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A new striking dendrobatid frog (Dendrobatidae: Aromobatinae, *Aromobates*) from the Venezuelan Andes

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Abstract

A new striking cloud frog of the genus *Aromobates* is described from the northwestern portion of the Cordillera de Merida in Venezuela. The new species is unique in several aspects, and its inclusion in *Aromobates* is supported by molecular analyses. This *Aromobates* is characterized by the presence of dark dorsolateral stripes, absence of pale dorsolateral, oblique lateral and ventrolateral stripes. Furthermore, it is the only non-aposematic *Aromobates* having dark to emerald green in life on dorsal surfaces and a highly ornamented pattern at both dorsal and ventral sides. This species is known from a single population in Carache (Trujillo State, Venezuela). Its population, although limited apparently to a small area, seems relatively abundant at the type locality and surroundings.

Key words: *Aromobates*, Dendrobatidae, Venezuela, Trujillo

Resumen

Se describe una nueva especie del género *Aromobates* de la porción noroccidental de la Cordillera de Mérida en Venezuela. La nueva especie es única en varios aspectos y su inclusión en *Aromobates* está apoyada por análisis moleculares. Se caracteriza por la presencia de líneas dorsolaterales oscuras, y por la ausencia de líneas dorsolateral, ventrolateral y oblicua lateral; y además es el único *Aromobates* de Venezuela que presenta cromatoforos verde oscuros a esmeralda en vida en las superficies dorsales; y posee un patrón único, tanto dorsal como ventralmente. Su población, aunque circunscrita a una pequeña área alrededor de la localidad tipo, parece abundante.

Palabras clave: *Aromobates*, Dendrobatidae, Venezuela, Trujillo

Introduction

The Venezuelan Andes (including the totality of the Cordillera de Merida and the northernmost portion of the Cordillera Oriental de Colombia; Barrio-Amorós 1998; Santos *et al.* 2009) harbor an astonishing diversity of dendrobatid frogs with 22 species (Barrio-Amorós 2009; Barrio-Amorós *et al.* 2010b). *Aromobates* is endemic to three relatively distinctive geographical areas (1) the Cordillera de Mérida, (2) the northernmost Eastern Cordillera Oriental de Colombia, and (3) the Sierra de Perijá (Rojas-Runjaic *et al.* 2011). Although the two last mountain chains share territory with Colombia, *Aromobates* is yet only known from Venezuela. This genus (sensu Grant *et al.* 2006) is monophyletic and it contains 13 described species (Rojas-Runjaic *et al.* 2011), but some more are to be published soon (Barrio-Amorós *et al.* in press). *Aromobates* was erected as a monotypic genus for one of the most extraordinary dendrobatid, *Aromobates nocturnus* Myers, Paolillo and Daly, 1991. This species is characterized by combination of autopomorphies including an extreme size (the largest dendrobatid reaching 64 mm), the presence of adductor mandibulae externus superficialis muscle, nocturnal and aquatic behavior (the only nocturnal and aquatic dendrobatid), and defensive mercaptanlike odor unique among dendrobatoids (Myers *et al.* 1991). Alternatively,

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La Marca (1994) erected the genus *Nephelobates* for those Andean dendrobatids having fang like teeth and a dermal covering of the cloaca. However, Grant *et al.* (2006) found that *Aromobates nocturnus* was nested among several *Nephelobates*. Moreover, both of La Marca's (1994) suggested synapomorphies were found to be symplesiomorphic as they were shared with other genera (Grant *et al.* 2006). Overall, current evidence strongly suggests that *Nephelobates* is a synonym of *Aromobates*.

Here, we describe a striking new species of *Aromobates*, detected after revising a series of specimens from Carache (Trujillo State, Venezuela) at the herpetological collection of the Museo de la Estación Biologica Rancho Grande (EBRG). These specimens were outstanding preserved compared with other congenerics, and the species is with no doubt the most patterned *Aromobates* known to date. In addition, we visited the original collection locality of these specimens during March of 2011 to determine the conservation status and to obtain details of their natural history. After a careful revision, we were unable to assign the museum and the field-collected specimens to any previously described species and, therefore, we herein name it.

Material and methods

All specimens examined are deposited in the following collections: Colección de Vertebrados, Universidad de los Andes, Mérida (CVULA); Museo de la Estación Biológica de Rancho Grande, Maracay (EBRG); Museo de Historia Natural La Salle, Caracas (MHNLS); Universidad de Puerto Rico at Mayaguez (UPRM). The diagnosis and description follows Barrio-Amorós & Santos (2009). Comparative data for Venezuelan congeners were taken from La Marca (1985), Péfaur (1985, 1993), Myers *et al.* (1991), Rivero (1978, 1980), Barrio-Amorós *et al.* (2010a), and from selected specimens (see Appendix). The toe webbing formula follows the system of Myers & Duellman (1982). Gender and maturity were determined by dissection (i.e., the presence of testes or oviducts), and/or secondary sexual characters (presence or absence of vocal sac or vocal slits). All measurements (in mm) were taken with a digital caliper to the nearest 0.1 mm. Measurements reported are only from adult frogs and include SVL: snout-vent length, straight length from tip of snout to vent; SL: shank length from outer edge of flexed knee to heel; FL: foot length from proximal edge of outer metatarsal tubercle to tip of toe IV; 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; EN: distance of anterior edge of eye to nostril; ED: horizontal eye diameter; TD: horizontal tympanum diameter; F3D: disc width of Finger III; T4D: disc width of Toe IV; 1FiL: length of Finger I from inner edge of thenar tubercle to tip of disc; 2FiL: length of Finger II from inner edge of thenar tubercle to tip of disc.

Calls were recorded at the type locality (Carache, Trujillo State, Venezuela) using a Sony HX1 camera with a setting for high definition (HD) video-recording. Sound was extracted from the HD videos using Audio Hijack Pro version 2.9.13 (Rogue Amoeba Software, LLC) under a 24-bit.AIFF high resolution audio format. Calls were analyzed and graphics elaborated using Praat 5.2.35 (http://www.fon.hum.uva.nl/praat/).

For the phylogenetic analyzes, the following procedures were performed. Total DNA was extracted using Qaigen DNeasy Blood & Tissue extraction kit. All PCR reactions were done using conditions and primers for the 12S-16S rRNA segment of mitochondrial genome (~2,400 bp) as described in Santos & Cannatella (2011). Sequences were validated using NCBI-BLAST by comparison against GenBank database to rule out contamination. Additional published sequences were obtained from GenBank including both dendrobatids and closely related hyloid frogs (for accession numbers see Fig. 1). Sequences were aligned using SATé (Simultaneous Alignment and Tree Estimation; Liu *et al.*, 2009). Tree estimation and nodal support were calculated as follows: (1) the molecular model of 12S-16S rRNA segment was determined using the AIC criterion implemented in jModelTest (Posada 2008), and the favored model was GTR+Γ+I; (2) a maximum likelihood (ML) phylogeny was inferred using RAxML 7.0.4 (Stamatakis 2006), from 20 different random starting numbers, and only the best score phylogeny is reported; and (3) nodal support values for the ML phylogeny were determined with 200 non-parametric bootstrap replicates using RAxML 7.0.4 analyses (Stamatakis 2006).

Results

We assign the collected specimens to *Aromobates*, as it possesses 11 of the 12 morphological characters for adults that Grant *et al.* (2006) determined for their genus definition. In general, the collected specimens character states

agree with Grant *et al.*'s definition of *Aromobates*, with the exception of character 3 (i.e., pale dorsolateral stripe assumed to be present in all species in the genus). Specifically, character 3 is problematic as it is not present in at least three species of *Aromobates* (namely *A. meridensis*, *A. nocturnus* and *A. leopardalis*; Barrio-Amorós *et al.* 2010a for *A. meridensis*; Myers *et al.* 1991 for *A. nocturnus*; Rivero 1976 and own data for *A. leopardalis*) plus the new one we describe herein. Furthermore some of Grant's defining characters are too general to be exclusive (e.g. character 6: webbing basal to extensive; character 8 of Grant el al. 2006: Finger I shorter than, equal to, or longer tan FII). A better definition of *Aromobates* is needed which is not based on molecular markers.

We found the following relationships of these specimens with other sympatric genera (*Mannophryne* and *Allobates*) within Aromobatinae. First, our specimens are not *Mannophryne* as all lack the black collar synapomorphy (as defined by Grant *et al.* 2006). Second, we found very difficult to exclude our specimens from *Allobates* on the basis of the morphological characters given by Grant *et al.* (2006). Specifically, the observed morphological variation of our specimens fits all of the 12 diagnostic characters of *Allobates* sensu Grant *et al.* (2006). We consider that the collected specimens are closer to *Aromobates* based in general morphological appearance (e.g., head shape) and geographical distribution (e.g., 12 species of *Aromobates* in the Cordillera de Merida from 700 to 3500 m versus two species of *Allobates*, from 400 to 1500 m). Additionally, our molecular results definitively excluded the collected paratopotype CVULA 8351 of the new species from *Allobates* and *Mannophryne* (Fig. 1). Therefore, a better definition of *Allobates* is needed not based on molecular markers alone.

***Aromobates ornatissimus* sp. nov**
English name: Ornate cloud frog
Spanish name: Sapito de niebla adornado

Holotype. Adult male, EBRG 5292, from Las Palmas, Municipio Carache, Estado Trujillo, Venezuela, 09º41'47''N, 70º08'24''W (9.6964 N–70.1400 W); elevation 2350 m, collected by Ramón Rivero the 4th of April, 2005.

Paratopotypes. Six adult males **(**EBRG 5285, 5287, 5290-94) and five adult females (EBRG 5282, 5288-89, 5298-99), all with the same data as the holotype. EBRG 6146-47, and CVULA 8351, collected by Ramón Rivero and César L. Barrio-Amorós, the 18th March 2011.

Referred specimens. Four juveniles (EBRG 5284, 5286, 5295, 5297), all with same data as the holotype.

Tadpoles. Unknown.

Diagnosis. (1) Skin on dorsum smooth (with notable tubercles posteriorly in life). (2) Paired dorsal scutes present on digits. (3) Distal tubercle on finger IV present. (4) Finger IV length reaches distal half of subarticular tubercle of finger III. (5) Finger I longer than II. (6) Digital discs present. (7) Finger discs barely expanded. (8) Finger fringes present, but weak on FII and III. (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 thick, long, to mid-tarsus, weakly curved. (16) Toe discs weakly expanded. (17) Toe webbing vestigial between TII and TIII and TIII and TIV. (18) Metatarsal fold absent. (19) External coloration with dark paracloacal marks, thighs with 4–6 transverse narrow bars, usually very conspicuous, sometimes less notorious; with dark brown (not pale) dorsolateral stripes; ventrolateral stripe absent; oblique lateral stripe absent; green chromatophores usually present. (20) Gular-chest markings absent. (21) Dermal collar absent. (22) Male throat coloration immaculate white to white with dark brown spotting; female throat coloration immaculate white to white with few irregular dark brown spots. (23) Male abdomen color white almost immaculate to spotted or reticulated to dark with white spots. (24) Female abdomen color pattern white with few to many small irregular dark brown spotting or reticulum. (25) Iris coloration black with metallic intrusions, gold-colored pupil ring. (26) Large intestine mainly unpigmented. (27) Enlarged white testes. (28) Median lingual process absent. (29) Tympanum inconspicuous, tympanic annulus absent. (30) Vocal sac distinct. (31) Teeth present on the maxillary arch. (32) Size small, males (*n*=8) 19.8–24.6 mm, mean=22.0±2.1; females (*n*=4) 24.2–25.5 mm, mean=24.8±0.5.

Comparisons. *Aromobates ornatissimus* (characters in parenthesis) differs by its smaller size from larger species of the genus, such as *A. alboguttatus* (Boulenger, 1903), *A. leopardalis* (Rivero, 1978), *A. meridensis* (Dole & Durant, 1973), *A. nocturnus* (Myers, Paolillo & Daly, 1991), and *A. capurinensis* (Péfaur, 1993), all with maximum SVL > 31.0 mm (up to 25.5 mm). *Aromobates meridensis* also lacks dorsolateral stripes and males have a strong

reticulation on the belly, but males have preaxial swelling on third finger (absent), and females lack spotting or reticulation on the belly (present). The call is also very different, being a fluttery trill in *A. meridensis* -Dole & Durant 1973; Barrio-Amorós *et al.* 2010a- (single notes). *Aromobates nocturnus* is *A. ornatissimus* largest congener, and we compare both as they might be sympatric and syntopic; its SVL reaches 62 mm (25.5 mm), it has fully webbed toes (basally webbed), belly coloration uniformly grey to mottled with grayish white in life (dark brown with small to large white spots or white with dark spots or reticulum), and distintive mercaptanlike odor (no apparent odor). Information about myological and osteological characteristics of *A. ornatissimus* are unknow. The seven other species of *Aromobates* (*A. duranti* (Péfaur, 1985), *A. haydeeae* (Rivero, 1978), *A. mayorgai* (Rivero, 1980), *A. molinarii* (La Marca, 1985), *A. orostoma* (Rivero, 1978), *A. saltuensis* (Rivero, 1980), and *A. serranus* (Péfaur, 1985)), are similar in size to *Aromobates ornatissimus*. *Aromobates duranti* is a slightly larger frog, up to 30.2 mm (up to 25.5 mm), and has also a dark venter with white spots, but it has clear pale dorsolateral stripes (absent), lateral oblique stripe present but indistinct (absent), skin smooth without tubercles (with tubercles posteriorly), and inhabits a different region of the Cordillera de Merida, separated by 140 km. *Aromobates haydeeae* has no fringes on fingers (fringes on FII and FIII), tarsal fold ill-defined (well defined), pale dorsolateral stripe present (absent), tympanum distinct inferiorly (inconspicuous), ventral parts orange (dark brown with white spots). *Aromobates mayorgai* has ventral parts yellow (dark brown with white spots), pale dorsolateral stripe present (absent), and occurs 165 km apart, in a different portion of the Cordillera de Merida, southwestern Sierra de la Culata. *Aromobates molinarii* has FII and II equal in length (FI longer than FII), fringes absent on fingers (fringes on FII and FIII), tarsal keel ill defined (weakly curved and well defined), toes moderately webbed (basally webbed), pale dorsolateral stripe present (absent), and toe webbing moderate (basal). *Aromobates orostoma* has no fringes on fingers (fringes on FII and FIII), tympanum distinct inferiorly (inconspicuous), ventral coloration immaculate (dark brown with white spots), pale dorsolateral stripe present (absent), and crossbars on hind limbs are not well defined (well-defined). *Aromobates saltuensis* has pale dorsolateral stripe present (absent), supratympanic bulge absent (ill-defined but present). *Aromobates serranus* has a distinct tympanum (indistinct), dorsum brown with blotches or reticulum (usually pale brown with dark spots or lines, but not reticulated), pale dorsolateral stripe present (absent), oblique lateral stripe present (absent). *Aromobates tokuko* from Sierra de Perijá—a separated Andean branch—has pale dorsolateral stripes present (absent), oblique lateral stripe present (absent), and ventral pattern absent (present). We also compare *Aromobates ornatissimus* with the two only Andean *Allobates*. *Allobates algorei* and *A. humilis* have no webbing on toes (vestigial between TII-III-IV-V), the ventrolateral stripe is present (absent), the oblique lateral stripe is present, diffuse (absent), and are ventrally patternless (striking pattern).

Phylogenetic relationships. *Aromobates ornatissimus* is well nested within Aromobatinae and has a high support as *Aromobates* (Fig. 1). This species is one of the closest living taxa to the crown of *Aromobates* and most likely resembles the oldest lineages of Aromobatinae and Dendrobatidae. Therefore, some of the unique and assumed basal characteristics associated to the putative oldest dendrobatid (i.e. *Aromobates nocturnus*), such as nocturnality, aquatic lifestyle, and defensive mercaptanlike odor might be derived rather than basal among dendrobatids (as Myers *et al.*, 1991).

Individuals of *Aromobates ornatissimus* were previously characterized using molecular markers at least two times (Fig. 1). Grant *et al.* (2006) provided nuclear and mitochondrial sequences from an individual collected by Walter Schargel (WES 626). The reported collection locality of this individual is a road from Humocaro Bajo to Agua de Obispo (approximate latitude 9.6945 N and longitude 70.0790 W) at 2400 m.a.s.l. (Trujillo State, Venezuela). Vences *et al.* (2003) provided a short 16S sequence from an individual identified as *Nephelobates* sp. ULABG 4445. The reported locality of collection is Agua de Obispo (latitude 9.70389 N, longitude 70.1072 W) at ~2200 m.a.s.l. (Trujillo State, Venezuela). Both localities (i.e., Grant's and Vences') and those reported here are within a 10 km radius and, therefore, likely represent a single population of *Aromobates ornatissimus*.

Description of the holotype. The holotype is an adult male of 24.4 mm (SVL): body slender and elongate, rounded in cross-section; dorsal skin, including dorsal surfaces of hind limbs, smooth in preservative (Fig. 2A); ventral skin smooth (Fig. 2B); vocal sac extended; head is longer than wide, HeL = 34.8% of SVL; HW = 30.3% SVL (Table 1); snout is truncate in profile (Fig. 3A), rounded in dorsal and ventral view (Fig. 3B); nares are situated laterally to the tip of snout; narial openings are barely visible when viewing the head from the front, barely visible when viewing dorsally; and not seen when viewing from a ventral aspect; canthus rostralis is rounded, the loreal region is little concave; interorbital region is little wider than the upper eyelid; snout longer than ED; tympanum is inconspicuous, about 2/3 of the tympanum is concealed posterodorsally by a low supratympanic bulge

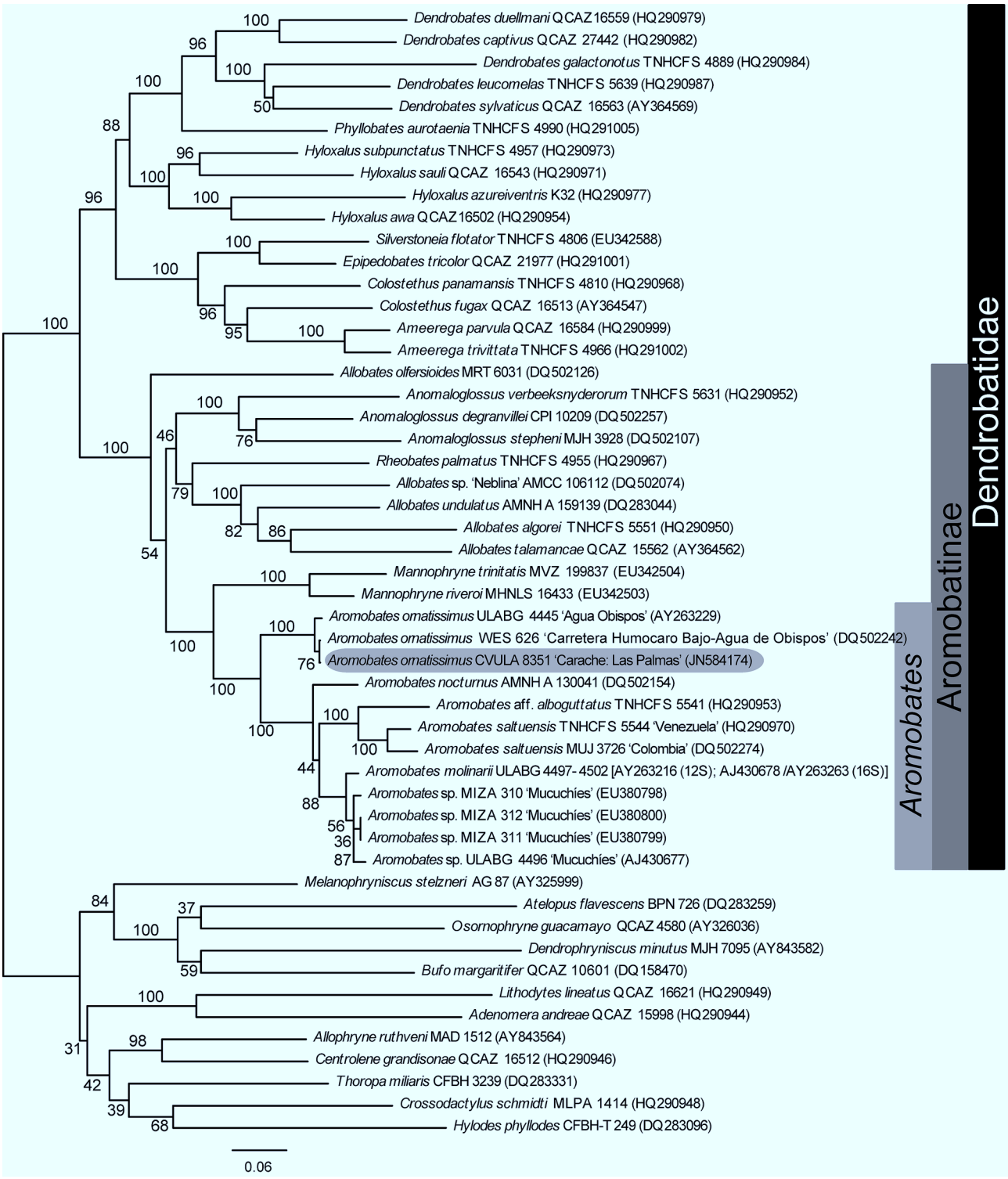

FIGURE 1. Maximum likelihood tree of *Aromobates ornatissimus* **sp. nov.**, other dendrobatids, and closely related hyloids. The phylogeny was inferred using a 12S-16S rRNA segment. Support values are based on 200 non-parametric bootstrap replicates. Museum catalog numbers and GenBank accession numbers are provided.

formed by the superficial slip of m. depressor mandibulae; tympanum is positioned closely behind eye and lower, close to the angle of jaws; teeth present on maxillary arch; vocal slits large and long, from mid-level of tongue to the angles of jaws; tongue rounded, half free posteriorly.

TABLE 1. Measurements (in mm) of adult males and females of *Aromobates ornatissimus* **sp. nov.** Abbreviations are defined in the materials and methods section. Values are means ± standard deviations; maximum and minimum values are in parentheses.

Character	Males (n= 8)	Females (n= 4)
SVL	22.0±2.1 (19.0–24.6)	24.8±0.5 (24.2–25.5)
SL	10.2±0.8 (8.8–11.3)	11.4±0.7 (10.5–11.1)
FL	10.4±1.0 (8.6–11.8)	11.4±0.5 (11.2–12.1)
HeL	8.2±0.5 (7.6–9.0)	8.8±0.2 (8.7–9.0)
HW	7.2±0.6 (6.4–8.0)	7.6±0.4 (7.2–8.1)
ED	2.7±0.2 (2.3–2.9)	*n*=3; 3.0±0.1 (2.9–3.1)
TD	*n*=3; 1.0±0.3 (0.7–1.2)	–
F3D	0.7±0.1 (0.6–0.8)	*n*=3; 0.9±0.1 (0.8–0.9)
T4D	0.8±0.1 (0.7–0.9)	*n*=3; 1.0±0.2 (0.8–1.1)
1FiL	4.0±0.4 (3.1–4.7)	*n*=3; 4.3±0.1 (4.3–4.4)
2FiL	3.6±0.4 (2.8–4.1)	*n*=3; 3.8±0.3 (3.5–4.0)

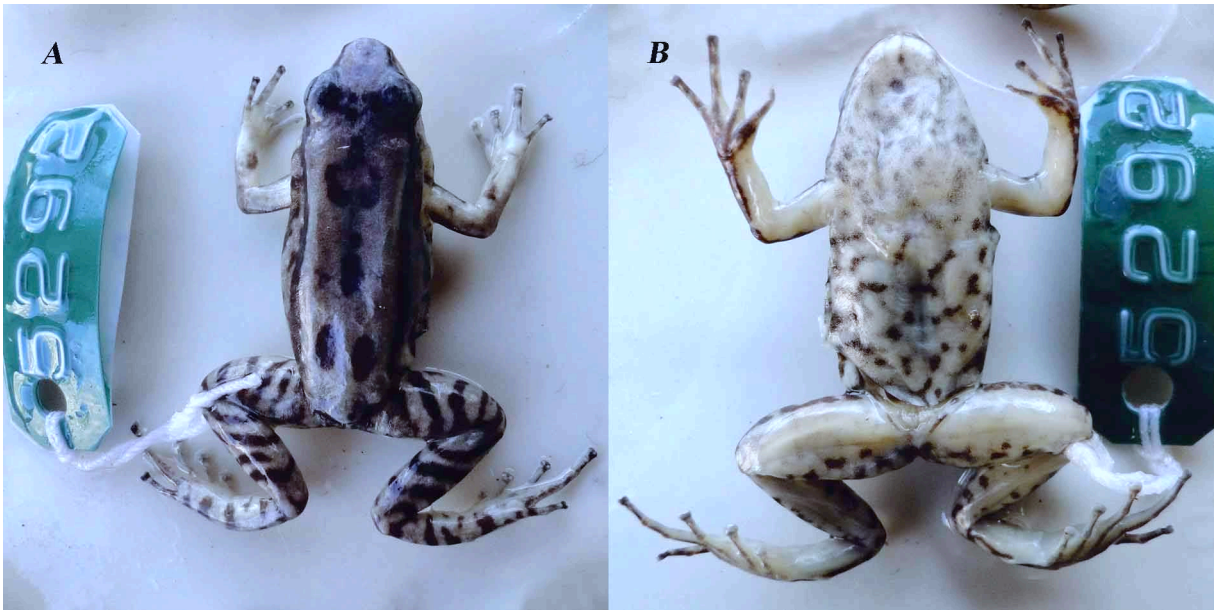

FIGURE 2. Dorsal (A) and ventral (B) views of the holotype (EBRG 5292) of *Aromobates ornatissimus* **sp. nov.**

Hand (Fig. 3C) of moderate size (26.1% SVL); relative lengths of adpressed fingers are III > I > II > IV; discs of all fingers are slightly expanded, horizontally oval; FIII is barely wider than distal end of adjacent phalanx; the base of palm has a large, nearly triangular palmar tubercle; and on base of FI there is a smaller (approximately 1/2 of the palmar tubercle), elliptical thenar tubercle; 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 low and indistinct on FII and FIII of right hand (well preserved), and very notable on all fingers of left hand (somewhat dehydrated). FIII is basally swollen on left hand, but not on right hand, possibly also due to a preservation artifact (see Variation).

Hind limbs are of moderate length, SL = 43.8% of SVL; relative lengths of adpressed toes are IV > III> V > II > I; TI is moderately long, the tip reaching the mid-subarticular tubercle of TII; toes are slightly expanded, TIV about 1.4 times wider than distal end of adjacent phalanx; feet (Fig. 3D) basally webbed; formula only applicable for TII – IV: II 2 – 3 III 3 2/3 – 4 IV; fringes on toes 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, thick, weakly curved, transverse across tarsus, from proximal edge of inner metatarsal tubercle to mid-tarsus; cloacal opening at upper level of thighs, with short tube flap or anal sheath.

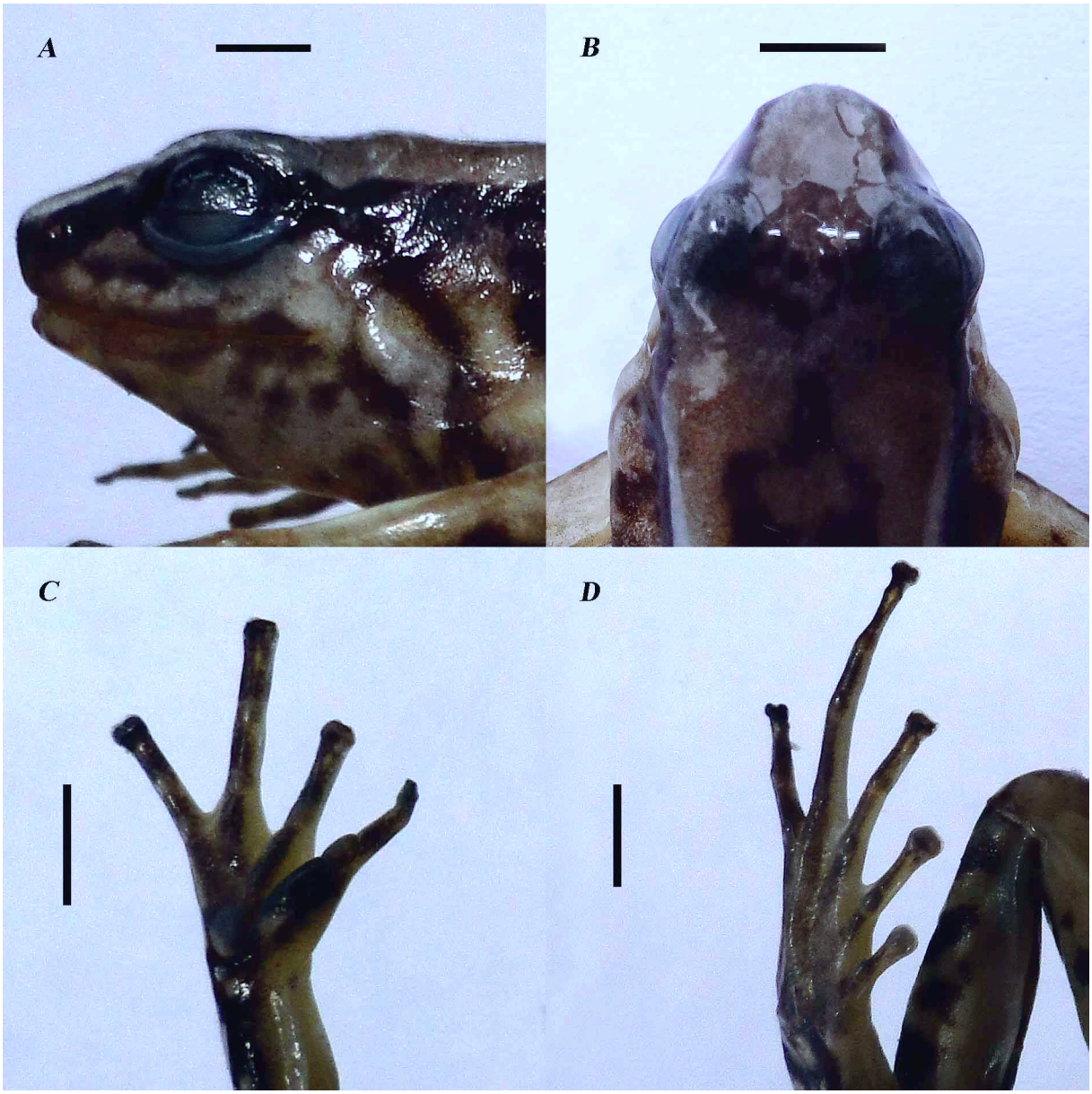

FIGURE 3. Lateral view of the head (A), dorsal view of the head (B), palmar view of the right hand (C) and plantar view of the right foot (D) of the holotype (EBRG 5292) of *Aromobates ornatissimus* **sp. nov.** Scale equals 2 mm.

Measurements of holotype (in mm) SVL: 24.4; SL: 10.7; FL: 10.7; HeL: 8.5; HW: 7.4; ETS: 3.9; EN: 1.5; ED: 2.7; TD: 1.2; F3D: 0.7; T4D: 0.8; 1FiL: 4.0; 2FiL: 3.6.

Color: In preservative dorsum pale brown with a clear pattern of dark brown marking as follows: interorbital irregular band, one round spot behind the head; two scapular "comma" like symmetrical spots; one longitudinal elongate mark; and two symmetrical longitudinally oval sacral spots. There are two symmetrical dark brown dorsolateral stripes (note that the dorsolateral stripes lacking are the pale ones), from the tip of snout through the canthal ridge, supratympanic area to the groin. Oblique lateral and ventrolateral stripes are absent. The flanks are pale brown below the dorsolateral stripes, with irregular dark brown marks that look similar to a dark oblique stripe, but that are part of an irregular reticulation of the flanks. Below this reticulation, the inferior part of the flanks becomes white. Arms are pale brown dorsally, with one irregular spot (oval on the left forearm, elongate on the right one), with dark brown stripes longitudinal anterior and posteriorly along the arm. Hind limbs pale brown, thighs crossed by many dark brown stripes (six on the left leg, five on the right), shanks crossed by four dark bands on each, and

tarsi also crossed by many vertical bands. Ventrally the chin, throat, chest and belly are white with irregular dark brown spotting. Thighs white anteriorly, spotted posteriorly. Palms of the hands and soles of the feet are dark brown.

Coloration in life. Description is based on two males, CVULA 8351, EBRG 6146 and one female EBRG 6147 (Fig. 4A, C, E). Background dorsal coloration pale to dark brown, with sometimes contrasting dorsal pattern (CVULA 8351, EBRG 6147), or not (EBRG 6146). The pattern, consisting in small spots or lines, is always dark brown. EBRG 6146 has an important portion of the back and flanks covered by dark green chromatophores (Fig. 4C). Green chromatophores are also appreciable in EBRG 6147 (Fig. 4E), but in less proportion; they are emerald green in EBRG 6147. CVULA 8351 lacks any green chromatophores (Fig. 4A). This species seems the only *Aromobates* to present some amount of green in the body. EBRG 6146 also shows some pale blue chromatophores on the flanks and along the extremities, but less dense than the green chromatophores (Fig. 4C). EBRG 6147 has a few pale blue chromatophores on the flanks and shanks (Fig. 4E). The dark dorsolateral stripes are present in all three specimens, ill-defined in CVULA 8351, little contrasting in EBRG 6146, or very contrasting in EBRG 6147. A dark brown canthal and supratympanic stripes are present and evident in EBRG 6147 (Fig. 4E). All types of pattern on dorsal surfaces (back marks and limbs crossbars) are always dark brown. The three specimens (CVULA 8351 and EBRG 6146-7) have white spots, large or small and irregular on the upper and lower lips. These specimens show axillary and groin marks; on CVULA 8351 and EBRG 6147 are yellow, while on EBRG 6146 are orange. Axillary and groin coloration extends to the ventral surfaces of arms and hind limbs, where it becomes paler. Ventrally, the background color is dark brown on the belly with contrasting white spots, varying from small on CVULA 8351 (Fig. 4B), to medium sized in EBRG 6146 (Fig. 4D), to large in EBRG 6147 (Fig. 4F). The throat color is sexually dimorphic, as the males have a dark brown vocal sac concealed behind the same pattern as on the belly. In the female, throat pattern is contrasting against the belly coloration. Iris coloration is pale to dark copper.

Variation. The dorsal pattern (http://images.morphbank.net/?id=705231&imgType=jpeg&sessionId=26djv87rehd8djt7t8qbkrgj52) observed in the holotype is similar in 6 specimens (holotype, EBRG 5282, 5288-91), while others are more spotted (EBRG 5287, 5293), less spotted or almost plain (EBRG 5285, 5294, 5299). Some specimens also have the cross barred limbs, but they are less evident. Ventrally, the pattern is more obvious on five males of the series: the most contrasting individual is EBRG 5291, while the less patterned is EBRG 5294. This last specimen and EBRG 5287 are subadult males and they are almost white without magnification (http://images.morphbank.net/?id=705231&imgType=jpeg&sessionId=26djv87rehd8djt7t8qbkrgj52). Under a microscope, both have the throat and chest with melanophores, but the belly is white in EBRG 5294 while it has some reticulation in EBRG 5287. One female (EBRG 5288) is completely white except for a few irregular spots on the belly, and a few melanophores seen with microscope, scattered across the ventral parts. Two females (EBRG 5289 and 5299) have white throats and chests, but their bellies are reticulated (EBRG 5299) or spotted (EBRG 5289). The female EBRG 5298 is darker and both its throat and belly have a profusion of small and irregular spotting.

The anal sheath is evident in the holotype and EBRG 5294, but it is not in the males EBRG 5282, 5291, 5293 or barely evident in EBRG 5285, 5287, and 5290. In females, the anal sheath is less evident that in males as evidenced in all specimens (EBRG 5288-89 and 5299). Our observations about the anal sheath agree with Grant *et al.* (2006), who suggested that the variation in this character might be caused by preservation artifacts.

The holotype has a basal swelling on the left hand FIII, but since there is no other specimen showing this character, we assume this might be an artifact. Specifically, the left hand of the holotype was a little dehydrated and thus, the swelling is due to the preservation. We could not find more sexually dimorphic characters other than the little bigger mean size of females (24.8 mm versus 22.0 mm of the males). However, the size range is large and some males are quite big (males up to 24.6 mm, females up to 25.5 mm). The coloration is mostly not sexually dimorphic with the exception of actively calling males, in which the vocal sac becomes dark.

Remarks. *Aromobates ornatissimus* stands next to the type species *A. nocturnus* and other two species, *A. leopardalis* and *A. meridensis*, in having no pale dorsolateral stripes*; Aromobates ornatissimus* is the only species with dark dorsolateral stripes (not pale as usual in other *Aromobates*), and with presence of green chromatophores (though probably not in all specimens, Fig 4A). The presence of green chromatophores is remarkable, as it is uncommon among non-aposematic dendrobatids in Venezuela. However, the presence of green chromatophores is also first reported herein for *Mannophryne oblitterata* and *M.* sp. aff *trinitatis* from northern lowlands of National Park Henri Pittier (F. Rojas-Runjaic, pers. com.). *Aromobates ornatissimus* is also the most ventrally ornamented

FIGURE 4. Living specimens of *Aromobates ornatissimus* **sp. nov.**, showing dorsal and ventral patterns and coloration. Dorsolateral (A) and ventral (B) views of CVULA 8351. Dorsolateral (C) and ventral (D) views of EBRG 6146. Dorsolateral (E) ventral (F) views of EBRG 6147. All specimens photographed are from the type locality.

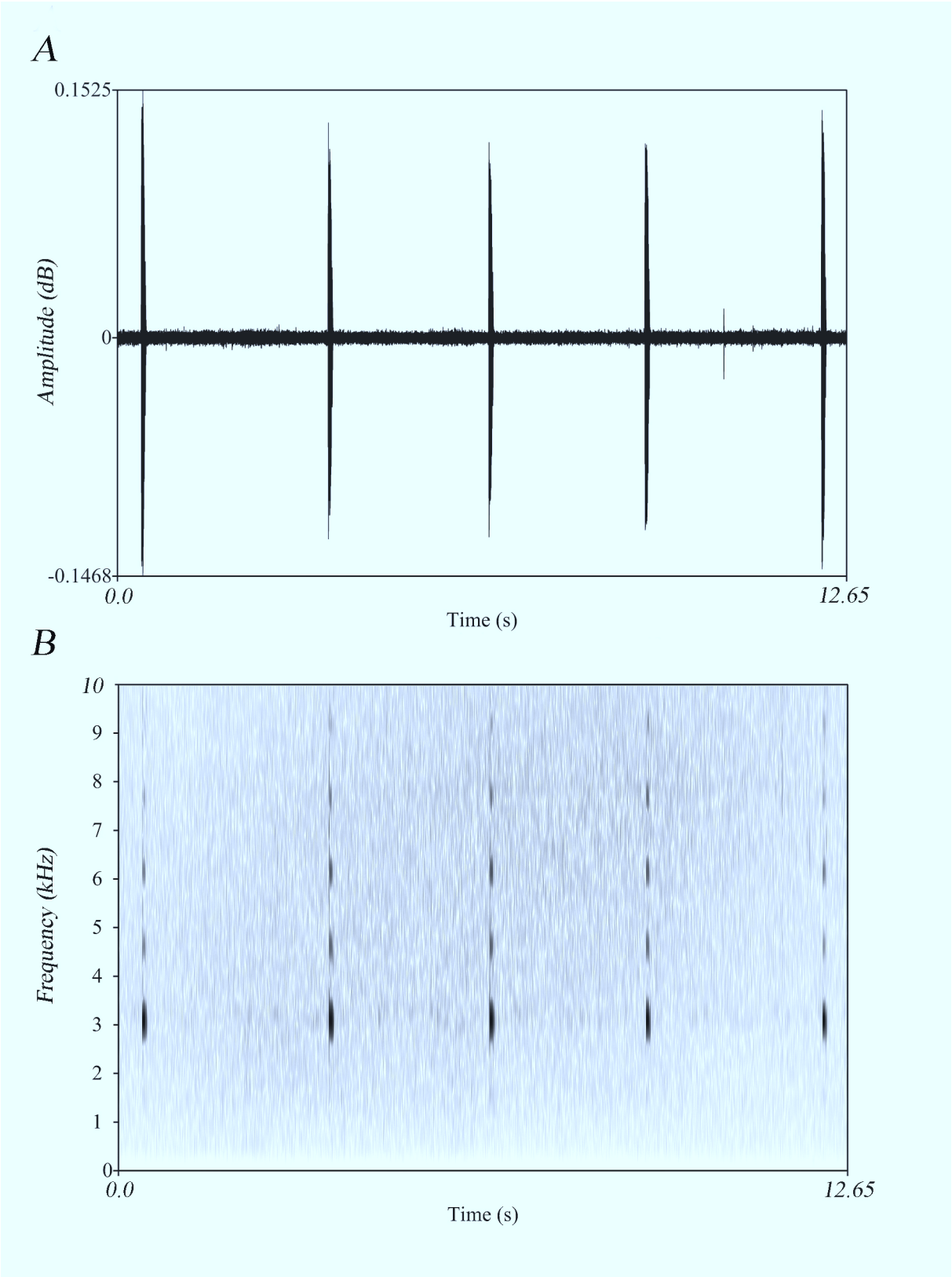

FIGURE 5. Series of 5 notes in the call of *Aromobates ornatissimus* **sp. nov.**, taken at 19ºC. (A) waveform and (B) spectrogram. Note distinct harmonics.

Aromobates; this ventral coloration is also evident in three other Venezuelan aromobatines. Two are congenerics from the same Cordillera de Merida, *Aromobates duranti* and *A. meridensis*, and on the other hand, *Anomaloglossus rufulus* from the Chimanta Massif in the Venezuelan Guayana (Barrio-Amorós & Santos, *in press*). The apose-

matic status of *Aromobates ornatissimus* and these other three species is unknown. *Aromobates ornatissimus* did not have a distinctive mercaptanlike odor and more likely lack a defensive mechanism required for aposematism.

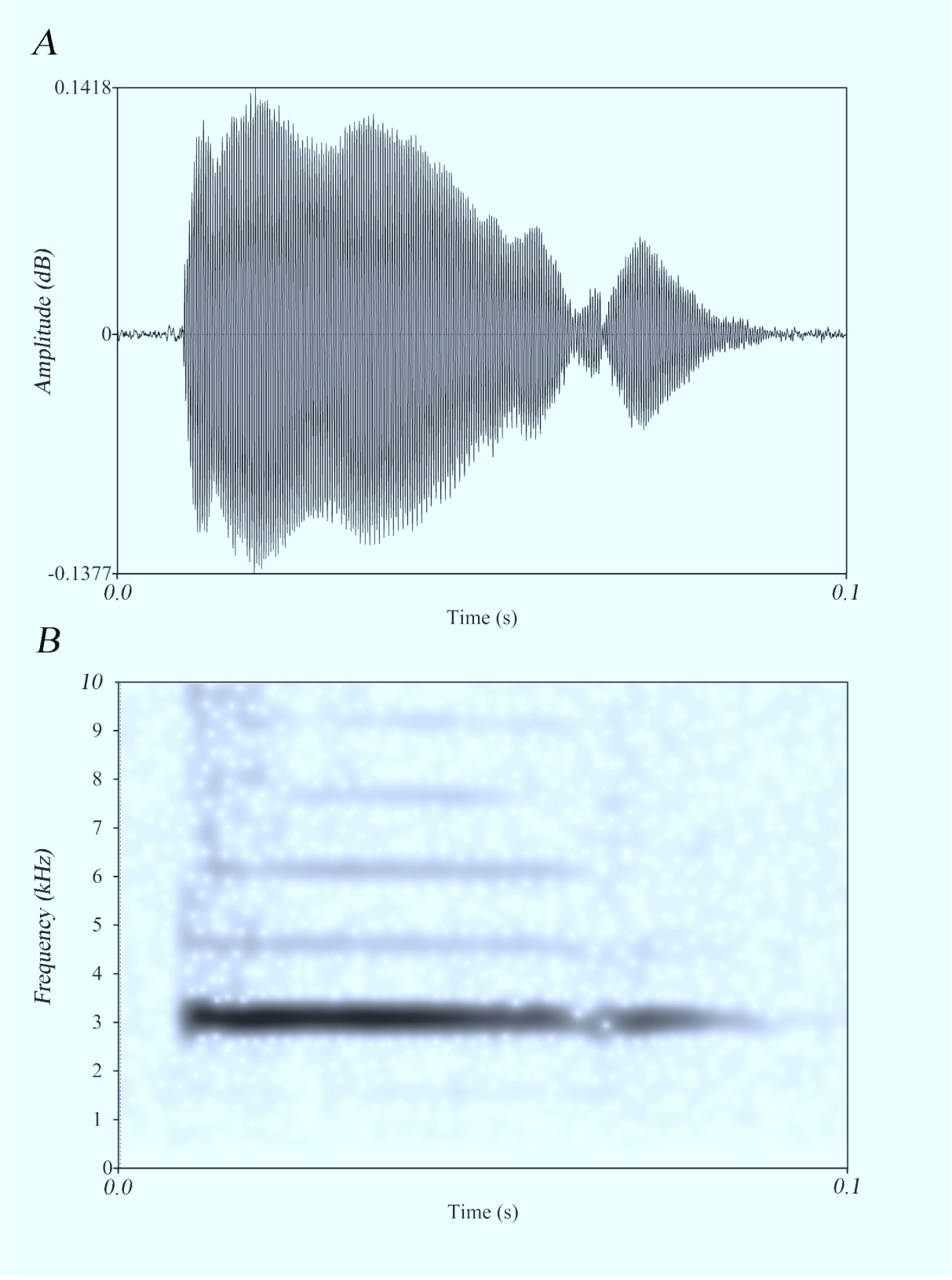

FIGURE 6. One note of the call of *Aromobates ornatissimus* **sp. nov.** taken at 19ºC. (A) waveform and (B) spectrogram.

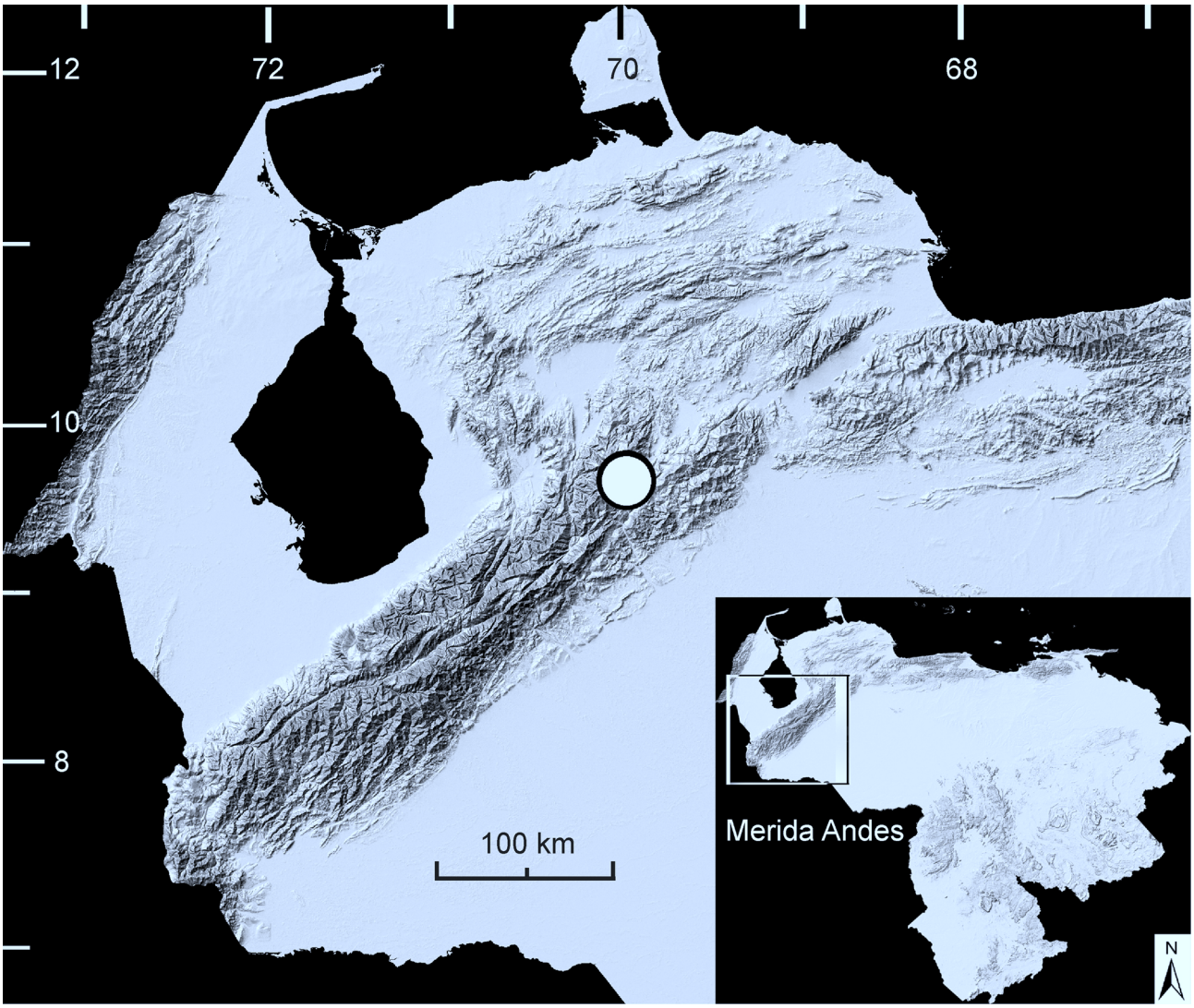

FIGURE 7. Distribution of *Aromobates ornatissimus* **sp. nov.** in the Venezuelan Andes.

Natural history. *Aromobates ornatissimus* is active during daytime. The type locality of this species is a creek in an open area (deforested for cattle meadows). The stream also goes through dwarf cloud forest. We found specimens both in the clearings and in the forest. The males were actively calling the 18th of March 2011, as this day was cloudy, and rain felt during the past weeks. The calling males are never exposed; they call among herbaceous junks, dense aquatic vegetation, or from holes in parts of the cascading stream. In the type locality, we did not found any specimen far from the stream. But in another locality nearby, in a primary cloud forest, the males called from along and away of small streams. We found one male calling from within an artificial abandoned stone-wall inside the cloud forest. No tadpoles were seen despite the fact that we went looking for them in nearby stream pools were the males were calling.

Vocalization. Four sets of vocalizations with a total of 35 pulses were recorded at 19ºC air temperature, during the morning of the 18th March 2011 at the type locality. Three sets were from isolated uncollected males with distant chorus on the background and one set from a chorus of at least 3 males. From one the sets representing a single male, we choose five notes of a continuous vocalization lasting a total of 12.65 sec for analysis; Fig. 5A shows waveform, Fig. 5B shows spectrogram. We examined the spectrogram of this set and we found a total of 6 to 7 harmonics per note with little frequency modulation as indicated in Fig. 5B. A single call consists on a single pulsed note emitted every 2.62 to 3.16 sec. The dominant frequency is at 3057-3120 Hz, (Fig 6A shows waveform of a single pulse; Fig. 6B shows the spectrogram). We also measured the note and inter-note duration and from each

variable the mean, SD and range in seconds are indicated as follows: note duration: 0.10±0.01 (0.08–0.11); inter-note duration: 2.86±0.25 (2.62–3.16).

Distribution. *Aromobates ornatissimus* is currently only known from five localities (1) at stream about 3 km before arriving to Las Palmas from Carache, (2) the type locality at Las Palmas, (3) at two streams within a cloud forest on the road from Aguas de Obispo to Barbacoas, (4) along the road from Humocaro Bajo to Agua de Obispo, and (5) at Aguas de Obispo. All of these localities are in the northwestern slopes of Páramo Cendé, Cordillera de Merida, Estado Trujillo (Fig 7).

Etymology. *ornatissimus* (from Latin *ornatus*), adjective meaning ornate, elegant or decorated, and *–issimus*, suffix indicating superlative, then something very ornate, in reference to the striking pattern of the species compared with the rest of congeners, which are less patterned.

Conservation. *Aromobates ornatissimus* is abundant at the type locality and surroundings (about 10 km in circumference). We did not explore exhaustively the type locality for potential conservation threats, but our impression is that *Aromobates ornatissimus* is surviving and reproducing. In appropriate areas, it was easy to listen from 5 to 20 males calling every 10 m along streams. Due to its reduced and apparently fragmented distributional range, we propose *Aromobates ornatissimus* as vulnerable VU B2ab(i,ii).

A note on *Aromobates nocturnus*. The general area of *Aromobates ornatissimus* also includes the type locality of *Aromobates nocturnus*, and we searched for this iconic species during the day and night in two different streams that resemble those on Figs 13 and 14 in Myers *et al.* (1991) without success. One of those streams was heavily polluted by cattle manure and the other had apparently suitable habitat, but devoid of any amphibian during the day or night. The current situation of *Aromobates nocturnus* might be extremely critical, likely extinct, despite it being at the highest category of risk (CR A2a; B2ab5) (Stuart *et al.* 2008). No concrete plans or actions for the conservation and preservation of the only known population of *A. nocturnus* exist.

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APPENDIX I. Specimens examined.

Allobates algorei (17).—VENEZUELA: Estado Táchira, Municipio Córdoba, Río Negro, EBRG 5560 (holotype), and EBRG 5561-64 (paratopotypes). Estado Táchira, Doradas, Uribante, CVULA 3790, 3830, 3835, 3838-39 (paratypes). Estado Táchira, La Honda, Uribante, CVULA 3690 (paratype). Estado Táchira, Río Doradas-Uribante (locality data is not very specific), CVULA 3832-33, 3836-37, 4700-03.

Allobates humilis (1).—VENEZUELA: Estado Barinas, San Ramón, Calderas, CLBA 5690 (field number; to be deposited at CVULA).

Aromobates alboguttatus (11).—VENEZUELA: Estado Mérida: Monte Zerpa, 2200 m, CVULA 1171, 1236–1238; La Mucuy, Parque Nacional Sierra Nevada, MHNLS 7089–7095.

Aromobates duranti (1).—VENEZUELA: Estado Mérida: Sierra de la Culata, CVULA 0845.

Aromobates haydeeae (5).—VENEZUELA: Estado Táchira: 15 km SW Zumbador, CVULA 0910-0911, 0917; Páramo Zumbador, Mesa del Aura CVULA 1067–1068.

Aromobates leopardalis (7).—VENEZUELA: Estado Mérida: Páramo de Mucubají, 3400 m, CVULA 5890, 5892, 3083–3084; Mucubají, Paratypes MHNLS 15093–15095 (ex-UPRM 5227, 5340 and 5232 respectively).

Aromobates mayorgai (4).—VENEZUELA: Estado Mérida: La Carbonera CVULA 0281; El Chorotal (El Sineral), carretera Mérida a La Azulita, Paratypes MHNLS 15119–15121 (ex-UPRM 5340, 5590 and 5591 respectively).

Aromobates meridensis (18).—VENEZUELA: Estado Mérida: Vía Mérida-La Azulita, 2000 m (CVULA 1448, 1491, 1670); La Empalizada, El Chorotal (CVULA 2167); El Chorotal (CVULA 2328–2389, 2335); Carretera 7 km N San Eusebio, El Chorotal, Distrito A. Bello (CVULA4767–4772); La Empalizada (CVULA 5056, 5060-5063).

Aromobates molinarii (2).—VENEZUELA: Estado Mérida: Cascada de Bailadores (CVULA 1873–1874).

Aromobates ornatissimus (19).—see type series.

Aromobates orostoma (3).—VENEZUELA: Estado Mérida: Km 590 Páramo Batallón y La Negra (CVULA 3529); Estado Táchira: Páramo La Negra, vía Pregonero, 2500 m (CVULA 3528, 3582).

Aromobates serranus (5).—VENEZUELA: Estado Mérida: Vía El Morro (CVULA 3376–3381).