SALAMANDRA **47**(3) | 155–160 | 20 August 2011 | ISSN 0036–3375

Redescription and generic assignation of *Dendrobates rufulus* Gorzula, 1990 (Anura: Dendrobatidae) from the Chimantá Massif, Venezuela

César Luis Barrio-Amorós [1] & Juan Carlos Santos [2,3]

[1)] Instituto de Biodiversidad Tropical, Apartado Postal 328, 1260 Escazú, Costa Rica

[2)] Section of Integrative Biology, University of Texas, 1 University Station C0930, Austin, Texas 78712 and Texas Memorial Museum, University of Texas, Austin, Texas 78712, USA

[3)] Current address: National Evolutionary Synthesis Center, Suite A200, 2024 W Main Street, Durham, North Carolina, 27705, USA

Corresponding author: César Luis Barrio-Amorós, e-mail: cesarlba@yahoo.com

Manuscript received: 8 March 2011

Abstract. *Dendrobates rufulus* Gorzula, 1990 is a poorly known dendrobatid, described from two specimens from the Chimantá Massif in the Venezuelan Guayana. We redescribe it based on six additional specimens and allocate this species to the genus *Anomaloglossus*. We also provide data on natural history, such as ecology, habitat, and vocalization.

Key words: Amphibia, *Anomaloglossus,* Dendrobatidae, tepui, Chimanta, Guayana, vocalization.

Resumen. *Dendrobates rufulus* Gorzula, 1990 es un dendrobátido poco conocido del Macizo de Chimantá en la Guayana venezolana. Se conocía de dos ejemplares; redescribimos la especie con base a seis nuevos ejemplares y lo colocamos en el género *Anomaloglossus*. Proveemos datos de historia natural, como ecología, vocalización y hábitat.

Palabras clave: Amphibia, *Anomaloglossus,* Dendrobatidae, tepuy, Chimantá, Guayana, vocalización.

Introduction

Dendrobates rufulus Gorzula, 1990 was described based on two specimens from the Chimantá Massif (Murey-tepui and Amuri-tepui) in the Venezuelan Guayana. Since the description of this species, its status has been limited to references in checklists and fauna accounts of the Venezuelan Guayana (Gorzula 1992, Gorzula & Señaris 1999, La Marca 1992, Walls 1994, Barrio-Amorós 1998, 2004, Lötters et al. 2007). The original description (Gorzula 1990) is little informative concerning its proper allocation to one of today's dendrobatoid (Grant et al. 2006, Lötters et al. 2007) or dendrobatid (Santos et al. 2009) genera. Walls (1994) treated *D. rufulus* as a member of *Epipedobates* sensu Myers (1987) based on the presence of teeth (absent in *Dendrobates* sensu Myers 1987) in the type material. Myers (1997) subsequently created the corresponding new combination as *Epipedobates rufulus*. Gorzula & Señaris (1999) and Jungfer & Böhme (2004) assigned the species to the *femoralis* species group of Silverstone (1976), i.e., the genus *Allobates* sensu Zimmermann & Zimmermann (1988), without discussing the rationale of this taxonomic change. The placement with *Allobates* was adopted by Grant et al. (2006), Lötters et al. (2007) and Santos et al. (2009) without further discussion. More recently, Barrio-Amorós & Santos (2009) suggested that this species might not be allocable to the genus *Allobates*.

In the course of ongoing research on dendrobatid frogs from the Venezuelan Guayana, we examined the holo- and paratype of *D. rufulus*. We found that a median lingual process (MLP), which is a synapomorphy of the genus *Anomaloglossus* (Grant et al. 2006), was present. Molecular data also supported *D. rufulus* to cluster within *Anomaloglossus* (authors' unpubl. data). In recent expeditions to the Churí-tepui in the Chimantá Massif (March 2006 and May 2009), six more specimens were obtained and the species' call was recorded. The purpose of this paper is to redescribe *D. rufulus* and formally allocate it to the genus *Anomaloglossus*.

Materials and methods

Measurements were taken with digital callipers to the nearest 0.1 mm. Abbreviations used throughout the text are: SVL: straight length from tip of snout to vent; ShL: shank length from outer edge of flexed knee to heel; ThL: thigh length from vent opening to flexed knee; HeL: head length from tip of snout to the posterior border of skull (posterior edge of the prootic bone, as noted through the skin); HW: head width between angle of jaws; InD: inter-narial distance between centres of nares; IOD: inter-orbital distance between proximal edges of eyelids; ED: horizontal eye diameter; TD: horizontal tympanum diameter; ETS: distance

between the anterior edge of the eye to the tip of snout; FD: disc width of Finger III; T4D: disc width of toe IV. All measurements are in mm.

The description scheme follows Barrio-Amorós & Santos (2009). We follow Santos et al. (2009) by regarding *Anomaloglossus* as a member of the Aromobatinae within the Dendrobatidae (contra Grant et al. 2006). Recordings were made with a Sony TCM-353V recorder and a Sony F-V5 microphone, and were analysed with Praat 5.2.01. Specimens examined are deposited at the Museo de Historia Natural La Salle, Caracas, Venezuela (MHNLS), and in the Colección de Vertebrados, Universidad de los Andes, Mérida, Venezuela (CVULA).

Anomaloglossus rufulus (Gorzula, 1990) comb. nov.
(Figs. 1–2)

Dendrobates rufulus Gorzula, 1990 "1988": 144; La Marca 1992: 33; Gorzula & Señaris 1999 "1998": 26.

Epipedobates rufulus – Myers 1997: 3; Barrio-Amorós 1998: 20; 2004: 9.

Allobates rufulus – Jungfer & Böhme 2004: 1; Grant et al. 2006: 28; Lötters et al. 2007: 312; Santos et al. 2009: Table S13.

Holotype: MHNLS 10361, an adult female from the central portion of the Murey (= Eruoda) tepui in the Chimantá Massif (CHIMANTA XVIII), 05°22' N, 62°05' W, 2,600 m altitude, Estado Bolívar, Venezuela, collected by Henry Briceño, 17 March 1986.

Paratype:. MHNLS 11188, an adult male, NW edge of the Amuri-tepui in the Chimanta Massif (CHIMANTA XXII), 05°08' N, 62°08' W, 2,100 m altitude, Estado Bolívar, Venezuela, collected by Stefan Gorzula, 27 January 1988.

Referred specimens: MHNLS 20245, an adult male, from the central sector of the Churí-tepui in the Chimantá Massif, 05°15' N, 62°01' W, 2,400 m altitude, collected by César L. Barrio-Amorós, 11 February 2007. CVULA 8294–96, three adult males, and CVULA 8297–98, two young and unsexed specimens, from the base camp of the Muchimuk Expedition 2009, northern face of the Churí-tepui, 05°16' N, 62°00' W, 2,325 m altitude, Estado Bolívar, Venezuela, collected by Javier Mesa and Charles Brewer-Carías, 26 May 2009.

Diagnosis: (1) Skin on dorsum smooth. (2) Paired scutes present on dorsal side of digits. (3) Distal tubercle on finger IV present but indistinct. (4) Finger IV length reaching distal subarticular tubercle of Finger III. (5) Finger I longer than Finger II. (6) Digital discs present. (7) Finger discs weakly expanded. (8) Finger fringes present or absent. (9) Metacarpal ridge absent. (10) Finger III not swollen in adult males. (11) Carpal pad absent. (12) Excrescences on thumb absent in males. (13) Thenar tubercle present, small. (14) Black arm gland absent in adult males. (15) Tarsal keel short, low, straight. (16) Toe discs weakly expanded. (17) Toe webbing absent. (18) Metatarsal fold absent. (19) External colouration with no paracloacal marks, dorsally dark brown with no pattern; dorsolateral, oblique lateral and ventrolateral stripes absent. (20) Gular-chest markings absent. (21) Dermal collar absent. (22) Male and female throat colouration dark with pale spots or white with dark spots (in young specimens). (23) Abdominal colour pattern in males dark with pale spotting to white with dark spotting. (24) Abdominal colour pattern in adult female dark with pale spots; colour unknown in live females. (25) Iris colouration metallic dirty bronze and golden pupil ring. (26) Large intestine mainly unpigmented. (27) Testes white with melanophores. (28) MLP present, small, round.

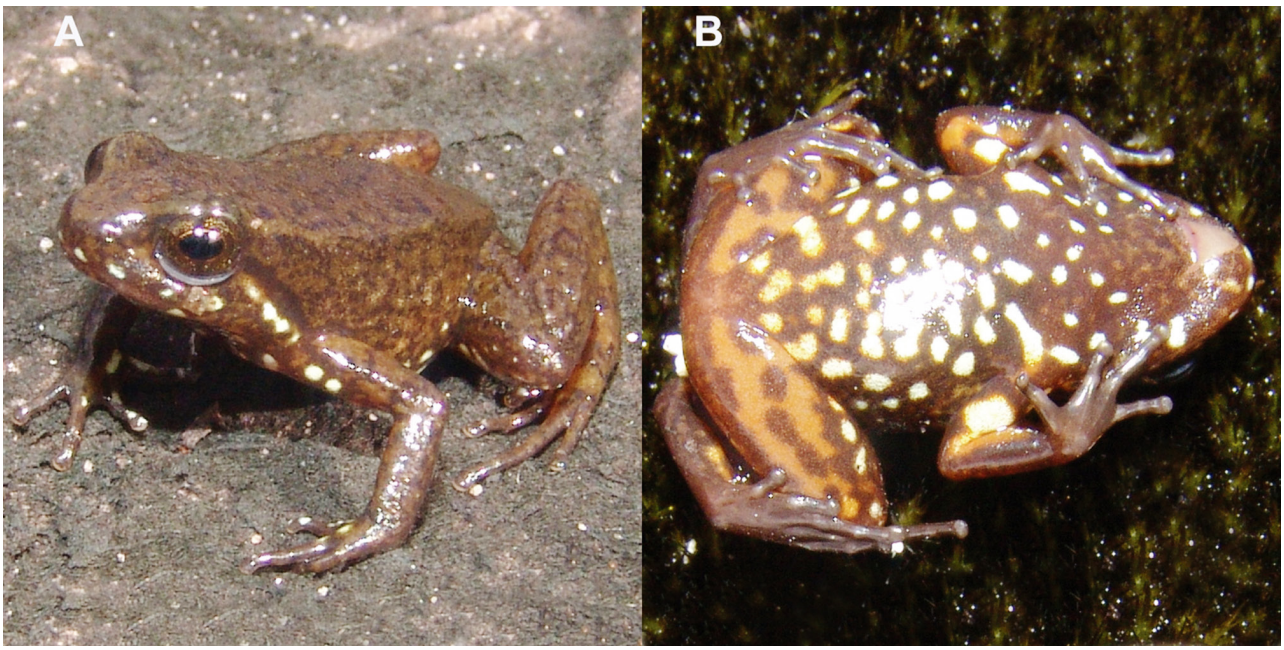

Figure 1. Live specimen (MHNLS 20245) of *Anomaloglossus rufulus* in (A) dorsolateral (B) ventral views.

(29) Tympanum distinct to inconspicuous, tympanic annulus absent. (30) Vocal sac not distinct. (31) Teeth present on the maxillary arch. (32) Size (SVL) small, males up to 20.4–22.4 mm (n = 5), mean 21.1 ± 0.9; only known female 23.4 mm.

This species can be easily distinguished from other *Anomaloglossus* by the lack of dorsolateral, oblique lateral, and ventrolateral stripes (at least one or more of these present in all other known species); its ventral pattern (both in life and preserved) consists of a dark brown background with white spots to whitish with small dark spots; reddish to orange undersides of thighs (no other known *Anomaloglossus* has such a contrasting ventral pattern).

Description of MHNLS 20245 (male): Dorsal and ventral skin smooth in preservative; shagreened in life with flat tubercles on the superior face of the thighs. Dorsal skin usually forming a well-defined rounded, posteriorly projecting flap well above the vent, which opens at the upper level of the thighs; anal tubercles and sheath absent. Head slightly longer than wide, HW 30.8% of SVL. Snout truncate in profile, round in dorsal and ventral views. Nares situated near the tip of snout and directed laterally; nares not visible from the front, barely visible dorsally, not visible from below. Canthus rostralis rounded, rather indistinct; loreal region flat. Interorbital region slightly wider than upper eyelid. Snout equal in length to eye diameter. Tympanum barely visible; its posterodorsal half hidden beneath superficial slip of the depressor mandibulae muscle; positioned right behind the eye and lower, close to the angle of jaws; TD 51.7% of ED. MLP short, rounded, not conspicuous (Fig. 2). Hand length moderate, 26.7% of SVL. Relative lengths of adpressed fingers III > IV > I > II; Finger I shorter than Finger II. Discs of all fingers barely expanded; Finger III disc 1.2 times the width of the distal end of the adjacent phalanx. Base of palm with a small, triangular, indistinct palmar tubercle; inner thenar tubercle on base of Finger I also indistinct; subarticular tubercles on Fingers I and II (one on each finger) large, flat, round, indistinct; on Finger III only the distal subarticular tubercle is distinct; on Finger IV no distinct subarticular tubercles; no supernumerary tubercles. No fringes on fingers. Hind limbs of moderate length; shank 44.6% of SVL. Relative lengths of adpressed toes IV > III > V > II > I, with Toe I reaching (when adpressed) the inferior edge of subarticular tubercle of Toe II. Toe discs moderately expanded; Toe IV disc 1.3 times the width of the distal end of the adjacent phalanx. Feet unwebbed, toes with very low fringes, missing on the external edges of Toes I and V. One to three non-protuberant subarticular tubercles on toes as follows: one each on Toes I and II, two on Toe III and V, three on Toe IV (all indistinct). Sole of foot with indistinct inner metatarsal tubercle and moderately protruding outer metatarsal tubercle. Narrow tarsal fold or keel, straight, but diagonal to the longitudinal axis of the tarsus, extending about half the length of tarsus, distally continuous with the narrow fringe on the free (preaxial) edge of Toe I. Maxillary teeth present, very small. Tongue longer than wide, elliptical, posterior half free; MLP small, longer than wide, positioned in the anterior third of tongue. Vocal slits evident, wide and long, extending from mid-level of tongue to posterior edge of tongue.

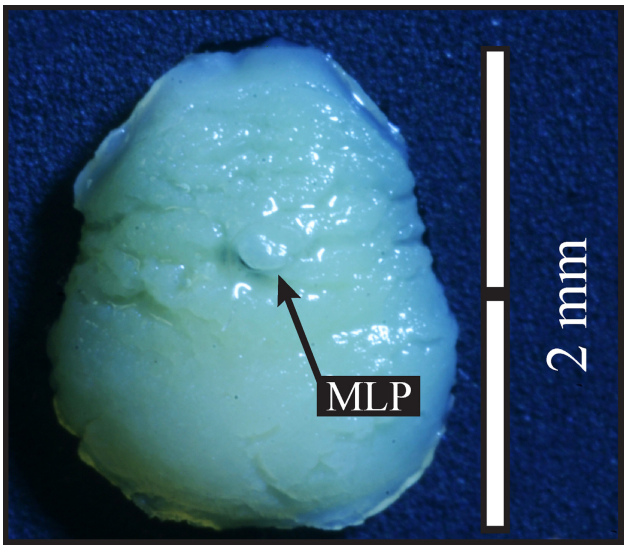

Figure 2. Tongue of *Anomaloglossus rufulus* (MHNLS 20245), showing the MLP.

In life, chocolate brown dorsally, without any pattern, but with small irregular dark brown spots all over the dorsal side including head and hind limbs. A wide dark brown supratympanic stripe with three bright white, rounded (due to the position in the photo) spots (which are elongated laterally) below, with the anterior spot covering the inferior half of the tympanum. Four small irregular white spots on upper lip. Loreal and infraocular regions light brown. Additional white marks on the supero-anterior part of the arm; upper arm also lighter than the dorsum. Two white round spots in the anterior part of the thigh. Limbs inconspicuously reticulated with light brown. Iris bronze, pupil round. Ventrally dark brown; throat with an underlying orange reticulation; round white spots in the posterior parts of throat and chest, belly with many white spots, becoming orange posteriorly and ending in a suffusion of orange marbling under the thighs. Two large white spots on upper arms and a longitudinal orange band on the forearm.

In preservative, dorsally dark brown without pattern or marks; only a few dirty white spots on each hand and a poorly-defined reticulation on the hind limbs. Ventrally dark brown (impression of being black) with small round, triangular to square white spots, larger posteriorly; a long longitudinal white band on the forearm, and marbling on the underside of the thighs.

Variation: The dorsal skin of CVULA 8296–8297 is smooth, while that of CVULA 8294–8295 are shagreened; skin on upper faces of thighs and shanks of MHNLS 11188 (male paratype) slightly tuberculate. In the female holotype and male paratype, the MLP is wider and conical, positioned on the anterior third of the tongue. The MLP protrudes and is conspicuous in CVULA 8295 (rounded) and CVULA 8296 (conical), less distinct in CVULA 8294, and even less so in CVULA 8297. The palmar tubercle is more prominent in the type specimens, with its shape ranging from oval to triangular. The thenar tubercle is only distinct (but small) in the paratype, while it is indistinct in the holotype, MHNLS 20245, CVULA 8295 and CVULA 8297. In the type specimens, the fringes on the toes are more dis-

tinct than in the more freshly preserved material. The toe webbing is basal between Toes II and III and Toes III and IV in the paratype and CVULA 8221–22, but barely evident in the holotype and CVULA 8220. The tarsal fold is distinct in the paratype, while it is low to indistinct in other specimens. An anal flap is barely distinct in the type material and completely absent in CVULA 8220. Gorzula (1990 "1988") noted the presence of fringes on fingers ("fino margen cutáneo lateral"), which were not evident during our examination of the specimens.

Gorzula (1990 "1988") mentioned light yellow spots on the venter. In contrast, CVULA 8220 has white ventral spots both in life and preservative. After 25 years in alcohol, the holotype is light brown on the dorsal side without any distinguishable pattern, and only a few, faded and small white spots are evident on the upper faces of the hands. The paratype is dark brown dorsally, with weakly defined black spotting that is only visible under a dissecting scope. CVULA 8221 and CVULA 8223 are dorsally dark brown with fine diffuse spotting (only evident under magnification), and the flanks are dark brown with no ornamentation (oblique lateral, dorsolateral and ventrolateral stripes absent). In these specimens, some white belly spots invade the lower part of the flanks. CVULA 8297–98 are paler, being dorsally light brown with slightly darker flanks. Ventrally, the holotype is light brown (similar to its dorsal side) with a profusion of faded white, mainly rounded and some irregularly shaped spots. Palms and soles are dark brown. Ventrally, the paratype is dark brown (similar to its dorsal side) with a profusion of creamy irregular white spots that are more clearly defined than in the holotype. MHNLS 20245, CVULA 8294–8295 are dark with white spots; it seems that there is an ontogenetic change, as the smaller individuals, a male (CVULA 8296) and one young, unsexed specimen (CVULA 8297), are white with fewer dark brown spots. CVULA 8298 is a juvenile with a completely white belly (with some scattered melanophores visible under magnification).

Vocalization: A single recorded call was analysed, taken at 17.5°C on the evening of 11 February 2007. The call has 18 pulsed notes (Fig. 3), lasting 2.8 seconds, with the last few notes losing in intensity. Notes were repeated at seven notes per second. The call's dominant frequency was 3,304 Hz (16.9 dB) while the fundamental frequency was 2,925 Hz. Note duration and inter-note interval were measured, respectively (mean ± SD and range in parentheses): 0.037 ± 0.004 (0.032–0.048) sec; 0.117 ± 0.011 (0.09–0.14) sec.

Natural history: During an expedition to the summit of Churí-tepui (massif of Chimantá) in February 2007, after a few dry days, one night of rain was enough to stimulate the vocalizing activity of many amphibians. During the day, one dendrobatid call was easily audible usually from deep (sometimes 10 to 60 m) crevices and inaccessible walls (Fig. 4). The animals stopped calling when approached, but

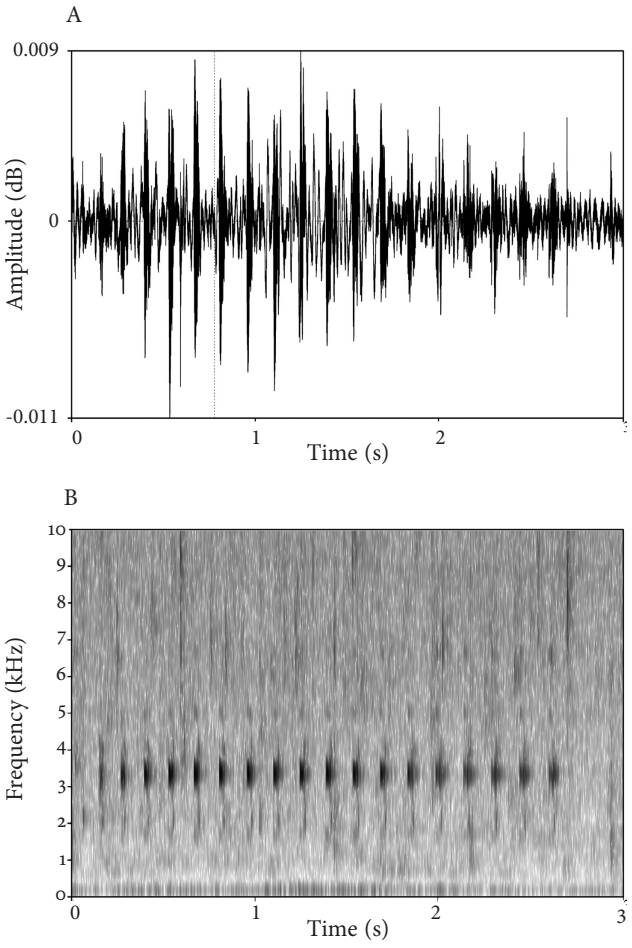

Figure 3. (A) Waveform and spectrogram (B) of a 3 sec sequence of the call of *Anomaloglossus rufulus*, taken at 17.5°C.

Figure 4. Microhabitat in a crevice on Churí-tepui.

Figure 5. General view of the habitat of *Anomaloglossus rufulus* on the summit of Churí Tepui at 2,400 m altitude.

continued after a while. Males that produced this call were those here redescribed as *Anomaloglossus rufulus* and were usually found in muddy soil among patches of vegetation (e.g., *Brochinnia tatei* with *Orectanthe sceptrum, Drosera roraimae, Heliamphora minor*). Gorzula (1990 "1988") mentioned that the holotype (a female) had been collected in an open zone with superficial flowing water from a dwarf forest of *Bonnetia roraimae*. He calculated that a calling male would be found every 100 m² in *Bonnetia* forest. The senior author of this paper has never heard the species call in *Bonnetia* forest but only in crevices (with up to four males aggregated in one spot).

Males showed aggressive behaviour by responding calls even to whistled imitations by humans. J. Mesa (pers. comm.) captured five individuals on a muddy trail covered by low vegetation (*Brochinnia*, *Orectanthe*, *Stegolepis*). He reported that these individuals were seen moving about among, and escaping into, this low vegetation (see Fig. 5 for a general habitat characterisation on the summit of Churí-tepui). Gorzula (1990 "1988") captured the holotype amongst the roots of a *Bonnetia* tree through digging.

A few predators are known from the summit of Chimantá, including the snakes *Thamnodynates chimanta* Roze, 1958 and *Leptodeira annulata* (Hallowell, 1845). They would appear capable of preying upon *A. rufulus*. It is unknown whether the ventral colour pattern has a deterrent effect on predators (e.g., aposematic colouration), as the presence of defensive alkaloids is unknown in *A. rufulus*. CVULA 8222 had in its stomach two ants and one ant larva (Hymenoptera), one fruit fly (Diptera), and two spiders (Arachnida), with all items measuring less than 2 mm.

The water in the creeks on the summit of Churí-tepui is acidic, with pH values of 3–5.5 (T. Lanczos, pers. com.), and one creek from where male *A. rufulus* were calling had a pH of 3.7. Some tadpoles, probably belonging to this species, were seen.

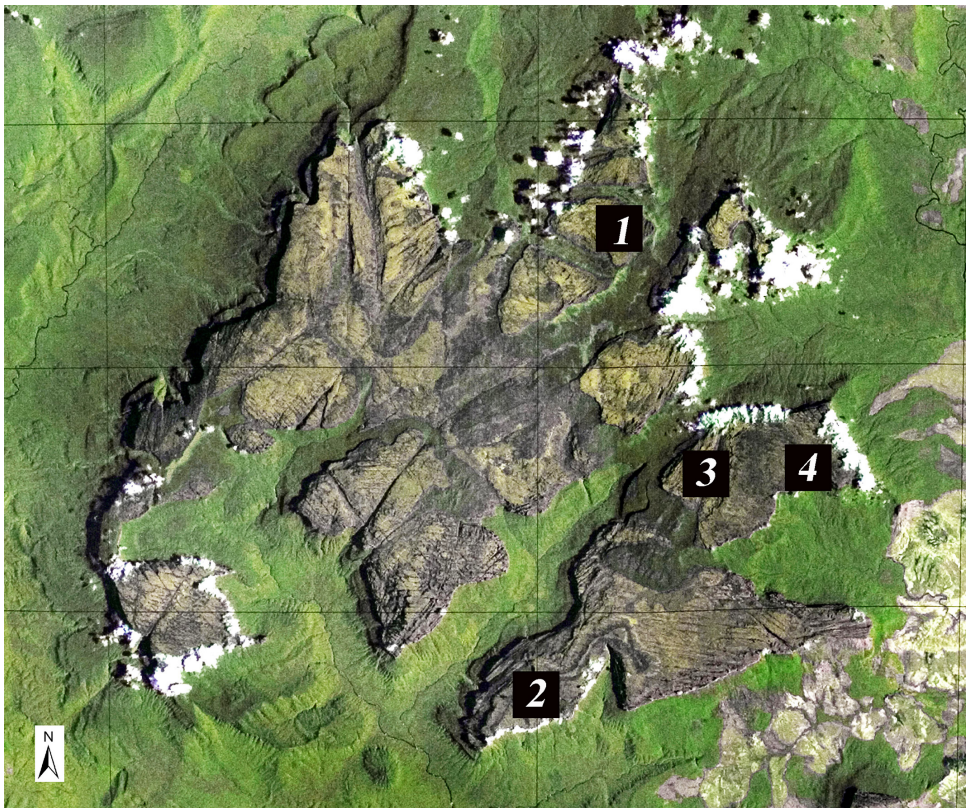

Figure 6. Known distribution of *Anomaloglossus rufulus* in the Massif of Chimanta, Venezuelan Guayana: 1 – Murey (= Eruoda) Tepui, type locality; 2 – Amuri Tepui (paratype); 3 – central sector of the Churí Tepui (CVULA 8220); 4 – eastern face of the Churí Tepui, locality of the base camp Muchimuk (CVULA 8221–25). Chimanta is located between 5°06' and 5°24' N and 61°57' and 62°20' W. Image created by Marek Audy.

Distribution: Gorzula (1990) heard *Anomaloglossus rufulus* calling at different localities in the Chimantá Massif (Apakará, Eruoda, Amurí- and Churí-tepuis), but not on other close-by tepuis such as Auyan, Aprada, Guaiquinima or in the Roraima-Ilu chain. Based on this, we tentatively consider the species a Chimantá Massif endemic (Fig. 6), as are other anuran amphibians, i.e., *Stefania ginesi* Rivero, 1968 and *Pristimantis muchimuk* Barrio-Amorós, Mesa, Brewer-Carías et McDiarmid, 2010.

Remarks**:** Gorzula (1990) stated that the head width was greater than the head length, but he did not explain how he had taken the respective measurements. Our evaluation of this character state suggests that the head is longer than wide. We found a similar disagreement in the lengths of Fingers I and II. Gorzula (1990) stated that Finger I was shorter than Finger II, while we came to the opposite conclusion.

Acknowledgements

The senior author is especially grateful to Charles Brewer-Carías who invited him to a series of expeditions to the Chimantá Massif. Ricardo Guerrero (Instituto de Zoología Tropical), Francisco Delascio (Jardín Botánico del Orinoco) and Hernán Biord (Sociedad Venezolana de Ciencias Naturales) were memorable companions in the field. Tomas Lánczos (Universitad Comenius, Bratislava, Slovakia) analysed the water samples. Javier Mesa collected the five specimens discussed herein. Special thanks go to Federico Mayoral for his endless support to our investigations. Finally, thanks to all expedition members who participated in the exploration of one of the last few virginal corners of the planet. The second author received funding through a National Science Foundation grant to David C. Cannatella (EF-0334952) and DDIG DEB-0710033. He was also supported by University of Texas EEB Graduate Research Fellowships and acknowledges the support by the National Evolutionary Synthesis Center (EF-0423641 and EF-0905606). We thank Stefan Gorzula for his kind support and review of the manuscript.

References

Barrio-Amorós, C. L. (1998): Sistemática y biogeografía de los anfibios (Amphibia) de Venezuela. – Acta Biologica Venezuelica, **18**: 1–93.

Barrio-Amorós, C. L. (2006): A new dendrobatid frog (Anura: Dendrobatidae: *Colostethus*) from Aprada tepui, southern Venezuela. – Zootaxa, **1110**: 59–68.

Barrio-Amorós, C. L. & C. Brewer-Carias (2008): Herpetological report of the 2002 Expedition to Sarisariñama, a tepui in Venezuelan Guayana, with description of five new species. – Zootaxa, **1942**: 1–68.

Barrio-Amorós, C. L. & J. C. Santos (2009): Description of a new *Allobates* (Amphibia: Anura: Dendrobatidae) from the eastern Andean piedmont, Venezuela. – Phyllomedusa, **8**: 89–104.

Barrio-Amorós, C. L., O. Fuentes & G. Rivas (2004): Two new species of *Colostethus* (Anura, Dendrobatidae) from Venezuelan Guayana. – Salamandra, **40**: 183–200.

Barrio-Amorós, C. L., J. C. Santos & O. Jovanovic (2010): A new dendrobatid frog (Anura: Dendrobatidae: *Anomaloglossus*) from the Orinoquian rainforest, southern Venezuela. – Zootaxa, **2413**: 37–50.

Barrio-Amorós C. L., A. Diaz de Pascual, J. J. Mueses-Cisneros, E. Infante & A. Chacon (2006): *Hyla vigilans* Solano, 1971, a second species for the genus *Scarthyla*, redescription and distribution in Venezuela and Colombia. – Zootaxa, **1349:** 1–18.

Gorzula, S. (1990 "1988"): Una nueva especie de *Dendrobates* (Amphibia: Dendrobatidae) del Macizo del Chimantá, Estado Bolívar, Venezuela. – Memoria Sociedad Ciencias Naturales La Salle, **48**: 143–149.

Gorzula, S. (1992): La herpetofauna del Macizo del Chimantá. – pp. 267–280 in Huber, O. (ed.): El Macizo del Chimantá, Escudo de Guayana, Venezuela. Un ensayo ecológico tepuyano. – Caracas: O. Todtmann Editores.

Gorzula, S. & J. C. Senaris (1999 "1998"): Contribution to the herpetofauna of the Venezuelan Guayana – I. A data base. – Scientia Guaianae, 8: xviii + 270 + 32 pp.

Grant, T., D. R. Frost, J. P. Caldwell, R. Gagliardo, C. F. B. Haddad, P. J. R. Kok, D. B. Means, B. P. Noonan, W. E. Schargel & W. C. Wheleer (2006): Phylogenetic systematics of dart-poison frogs and their relatives (Amphibia: Athesphatanura: Dendrobatidae). – Bulletin American Museum of Natural History**, 299:** 1–262.

Jungfer, K.-H. & W. Böhme (2004): A new poison-dart frog (*Dendrobates*) from northern central Guyana (Amphibia: Anura: Dendrobatidae). – Salamandra, **40**: 1–6.

La Marca, E. (1992): Catálogo taxonómico, biogeográfico y bibliográfico de las ranas de Venezuela. – Cuadernos Geográficos U.L.A. Mérida, 9: 1–197.

Lötters, S., K.-H. Jungfer, F. W. Henkel & W. Schmidt (2007): Poison frogs. Biology, species & captive care. – Frankfurt am Main: Edition Chimaira.

Myers, C. W. (1987): New generic names for some Neotropical poison frogs (Dendrobatidae). – Papeis Avulsos Zoologia, **36**: 301–306.

Myers, C. W. (1997): Preliminary remarks on the summit herpetofauna of Auyantepui, eastern Venezuela. – Acta Terramaris, **10**: 1–8.

Santos J. C., L. A. Coloma, K. Summers, J. P. Caldwell & R. Ree (2009): Amazonian amphibian diversity is primarily derived from Late Miocene Andean lineages. – PLoS Biology, **7**: e1000056. doi:10.1371/journal.pbio.1000056.

Silverstone, P. (1976): A revision of the poison arrow frogs of the genus *Phyllobates* Bibron in Sagra (Family Dendrobatidae). – Natural History Museum Los Angeles Contributions in Science Bulletin, **27**: 1–53.

Walls, J. G. (1994): Jewels of the rainforest. poison frogs of the family Dendrobatidae. Neptune City: T.F.H.

Zimmermann, H. & E. Zimmermann (1988) Etho-Taxonomie und zoogeographische Artengruppenbildung bei Pfeilgiftfröschen (Anura: Dendrobatidae). – Salamandra, **24**: 125–160.