Islands in the sky : species diversity, evolutionary history, and patterns of endemism of the Pantepui Herpetofauna

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A NEW SPECIES OF *ANOMALOGLOSSUS* (ANURA: AROMOBATIDAE) FROM THE PAKARAIMA MOUNTAINS OF GUYANA

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Abstract

We describe a new species of *Anomaloglossus* from the Pakaraima Mountains of Guyana. *Anomaloglossus megacephalus* **sp. nov.** is currently known from Maringma Tepui at 1060 m elevation and from Mt. Ayanganna at 1490 m elevation. The new species can be distinguished from all known congeners by the following combination of characters: relatively large size (females up to 28.3 mm), head large, Finger I subequal or shorter than II, the tip of Finger IV surpassing the base of the distal tubercle on Finger III when fingers are adpressed, fingers with preaxial keel-like lateral folds, best developed on Fingers II and III, toes moderately webbed with folded flaplike fringing, symmetrical cloacal tubercles present, dorsolateral stripe absent, ventrolateral stripe present, inconspicuous, oblique lateral stripe present, often broken in spots. *Anomaloglossus megacephalus* has been previously confused with *A. tepuyensis*, a taxon described from Auyantepui in Venezuela.

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Text and figures remain unchanged, only the format was adapted to fit the thesis layout

INTRODUCTION

The genus *Anomaloglossus* contains twenty-four species—some of them previously assigned to the genus *Colostethus*—many of which apparently have restricted distribution ranges (Grant *et al*. 2006). *Anomaloglossus* species are easily distinguished from other Aromobatidae by the synapomorphic presence of a median lingual process (Grant *et al*. 2006).

Anomaloglossus species display considerable variation in reproductive biology. The six species for which data on reproductive behaviour are available have terrestrial eggs (*i.e*. non-aquatic). After hatching, tadpoles are transported on males' dorsum to a suitable body of water, except in *A. stepheni* (Martins, 1989) (tadpole endotrophic, nidicolous), and in *A. degranvillei* (Lescure, 1975) (tadpole endotrophic, developing on the male's back). In phytotelm-breeding species like *A. beebei* (Noble, 1923), tadpoles hatch from eggs laid on leaves above the water-filled axis of bromeliads and slide into the bromeliad tank; males transport them only occasionally, for instance when there is no food in the bromeliad tank (Kok *et al*. 2005). Maternal care (here laying of trophic eggs) is reported in two species [*A. beebei* and *A. kaiei* (Kok, Sambhu, Roopsind, Lenglet & Bourne, 2006a)]. Tadpole deposition sites are invariable within species and range from phytotelmata [*e.g*. *A. beebei*, *A. roraima* (La Marca, 1998)], to small forest puddles [*e.g*. *A. kaiei*, *A. praderioi* (La Marca, 1998)] and to running water [*e.g*. *A. tepuyensis* (La Marca, 1998)].

The genus is reported to occur on the Pacific slopes of the Andes in Colombia and Ecuador (three species), in the Amazonas state of Brazil (one species) and in the Guiana Shield (21 species), where most species (16 species, 67% of all known *Anomaloglossus*) occur in the uplands and highlands of the Pantepui region, a biogeographic province referring to the complex of mountains mainly derived from the sandstone of the Roraima Group in southern Venezuela, west-central Guyana and northern Brazil [see Myers & Grant (2009), Barrio-Amorós *et al*. (2010), Frost (2010), and Kok (2010) for number of known species and detailed species distributions].

Because of the sometimes large intraspecific variability, *Anomaloglossus* can be morphologically difficult to distinguish [*e.g*. *A. baeobatrachus* (Boistel & de Massary, 1999) and *A. stepheni*], particularly in preservative. Several areas within the distribution of the genus are still largely unexplored and cryptic species are probably not uncommon in the genus (Fouquet *et al*. 2007).

Grant *et al*. (2006) included an *Anomaloglossus* specimen collected during the Royal Ontario Museum Ayanganna Expedition in 2000 in their phylogenetic study, and cautiously identified it as *A. tepuyensis*—a species described from Auyantepui in Venezuela—on the basis of morphology. Grant *et al*. (2006: 120) aptly mentioned that their identification "*will likely require revision*" and predicted "*additional specimens and/or molecular data will reveal that these are different species*". MacCulloch & Lathrop (2009) followed Grant *et al*.'s (2006) tentative identification. In the meantime two additional *Anomaloglossus* specimens became available from Mt. Ayanganna and Maringma Tepui, Guyana and PJRK had the opportunity to examine the type series of most *Anomaloglossus* from the Pantepui region in the context of a taxonomic redefinition of the Pantepui species. Direct comparisons indicated that the specimens from Guyana are not conspecific with *A. tepuyensis* from the type locality and further morphological comparisons showed that the Guyanese populations represent an undescribed taxon, which is described herein.

MATERIAL AND METHODS

Specimens were collected by hand and euthanized by immersion in Xylocaine or in a mixture of clove oil, ethanol and water. Tissue (a piece of liver or thigh muscle) was removed from most specimens and preserved in 95-100% ethanol. Whole individuals were fixed in 10% formalin and later transferred to 70% ethanol for permanent storage. Specimens have been deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRSNB) and the Royal Ontario Museum (ROM); tissue samples were deposited in the Amphibian Evolution Lab, Biology Department, Vrije Universiteit Brussel (VUB) and ROM (see Appendix for material examined).

Coordinates and elevations were acquired using a Garmin 60CSx Global Positioning System unit and referenced to map datum WGS84.

All morphometric data were taken from the preserved specimens by the same person (BW) [except HL2, HL3, HW, and BEL (taken by PJRK)], to the nearest 0.01 mm and rounded to the nearest 0.1 mm, under a Leica stereo dissecting microscope using an electronic digital caliper. For ease of comparison, the description mainly follows the pattern of recent descriptions in the genus (*e.g.* Kok *et al.* 2006a, Myers & Donnelly 2008, Kok 2010). Measurements were taken and abbreviated as follows: (1) snout-vent length (SVL); (2) head length from corner of mouth to tip of snout (HL1); (3) head length from angle of jaw to tip of snout (HL2); (4) midline distance from snout tip to an imaginary line between anterior arm insertions when arms at right angle with body (HL3); (5) head width at level of angle of jaws (HW); (6) snout length from anterior corner of eye to tip of snout (SL); (7) eye to naris distance from anterior corner of eye to posterior margin of naris (EN); (8) internarial distance (IN); (9) eye length (EL); (10) interorbital distance (IO); (11) greatest length of tympanum from its anterior margin to its posterior margin (TYM); (12) forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow (FAL); (13) length of Finger I from proximal edge of palmar tubercle to tip of finger (HAND I); (14) length of Finger II from proximal edge of palmar tubercle to tip of finger (HAND II); (15) length of Finger III from proximal edge of palmar tubercle to tip of finger (HAND III, also equivalent to hand length); (16) length of Finger IV from proximal edge of palmar tubercle to tip of finger (HAND IV); (17) width of disc on Finger III (WFD); (18) foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV (FL); (19) width of disc on Toe IV (WTD); (20) tibia length from outer edge of flexed knee to heel (TIL); (21) upper arm length from anterior insertion with the body to outer edge of flexed elbow (AL); (22) midline distance from an imaginary line between anterior arm insertions when arms at right angle with body to an imaginary line between anterior thigh insertions when thighs at right angle with body (BEL).

Webbing formulae follow Savage & Heyer (1967), with modifications proposed by Myers & Duellman (1982) and Savage & Heyer (1997). 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.

Colour pattern in life was taken from field notes and colour photographs. Sex and maturity were determined by the presence/absence of vocal slit(s) and by dissection. Internal soft anatomy was examined by dissection of preserved specimens.

Comparisons of external character states are based both on original descriptions and examination of museum specimens, usually including the type series (see Appendix for

material examined). Since examination of comparative type series sometimes revealed discrepancies between type specimens and original descriptions, our diagnoses may differ from those usually proposed.

Taxonomy follows Grant *et al*. (2006). Institutional acronyms follow Frost (2010).

NEW SPECIES DESCRIPTION

Anomaloglossus megacephalus sp. nov.

Figs. 1–4; Table 1

Anomaloglossus tepuyensis (La Marca, 1998) in part; Grant *et al*. (2006: 120, 158)
Anomaloglossus tepuyensis (La Marca, 1997 [sic]); MacCulloch & Lathrop (2009: 11, figs. 5–6, plate B)

Holotype. IRSNB 1986 (field number PK 1881), an adult female collected by Philippe J. R. Kok, Paul Benjamin and Claudius Perry, 20 November 2007 at 16h30, eastern base of Mount Maringma, Cuyuni-Mazaruni District, Guyana (05° 12' 37"N, 060° 33' 59"W, 1060 m elevation).

Paratypes. ROM 39637-38, adult females collected by Amy Lathrop and Carter Cox, 28 October 2000, northeastern plateau of Mount Ayanganna, Cuyuni-Mazaruni District, Guyana (05° 24' N, 59° 57' W, 1490 m elevation).

Etymology. The specific epithet is a combination of *mega* (Greek meaning "large") and *cephalus* (Greek meaning "head"), which refers to the large head of the species and is used as a noun in apposition.

Adult definition and diagnosis. (1) large-sized *Anomaloglossus* (male unknown, female 27.3–28.3 mm SVL); (2) body robust, but relatively more slender than most known congeners, head large; (3) skin on dorsum smooth to granular, more tuberculate posteriorly, skin on venter smooth to slightly granular; (4) Finger I subequal or shorter than II; (5) tip of Finger IV surpassing the base of the distal subarticular tubercle on Finger III when fingers adpressed; (6) distal tubercle on Finger IV present; (7) condition of Finger III in males unknown; (8) fingers with keel-like lateral folds (*sensu* Myers & Donnelly 2008), best developed preaxially on Fingers II and III; (9) toes moderately webbed, with well-developed folded flaplike fringing (*sensu* Myers & Donnelly 2008); (10) tarsal keel well-defined, weakly curved, slightly tuberclelike; (11) presence of black arm gland in males (*sensu* Grant & Castro-Herrera 1998, see also Grant *et al*. 2006) unknown; (12) symmetrical cloacal tubercles present; (13) pale paracloacal mark present; (14) dorsolateral stripe absent in female (condition unknown in males); (15) ventrolateral stripe present, inconspicuous; (16) oblique lateral stripe present, broken in spots or relatively well-defined; (17) condition of sexual dichromatism in throat colour unknown; (18) condition of sexual dichromatism in ventral colouration unknown; (19) iris with metallic pigmentation and pupil ring; (20) large intestine anteriorly pigmented; (21) colour of testes unknown; (22)

mature oocytes partly pigmented; (23) median lingual process short, wider than long, tapered (24) maxillary teeth present, small.

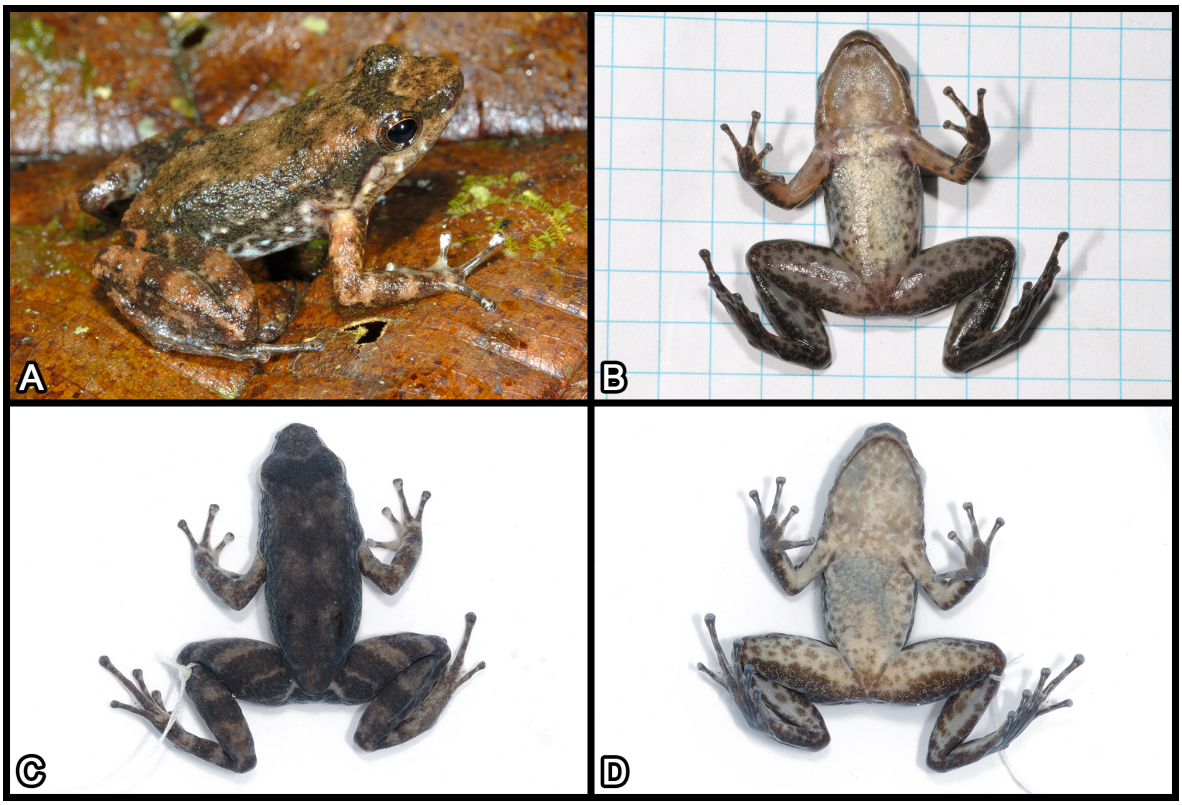

Figure **1.** *Anomaloglossus megacephalus* **sp. nov.** A: Dorsolateral view of the holotype in life (IRSNB 1986, 27.3 mm SVL). B: Ventral view of the holotype in life. C: Dorsal view of the preserved holotype. D: Ventral view of the preserved holotype. Photos by PJRK.

Description of the Holotype. An adult female 27.3 mm SVL in excellent condition of preservation. Dorsal skin granular, more tuberculate posteriorly; ventral skin slightly granular. In preservative, a barely distinct epidermal ridge borders the tip of snout dorsally. Dorsal surface of hind limbs granular and tuberculate, with two distinct symmetrical enlarged tubercles located laterally between urostyle and vent (Fig. 1; see Grant *et al*. 1997 for a description and illustration of the cloacal tubercles).

Head longer than wide (HL2 > HW), greatest width 34% of SVL. Snout bluntly pointed in lateral view, extending past the lower jaw, bluntly pointed in ventral and dorsal views. Nares located close to tip of snout, directed posterolaterally; nares visible from front, barely visible from above and below; posterior rim of naris bordered behind by a crescent-shaped ridge; rim bearing a small tuberclelike prominence posterodorsally, this "bump" is distinct in frontal, dorsal and ventral views; internarial distance 40% of greatest head width. Canthus rostralis well defined; loreal region straight, sloping outward to lip. Interorbital distance 83% of eye length, 90% of upper eyelid width. Snout length 123% of eye length, 49% of head length; distance from anterior corner of eye to posterior margin of naris 60% of eye length. Postrictal tubercles inconspicuous. Tympanic membrane inconspicuous, round, concealed posterodorsally by a diffuse supratympanic swelling; tympanic annulus

prominent anteroventrally; tympanum 43% of eye length, separated from eye by a distance equal to 23% of eye length. Midline distance from tip of snout to arm insertion greater than distance from arm insertion to thigh insertion (HL3 > BEL).

Forearm slightly longer than upper arm, no distinct ulnar fold. Hand moderate in size, HAND III 27% of SVL, 78% of HW. Relative length of fingers III > IV > I ≥ II. Fingers unwebbed. Discs of fingers expanded, disc on Finger IV widest, discs on other fingers subequal. Fingers with keel-like lateral folds (*sensu* Myers & Donnelly 2008), best developed pre- and (slightly) postaxially on Finger II and preaxially on Finger III (Fig. 2 A).

Palmar tubercle large, rounded, slightly heart-shaped; thenar tubercle smaller, elliptical; one or two round to ovoid subarticular tubercles (one each on Fingers I and II, two each on Fingers III and IV, with distal tubercles on Finger III and IV slightly less conspicuous). A very low, barely distinct outer metacarpal fringe. Tip of Finger IV distinctly surpassing the base of distal subarticular tubercle on Finger III when fingers adpressed. No fleshy supracarpal fold atop wrist (Fig. 2 A).

Hind limbs robust, moderately long, with heel of adpressed leg reaching anterior corner of eye; TIL 49% of SVL. Relative lengths of adpressed toes IV > III > V > II > I; first toe short, slightly surpassing the base of subarticular tubercle of second toe. Toe discs expanded, slightly larger than finger discs, largest on Toes II and IV. Feet moderately webbed; all toes with well developed folded flaplike fringing (*sensu* Myers & Donnelly 2008), except on postaxial edge of Toe V on the right side. Webbing formula **I** 0^{+}–2^{-} **II** 1^{-}–2 1/2 **III** 2^{-}–3^{+} **IV** 3 1/3–2^{-} **V** (Fig. 2 A).

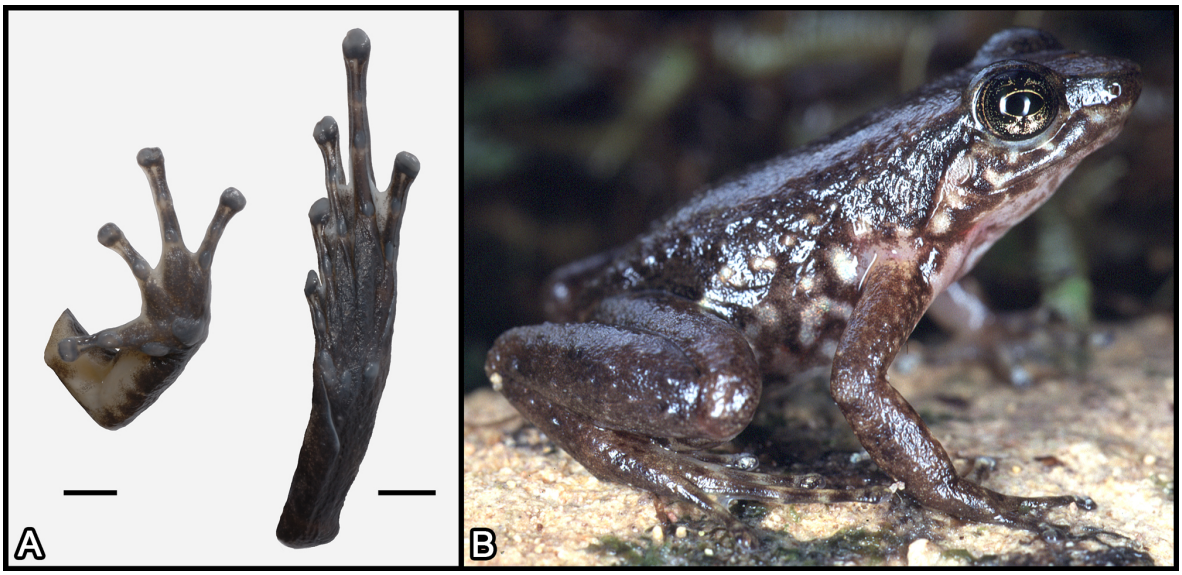

Figure **2.** *Anomaloglossus megacephalus* **sp. nov.** A: Ventral views of left hand (left) and left foot (right) of the female holotype (IRSNB 1986, 27.3 mm SVL). Scale bars are 2 mm. B: ROM 39638, female paratype (27.9 mm SVL), from Mt. Ayanganna. Photos by PJRK (A) and AL (B).

Inner metatarsal tubercle small, elliptical; outer metatarsal tubercle small, round, about half the size of the inner; a distinct oval medial metatarsal tubercle present on both sides. 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 strong outer metatarsal fold coextensive with the folded flaplike fringing on Toe V, almost reaching the outer metatarsal tubercle on the left side; outer metatarsal fold absent on the right side. A slightly tuberclelike tarsal keel weakly curved at proximal end, extending proximolaterad from preaxial edge of inner metatarsal tubercle, not continuous with the fringe along the outer edge of the first toe (Fig. 2 A).

Maxillary teeth present, small. Tongue longer than wide, wider and free posteriorly, with rounded margin; median lingual process short, wider than long, tapered.

Figure **3.** *Anomaloglossus megacephalus* **sp. nov.**, showing intra- and interpopulational variation in dorsal (A) and ventral (B) pattern in preservative. Two upper specimens are from Mt. Ayanganna: ROM 39637 (upper left, female 28.3 mm SVL) and ROM 39638 (upper right, female 27.9 mm SVL). Lower specimen is the holotype (female 27.3 mm) from Maringma Tepui. Photos by PJRK.

Colour of the Holotype in life. Dorsal ground colour medium brown, with a dark brown V-shaped interorbital bar slightly outlined with light creamish brown, followed by two less defined dark brown bars, the first more or less V-shaped, at the level of arm insertion, the second just anterior to sacrum. Small, poorly defined, dark brown flecks on snout, between and on dorsal bars. Upper surface of arm light brown with well-defined dark brown transverse bands on forearm and wrist, a less defined one on elbow; upper surface of thigh, shank, and foot light brown with well-defined dark brown transverse bands. A yellow wash on the anterior face of the thigh. Flanks dark brown, slightly lighter ventrally with a few bluish irregular spots and a few whitish irregular blotches on the lower part forming a broken inconspicuous ventrolateral stripe. A few white spots (covering small tubercles) form a broken oblique lateral stripe that does not extend to arm insertion. No dorsolateral stripe. Upper lip creamish brown suffused with melanophores, two bluish marks below eye; loreal region and side of head dark brown; tympanum area light creamish brown concealed in a poorly defined light stripe from posterior corner of eye to arm insertion. A dark brown stripe is present on the anterior edge of upper arm, tapering from arm insertion to forearm. Throat light brown, blotched with white and dark brown; belly light grey, blotched with dark brown, blotches more numerous and larger laterally. Undersurface of upper arm light brown with a few dark markings; undersurface of forearm blackish; undersurface of thigh

and shank light grey blotched with dark brown; rear of thigh and cloacal region blackish. Pale reddish orange paracloacal marks present. Tip of digits whitish. Palms and soles black. Iris mostly orange-bronze, darkened with black suffusion, with two oblique metallic white marks separated by a black triangular mark below pupil (Fig. 1 A–B).

Colour of the Holotype in preservative. Dorsal ground colour brown, with a dark brown V-shaped interorbital bar slightly outlined with light brown, followed by two less defined dark brown bars, the first more or less V-shaped, at the level of arm insertion, the second just anterior to sacrum. Small, poorly defined, dark brown flecks on snout, between and on dorsal bars. Upper surface of arm light brown with well-defined dark brown transverse bands on elbow, forearm and wrist; upper surface of leg light brown with well-defined dark brown transverse bands on thigh, shank, and foot. Flanks dark brown, with some irregular spots and a few whitish irregular blotches on the lower part forming a broken inconspicuous ventrolateral stripe. A few white spots (covering small tubercles) form a broken oblique lateral stripe that does not extend to arm insertion. No dorsolateral stripe. Upper lip dirty brown suffused with melanophores, two whitish marks below eye; loreal region and side of head black; distinct whitish stripe extending from posterior corner of eye to arm insertion including most of tympanum. A dark brown stripe is present on the anterior edge of upper arm, tapering from arm insertion to forearm. Throat and belly whitish, blotched with dark brown. Undersurface of upper arm whitish with a few dark markings; undersurface of forearm blackish; undersurface of thigh whitish blotched with dark brown; undersurface of shank light grey blotched with dark brown; rear of thigh and cloacal region blackish. Light brown paracloacal marks present. Palms and soles black (Fig. 1 B–C).

Variation. See Table 1 for morphometric measurements of the holotype and the paratypes and Figs. 2 B and 3 for intra- and interpopulational variation.

Symmetrical enlarged cloacal tubercles are clearly visible in the holotype. Those tubercles are present, but less visible in the paratypes probably due to an artefact of preservation (cloacal tubercles are most visible in well preserved specimens).

Only the holotype and one paratype have a medial metatarsal tubercle, a character that is sometimes present in other *Anomaloglossus* species as well.

Only the holotype lacks folded flaplike fringing on the postaxial edge of Toe V and a coextensive strong outer metatarsal fold on the right side, indicating an aberrant condition.

An additional difference between the holotype and the paratypes is the length of Finger I, which is slightly longer than II in the holotype on the left hand (*vs*. shorter in the two paratypes), and subequal on the right hand (*vs*. shorter in the two paratypes).

Toe webbing variation in females (male unknown) is **I** 0^{+}-2^{-} **II** (1^{-}-$1^{1/2}$)–($2^{1/2}$-3^{-}) **III** (2^{-}-2)–(3^{+}-$3^{1/2}$) **IV** ($3^{1/3}$- $3^{1/2}$)–(2^{-}-2) **V**.

The condition of the oblique lateral stripe is variable among specimens, from a series of light spots/blotches extending diagonally from the groin across the flanks and barely reaching the level of the insertion of the arm (*e.g*. IRSNB 1986) to an almost solid, clearly visible stripe extending diagonally from the groin across the flanks to the level of the insertion of the arm, then breaking in a series of light spots almost reaching the eye (*e.g*. ROM 39638). Slight variation also occurs between the right and the left flank.

In life, ROM 39638 was darker and the dark dorsal bars less detectable (Fig. 2 B).

Character	IRSNB 1986	ROM 39637	ROM 39638
SVL	27.3	28.3	27.9
HL1	8.8	8.5	9.1
HL2	10.5	10.7	10.8
HL3	12.2	10.8	11.7
HW	9.2	9.9	9.6
SL	4.3	4.4	4.2
EN	2.1	2.2	2.3
IN	3.8	3.5	3.6
EL	3.5	3.6	3.5
IO	2.9	3.1	2.8
TYM	1.5	1.4	1.5
FAL	5.7	5.8	6.6
HAND I	5.4	5.0	5.6
HAND II	5.2	5.9	5.9
HAND III	7.3	8.0	7.6
HAND IV	6.0	6.2	6.1
WFD	0.9	1.0	1.1
FL	12.7	13.4	14.3
WTD	1.2	1.2	1.2
TIL	13.5	13.9	14.5
AL	5.7	5.6	5.6
BEL	10.5	10.8	12.0

Table **1.** Morphometric measurements (in mm) of the type series of *Anomaloglossus megacephalus*. Abbreviations are defined in the text. Male is unknown.

Tadpole description. Two tadpoles were collected in a stream at 1490 m on Mt. Ayanganna. Description and illustrations of one of the two stage-25 tadpoles are provided in MacCulloch and Lathrop (2009: 11, under *Anomaloglossus tepuyensis*).

Comparison with other known *Anomaloglossus* tadpoles occurring in the Pantepui region.- Tadpoles of *A. megacephalus* most resemble those of *A. parkerae* (Meinhardt & Parmalee, 1996) and *A. tepuyensis*, which are also deposited in streams. The tadpole of *A. parkerae* was described by Duellman (1997), that of *A. tepuyensis* by Myers & Donnelly (2008). Both descriptions contain drawings and written descriptions. Two items are noteworthy: (1) Duellman (1997) describes the oral disc of *A. parkerae* as "not emarginate", whereas Myers & Donnelly (2008) describe the oral disc of *A. tepuyensis* as "emarginate". The oral disc margins of these two species are very similar (Duellman 1997, fig. 12; Myers & Donnelly 2008, fig. 17) and we follow Grant *et al.* (2006) in describing the oral discs of *Anomaloglossus* as emarginate; (2) Duellman (1997) describes the LTRF of *A. parkerae* as 2(1)/3, although the oral disc illustrated shows a LTRF 2(2)/3. This is obviously an error and the LTRF of *A. parkerae* is 2(2)/3, like in *A. tepuyensis* and *A.*

megacephalus.

Although there are few quantifiable differences among the larvae of *Anomaloglossus megacephalus*, *A. parkerae* and *A. tepuyensis*, the tadpole of *A. megacephalus* markedly differs from that of *A. parkerae* and *A. tepuyensis* in having a longer tail [tail length of stage-25 tadpoles is 68% of total length in *A. megacephalus* (n=2) *vs*. 62-63% in *A. parkerae* (n=4) and *A. tepuyensis* (n=29) tadpoles in the same stage], in having the maximum height of tail similar to body height (distinctly higher in *A. parkerae* and *A. tepuyensis*), and in having the upper fin noticeably lower than tail musculature at midtail (higher or equal in *A. parkerae* and *A. tepuyensis*).

When compared to other known *Anomaloglossus* tadpoles from the Pantepui region, *A. megacephalus* differs from *A. beebei* and *A. roraima* by stream habitat (phytotelmata habitat in *A. beebei* and *A. roraima*); from *A. kaiei* and *A. praderioi* in having the upper fin slightly increasing in length from tail-body junction [first quarter of upper fin straight before increasing in length to about midlength in *A. kaiei* (n=30) and *A. praderioi* (n=11)]; and from *A. tamacuarensis* (Myers & Donnelly, 1997) in having a longer tail [body length of stage-25 tadpoles is 68% of total length in *A. megacephalus* (n=2) *vs*. 63-65% in *A. tamacuarensis* (n=12) tadpoles in the same stage], and in having less marginal papillae and shorter lateral processes.

Distribution and ecology. *Anomaloglossus megacephalus* is currently only known from the eastern base of Maringma Tepui, Guyana, where it occurs at 1060 m elevation in low-canopy forest, and from the northeast plateau of Mt. Ayanganna, Guyana on the basis of two specimens collected at 1490 m elevation in dense low-canopy, high-tepui forest (Fig. 4).

Anomaloglossus megacephalus appears to be uncommon and elusive, with only three specimens collected. It is a diurnal species, the holotype was found on the sandy bank of a small forest stream. The Ayanganna specimens were collected in wet forest not closely associated with stream banks.

Egg deposition site unknown. Tadpoles are deposited in streams. Advertisement call is unknown.

Distinguishing among *Anomaloglossus* species from the Pantepui region. We first present a focussed comparison between the new species and the ten *Anomaloglossus* species known to occur in the Eastern Pantepui District (*i.e*. east of the Rio Caroní). The Rio Caroní likely acts as a biogeographic barrier for *Anomaloglossus* species since no species has been reported to occur on both sides of the river in the Guiana highlands of Venezuela and Guyana (it must be noted that very few Pantepui anurans are known to occur on both sides of the river). But, in order to provide a more comprehensive comparison, we also compared the new species with the six known *Anomaloglossus* species that occur in the Western Pantepui District (*i.e*. west of the Rio Caroní) in the Guiana highlands of Venezuela.

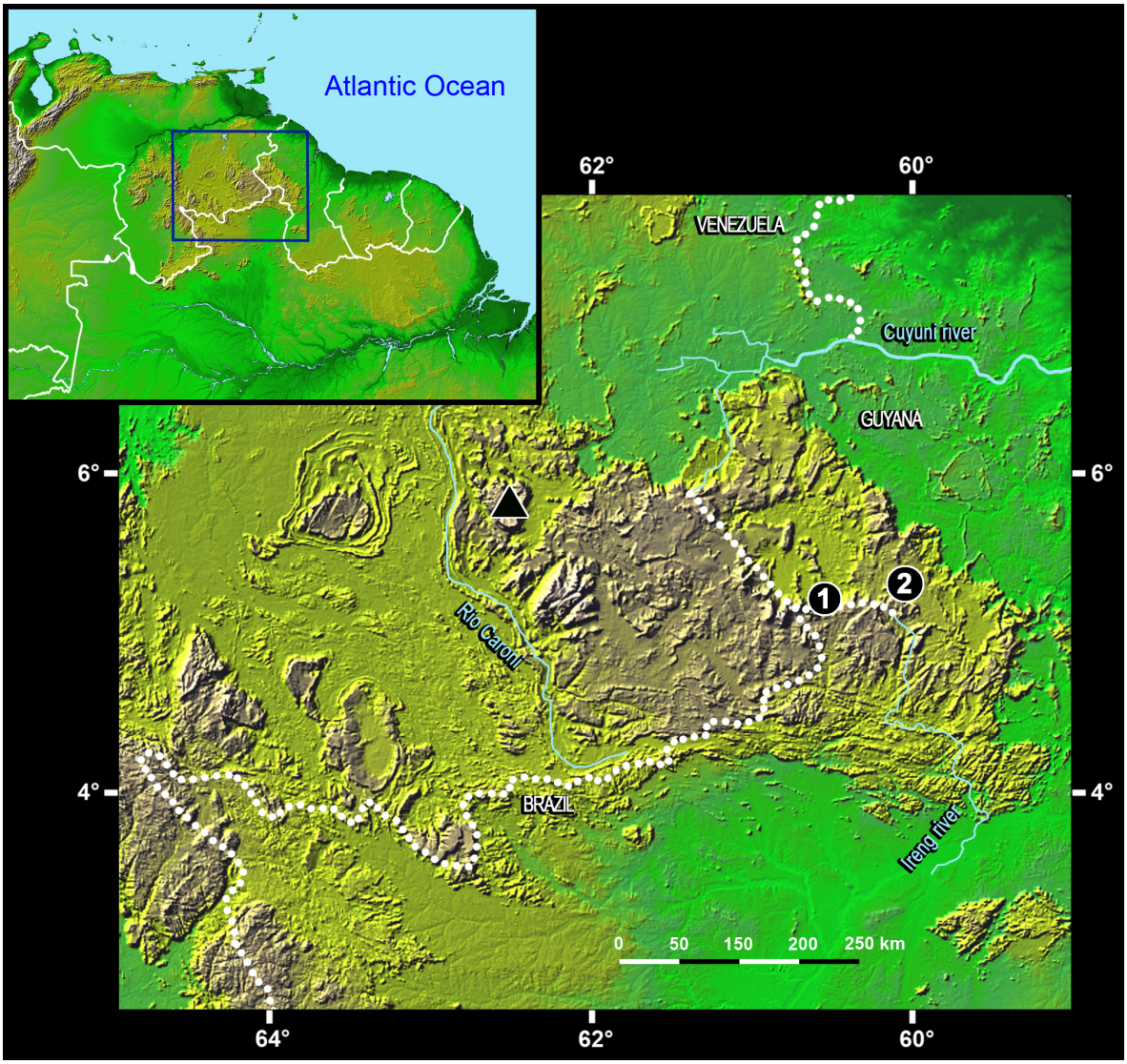

Figure **4.** Map of the eastern Pantepui region showing the known distributions of *Anomaloglossus megacephalus* **sp. nov.** (circles): 1 = type locality, Mount Maringma, Guyana; 2 = Mount Ayanganna, Guyana. The type locality of *A. tepuyensis* is indicated by a triangle. Maps elaborated after a radar image of South America by NASA/JPL/NIMA available at http://photojournal.jpl.nasa.gov/catalog/PIA03388.

Eastern Pantepui *Anomaloglossus* species.

Anomaloglossus megacephalus can be distinguished from *A. beebei* by (characters of *A. beebei* in parentheses, see also Kok *et al*. 2006b and Kok & Kalamandeen 2008) its larger size, female SVL max 28.3 mm [n=3] in *A. megacephalus* (18.7 mm in *A. beebei*, n=27), fingers with keel-like lateral folds, best developed preaxially on Fingers II and III (fringes not folded), toes with folded flaplike fringing (fringes not folded), throat in adult female blotched (immaculate), palm dark brown to black (yellowish), distinct dark bands on thigh and shank (absent), dark interorbital V-shaped band (absent).

Anomaloglossus megacephalus can be distinguished from *A. breweri* (Barrio-Amorós, 2006) by (characters of *A. breweri* in parentheses) its larger size, female SVL max 28.3 mm [n=3] in *A. megacephalus* (23.8 mm in *A. breweri*, n=1), throat in adult female blotched (immaculate), median lingual process short, wider than long, tapered (distinctly longer than

wide, tip pointed).

Anomaloglossus megacephalus can be distinguished from *A. kaiei* by (characters of *A. kaiei* in parentheses, see also Kok & Kalamandeen 2008) its larger size, female SVL max 28.3 mm [n=3] in *A. megacephalus* (19.8 mm in *A. kaiei*, n=25), fingers with keel-like lateral folds, best developed preaxially on Fingers II and III (fringes not folded), toes moderately webbed (basally webbed), dorsolateral stripe absent (present), oblique lateral stripe present (absent), throat in adult female blotched (immaculate).

Anomaloglossus megacephalus can be distinguished from *A. murisipanensis* (La Marca, 1998) in having (characters of *A. murisipanensis* in parentheses, all based on the preserved holotype, which is a juvenile and the only known specimen) fingers with keel-like lateral folds, best developed preaxially on Fingers II and III (fringes barely detectable), more webbing on toes, symmetrical cloacal tubercles present (absent), tarsal keel weakly to distinctly curved, slightly tuberclelike (straight, not tuberclelike), oblique lateral stripe always present, even if broken in spots (not distinguishable), no white stripe between naris and eye in preservative (present).

Anomaloglossus megacephalus can be distinguished from *A. praderioi* by (characters of *A. praderioi* in parentheses, see also Kok 2010) its larger size, female SVL max 28.3 mm (n=3) in *A. megacephalus* (22.7 mm in *A. praderioi*, n=1), Finger IV longer than I (equal), tip of Finger IV always surpassing the base of the distal subarticular tubercle on Finger III when fingers adpressed (barely reaching the base), toes moderately webbed with folded flaplike fringing (basally webbed, folded flaplike fringing not present on all toes), dorsolateral stripe absent (present), oblique lateral stripe present (absent), throat in adult female blotched (immaculate).

Anomaloglossus megacephalus can be distinguished from *A. roraima* in having (characters of *A. roraima* in parentheses) fingers with keel-like lateral folds, best developed preaxially on Fingers II and III (fringes barely distinct, not distinctly folded), all toes with folded flaplike fringing (absent), webbing on toes moderate (absent).

Anomaloglossus megacephalus can be distinguished from *A. rufulus* (Gorzula, 1990) in having (characters of *A. rufulus* in parentheses) webbing on toes moderate (rudimentary), and most remarkably by ventral colour pattern; light with a few dark brown blotches in *A. megacephalus* (dark brown marbled with white blotches in *A. rufulus*).

The new species superficially most resembles *A. parkerae*, *A. tepuyensis* (with which it has been confused), and *A. triunfo* (Barrio-Amorós, Fuentes-Ramos & Rivas-Fuenmayor, 2004), in sharing a similar dorsal pattern. It should be noted that *A. triunfo* is a possible synonym of *A. tepuyensis* (Kok & Barrio-Amorós unpubl. data, see also comments by Myers & Donnelly 2008). *Anomaloglossus parkerae* is distinguished from *A. tepuyensis* and *A. triunfo* only by a few characters such as size, definition of dorsal pattern, and condition of finger and toe fringes (Myers & Donnelly 2008). Adults of *A. megacephalus* can notably be distinguished from those three similar taxa in having a more slender body (*Anomaloglossus parkerae*, *A. tepuyensis* and *A. triunfo* are distinctly stockier frogs), a comparatively longer snout and a larger, somewhat more massive head [See Fig. 5 for close comparison between *A. megacephalus* and *A. tepuyensis* and *A. parkerae*; compare also with Duellman's (1997: 10) colour plate of *A. parkerae*, fig. 30 (showing *A. parkerae*) in Lötters *et al*. (2007), and figs. 13, 15 and 16 illustrating *A. tepuyensis* in Myers & Donnelly (2008); see also below for further comments], and in having symmetrical cloacal tubercles (absent in all females of *A. parkerae*, *A. tepuyensis* and *A. triunfo* examined).

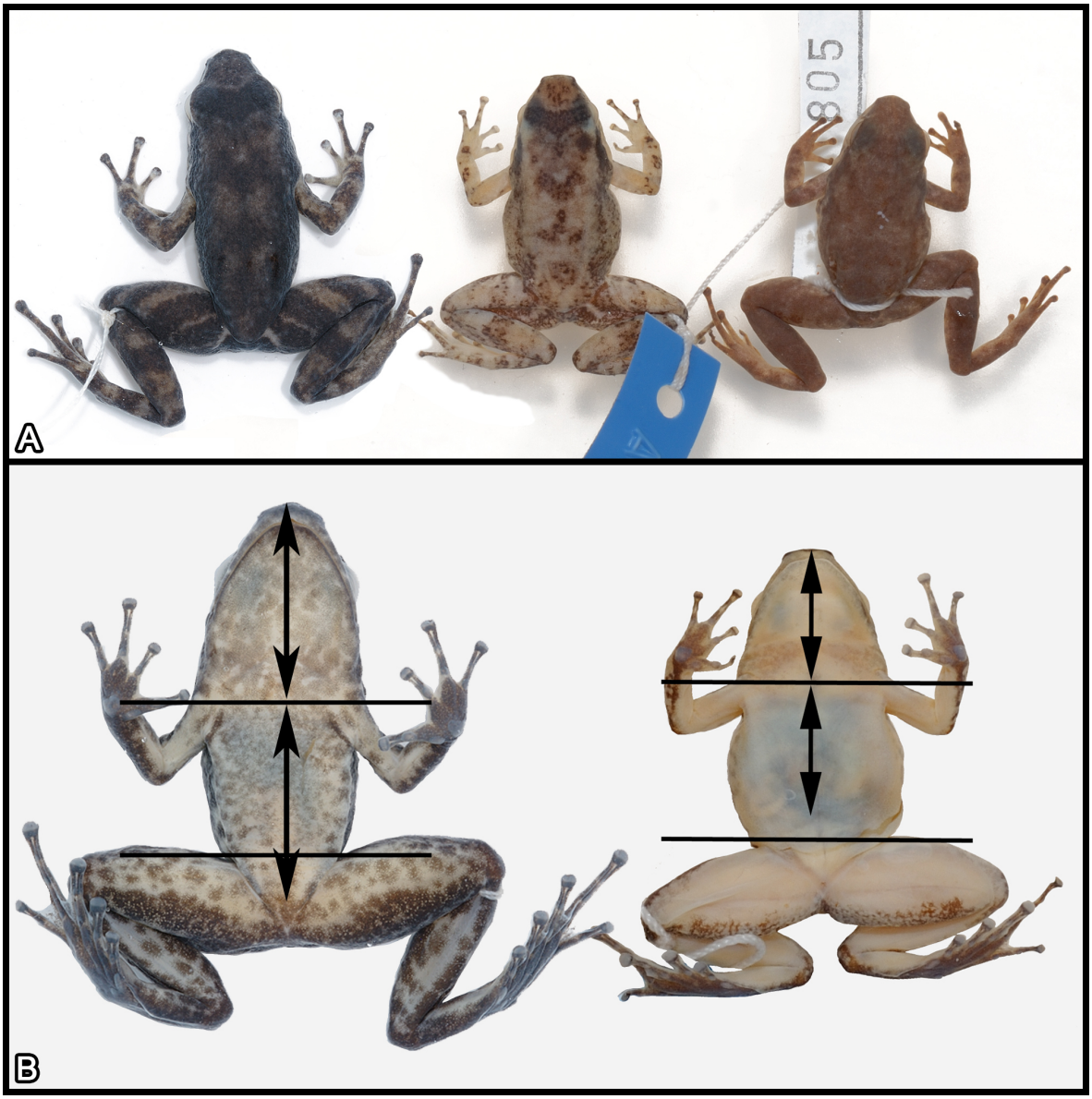

Figure **5.** Comparison of *Anomaloglossus megacephalus* **sp. nov.** and the similar *A. tepuyensis* and *A. parkerae*. A: Dorsal view of preserved specimens of (from left to right) *A. megacephalus* **sp. nov.** (IRSNB 1986, 27.3 mm SVL)**,** *A. tepuyensis* (MHNLS 17401, 23.3 mm SVL) and *A. parkerae* (MHNLS 11089, 23.2 mm SVL). B: Comparison between midline distance from snout tip to an imaginary line between anterior arm insertions and the same distance reported posteriorly from the same imaginary line in *A. megacephalus* **sp. nov.** and *A. tepuyensis*. In most *A. megacephalus* specimens (left, IRSNB 1986, 27.3 mm SVL) the distance reaches or surpasses the anterior insertion of thigh, whereas in all specimens of *A. tepuyensis* examined (right, MHNLS 17401, 23.3 mm SVL), the distance fails to reach the thigh. Photos by PJRK.

Direct comparison of specimens shows a difference in head size in *Anomaloglossus megacephalus* compared to the similar *A. parkerae*, *A. tepuyensis* and *A. triunfo*, as confirmed by plotting of morphometric proportions. Comparison of HL3 with BEL indicates that the new species proportionally has a longer head than *A. tepuyensis* (Fig. 6). In order to distinguish between those similar species, the midline distance from the tip of the snout to an imaginary line between anterior insertions of upper arms is measured, and that distance is then extended posteriorly from the same imaginary line. In two of the three

available *A. megacephalus* adult specimens the distance reaches or surpasses the anterior insertion of thigh, whereas in all adult specimens of *A. parkerae*, *A. tepuyensis* and *A. triunfo* examined (n = 20), the distance fails to reach the thigh insertion (see Fig. 5 B). It is noteworthy to mention that the only specimen of *A. megacephalus* in which HL3 is not longer than BEL is in poor preservation state.

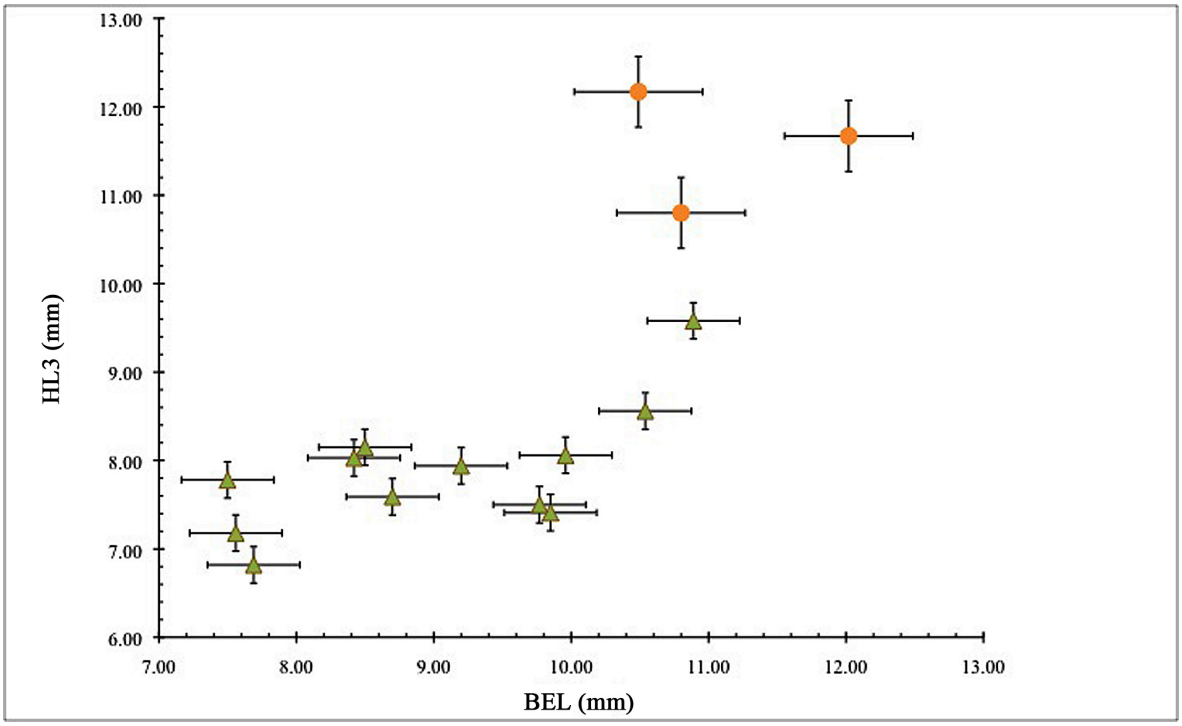

Figure **6.** Graph showing correlation between HL3 and BEL with standard errors for adult female specimens of *Anomaloglossus tepuyensis* (green triangles) and *A. megacephalus* **sp. nov**. (orange circles). Abbreviations are defined in the text. The graph clearly shows that the head of *A. megacephalus* **sp. nov**. is proportionally longer that the head of *A. tepuyensis*.

Western Pantepui *Anomaloglossus* species.

Among the Western Pantepui *Anomaloglossus* species, *A. ayarzaguenai* (La Marca, 1998) and *A. moffetti* Barrio-Amorós and Brewer-Carías, 2008 are the geographically closest species to *A. megacephalus* (*ca.* 400 km airline to the west). *Anomaloglossus ayarzaguenai* and *A. moffetti* are very similar to each other, geographically close (from Cerro Jaua and Cerro Sarisariñama, respectively) and possible synonyms (Kok & Barrio-Amorós unpubl. data). *Anomaloglossus megacephalus* is distinguished from *A. ayarzaguenai* and *A. moffetti* in having a comparatively longer snout, and a larger, somewhat more massive head [compare Figs. 1 and 2 B with fig. 4 a–c illustrating *A. moffetti* in Barrio-Amorós & Brewer-Carías (2008)], in having a distinct tympanum in life (barely distinct in *A. ayarzaguenai* and *A. moffetti*), separated from eye by 42–60% of its greatest length (25% or less in *A. ayarzaguenai* and *A. moffetti*), and in lacking a dark area spotted with white ventrolaterally at the level of arm insertion (always present in *A. ayarzaguenai* and *A. moffetti*).

Anomaloglossus megacephalus mostly differs from *A. guanayensis* (La Marca, 1998) by (characters of *A. guanayensis* in parentheses) its larger size, female SVL max 28.3 mm

(n=3) in *A. megacephalus* (23.5 mm in *A. guanayensis*, n=3), and in having less developed keel-like lateral folds on fingers (extensive, present pre- and postaxially on all fingers).

Anomaloglossus megacephalus can be distinguished from *A. parimae* (La Marca, 1998) by (characters of *A. parimae* in parentheses) its larger size, female SVL max 28.3 mm (n=3) in *A. megacephalus* (23.1 mm in *A. parimae*, n=2), in having a short, wider than long median lingual process (slender, noticeably longer than wide), and in having distinctly more webbing on toes.

Anomaloglossus megacephalus can be distinguished from *A. shrevei* (Rivero, 1961) in having (characters of *A. shrevei* in parentheses) a weakly to distinctly curved, slightly tuberclelike tarsal keel, (short, straight, not tuberclelike), less developed keel-like lateral folds on fingers (extensive, present pre- and postaxially on all fingers), and dark blotches on throat and belly (throat and belly immaculate).

Anomaloglossus megacephalus mostly differs from *A. tamacuarensis* by (characters of *A. tamacuarensis* in parentheses) its larger size, female SVL max 28.3 mm (n=3) in *A. megacephalus* (25.0 mm in *A. tamacuarensis*, n=2), in having a comparatively longer snout, and a larger, somewhat more massive head [compare Figs. 1 and 2 B with figs. 11 and 13 illustrating *A. tamacuarensis* in Myers & Donnelly (1997)], less developed keel-like lateral folds on fingers (extensive, present pre- and postaxially on all fingers), a conspicuous tympanum (inconspicuous), and in having a short, wider than long median lingual process (slender, noticeably longer than wide).

Discussion. Although progress has been made, we are still far from having a full understanding of the *Anomaloglossus* species richness in the Pantepui region. Based on the material available to us, there are at least two undescribed *Anomaloglossus* species in the Ayanganna and Wokomung massifs in Guyana. One of them was reported as *A.* "Ayanganna" in Grant *et al.* (2006) and subsequently as *A.* cf. *praderioi* in Kok (2010). Another possible undescribed species occurs on Mt. Wokomung, but additional evidence is needed to formally exclude conspecificity with *A. megacephalus*.

Grant *et al.* (2006) reported another undescribed species from the area (*A.* "Thomasing") from Mt. Tomasing, Guyana that we have not examined, but which—according to the data provided by Grant *et al.* (2006)—is closely related (and possibly conspecific) with *A. megacephalus*. More data (ecological, morphological and molecular) are needed to resolve this.

Species limits are sometimes difficult to define on morphology alone, and as pointed out by Kok (2010), any new *Anomaloglossus* description should ideally include tadpole and call descriptions, and data on natural history. However, this is sometimes hardly achievable, especially in regions difficult to explore and where additional expeditions are unlikely in the near future.

Our preliminary molecular results indicate that uncorrected pairwise distances based on a fragment of *ca.* 550 base pairs of the 16S rRNA gene (GenBank accession number DQ502128 + the authors unpublished data) between *Anomaloglossus tepuyensis* from the type locality and *A. megacephalus* varies between 6.9 and 7.1%, while uncorrected pairwise distance between known populations of *A. megacephalus* is only 0.17%. It should be stressed that low genetic distances (based on a fragment of the 16S rRNA gene) between morphologically well distinguishable sister taxa is not uncommon in the genus (the authors, unpubl. data). The same was recently reported in the genus *Ameerega* (Dendrobatidae,

sister group of Aromobatidae), in which genetic distances of *ca*. 2% (based on a fragment of the 16S rRNA gene) or less between species is not uncommon (see Lötters *et al*. 2005, 2009). This emphasizes the need for integrative taxonomy and shows the limits of the use of a universal threshold of genetic distance to identify amphibian species.

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APPENDIX 1. ADDITIONAL MATERIAL EXAMINED

Anomaloglossus ayarzaguenai.— Venezuela: *Estado Bolívar*: Cerro Jaua, MHNLS 12949 (holotype), MHNLS 12950–51 (paratypes).

Anomaloglossus beebei.— Guyana: *Potaro-Siparuni District*: Kaieteur National Park, IRSNB 13721–26, 13728–54, ULABG 6817 (ex IRSNB 13727), IRSNB 13779–81 (tadpoles).

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

Anomaloglossus guanayensis.— Venezuela: *Estado Bolívar*: Serranía de Guanay, MHNLS 10708 (holotype), MHNLS 10712–10714 (paratypes), 10716–10717 (paratypes), 10724–10725 (paratypes).

Anomaloglossus kaiei.— Guyana: *Potaro-Siparuni District*: Kaieteur National Park, IRSNB 1938 (holotype), IRSNB 1939–64 (paratypes), IRSNB 14419 (2 specimens), IRSNB 14422–26, IRSNB 14433–35, IRSNB 14437–40, IRSNB 14443, IRSNB 14446–51, IRSNB 14454–57, IRSNB 13755–78 (tadpoles), IRSNB 14432 (tadpoles), IRSNB 14436 (tadpole), IRSNB 14444–45 (tadpoles), IRSNB 14452–53 (tadpoles), ROM 42999, Mount Wokomung, ROM 43321, ROM 43327, ROM 43330, ROM 43333; *Cuyuni-Mazaruni District*: Wayalayeng, IRSNB 14922–24, Maringma Tepui, IRSNB 14925–31.

Anomaloglossus moffetti.— Venezuela: *Estado Bolívar*: Sarisariñama-tepui, EBRG 4645 (holotype), EBRG 4646–51 (paratypes).

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

Anomaloglossus parimae.— Venezuela: *Estado Amazonas*: Cerro Delgado Chalbaud, ULABG 4221 (holotype), ULABG 4212–20 (paratypes), ULABG 4222–26 (paratypes).

Anomaloglossus parkerae.— Venezuela: *Estado Bolívar*: Sierra de Lema, Salto El Danto, MHNLS 2901, MHNLS 11088–89 (topotypic specimens).

Anomaloglossus praderioi.— Guyana: *Cuyuni-Mazaruni District*: Maringma Tepui, IRSNB 14403–13, IRSNB 14414–16 (tadpoles); Venezuela: *Estado Bolívar*: Mount Roraima ULABG 4196 (holotype), MHNLS 11272 (paratype), Sierra de Lema, EBRG 5569.

Anomaloglossus roraima.— Venezuela: *Estado Bolívar*: Mount Roraima, ULABG 4197 (holotype).

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

Anomaloglossus tamacuarensis.— Venezuela: *Estado Amazonas*: Sierra Tapirapecó, north base of Pico Tamacuari, MBUCV 6430–33 (paratypes).

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).