

Description of a new *Allobates* (Anura, Dendrobatidae) from the eastern Andean piedmont, Venezuela

César Luis Barrio-Amorós¹ and Juan Carlos Santos^{2,3}

^{1,4}Fundación AndígenA., Apartado Postal 210, 5101-A Mérida, Venezuela. E-mail: atelopus@andigena.org.

² University of Texas at Austin, Integrative Biology, 1 University Station C0930 - Austin TX 78705, USA.

³ Current address: National Evolutionary Synthesis Center, 2024 W, Main Street, Suite A200, Durham, NC 27705-4667, USA. E-mail: juan.santos@duke.edu.

Abstract

Description of a new *Allobates* (Anura, Dendrobatidae) from the eastern Andean piedmont, Venezuela. We describe a new nurse frog in the genus *Allobates* (Dendrobatidae) from Río Negro, Municipio Córdoba, Estado Táchira, in western Venezuela. This species is a leaf litter inhabitant of primary and secondary lowland rainforest at altitudes from 400 to 1000 m. The new species is similar to the species in the *Allobates marchesianus* group and is restricted to the slopes of the western Venezuelan Andes. It differs from its congeners by having an irregularly spotted dorsal pattern, diffuse oblique lateral stripe, ventrolateral stripe and yellowish belly on males.

Keywords: Anura, Dendrobatidae, *Allobates*, new species, Venezuela, Colombia.

Resumen

Descripción de una nueva especie de *Allobates* (Anura, Dendrobatidae) del Este del piemonte andino, Venezuela. Describimos un nuevo sapito niñera del género *Allobates* (Dendrobatidae) proveniente de Río Negro, Municipio Córdoba, Estado Táchira, oeste de Venezuela. Esta nueva especie es habitante terrestre de bosque tropical primario y secundario en tierras bajas y medias entre los 400 y 1000 msnm. La nueva especie es similar a especies del grupo de *Allobates marchesianus* y su distribución se restringe a las faldas occidentales de los Andes Venezolanos. Difiere de sus congéneres por su patrón dorsal manchado irregularmente, con línea oblicua lateral difusa, línea ventro-lateral presente, y vientre de color amarillo en los machos.

Palabras clave: Anura, Dendrobatidae, *Allobates*, especie nueva, Venezuela, Colombia.

Resumo

Descrição de uma nova espécie de *Allobates* (Anura, Dendrobatidae) do leste do piemonte andino, Venezuela. Descrevemos aqui uma nova espécie de anuro do género *Allobates* (Dendrobatidae) proveniente de Río Negro, Município de Córdoba, Estado de Táchira, oeste da Venezuela. Trata-se de um anfíbio terrestre que habita a floresta tropical primária e secundária de baixas e médias altitudes, entre 400 e 1000 m. A nova espécie é similar àquelas do grupo de *Allobates marchesianus*, e sua distribuição geográfica se restringe às encostas ocidentais dos Andes venezuelanos. Difere de seus congêneres por seu padrão dorsal com manchas irregulares, com linha lateral oblíqua difusa, linha ventro-lateral presente e ventre amarelo nos machos.

Palavras-chave: Anura, Dendrobatidae, *Allobates*, espécie nova, Venezuela, Colômbia.

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Introduction

After a major revision of dendrobatoid frogs (Grant *et al.* 2006) and subsequent taxonomic corrections (Santos *et al.* 2009, Barrio-Amorós *et al.* in press), the diversity of these frogs is still much underestimated. Venezuela has revealed to have an extraordinarily diverse and endemic dendrobatid fauna, consisting of at least 55 species distributed throughout the country's diverse geography (e.g., 20 spp. in the Andes, 13 spp. in the Cordillera de la Costa, 22 spp. in the Venezuelan Guiana), almost all endemic (see Barrio-Amorós 1998, 2004, and Barrio-Amorós and Fuentes 1999 for a general overview).

Venezuelan dendrobatids consists of the nearly endemic genera *Anomaloglossus* (16 spp.), *Aromobates* (12 spp.), and *Mannophryne* (14 spp.). Other less diverse genera in Venezuela are *Dendrobates* (2 spp.; after *Minyobates* was synonymized with *Dendrobates* by Santos *et al.* 2009), *Ameerega* (2 spp.) and one "*Prostherapis*" (see Grant *et al.* 2006) and *Allobates* (10 spp. considering the one described here). In an ongoing general review of Andean dendrobatids, we discovered a new species of *Allobates* at both sides of the Táchira Depression (which separates the Cordillera Oriental de Colombia from the Cordillera de Mérida at an altitude of around 450 m). It is the purpose of this paper to describe this new species.

Material and Methods

Frogs were captured, euthanized and preserved under the guidelines of the IACUC (Institutional Animal Care and Use Committee) protocol 05111001. We follow Grant *et al.* (2006) in scoring valid diagnostic characters (Appendix I), in order to unify criteria among dendrobatid taxonomists.

The description follows Barrio-Amorós *et al.* (2006). Comparative data for Venezuelan *Allobates* were taken from Test (1956), Rivero

et al. (1986), La Marca (1993), Myers and Donnelly (2001), La Marca *et al.* (2002, 2006), and Barrio-Amorós *et al.* (2006). Sex was determined by dissection (presence of mature testes or oviducts), and identification of secondary sexual characters (i.e. presence or absence of vocal slits, or by direct observation of calling males). Measurements (in mm) were taken with a calliper to the nearest 0.1 mm. Measurements taken exclusively on adult frogs are as follows: SVL: straight length from tip of snout to vent; SL: shank length from outer edge of flexed knee to heel; ThL: thigh length from vent opening to flexed knee; FL: foot length from proximal edge of outer metatarsal tubercle to tip of toe IV; HaL: hand length from proximal edge of palmar tubercle to tip of finger III; HeL: head length from tip of snout to the posterior border of skull (posterior edge of prootic, noted through the skin); HW: head width between angle of jaws; InD: inter-narial distance between centers of nares; EN: distance of anterior edge of eye to nostril; ED: horizontal eye diameter; TD: horizontal tympanum diameter; ETS: distance between the anterior corner of the eye to the tip of the snout; FD: width of Finger III; T4D: width of toe IV; 1FiL: length of Finger I from inner edge of thenar tubercle to tip of finger; 2FiL: length of Finger II from inner edge of thenar tubercle to the tip of finger. Fingers are abbreviated as F, followed by the number of the finger in Roman numerals; toes as T.

All specimens examined are housed in the following collections: Colección de Vertebrados, Universidad de los Andes, Mérida (CVULA); Museo de la Estación Biológica de Rancho Grande, Maracay (EBRG); Colección de Herpetología del Museo de Biología de la Universidad Central de Venezuela, Caracas (MBUCV); Museo de Historia Natural La Salle, Caracas (MHNLS) (Appendix II).

We recorded two males of the new species from Rio Negro (voucher numbers EBRG 5562-63, SVL 19.3 and 19.4 mm respectively). Frogs

were calling actively from the forest floor and between roots of shrubs. The advertisement call was recorded using a portable Sony stereo cassette recorder WM-D6C and a Sennheiser ME67 directional microphone onto a TDK MA90 metal bias tape cassettes. The frogs were recorded at approximately one meter from the animals and the temperature of the substrate was registered. Recordings were digitized using Cool Edit Pro version 2 (Syntrillium Software, CA) at a sampling rate of 44100 HZ with sample size of 32 bits. Advertisement calls were analyzed using SoundRuler version 0.960 (Gridi-Papp 2007). The call parameters measured follow definitions of Cocroft and Ryan (1995) and Moriarty-Lemmon (2009).

The list of measurements included (Appendix III) are call length, inter-call duration, rise time (duration from the beginning 10% of amplitude to the maximum amplitude), fall time (duration from the maximum amplitude to the end 90% of amplitude), rate (inverse of the time between the maximum amplitude of to consecutive calls), duty cycle (unitless measurement obtained by dividing the pulse length by the interval between two consecutive pulses), shape (unitless measurement obtained by dividing the duration of the pulse rise time over pulse length), dominant frequency, and crest factor (unitless measurement maximum amplitude divided by the root mean square of the amplitude). All variables measured here are adequate to better characterize the call of this new species in hope of further research will elucidate their phylogenetic and behavioural relevance in the context of the entire family Dendrobatidae.

Species Description

Allobates algorei sp. nov.

(Figures 1–4)

Colostethus humilis Barrio-Amorós and García-Porta, 2003: 34.

English name - spotted nurse frog.

Spanish name: sapito niñera moteado.

Holotype - Adult male, EBRG 5560, from Río Negro, Municipio Córdoba, Estado Táchira, Venezuela, “07°34.723’ N, 72°10.739’ W”, elevation 482 m, collected on 10 June, 2007.

Paratopotypes - EBRG 5561-64, adult males, with the same data as the holotype.

Paratypes - CVULA 3790 (male), 3830 (female), 3835 (male), 3838 (male), and 3839 (female), all from Doradas, Uribante, Estado Táchira, Venezuela; CVULA 3690 (female) from La Honda, Uribante, Estado Táchira, Venezuela.

Referred specimens - The following specimens, CVULA 3832-33, 3836-37, 4700-03 are from Río Doradas-Uribante (locality data is not very specific), Estado Táchira, Venezuela. These specimens are immature or juveniles and were not considered paratypes.

Etymology - We name this species after the former American vice-president and Nobel Peace Laureate Al Gore to recognize his ecumenical efforts to alert the people of the planet about the global warming crisis (Gore 2006). Amphibians are among the organisms most affected by this crisis, even without direct prosecution by humans (Pounds *et al.* 2006). Concretely, the Andes of Venezuela have suffered an evident decimation of amphibian populations due to known and unknown causes (La Marca and Reinhaller 1991, Barrio-Amorós 2001, Lampo *et al.* 2008).

Definition (see Appendix I for character explanation) - (1) Skin on dorsum slightly granular. (2) Paired dorsal scutes present on digits. (3) Distal tubercle on finger IV present but indistinct. (4) Finger IV length almost reaches distal subarticular tubercle of finger III. (5) Finger I longer than II. (6) Digitals present. (7) Fingers weakly expanded. (8) Finger fringes absent. (9) Metacarpal ridge absent. (10) Finger III not swollen in adult males. (11) Carpal pad absent. (12) Male excrescences on thumb absent. (13) Thenar tubercle present, small. (14) Black arm gland in adult males absent. (15) Tarsal keel short, tubercle-like. (16) Toes

weakly expanded. (17) Toe webbing absent. (18) Metatarsal fold absent. (19) External coloration with paracloacal marks whitish, thigh dorsally orange with one transverse narrow bar; lacking dorsolateral stripes; ventrolateral stripe present but not lineal; oblique lateral stripe partial, diffuse. (20) Gular-chest markings absent. (21) Dermal collar absent. (22) Male throat coloration evenly stippled grey with a profusion of melanophores; female throat coloration free or nearly free of melanophores. (23) Male abdomen color pattern immaculate, pale yellow. (24) Female abdomen color pattern free or nearly free of melanophores; color unknown on living females. (25) Iris coloration metallic dirty bronze gold-colored pupil ring. (26) Large intestine mainly unpigmented. (27) Testis white with melanophores. (28) Median lingual process absent. (29) Tympanum inconspicuous, tympanic annulus absent. (30) Vocal sac not distinct. (31) Teeth present on the maxillary arch. (32) Size small, males ($n=8$) 17.2–19.5 mm, mean=18.9±0.7; females ($n=3$) 17–18 mm, mean=17.7±0.6.

Comparisons - We compare *Allobates algorei* sp. nov. to other *Allobates* from Venezuela (*A. bromelicola*, *A. caribe*, *A. mandelorum*, *A. pittieri*, *A. sanmartini*, *A. undulatus*) and especially to *A. humilis*, the most similar congener in the Venezuelan Andes. Some of our data contradict the assertion of Jungfer and Böhme (2004), followed by Grant *et al.* (2006), that the species *rufulus* is a member of *Allobates* (Barrio-Amorós and Santos pers. obs.), and we therefore do not consider it in our comparisons with *A. algorei*. *Allobates brunneus* and *A. marchesianus* were mentioned as part of the Venezuelan fauna (Rivero 1961, Morales 1994, La Marca 1996, Barrio-Amorós 1998, 2004); but these species were later demonstrated not to be conspecific with Venezuelan specimens (Caldwell *et al.* 2002, Lima *et al.* 2009); they still lack a definitive specific assignment.

Allobates algorei sp. nov. (character states in parentheses) differs from *A. bromelicola*

(Test, 1956) by having dorsolateral whitish stripes (absent), black tip of digits (black with white dermal scutes) and arboreal habits (terrestrial). *Allobates caribe* (Barrio-Amorós, Rivas and Kaiser, 2006) has a smooth dorsum (smooth to slightly granular), FI = FII (FI > FII), rudimentary toe webbing (absent), ventrolateral line absent (present), oblique lateral stripe absent (present), and dorsolateral pattern absent (present). *Allobates pittieri* (La Marca, Manzanilla and Mijares, 2004 “2006”) has the disk of FIII not expanded (weakly expanded), basal toe webbing (absent), a small anal sheath (absent), and fringes on toes (absent). *Allobates undulatus* (Myers and Donnelly, 2001) has a swollen supracarpal pad (absent), an unusual small subarticular tubercle at the base of TV (absent), basal toe webbing between TIII and TIV (absent), and black sides (black lateral band fading posteriorly). *Allobates sanmartini* (Rivero, Langone and Prigioni, 1986) has pustular dorsal skin (slightly granular), FI equal or shorter than FII (FI > FII), fringes on toes (absent), and toe webbing (absent). *Allobates mandelorum* (Schmidt, 1932) has extensive toe webbing (absent) and a marbled ventral pattern on females (absent). *Allobates humilis* (Rivero, 1978) is the geographically closest relative, although separated by at least 200 km to the northeast. It differs from *A. algorei* by having a diamondback pattern (waving wide vertebral band surrounded by multiple small spots), absence of ventrolateral stripe (present), of FIII 1.8 wider than adjacent phalanx (1.2).

Description of the holotype - The holotype is an adult male of 19.5 mm (SVL): body slender and elongate, quadrangular in cross-section; dorsal skin, including dorsal surfaces of hind limbs, smooth in preservative, bearing small, non-keratinized tubercles in life (Fig 1A,C); ventral skin smooth (Figure 1B,D); head is longer than wide, HeL = 41% of SVL; HW = 33.3% SVL (Table 1); snout is subacuminate in profile (Figure 2A), nearly rounded in dorsal

and ventral view (Figures 2B, 2C); nares are situated laterally to the tip of snout; narial openings are visible when viewing the head from the front, not when viewing dorsally; and barely visible when viewing from a ventral aspect; canthus rostralis is rounded, the loreal region is little concave; interorbital region is as wide as the upper eyelid; snout longer than ED; tympanum is inconspicuous, about 2/3 of the tympanum is concealed posterodorsally by a low supratympanic bulge formed by the superficial slip of *m. depressor mandibulae*; tympanum is positioned closely behind eye and lower, nearly touching angle of jaws; teeth present on maxillary arch; vocal slits large and long, from mid level of tongue to the angles of jaws; tongue slightly cordiform and free posteriorly.

Hand (Figure 3A) of moderate size (25.6% SVL); relative lengths of adressed fingers are III > I > II > IV; s of all fingers are slightly expanded and round; FIII is 1.2 times wider than distal end of adjacent phalanx; the base of palm has a large, rounded palmar tubercle; small (approximately 1/3 of the palmar tubercle), slightly elliptical thenar tubercle on base of FI; one or two subarticular tubercles on fingers (one each on FI and FII, two each on FIII and FIV, the distal one of FIV inconspicuous); and all tubercles are flat and round; without supernumerary tubercles; fringes on fingers are absent.

Hind limbs are of moderate length, SL = 49.2% of SVL; relative lengths of adressed toes are IV > II > V > III > I; TI is short, the tip not reaching the subarticular tubercle of TII;

Table 1 - Measurements (in mm) of adult male and female *Allobates algorei* sp. nov. from the type locality and the Río Doradas. Abbreviations are as described in the text. Values include range and mean ± standard deviation.

Character	Males (n = 8)		Females (n = 3)	
	Range	Mean ± SE	Range	Mean ± SE
SVL	17.2–19.5	18.9 ± 0.7	17.0–18.0	17.7 ± 0.6
SL	8.0–9.6	8.6 ± 0.4	8.2–8.5	8.3 ± 0.2
HaL	4.3–5.0	4.7 ± 0.2	4.2–4.6	4.4 ± 0.2
FL	7.0–9.0	8.1 ± 0.6	7.6–8.0	7.8 ± 0.2
ThL	7.3– 9.0	8.1 ± 0.6	7.8 –8.2	8.0 ± 0.2
HeL	7.0–8.0	7.5 ± 0.4	6.6–7.2	6.9 ± 0.3
HW	5.2–7.0	6.1 ± 0.5	5.2– 5.4	5.3 ± 0.1
InD	2.1–2.7	2.3 ± 0.2	2.0–2.6	2.4 ± 0.3
EN	1.3–2.0	1.6 ± 0.2	1.5–1.7	1.6 ± 0.1
ED	2.0–2.8	2.4 ± 0.2	2.0–2.2	2.1 ± 0.1
TD	0.8–1.0	0.8 ± 0.1	0.6–1.0	0.8 ± 0.3
ETS	2.9 –3.0	3.0 ± 0.1	2.6 –3.0	2.8 ± 0.2
FD	0.4–0.7	0.6 ± 0.1	0.3–0.5	0.4 ± 0.1
T4D	0.4–0.6	0.5 ± 0.1	0.4–0.5	0.4 ± 0.1
1FiL	2.9–3.2	3.0 ± 0.1	2.2–2.9	2.6 ± 0.4
2FiL	2.5–2.9	2.7 ± 0.2	2.0–2.5	2.3 ± 0.3

toes are slightly expanded, about 1.4 times wider than distal end of adjacent phalanx; feet (Figure 3B) are unwebbed; fringes on toes are absent; one to three non-protuberant, small subarticular tubercles are present (one on TI and TII, two on TIII and TV, three on TIV, proximal one almost indistinct); two metatarsal tubercles present, including a small round outer, and a similar in size oval inner tarsal tubercle; well defined tarsal keel present at 1.2 mm from proximal edge of inner metatarsal tubercle, short, transverse across tarsus; cloacal opening at upper level of thighs, without flap.

Color - In life (Figure 1A), the dorsal background color is orange brown, with a dark brown interorbital region that extends as a wide vertebral band to the posterior part of the dorsum not reaching the cloacal opening. This band is not solid and it is bordered by straight parallel small brown spots forming para-vertebral rows; on the posterior part of the dorsum there are many small dark brown spots, coinciding to small non-keratinized tubercles. Paracloacal marks consist of elongate whitish curved stripes at the base of the thighs. The sides of the body have a black lateral band from the tip of the snout and continuing to the groin, covering the superior half of the tympanum and fading posteriorly in color intensity but widening to twice its anterior width; a whitish, diffuse (sometimes spotted; Figure 1C) and incomplete oblique lateral stripe is present from groin to midbody. An irregular white ivory ventrolateral stripe is found along the inferior edge of the lateral band. Anterior sides of the arms are pale orange with no marks; posteriorly there is a dark brown longitudinal stripe along the arm that is particularly noticeable at elbow level. Fingers pale orange, with ill-defined cross-bars; a white ring is present anterior to finger disks; disks are black with white digital scutes. Dorsal surfaces of hind limbs are pale brownish orange with one transverse narrow dark brown bar on thigh, shank and tarsus. Toes are dark brown with a white ring anterior to

finger disks; disks black with white digital scutes.

Ventrally (Figure 1B, D) the throat is dirty white, the chest and inferior arms are pinkish, the belly is whitish anteriorly, light yellow posteriorly, thighs are pale orange and shanks and tarsi are greyish. Palms are light brown and soles blackish. Iris is dirty bronze, with a golden pupil ring.

In preservative the colors brown and orange fade to grey and pale grey. Dark brown coloration turned into blackish grey. The dorsum is brown with dark brown markings; arms and legs are pale brown (Figure 4A); the ventral side is pale yellow with a profusion of melanophores on the throat; palms and soles are dark brown (Figure 4B); after two years the yellow coloration has faded to white.

Variation - All animals from the type locality have the same dorsal pattern, with more or less contrast. Ventrally, they are almost identical, except for the yellow from the belly that can be more or less intense (probably related to reproductive season). The series from Doradas (CVULA 3790, 3830, 3835, 3838, 3839, and 3690) was collected in 1985 and preserved specimens present a brownish general coloration, probably due to different procedures during preservation. Therefore, they have a brownish general coloration. Otherwise, they are almost identical in all characters stated. A female (CVULA 3830) has the most striking oblique lateral stripe, while in other animals (CVULA 3790, 3838, two males) the oblique lateral stripe is indistinct. Paracloacal marks can be present (EBRG 5563, 5561, holotype, and becoming more diffuse on EBRG 5562 and 5564). EBRG 5562 has a swollen left FI (Figure 3C), although this is obviously an anomaly.

Sexual differences - The mean SVL for females (17.7 ± 0.6 mm; N=3) is smaller than the mean SVL for males (18.9 ± 0.7 mm; N=8) (Table1), but the sample we have available is too small to be statistically tested. Many other *Allobates* are known to have females larger than

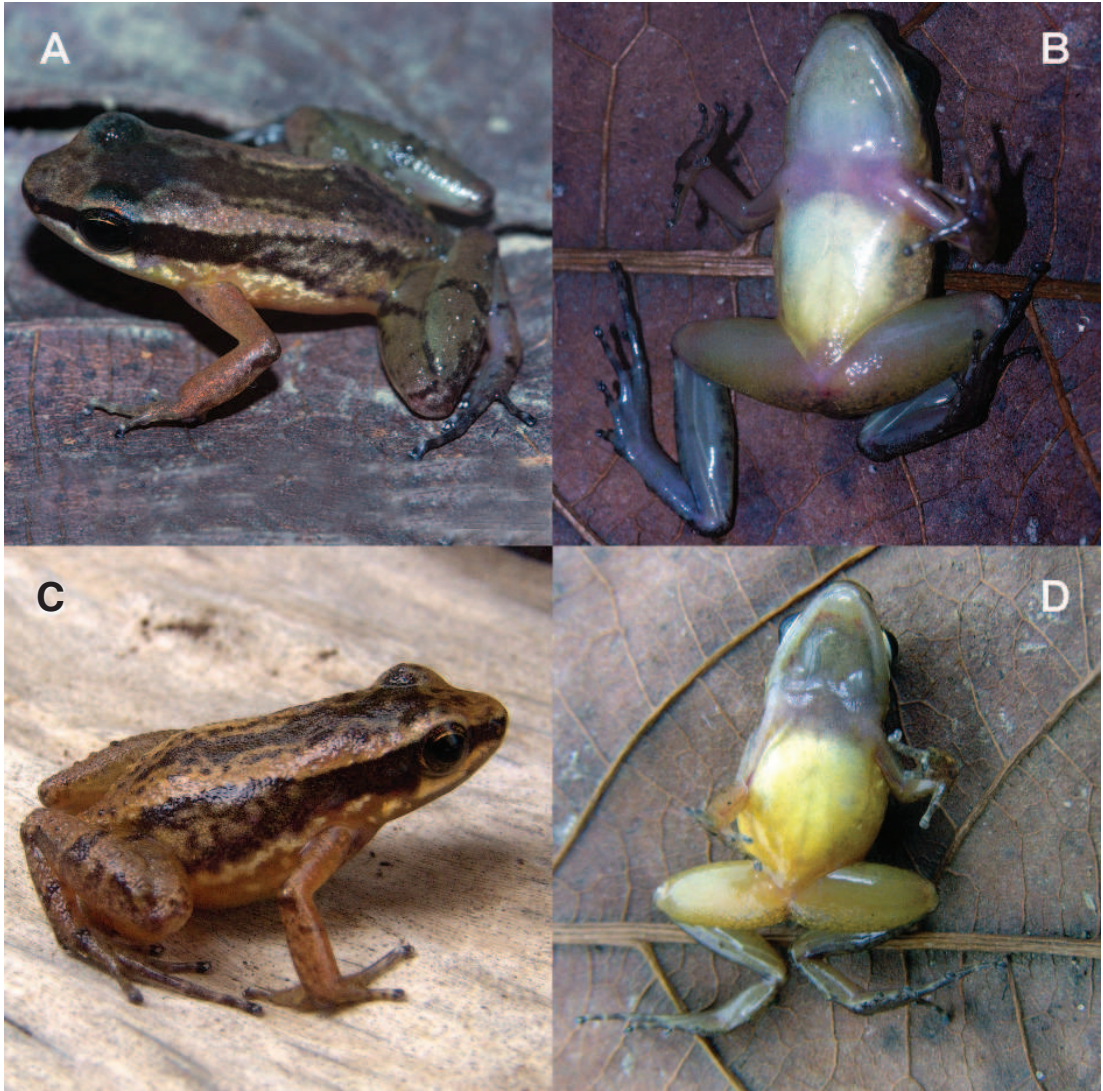


Figure 1 - Dorsolateral (A) and ventral (B) views of EBRG 5560, the holotype of *Allobates algorei* sp. nov. Dorsolateral (C) and ventral (D) views of a living, uncollected male of *A. algorei*.

males (e.g. *A. brunneus*, *A. femoralis*, *A. granti*, *A. myersi*, *A. marchesianus*, *A. subfolianidicans*; Lima *et al.* 2009, Lötters *et al.* 2007, Kok *et al.* 2006, Caldwell *et al.* 2002, Lima *et al.* 2007, respectively; in *A. olfersioides* and *A. zaparo*, the female size is the same as for males; Verdade and Rodrigues 2007, Lötters *et al.*

2007, respectively). In *A. algorei*, the most striking sexually dimorphic character is the ventral coloration; although both sexes seem immaculate ventrally, it is possible to see under magnification a profusion of melanophores on the throat and chest of males, which is absent in females.

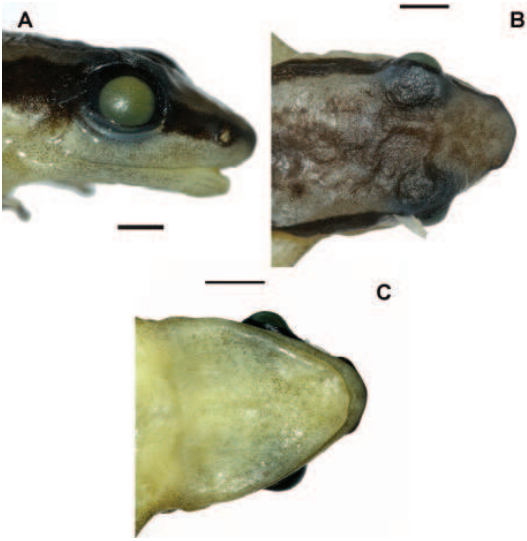


Figure 2 - Lateral (A), dorsal (B), and ventral (C) views of the head of EBRG 5560, holotype of *Allobates algorei* sp. nov. Scale of A = 1 mm; scales of B and C = 2 mm.

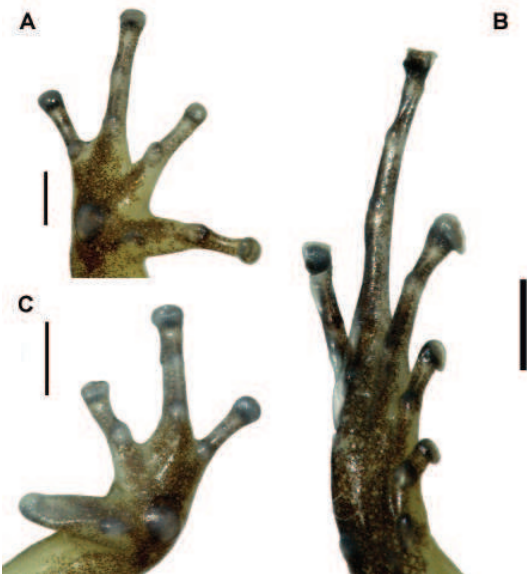


Figure 3 - Palmar (A) and plantar (B) views of the right hand and foot of EBRG 5560, the holotype of *Allobates algorei* sp. nov. (C) Anomalous left thumb of paratype EBRG 5562. Scales = 1 mm.

Natural history - Males usually call from between shrub roots and concealed leaf litter debris inside the forest (Río Negro) or at disturbed but shady areas (along the road from San Cristobal to El Piñal), and are normally difficult to locate. Animals were actively collected while calling within dense vegetation during the day and especially at dusk. The males seem to exhibit aggressive behaviour to each other as they reply aggressively to their recorded call.

Vocalization - Males of *Allobates algorei* have single note call produced at an overall constant rate (Figure 5A), from 2-3 notes per second, with a dominant frequency at 5065 Hz. Figure 5B shows the waveform and spectrogram of *Allobates humilis* from San Ramón, Estado Barinas, Venezuela, for comparative purposes. The most striking differences between the advertisement call of *A. algorei* and *A. humilis* are the number of notes per second (2-3 on *A. algorei*; 4 on *A. humilis*), and the dominant frequency (5065 Hz on *A. algorei*; 4200 Hz on *A. humilis*).

Distribution - *Allobates algorei* sp. nov. is only known from a few localities: the type locality, and the road between San Cristóbal and El Piñal (07°39.225' N, 72°11.482' W, elevation 529 m), both lying in the Cordillera oriental de Colombia and represented by a



Figure 4 - Dorsal (A) and ventral (B) views of EBRG 5560, the holotype of *Allobates algorei* sp. nov.

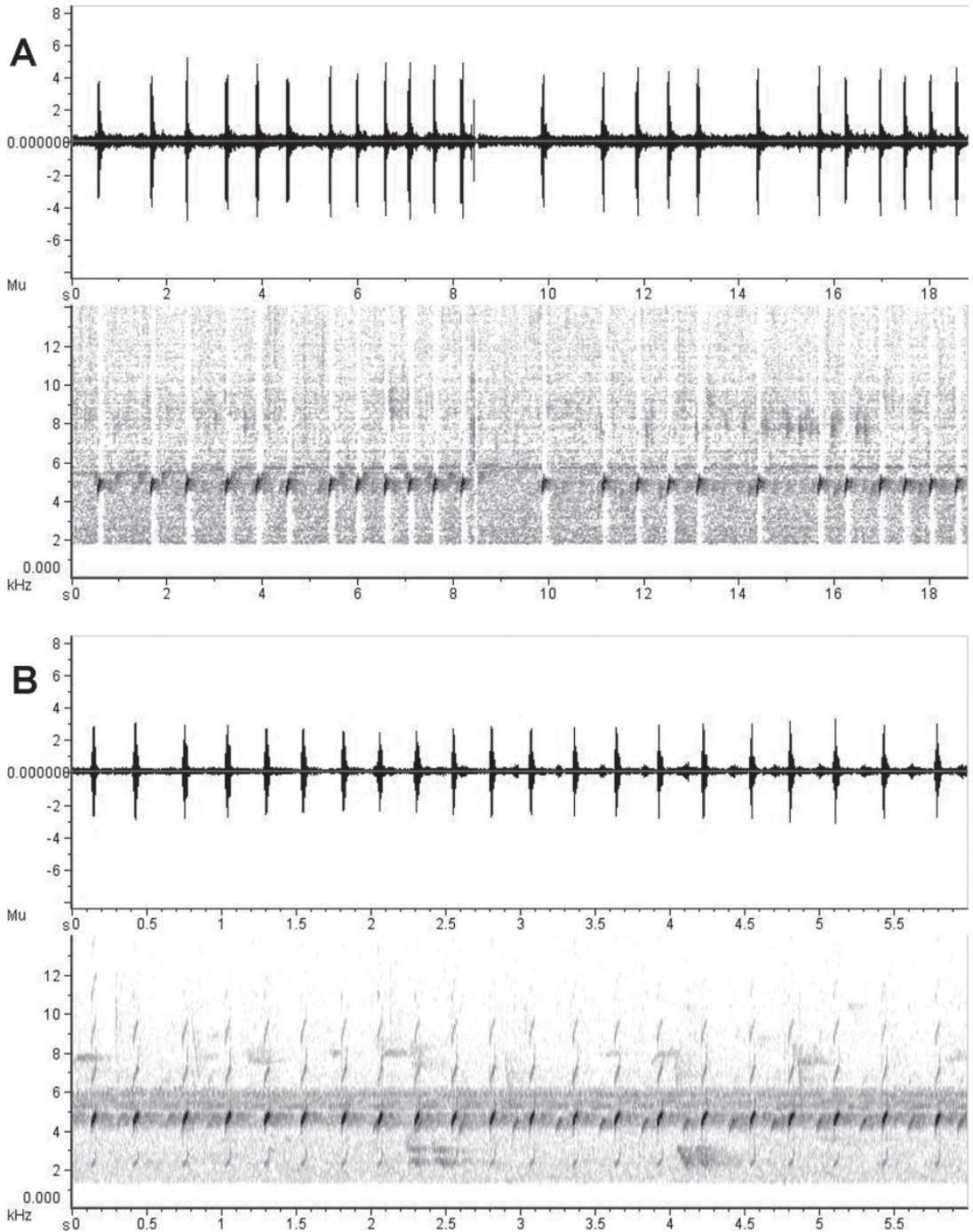


Figure 5 - Waveform and spectrogram of a 19 s sequence of the call of *Allobates algoeiri* sp. nov. (A). Waveform and spectrogram of a 6 s trill call of *Allobates humilis* (B). Indistinct harmonics can be seen in calls of both species.

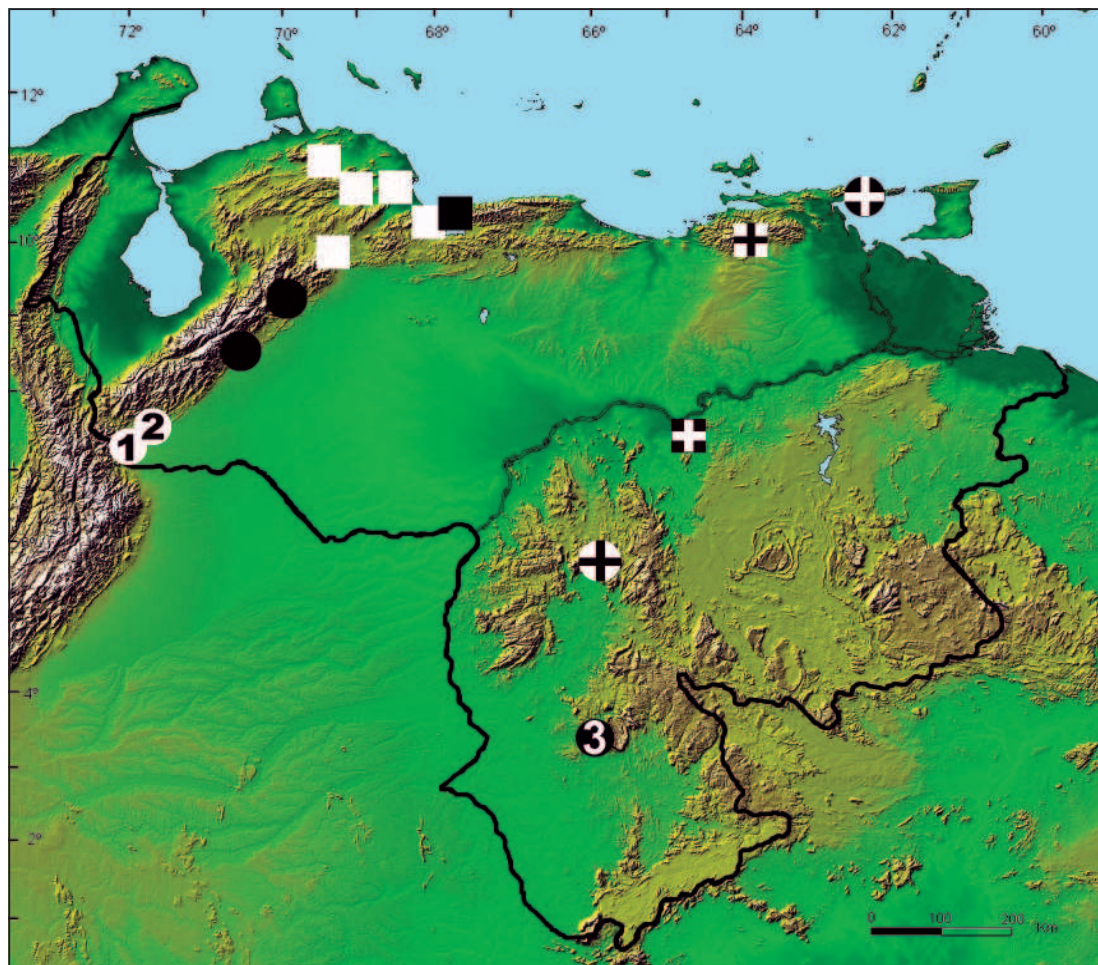


Figure 6 - Distribution of Venezuelan *Allobates*. *Allobates algorei* sp. nov. (white circles): 1- type locality. 2- río Doradas-Uribante; *A. aff. marchesianus* and *A. cf. brunneus* (black circle with white 3); *A. humilis* (black circles); *A. pittieri* (white squares); *A. bromelicola* (black square); *A. mandelorum* (white square with black cross); *A. caribe* (black circle with white cross); *A. sanmartini* (black square with white cross); *A. undulatus* (white circle with black cross).

single white circle in Figure 6, and Río Doradas-Uribante, in the southwesternmost Cordillera de Mérida. Due to the proximity of the international boundary line, the species could also be present in Colombia. Re-examining the material identified as *A. humilis* from Río Doradas, reported by Barrio-Amorós and García-Porta (2003), it became evident that it belongs to this new species. Figure 6 provides

the known distribution for *A. algorei* sp. nov. including the other Venezuelan *Allobates* species (except *rufulus*).

Discussion

Neobatrachia is undergoing an intense taxonomic rearrangement to address the issues of a monophyletic nomenclature (e.g., Heinicke

et al. 2009), and dendrobatid taxonomy is not an exception (Grant *et al.* 2006, and supplementary text of Santos *et al.* 2009). Our description of *Allobates algorei* sp. nov. has not the intention to address the issues of the Dendrobatoidea systematics (*sensu* Grant *et al.* 2006), however, we adhere to the taxonomic conservatism (Pauly *et al.* 2009). Our classification follows Santos *et al.* (2009), in which the family Dendrobatidae correspond to Dendrobatidae plus Aromobatidae of Grant *et al.* (2006) In our view, the arguments in Grant *et al.* (2006) are few compared to the historical monophyly of the group.

The genus *Allobates* as currently understood (after Grant *et al.* 2006 and Santos *et al.* 2009) appears to be quite speciose. Ten species (including *A. algorei* sp. nov. but without *A. rufulus*) have been reported to Venezuela, although three are poorly diagnosed. *Dendrobates rufulus* has been transferred to *Allobates* by Jungfer and Böhme (2004) with no further explanation. Even though we agree that this species is not a member of *Dendrobates* nor *Ameerega* (it was assigned to *Epipedobates* = *Ameerega* by Myers 1997), neither is an *Allobates* (Barrio-Amorós and Santos, in prep.). Rivero (1961) mentioned *A. brunneus* from the base of Monte Duida, Estado Amazonas, Venezuela. Examining the same specimens mentioned by Rivero (1961), Morales (1994) believed them to be *A. marchesianus*. However, Caldwell *et al.* (2002) did not concur, and most probably Rivero's specimens belong to a different or undescribed species similar to *A. marchesianus*. La Marca (1996) collected some specimens in the same area, the foothills of the Monte Duida, and considered them to be *A. brunneus*. Lima *et al.* (2009) redescribed the species from the type locality (about 2300 km SE), and the Venezuelan specimens are in need of reliable identification.

The presence of two allopatric species of *Allobates* in the eastern versant of the Venezuelan Andes is not surprising. The other species, *A. humilis*, is poorly known (Figure 7),




Figure 7 - *Allobates humilis* from San Ramón, Calderas, Estado Barinas, Venezuela. Note the diamondback pattern, the dark flank and a much better defined ventrolateral stripe and compare with Figure 1A, C.

described only from a single juvenile by Rivero (1978) and redescribed based on an adult male by La Marca *et al.* (2002).

Venezuela is the 8th most diverse country in terms of amphibians in the world (Barrio-Amorós 2009), and every year there is a significant increase in the number of known taxa. The description of *A. algorei* is yet another example of how increased effort in alpha taxonomic investigations can help us to understand the true diversity of the family Dendrobatidae.

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References

- Barrio, C. L. and O. Fuentes. 1999. Sinopsis de la familia Dendrobatidae (Amphibia: Anura) de Venezuela. *Acta Biologica Venezuelica* 19: 1–10.
- Barrio-Amorós, C. L. 1998. Sistemática y biogeografía de los anfibios (Amphibia) de Venezuela. *Acta Biologica Venezuelica* 18: 1–93.
- Barrio-Amorós, C. L. 2001. Amphibian Decline in Venezuela – the state of knowledge. *Froglog* 47: 2–4.
- Barrio-Amorós, C. L. 2004. Amphibians of Venezuela, Systematic list, distribution and references; an update. *Revista Ecología Latino Americana* 9: 1–48.
- Barrio-Amorós, C. L. 2009. Riqueza y Endemismo. Pp. 25–39 in C. Molina, J. C. Señaris, M. Lampo, and A. Rial (eds.), *Anfibios de Venezuela – estado del conocimiento y recomendaciones para su conservación*. Ediciones Grupo TEI, Caracas.
- Barrio-Amorós, C. L. and J. Garcia-Porta. 2003. Geographic Distribution: Anura: *Colostethus humilis*. *Herpetological Review* 34: 380.
- Barrio-Amorós, C. L., G. Rivas and H. Kaiser. 2006. New species of *Colostethus* (Anura, Dendrobatidae) from the Peninsula de Paria, Venezuela. *Journal of Herpetology* 40: 371–377.
- Barrio-Amorós, C. L., J. C. Santos and O. Jovanovic. A new dendrobatid frog (Anura: Dendrobatidae: *Anomaloglossus*) from the Orinoquian rainforest, southern Venezuela. *Zootaxa*. In press.
- Caldwell, J. P., A. P. Lima and C. Keller. 2002. Redescription of *Colostethus marchesianus* (Melin, 1941) from its type locality. *Copeia* 2002: 157–165.
- Cocroft, R. B. and M. J. Ryan. 1995. Patterns of advertisement call evolution in toads and chorus frogs. *Animal Behaviour* 49: 283–303.
- Gore, A. 2006. *Una verdad incómoda*. Editorial Gedisa. Barcelona. 328 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, and W. C. Wheeler. 2006. Phylogenetic systematics of dart-poison frogs and their relatives (Amphibia: Athesphatanura: Dendrobatidae). *Bulletin of the American Museum of Natural History* 299: 1–262.
- Gridi-Papp, M (ed.). 2003–2007. *SoundRuler – acoustic analysis for research and teaching*. <http://soundruler.sourceforge.net>.
- Heinicke, M. P., W. E. Duellman, L. Trueb, D. B. Means, R. D. MacCulloch, and S. B. Hedges. 2009. A new frog family (Anura: Terrarana) from South America and an expanded direct-developing clade revealed by molecular phylogeny. *Zootaxa* 2009: 1–35.
- Jungfer, K. H. and W. Böhme. 2004. A new poison-dart frog (*Dendrobates*) from northern central Guyana. *Salamandra* 40: 1–6.
- Kaplan, M. 1997. A new species of *Colostethus* from the Sierra Nevada de Santa Marta (Colombia) with comments on intergeneric relationships within the Dendrobatidae. *Journal of Herpetology* 31: 369–375.
- Kok, P. J. R., R. D. MacCulloch, P. Gaucher, E. H. Poelman, G. R. Bourne, A. Lathrop, and G. L. Lenglet. 2006. A new species of *Colostethus* (Anura, Dendrobatidae) from French Guiana, with a redescription of *Colostethus beebei* (Noble, 1923) from its type locality. *Phyllomedusa* 5: 43–66.
- Lampo, M, D. Sánchez, A. Nicolás, M. Márquez, F. Nava, C. Z. García, M. Rinaldi, A. Rodríguez-Contreras, F. León, B. Han, and A. Chacón-Ortiz 2008. *Batrachochytrium dendrobatidis* in Venezuela. *Herpetological Review* 39: 449–454.
- La Marca, E. 1993. Phylogenetic relationships and taxonomy of *Colostethus mandelorum* (Anura: Dendrobatidae) with notes on coloration, natural history and description of the tadpole. *Bulletin of the Maryland Herpetological Society* 29: 4–19.
- La Marca, E. 1996. Ranas del género *Colostethus* (Amphibia: Anura: Dendrobatidae) de la Guayana Venezolana, con la descripción de siete nuevas especies. *Publicaciones de la Asociación Amigos de Doñana* 9: 1–64.
- La Marca, E. & H. P. Reinthaler. 1991. Population changes in *Atelopus* species of the Cordillera de Mérida, Venezuela. *Herpetological Review* 22: 125–128.
- La Marca, E., J. Manzanilla and A. Mijares-Urrutia. 2006. “2004”. Revisión taxonómica del *Colostethus* del Norte de Venezuela confundido durante largo tiempo con *C. brunneus*. *Herpetotropicos* 1: 40–50.
- La Marca, E., M. Vences and S. Lötters. 2002. Rediscovery and mitochondrial relationships of the dendrobatid frog *Colostethus humilis* suggest parallel colonization of the Andes by poison frogs. *Studies on Neotropical Fauna and Environment* 37: 233–240.
- Lima, A. P., J. P. Caldwell and C. Strüssmann. 2009. Redescription of *Allobates brunneus* (Cope) 1887

- (Anura: Aromobatidae: Allobatinae), with a description of the tadpole, call, and reproductive behaviour. *Zootaxa* 1988: 1–16.
- Lima, A. P., D. E. A. Sánchez and J. R. D. Souza. 2007. A new Amazonian species of the frog genus *Colostethus* (Dendrobatidae) that lays its eggs on undersides of leaves. *Copeia* 2007: 114–122.
- Lötters, S., K. H. Jungfer, F. W. Henkel, and W. Schmidt. 2007. *Poison Frogs, Biology, Species & Captive Husbandry*. Edition Chimaira & Serpents Tale. 668 pp.
- Morales, V. R. 1994. Taxonomía de algunos *Colostethus* (Anura: Dendrobatidae) de Sudamérica, con descripción de dos especies nuevas. *Revista Española de Herpetología* 8: 95–103.
- Moriarty-Lemmon, E. 2009. Diversification of conspecific signals in sympatry: geographic overlap drives multidimensional reproductive character displacement in frogs. *Evolution* 63: 1155–1170.
- Myers, C. M. 1997. Preliminary remarks on the summit herpetofauna of Auyantepui, eastern Venezuela. *Acta Terramaris* 10: 1–8.
- Myers, C. W. and M. A. Donnelly. 2001. Herpetofauna of the Yutajé-Corocoro Massif, Venezuela: second report from the Robert G. Goelet American Museum Terramar Expedition to the northwestern tepuis. *Bulletin of the American Museum of Natural History* 261: 1–85.
- Pauly, G. B., D. M. Hillis and D. C. Cannatella. 2009. Taxonomic freedom and the role of official lists of species names. *Herpetologica* 65: 115–128.
- Pounds, J. A., J. A. Consuegra, M. P. L. Fogden, P. N. Foster, K. L. Masters, R. Puschendorf, S. R. Ron, G. A. Sánchez-Azofeifa, and C. J. Still. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439: 161–167.
- Rivero, J. A. 1961. Salientia of Venezuela. *Bulletin of the Museum of Comparative Zoology* 126: 1–267.
- Rivero, J. A. 1978. Notas sobre los anfibios de Venezuela. III. Nuevos *Colostethus* de los Andes Venezolanos. *Memoria de la Sociedad de Ciencias Naturales La Salle* 38: 95–111.
- Rivero, J. A., J. A. Langone and C. M. Prigioni. 1986. Anfibios anuros colectados por la Expedición del Museo Nacional de Historia Natural de Montevideo al Río Caura, Estado Bolívar, Venezuela; con la descripción de una nueva especie de *Colostethus* (Dendrobatidae). *Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo* 11: 1–15.
- Santos, J. C., L. A. Coloma and D. C. Cannatella. 2003. Multiple, recurring origins of aposematism and diet specialization in poison frogs. *PNAS* 100: 12792–12797.
- Santos J. C., L. A. Coloma, K. Summers, J. P. Caldwell, and R. Ree. 2009. Amazonian amphibian diversity is primarily derived from late Miocene Andean lineages. *PLoS Biol*, 7, e1000056. doi:10.1371/journal.pbio.1000056, 1–14.
- Test, F. H. 1956. Two new dendrobatid frogs from Northern Venezuela. *Occasional Papers of the Museum of Zoology, University of Michigan* 577: 1–9.
- Vences, M., J. Kosuch, R. Boistel, C. Haddad, E. La Marca, S. Lotters, and M. Veith. 2003. Convergent evolution of aposematic coloration in Neotropical poison frogs: a molecular phylogenetic perspective. *Organisms, Diversity & Evolution* 3: 215–226.
- Vences, M., J. Kosuch, S. Lötters, A. Widmer, K. H. Jungfer, J. Köler, and M. Veith. 2000. Phylogeny and classification of Poison frogs (Amphibia: Dendrobatidae), based on mitochondrial 16S and 12S ribosomal RNA gene sequences. *Molecular Phylogenetics and Evolution* 15: 34–40.
- Verdade, V. K. and M. T. Rodrigues. 2007. Taxonomic review of *Allobates* (Anura, Aromobatidae) from the Atlantic forest, Brazil. *Journal of Herpetology* 41: 566–580.

Appendix I – Species characters and states.

We consider the following characters (modified from Grant *et al.* 2006) to be appropriate for species definitions of dendrobatids, including those that are easy to observe in living, and recent or old preserved specimens. Some characters can change during preservation, depending on the liquids used, preservation method, or time. We did not included internal characters (such as osteological or myological), and only some coloration of internal parts that are easy to see after a simple abdominal dissection. Behaviour is excluded as a character as it is meaningless when working with preserved specimens.

- 1 - Dorsal skin texture: smooth; posteriorly granular; strongly granular; spiculate.
- 2 - Paired dorsal digital scutes: absent; present.
- 3 - Distal tubercle on FIV: absent; present.
- 4 - Finger IV length: surpassing distal subarticular tubercle of FIII; reaching distal half of distal subarticular tubercle of FIII; not reaching distal subarticular tubercle of FIII.
- 5 - Relative length of FI and FII: FII 20% or longer than FI; FII less than 20% than FI; FI and FII equal; FI longer than II. The measurement is taken from the same point at the base of the palmar tubercle to the tip of finger I and II in order to be consistent with Kaplan (1997) and Grant *et al.* (2006).
- 6 - Digital s: absent; present.
- 7 - Expansion of finger s: unexpanded; weakly expanded; moderately expanded; greatly expanded.
- 8 - Absence or presence of finger fringes (applicable to all fingers and toes): absent; present.
- 9 - Metacarpal ridge: absent; weak.
- 10 - FIII swelling in adult males: absent; present (if swollen): weak preaxial swelling; strong preaxial swelling; swelling extending from wrist, mainly preaxial on digit.
- 11 - Carpal pad: absent; present.
- 12 - Male excrescences on thumb: absent; present.
- 13 - Thenar tubercle: inconspicuous; conspicuous.
- 14 - Black arm gland in adult males: absent; present.
- 15 - Tarsal keel (or fringe): absent; present: when present, straight or very weakly curved; tubercle-like and strongly curved; short, tubercle-like; weak, short dermal thickening, not extended from metatarsal tubercle.
- 16 - Expansion of toe s: unexpanded; weakly expanded; moderately expanded.
- 17 - Toe webbing: absent; without fringe; with fringe (or two phalanges free); 1.5 phalanges free; one phalanx free; less than one phalanx free (full to almost full webbed).
- 18 - Metatarsal fold: absent; weak; strong.
- 19 - External coloration pattern: pale paracloacal mark (absent; present); thigh dorsal color pattern (solid dark; dark with pale spots/bands; solid pale; brown or pale with dark brown bands/blotches); pale lateral stripes (dorsolateral stripe: absent, present in juveniles only; anterior, narrow, faint; complete)(ventrolateral stripe: absent; series of spots; straight)(oblique lateral stripe: absent; series of spots; diffuse; straight)(oblique lateral stripe length: partial; complete).
- 20 - Gular-chest markings: absent; present.
- 21 - Dermal collar: absent; faint; present.
- 22 - Throat coloration: pale, free or almost free of melanophores; dark due to the absence of iridiophores (inconspicuous in long preserved specimens); evenly stippled gray; pale with discrete dark spots/reticulation/marbling; solid dark; dark with discrete pale spots/reticulation/marbling.

- 23 - Male abdomen color pattern: pale, free or almost free of melanophores; pale with rete dark spotting/reticulation/marbling; evenly stippled; dark with rete pale spotting/reticulation/marbling; irregular (clumped) stippling or faint, diffuse spotting; solid dark.
 - 24 - Female abdomen color pattern: pale, free or almost free of melanophores; pale with rete dark spotting/reticulation/marbling; dark with rete pale spotting/reticulation/marbling; irregular (clumped) stippling or faint, diffuse spotting; evenly stippled; solid dark.
 - 25 - Iris coloration: lacking metallic pigmentation and pupil ring; having metallic pigmentation and pupil ring.
 - 26 - Large intestine color: unpigmented; pigmented anteriorly; extensively pigmented.
 - 27 - Adult testis color: unpigmented; pigments are restricted to the medial line of testicles; entirely pigmented.
 - 28 - Medium Lingual Process (MLP): absent; present. If present: short, bumplike; elongate; blunt tip; tip tapering to point; smooth; rugose; upright oriented; posteriorly reclined; non-retractile; retractile; with associated pit; without associated pit.
 - 29 - Tympanum: absent; inconspicuous or ill-defined; well defined; tympanic annulus present/absent. Always concealed posterodorsally by low supratympanic bulge formed by superficial slip of m. depressor mandibulae.
 - 30 - Vocal sac structure: absent; median, subgular.
 - 31 - Presence / absence of teeth: absent; present; pedicellate; nonpedicellate.
 - 32 - Size: range: 11-14 mm (very small); 15-20 mm (small); 21-25 mm (moderately small); 26-30 (moderate); 31-35 (moderately large); 36-45 mm (large); more than 46 mm (very large).
-

Appendix II – Species examined.

Allobates algorei: EBRG 5560 (holotype), and EBRG 5561-64 (paratopotypes), from Río Negro, Municipio Córdoba, Estado Táchira, Venezuela, “07°34.723’N, 72°10.739’ W”, elevation 482 m. CVULA 3790, 3830, 3835, 3838-39 (paratypes), from Doradas, Uribante, Estado Táchira, Venezuela; CVULA 3690 (paratype) from La Honda, Uribante, Estado Táchira, Venezuela. CVULA 3832-33, 3836-37, 4700-03 from Río Doradas-Uribante (locality data is not very specific), estado Táchira, Venezuela.

Allobates bromelicola: MBUCV 5123, from Rancho Grande, Estado Miranda [sic]= Estado Aragua, altitude 200 m [sic]= 1100 m.

Allobates caribe: MHNLS 17462 (holotype), 17463 and 17490 (paratypes), all from southern slope of Cerro El Humo, Península de Paria, Estado Sucre, Venezuela, elevation 1050 m.

Allobates humilis: CLBA 5690 (field number; to be deposited at CVULA), from San Ramón, Calderas, Estado Barinas, Venezuela.

Allobates pittieri: MBUCV 1996, from Rancho Grande, Estado Aragua, Venezuela. EBRG 3879, Sierra San Luis, Cerro Galicia, Estado Falcón, elev. 1300 m. EBRG 3946-7, Cerro Paraguaniba, Sierra de San Luis, Estado Falcón.

Allobates undulatus: EBRG 3040-2 (paratypes) (Cerro Yutajé, elev. 1750 m., 5° 46’N-66° 08’W, estado Amazonas, Venezuela).

Appendix III – Advertisement call of *Allobates algorei* and closely related species.

	<i>A. algorei</i>	<i>A. caeruleodactylus</i>	<i>A. humilis</i>	<i>A. marchesianus</i>	<i>A. juanii</i>	<i>A. trilineatus</i>
Male size (mm)	19.19-19.42	15.5	–	15.8 ^b	20.8	16.0
Temperature (°C)	23.5 (substrate)	24.0 (air temperature)	19.5 (air temperature)	24.0-26.0	21.9	27.0
Number of calls (individuals)	51 (3)	(1)	9 (1) ^a	5(1) rete call	93 (1)	26(1)
Call length (ms)	41.67 ± 8.66 (n = 51)	62	–	5(1) continuous call 4030 ± 440 (rete)	59.4-1256.2 ^c	1260 ± 29.8 (n = 26)
Call interval (ms)	462.58 ± 67.02 (n = 33)	–	428 ± 134 (n = 51) ^a	–	2000-4000	–
Note length (ms)	41.67 ± 8.66 (n = 51)	62	47 ± 3 (n = 51)	41 ± 3 (rete) 45 ± 5 (continuous)	62.03 ± 0.94 (n = 20)	43.79 ± 0.15 (n = 19) ^d
Pulse interval (ms)	462.58 ± 67.02 (n = 33)	–	428 ± 134 (n = 51)	156 ± 27 (rete) 182 ± 40 (continuous)	389.12 ± 18.89 (n = 11)	77.92 ± 1.25 (n = 17) ^d
Call rate per second	3.61 ± 0.39 (n = 32)	2.5	1.8-2.5 ^a	0.05 ± 0.003 (rete) 2.22 ± 0.49 (continuous)	0.52	0.15 (n = 27)
Call duty cycle	0.11 ± 0.03 (n = 33)	–	0.11 ^a	–	–	–
Call shape	0.78 ± 0.22 (n = 51)	–	–	–	–	–
Frequency range (Hz)	4737-5254 (n = 51)	5540-6640	3700-4400	5180-6470 (rete) 4890-6520 (continuous)	3880-4160	4920-6040 (n = 23)
Dominant frequency (Hz)	5065 ± 151 (n = 51)	5540-6640	4200	5180-6470 (rete) 4890-6520 (continuous)	4120-4560	4920-6040 (n = 23)
Call crest factor	2.60 ± 0.24 (n = 51)	–	–	–	–	–
Call continuity	continuous	continuous	rete ^a	continuous/rete	rete	rete
Number of harmonics	4		4			

^a La Marca *et al.* (2002) assumed that the call is a series of single pulse notes. However, they indicate the calls were repeated at irregular intervals. We disagree and they might be a single pulse call with several repeated bouts, repeated at irregular intervals.

^b Size of the males analyzed were not provided, the size indicated came from the species diagnosis.

^c Calls were described as single notes, couplets, triplets, and quadruplets.

^d Pulse length and interval for the first and second note are not included as the original description indicated them to be shorter than the other notes in the call.