma, which indicates that several clutches can be deposited in a same plant.



Figure 11. Habitat of *Anomaloglossus roraima*. **A:** Patch of *Brocchinia tatei* on the upper northern slope of Mount Roraima, Guyana, at ca. 2300 m elevation. **B:** A large *Brocchinia tatei* on the upper northern slope of Mount Roraima, Guyana, at ca. 2300 m elevation. **C:** Numerous *Brocchinia tatei* between escarpments on the summit of Wei-Assipu-tepui, Guyana, at ca. 2150 m elevation. **D:** Thick vegetation including a *Brocchinia tatei* on the summit of Maringma-tepui, Guyana, at ca. 2100 m elevation. Photos A-B by D. Bruce Means, C-D by Philippe J.R. Kok.

In phytotelmata of *Brocchinia tatei* on Wei-Assipu-tepui and at the base of the ultimate cliffs of the "Prow" of Mount Roraima, we found abundant small (<15 cm), brown earthworms (Clitellata: Glossoscolecidae) and a small aquatic cricket, *Hydrolutos roraimae* (Orthoptera: Anostostomatidae) that may be a predator on frog eggs and tadpoles.

Phylogenetic relationships.- As highlighted by Grant *et al.* (2006) and Kok *et al.* (2012), *Anomaloglossus roraima* is sister to *A. beebei*. Both species are the only known *Anomaloglossus* that use bromeliad phytotelmata as habitat for their larvae. Kok *et al.* (2012, supplementary material) showed that the clade containing *A. beebei* and *A. roraima* (arboreal tadpoles with confirmed trophic egg-laying in *A. beebei*, highly hypothesized in *A. roraima*) is sister to a clade containing *A. kaiei*, *A. praderioi*, and a still undescribed taxon from Mount Wokomung (lentic tadpoles with confirmed trophic egg-laying in *A. kaiei*, potential in *A. praderioi* and the still unnamed taxon). The clade containing these species with arboreal/lentic tadpoles diverged from clades containing species mostly with lotic or endotrophic tadpoles.

Discussion. Comparison of our specimens with the holotype of *Anomaloglossus roraima* leaves no doubt about their belonging to the same species. Our additional specimens also agree well with the original species definition (La Marca, 1998) except in a few aspects that are mostly La Marca's misinterpretation of character states and inconsistencies in illustrations. Several important diagnostic characters were unknown by La Marca because his description is based on a single immature female. We hope that our detailed redescription will facilitate specimens' identification.

Like many other *Anomaloglossus* species, *A. roraima* displays an impressive intraspecific variation in color pattern. This phenotypic variability, coupled with the fact that the species occurs on different tepuis, could lead to inappropriate taxonomic decisions (*i.e.* describing populations from different tepuis as new), which has been done in the past with other Pantepui taxa (see Kok *et al.*, 2012). Genetic divergences between populations of *A. roraima* from different tepuis are surprisingly low (0–0.2% in 16S, less than 0.8% in ND1, see Kok *et al.*, 2012) and strongly advocate against the recognition of these populations as separate species, as also indicated by morphological and call analyses.

In their supplementary material, Santos *et al.* (2009) argued that the taxonomic division of Dendrobatidae into two families by Grant *et al.* (2006) [referred by Santos and colleagues to as Allobatidae (*lapsus calami* for Aromobatidae) and Dendrobatidae] is "unnecessary and adds no new information". They thus proposed to return Dendrobatidae to a single family. Apart from the fact that Santos *et al.* (2009) consistently use "Allobatidae" instead of Aromobatidae—which might arise questions about their proper reading of Grant *et al.* (2006)—their proposition is in contradiction with the topology of the phylogenetic trees these authors proposed which, as mentioned by Santos *et al.* (2009) themselves, is similar to the phylogenetic hypotheses of Grant *et al.* (2006). We disagree with Santos *et al.* (2009) and still consider Aromobatidae as a distinct family and refer the reader to Brown *et al.* (2011) for further discussion about the relevance and adequacy of the taxonomic corrections proposed by Santos *et al.* (2009).

Due to its restricted range (area of occupancy severely fragmented and estimated to be less than 2000 km², with species found at less than 10 locations) and continuing decline of habitat quality caused by (1) the many local fires affecting tepui slope vegetation ignited by Amerindians in Venezuela (see Tate, 1930; Means, 1995), (2) an increase of mostly unregulated tourism on Mount Roraima (Castillo, 2005), and (3) global warming (Nogué *et*

al., 2009) we suggest that *Anomaloglossus roraima* be classified as “Vulnerable” (VU) in accordance with the criteria B2 a, b (iii) of IUCN (2001).

Resumen

La rana *Anomaloglossus roraima* fue originalmente descrito como *Colostethus roraima* por E. La Marca en 1998 con base a un único e inmaduro ejemplar hembra, recolectado a 2700 m de elevación sobre la parte alta del monte Roraima, un tepui (macizo montañoso) localizado en el sureste de Venezuela. Se ofrece una redescrición de la especie con base a nuevos ejemplares del Wei-Assipu-tepui y Maringma-tepui en Guyana. La redescrición incluye su vocalización y descripción de la larva. *Anomaloglossus roraima* es una especie de pequeño tamaño y se diferencia de otras especies dentro del genero por tener el dedo de la mano I < II con aristas pre-y postaxiales que son angostas y sin doblés; dedos del pie sin membrana (aunque una membrana rudimentaria esta algunas veces presente entre los dedos III y IV) y con aristas pre-y postaxiales que son angostas y sin doblés; tubérculos cloacales simétricos presentes; línea dorsolateral usualmente presente, con frecuencia inconspicua; línea ventrolateral ausente, línea lateral oblicua ausente; sin un obvio dicromatismo sexual en la garganta, pecho y en el diseño de la coloración ventral. La larva es grande, negra, exotrofica, arbórea, LTRF 2(2)/3. El canto de llamado reproductivo consiste de una única nota repetida a una tasa de 8.5–17 notas/minuto, con una frecuencia dominante que va de 4107 a 4362 Hz. La especie esta restringida a una pequeña área dentro de la Cadena de Tepuyes del Este, en el sureste de Venezuela y oeste de Guyana, donde esta habita principalmente sobre grandes bromelias en arbustales y vegetación rala altotepuyana, en elevaciones entre 1860–2700 m sobre el nivel del mar. El descubrimiento de esta especie en diferentes cimas de tepuyes y en sus laderas, la cual había sido previamente señalada como un habitante restringido a las tierras altas, es importante para el entendimiento de la biogeografía del la región del Pantepui.

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APPENDIX . ADDITIONAL SPECIMENS EXAMINED

Anomaloglossus beebei.— Guyana: *Potaro-Siparuni District*: Kaieteur National Park, IRSNB 13721-26, 13728-53, ULABG 6817 (ex IRSNB 13727), IRSNB 13754 (tadpoles), IRSNB 13779-81 (tadpoles).

Anomaloglossus breweri.— Venezuela: *Estado Bolívar*: Aprada Tepui, Cueva del Fantasma, MHNLS 17044 (holotype), MHNLS 17045-46 (paratypes).

Anomaloglossus kaiei.— Guyana: *Potaro-Siparuni District*: Kaieteur National Park, IRSNB 1938 (holotype), IRSNB 1939-64 (paratypes), IRSNB 14420-57, IRSNB 13755-78 (tadpoles), ROM 42999; Cuyuni-Mazaruni District, Wayalayeng, IRSNB 14922-24, Maringma Tepui, IRSNB 14925-31, Mount Wokomung, ROM 43321, ROM 43327, ROM 43330, ROM 43333.

Anomaloglossus murisipanensis.— Venezuela: *Estado Bolívar*: Murisipan-Tepui, MHNLS 11385 (holotype).

Anomaloglossus parkerae.— Venezuela: *Estado Bolívar*: Sierra de Lema, Salto El Danto, MHNLS 2901, MHNLS 11088-89.

Anomaloglossus praderioi.— Guyana: *Cuyuni-Mazaruni District*: Maringma Tepui, IRSNB 11403-13, IRSNB 14414-16 (tadpoles); Venezuela: *Estado Bolívar*: Mount Roraima ULABG 4196 (holotype), MHNLS 11272 (paratype), Sierra de Lema, EBRG 5569.

Anomaloglossus cf praderioi.— Guyana: *Cuyuni-Mazaruni District*: Mount Wokomung, ROM 43320, ROM 43322-26, ROM 43328-29, ROM 43331-32, ROM 43896, Mount Ayanganna ROM 39639.

Anomaloglossus roraima.— Guyana, *Cuyuni-Mazaruni District*: Wei-Assipu-tepui, IRSNB 15851, IRSNB 15865, IRSNB 15904-11, 15903 a-g (tadpoles), Maringma-tepui, IRSNB 15864, IRSNB 15883-901, 15902 a-m (tadpoles). Venezuela, *Estado Bolívar*: Mount Roraima, ULABG 4197 (holotype).

Anomaloglossus rufulus.— Venezuela: *Estado Bolívar*: Amuri-Tepui, Chimantá Massif, MHNLS 10361 (holotype).

Anomaloglossus tepuyensis.— Venezuela: *Estado Bolívar*, Auyantepui: ULABG 2557 (holotype), Cucurital River, MHNLS 14404-05, Purumay River, MHNLS 14924-25, MHNLS 14940-41, MHNLS 15687, Quebrada Atapere, MHNLS 15924, MHNLS 17359-60, MHNLS 17383, Quebrada Tucutupan, MHNLS 17401, Quebrada Rutapa, MHNLS 17361.

Anomaloglossus triunfo.— Venezuela: *Estado Bolívar*: Cerro Santa Rosa, Serranía del Supamo, EBRG 4756 (holotype), EBRG 4757-59 (paratypes).

