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A Name for the Species of *Allobates* (Anura: Dendrobatoidea: Aromobatidae) from the Magdalena Valley of Colombia

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We describe a new species of *Allobates* from the Magdalena Valley in Colombia. The new species and its sister species, *A. talamancae*, are the only two species of *Allobates* known to occur west of the Andes. The new species differs from *A. talamancae* in being smaller, possessing a diffuse pale oblique lateral stripe, and exhibiting strong swelling of finger III in adult males. Tadpoles also differ in the relative size of anterior and posterior labial papillae; in the new species anterior papillae are conspicuously larger than posterior papillae, whereas in *A. talamancae* they are subequal in size. *Allobates talamancae* and the new species are allopatric. Among the *cis*-Andean species of *Allobates*, the new species most resembles *A. melanolaemus*, which also possesses a diffuse pale oblique lateral stripe and a solid black throat in adult males, but from which it differs in being smaller and adult males having finger III strongly swollen and solid black pigmentation covering the chest and most of the belly.

Se describe una nueva especie de *Allobates* del Valle del Magdalena en Colombia. Esta especie y su especie hermana, *A. talamancae*, son las únicas dos especies de *Allobates* que ocurren al occidente de los Andes. La nueva especie difiere de *A. talamancae* por ser más pequeña, poseer una difusa franja oblicualateral pálida, y tener el dedo III de la mano en los machos adultos fuertemente ensanchado. Además, las larvas difieren en el tamaño relativo de las papilas del labio anterior y posterior. Entre las especies *cis*-andinas de *Allobates*, la más parecida es *A. melanolaemus*, con la cual comparte la difusa franja oblicualateral pálida y la garganta negra en los machos adultos. La nueva especie se diferencia de *A. melanolaemus* por su menor tamaño y porque los machos adultos exhiben el dedo III de la mano fuertemente ensanchado y la pigmentación del pecho y del abdomen negra.

ALLOBATES is a large radiation (45 named species) of aromobatid frogs distributed almost exclusively east of the Andes (Grant et al., 2006). There are two known exceptions to the *cis*-Andean distribution: *Allobates talamancae*, which occurs in Central America and the Pacific lowlands of Colombia and northern Ecuador (Coloma, 1995), and its sister species, an undescribed species from the Magdalena Valley in Colombia, referred to by Grant et al. (2006) as ''Magdalena species.'' These two species are united by extensive evidence from DNA sequences, as well as by the unambiguous synapomorphies of the solid black throat of adult males and tadpole transport carried out exclusively by female nurse frogs (Grant et al., 2006); no other aromobatid is known to have exclusively female nurse frogs. The purpose of this paper is to describe this new species of *Allobates*.

MATERIALS AND METHODS

Prior to fixation in formalin, the right leg of the holotype was removed as a tissue sample and fixed in 95% ethanol for DNA extraction and analysis (Grant et al., 2006); otherwise, material was prepared following standard procedures (McDiarmid, 1994). Measurements were taken to 0.1 mm with dial or digital calipers. Unless otherwise noted, measurements and proportions are reported for adults only, as determined by examination of gonads and secondary sex characters. Males with vocal slits on both sides of the mouth were scored as adult, those with only one as subadult, and those lacking slits on both sides as juvenile. Females with expanded, convoluted oviducts and enlarged ova were considered to be adult, those with only weakly expanded, non- or weakly convoluted oviducts and poorly differentiated ova to be subadult, and those with small, undifferentiated ova and unexpanded, straight oviducts to be juvenile. Statistical summaries of measurements are reported as the sample mean ± standard deviation. Toe webbing formulas follow Myers and Duellman (1982; see also Savage and Heyer, 1967, 1997). Ear terminology follows Lynch and Duellman (1997). Relative lengths of fingers I and II were determined following Kaplan (1997; see also Grant et al., 2006). Comparisons focus on closely related species and potentially sympatric species formerly placed in *Colostethus* and now divided among

Fig. 1. Palmar view of the hand of adult male holotype MUJ 3520 (hand length 3.8 mm) of *Allobates niputidea*. Note the strong preaxial swelling of finger III.

Colostethus sensu stricto, *Rheobates*, and *Silverstoneia*. Diagnostic characters follow Grant et al. (2006; see also Coloma, 1995; Grant and Rodríguez, 2001). Larval terminology follows Altig and McDiarmid (1999); larval staging follows Gosner (1960). Institutional abbreviations follow Leviton et al. (1985), with the following exceptions: ICN (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia), MHUA (Museo de Historia Natural, Universidad de Antioquia, Medellín, Colombia), and MUJ (Museo de Historia Natural, Pontificia Universidad Javeriana, Bogotá, Colombia).

Allobates niputidea, new species
Figures 1–5

Holotype.—MUJ 3520 (field number MAR 159), adult male, Colombia, Departamento de Caldas, Municipio de La Dorada, Vereda San Roque, Reserva Natural Privada Riomanso, 280 m, 5°40′N, 74°46′W, 9 Sept. 2004, Marco Antonio Rada.

Paratypes.—All from Colombia. ICN 47969–47970, Departamento de Boyacá, Municipio Puerto Boyacá, Serranía las Quinchas; MUJ 2899–2917, 2987, Departamento de Santander, Municipio de Cimitarra, Vereda Los Indios, sitio El Triángulo, Finca Las Camelias, 240 m; MUJ 2927–2928, Departamento de Santander, Municipio de Cimitarra, Inspección de Policía Puerto Araujo, Hacienda El Manantial, 180 m; MUJ 2918–2926, Departamento de Santander, Municipio de Puerto Parra, Vereda Aguas Negras, Hacienda el Paso, 185 m; MHUA 1830–1831, Departamento de Santander, Municipio de Puerto Parra, La Olinda, 145 m; MHUA 2070, 2072, Departamento de Antioquia, Municipio de Puerto Nare, La Suiza, 230 m; MHUA 2147–2151, Departamento de Antioquia, Municipio de Puerto Nare, La Brasilia, 320 m; MHUA 2515, Departamento de Antioquia, Municipio de Caucasia, La Leyenda, 70 m.

Paratopotypes.—MUJ 3519, 3521, 3522–3534, 3544.

Diagnosis.—A small species (maximum SVL of adult males approximately 17 mm, females approximately 18 mm) of *Allobates*; dorsal skin texture posteriorly granular; finger I > finger II; adpressed finger IV reaching midway to distal subarticular tubercle of finger III, shorter than finger II; preaxial surface of finger III strongly swollen in adult males; throat and (usually) chest and anterior belly black in adult males, immaculate white (unpigmented) or with sparse, inconspicuous melanophores in adult females; black arm band of adult males absent; testes white; toes II–IV basally webbed (**II** 2–3.5 **III** 2.5–4 **IV**); pale dorsolateral stripe present; pale ventrolateral stripe present; oblique lateral stripe present as a diffuse, inconspicuous, pale region or group of small spots that extends from the groin to midway along the flanks; conspicuous pale paracloacal marks present; median lingual process absent.

Comparisons.—The most conspicuous differences between *Allobates niputidea* and its allopatric sister species *A. talamancae* are its smaller size (male *A. talamancae* 21.1–23.9 mm SVL, $n = 12$, $\bar{x} = 22.00 \pm 0.86$; females 21.4–25.1 mm SVL, $n = 12$, $\bar{x} = 22.87 \pm 1.12$), the presence of a diffuse pale oblique lateral stripe (absent in *A. talamancae*), and presence of swollen finger III of adult males (not swollen in *A. talamancae*). Tadpoles also differ in the relative size of anterior and posterior labial papillae; in *A. niputidea* anterior papillae are conspicuously larger than posterior papillae, whereas in *A. talamancae* they are subequal in size (Savage, 2002:381, fig. 7.123). *Allobates niputidea* resembles many *cis*-Andean species of *Allobates*, but it most resembles *A. melanolaemus*, which also possesses a diffuse pale oblique lateral stripe and

a solid black throat in adult males. However, *A. niputidea* differs in smaller size (male *A. melanolaemus* 21.1–23.4 mm SVL, $n = 11$, $\bar{x} = 22.16 \pm 0.22$; females 21.3–23.6 mm SVL, $n = 14$, $\bar{x} = 22.24 \pm 0.22$), strongly swollen finger III (weakly swollen in *A. melanolaemus*), and black ventral coloration of adult males covering the throat, chest, and most of belly (confined to throat in *A. melanolaemus*, chest and belly with gray stippling; Grant and Rodríguez, 2001). Morales (2002 ''2000'':36) reported that the throat in adult males of *A. masniger* is ''obscuro'' but did not specify the color. Examination of paratype USNM 303590 showed the throat, chest, and anterior belly to be stippled gray, not solid black, and we confirm Morales's (2002 ''2000'') statement that finger III of adult males is not swollen.

Among other genera of dendrobatoids, *Allobates niputidea* most resembles *Colostethus furviventris*, with which it shares solid black coloration of the throat, chest, and anterior belly in adult males, a conspicuously swollen finger III in adult males, and a diffuse pale dorsolateral stripe, among other character-states. Based on Rivero and Serna's (1991) description, *Allobates niputidea* differs in being smaller (*C. furviventris* females reach 26 mm SVL and males reach over 24 mm SVL), possessing basal webbing between toes III–IV (absent in *C. furviventris*), lacking conspicuous white spots on the forearms of males (present in *C. furviventris*), and having the pale oblique lateral stripe present as a diffuse, inconspicuous, pale region or group of small spots that extends from the groin to midway along the flanks (present as a well defined, conspicuous stripe extending from the groin midway along flank in *C. furviventris*). Furthermore, although adult males of both species possess solid black ventral coloration, in *A. niputidea* the black coloration fades posteriorly, whereas in *C. furviventris* it breaks into spots or a marbled pattern (compare Fig. 4A, below, with Rivero and Serna, 1991:483, fig. 3), and the two species occur at vastly different elevations (*A. niputidea* occurs below 350 m in the Magdalena Valley, whereas *C. furviventris* is found at 1500 m in the northern part of the Cordillera Occidental).

Allobates niputidea occurs in macrosympatry with the distantly related dendrobatid *Colostethus inguinalis*, from which it is readily distinguished by much smaller size (*C. inguinalis* males reach approximately 27 mm SVL and females reach approximately 30 mm SVL), presence of the pale dorsolateral stripes (absent in *C. inguinalis*), coloration of the otic region (tympanum entirely dark or horizontally divided in dorsally dark and ventrally pale coloration in *A. niputidea*; posterodorsal portion of tympanum dark in *C. inguinalis*), and basal webbing between toes II–IV (in *C. inguinalis* toes I–IV moderately webbed, toes IV–V free or basally webbed; webbing formula **I** 1½ or 2^{-}–2^{+} **II** 1½ or 2^{-}–3½ or 3^{+} **III** 2½–3½ or 4 **IV** 4½–3^{-} **V** [when present between IV and V]). These species further differ in that *A. niputidea* is a forest-dweller whereas *C. inguinalis* is riparian (Grant, 2004).

Although *Allobates niputidea* is not known to occur in sympatry with additional species of the former *Colostethus sensu lato*, sampling is far from complete, and other potentially sympatric species include the aromobatid *Rheobates palmatus* and the dendrobatids *Colostethus pratti* and *Silverstoneia nubicola*. *Allobates niputidea* is readily distinguished from *R. palmatus* by its smaller size (both sexes to at least 30 mm SVL in *R. palmatus*), presence of a pale dorsolateral stripe (absent in *R. palmatus*), solid black throat, chest, and belly coloration in adult males (grey or brown in *R. palmatus*), and basal webbing between toes II–IV (all toes extensively webbed in *R. palmatus*). *Allobates niputidea* differs from *C. pratti* in smaller size (adult males to approximately 24 mm and adult females to approximately 25 mm in *C. pratti*), solid black throat, chest, and belly coloration in adult males (pale gray or brown with irregular white spots, forming a faint mottled or reticulated pattern in *C. pratti*), and webbing between toes II–IV (absent in *C. pratti*). And *A. niputidea* differs from *S. nubicola* in smaller SVL (adult males to approximately 21 mm and adult females to approximately 22 mm in *S. nubicola*), presence of the pale dorsolateral stripe (absent in *S. nubicola*), and oblique lateral stripe present as a diffuse, inconspicuous, pale region or group of small spots that extends from the groin to midway along the flanks (pale oblique lateral stripe well defined and extending to eye in *S. nubicola*).

Measurements of holotype (in mm).—SVL 16.7; forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow 3.8; hand length from proximal edge of palmar tubercle to tip of third finger 4.1; shank length from outer edges of flexed knee to heel 7.9; foot length from proximal edge of outer metatarsal tubercle to tip of fourth toe 6.7; head width between angle of jaws 5.8; head length diagonally from corner of mouth to tip of snout 5.5; eye length from posterior to anterior corner 2.3; eye to naris distance from anterior corner of eye to center of naris 1.7; distance between centers of nares 2.5; snout length from anterior corner of eye to tip of snout 3.1; interorbital distance 2.1; greatest diameter of tympanum 1.0.

Description.—Adult males 15.7–16.9 mm SVL ($n = 16$; $\bar{x} = 16.49 \pm 0.34$); testes unpigmented

(white), testis length approximately 2/3 eye length. Adult females 16.4–18.0 mm SVL (n = 17; $\bar{x}$ = 17.26 ± 0.52); mature oviducts unpigmented (white); mature ova approximately 1 mm in diameter, animal pole dark brown. MUJ 2916 is a subadult female of 15.8 mm SVL with barely convoluted oviducts and weakly differentiated ova.

Ventral and lateral surfaces smooth. Dorsal surfaces with granules scattered irregularly in sacral region and (to a lesser degree) on thigh and shank. Postrictal and preaxillary tubercles (one each) elongate. Head width between angle of jaws 30–35% SVL, 1.0–1.1 times head length. Interorbital distance 30–38% head width between angle of jaws. Canthus rostralis gently rounded. Loreal region flat or weakly concave, not sloping to lips. Eye length 41–50% of diagonal head length. Eye–naris distance 60–81% snout length and 58–82% eye length. Nares slightly protuberant, directed posterodorsad. Tympanum well defined in well preserved specimens, concealed posterodorsally by low supratympanic bulge formed by superficial slip of m. depressor mandibulae. Diagonal length of externally visible tympanum 34–54% eye length. Teeth present on maxillary arch.

Hand length 22–33% of SVL, 0.9–1.1 times forearm length. Finger discs weakly to moderately expanded. Finger III of adult males strongly swollen along preaxial side; postaxial swelling not detected (Fig. 1). Finger III not swollen in adult females or juveniles. Fingers lacking fringes. Metacarpal fold absent, although lateral edge of palm lacking melanophores. Finger I longer than finger II; finger II extended to midlevel of distal subarticular tubercle of finger III; finger IV extended midway between proximal and distal subarticular tubercles of finger III. Relative finger lengths IV < II < I < III. Subarticular tubercles 1–1–2–1 (usually) or 1–1–2–2 (rarely, e.g., adult male MUJ 3522). All tubercles strongly protuberant; subarticular and thenar tubercles elliptical; palmar tubercle subcircular.

Shank and foot length 41–49% and 34–43% of SVL, respectively. Relative lengths of appressed toes I < II < V < III < IV (Fig. 2). Toe III extended just past penultimate subarticular tubercle of toe IV; toe V extended approximately midway between basal and penultimate subarticular tubercles. Webbing basal between toes II–IV, lacking between others (formula **II** 2–3.5 **III** 2.5–4 **IV**). Fringes absent. Discs weakly to moderately expanded. Tubercles strongly protuberant except proximal tubercle of toe IV weak and poorly defined in some specimens. Subarticular tubercles 1–1–2–3–2. Inner metatarsal tubercle elongate. Outer metatarsal tubercle

Fig. 2. Plantar view of the foot of adult male MUJ 3544 (foot length 7.0 mm) of *Allobates niputidea*.

subcircular, diameter roughly half length of inner metatarsal tubercle. Medial metatarsal tubercle absent, but thickening of skin notable in most specimens (for discussion of relevance see Myers et al., 1991:23–24). Outer metatarsal fold absent. Tarsal keel prominent, short, tubercle-like, not contacting inner metatarsal tubercle, situated at point ca. one-quarter tarsal length from proximal edge of inner metatarsal tubercle.

Coloration in preservative.—Dorsum (Fig. 3A) dark brown or brown with dark brown blotches; granules dark brown. Pale dorsolateral stripe varying from inconspicuous paler brown to conspicuous cream or whitish gray, extending from posterior edge of eyelid (i.e., not extending along canthus rostralis) toward (and reaching in some specimens, e.g., MUJ 3529) tip of urostyle, not dropping toward base of thighs. Flank (Fig. 3B) dark brown broken by diffuse, inconspicuous, pale region or group of small spots extending from groin to point midway to arm insertion. Ventrolateral stripe well defined, straight, white, extending from groin, above arm insertion, either below or across lower portion of tympanum, and along upper lip toward or around snout (i.e., continuous with white stripe along upper lip). Flank below ventrolateral stripe (i.e., lower flank in lateral view, lateral belly in ventral view) mottled or spotted black or brown and white. Otic region dark brown, bordered above by pale dorsolateral stripe and below by pale ventrolateral stripe; tympanum either entirely dark brown or divided in dark brown upper and white (from ventrolateral stripe) lower portions. Loreal region and snout above white upper lip stripe dark brown.

Ventral coloration sexually dimorphic (Fig. 4). Adult males black anteriorly (i.e., entire throat, chest, anterior belly), fading to gray posteriorly; ventral coloration darkens ontogenetically. Females white, immaculate or with occasional, sparsely scattered melanophores. Lateral belly of both sexes mottled or spotted black or brown and white.

Dorsal surface of arm ranging from whitish gray or tan with brown or dark brown spots and blotches to solid dark brown. Dorsal and posterior surfaces of proximal portion of upper arm lacking melanophores, forming flash mark. Anterior and posterior surfaces dark brown, forming dark brown longitudinal stripes, broken ventrally by tiny white spots; ventrally white or cream. Palmar surfaces brown; contact surfaces gray or lacking melanophores. Dorsally fingers I and II mostly white or gray with brown blotches; fingers III and IV mostly brown with small white or gray blotches.

Dorsal surface of thigh gray or brown, lacking well defined transverse bands. Anterior surface of thigh gray or pale brown with diffuse dark brown longitudinal stripe; posterior surface gray or pale brown with dark brown mottling or dark brown with gray or pale brown spots and distinct crescent-shaped whitish gray or tan paracloacal mark at base of thigh, extending distad along posterior surface of thigh. Upper portion of posterior surface of thigh (i.e., dorsal and distal to paracloacal mark) brown or dark brown, forming diffuse longitudinal line. Exposed surfaces of shank and foot tan or dark brown with brown or dark brown blotches and spots. Ventral surface of thigh and concealed surfaces of shank and foot immaculate white or cream. Plantar surfaces brown; contact surfaces gray or lacking melanophores.

Coloration in life.—Based on field notes deposited at MUJ. MUJ 2900 (adult female): Dorsum brown with cream dorsolateral stripe; arms and legs dorsally pale brown; ventral surfaces cream; posterior thigh brown with tiny white spots; iris copper; palmar and plantar surfaces pale brown.

Larvae.—Six larvae in stage 25 (Fig. 5) were taken from the back of female nurse frog MUJ 3534. Body oval, slightly compressed at level of spiracle; length 3.0–3.1 mm ($\bar{x}$ = 3.05 ± 0.05 mm); maximum width 1.9–2.0 mm ($\bar{x}$ = 1.97 ± 0.05 mm); maximum height 1.1–1.2 mm ($\bar{x}$ = 1.13 ± 0.05 mm). Eyes positioned dorsally, oriented dorsolaterally; interorbital distance 1.2–1.3 mm ($\bar{x}$ = 1.28 ± 0.04 mm). Internarial distance 0.7–0.8 mm ($\bar{x}$ = 0.78 ± 0.04 mm). Lateral-line stitches absent. Tail tip broadly rounded; length 5.7–6.0 mm ($\bar{x}$ = 5.83 ± 0.12 mm); maximum height 1.2–1.5 mm ($\bar{x}$ = 1.40 ± 0.11 mm). Spiracle sinistral, oriented posterodorsally. Vent tube dextral. Tail muscle width 0.7–0.8 mm ($\bar{x}$ = 0.78 ± 0.04 mm) and height 0.9–1.1 mm ($\bar{x}$ = 0.97 ± 0.08 mm). Oral disc emarginate, positioned anteroventrally; width 0.8–0.9 mm ($\bar{x}$ = 0.87 ± 0.05 mm). Anterior margin of oral disc with wide dorsal gap in marginal papillae. Marginal papillae of anterior and posterior labia uniserial, conical, short. Anterior marginal papillae (4–5 on each side, $\bar{x}$ = 4.5 ± 0.52; bilaterally asymmetrical in two individuals) conspicuously larger than posterior papillae (30–35, $\bar{x}$ = 31.5 ± 1.87). Labial teeth weakly keratinized, labial tooth row formula 2(2)/3; gap in A-2 broad. Upper and lower jaw sheaths serrated, narrowly keratinized upper jaw sheath gently curved, not pointed (weakly pointed in single specimen). In preservative, body dorsally uniformly brown with cream flecks;

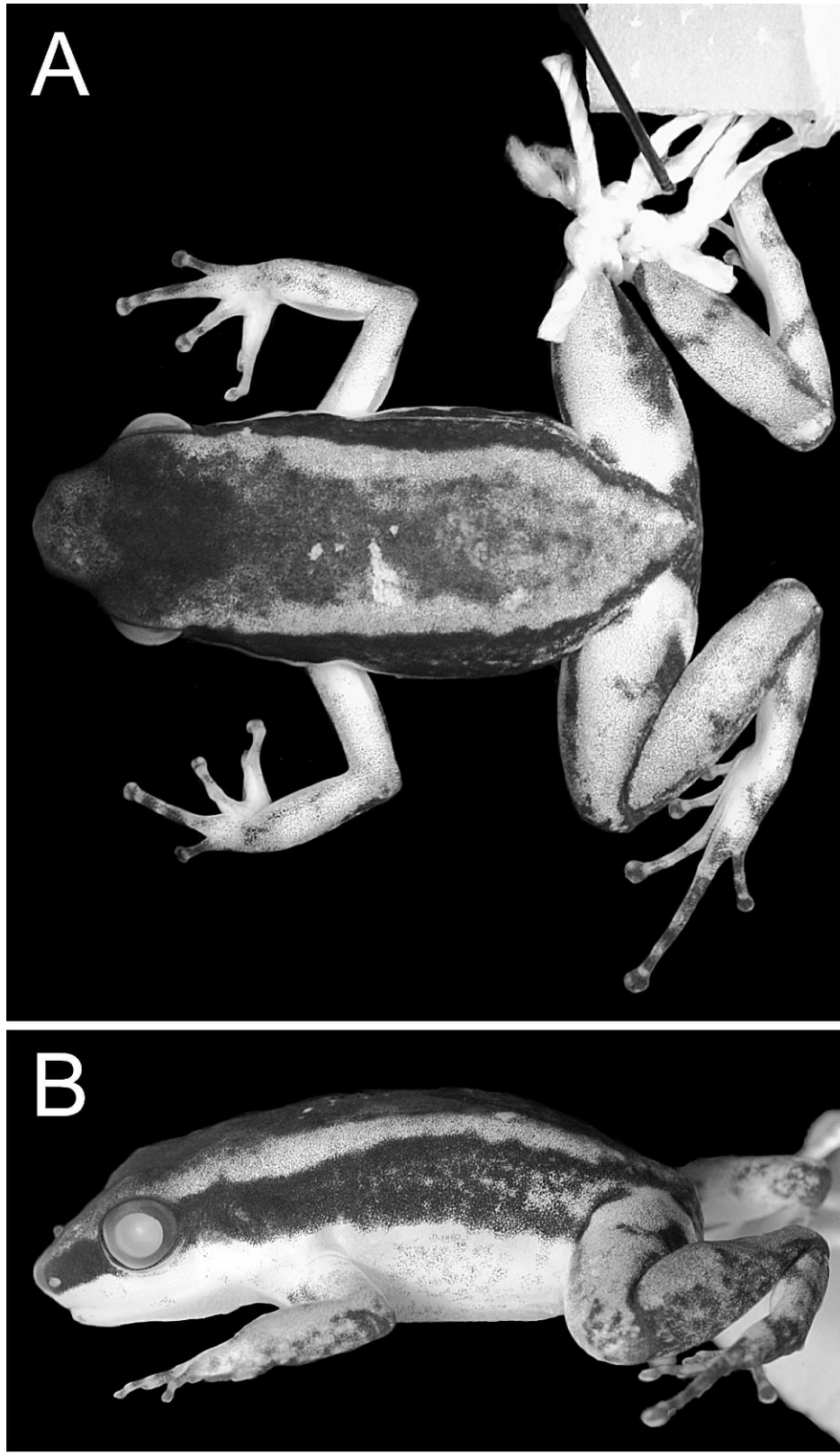

Fig. 3. Dorsal (A) and lateral (B) view of adult female MUJ 3529 (SVL = 17.3 mm) of *Allobates niputidea*. Note the diffuse pale oblique lateral stripe extending from the groin area in (B).

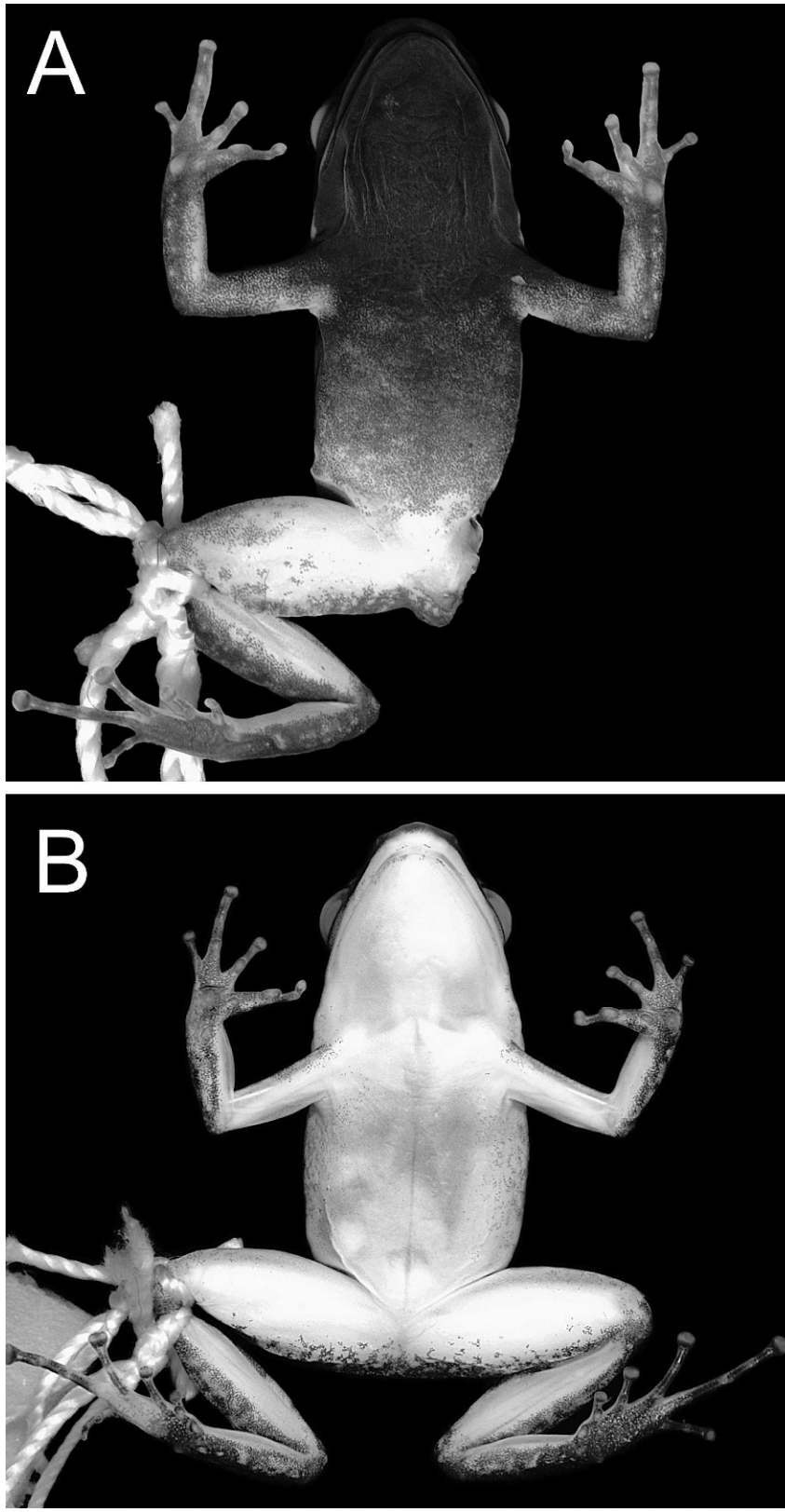

Fig. 4. Ventral views of adults showing sexual dimorphism in coloration of *Allobates niputidea*. (A) Adult male holotype MUJ 3520 (SVL = 16.7 mm). (B) Adult female MUJ 3529 (SVL = 17.3 mm).

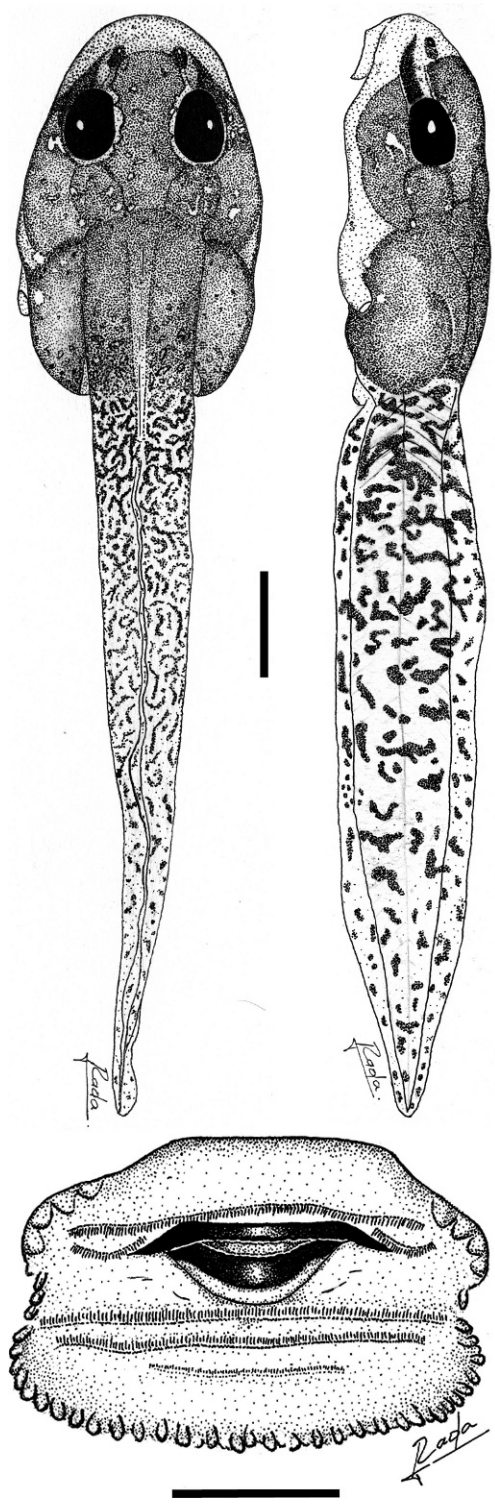

Fig. 5. Stage 25 larva of *Allobates niputidea* taken from the back of female nurse from MUJ 3534. Upper left: Dorsal view. Upper right: Lateral (sinistral) view. Lower: Mouth. Upper scale bar = 1 mm. Lower scale bar = 0.25 mm.

laterally brown with conspicuous diffuse cream loreal stripe bordered above and below by dark brown; ventrally brown anterior to level of spiracle, cream from level of spiracle to base of tail. Tail (including both fins) with extensive irregular brown mottling on cream ground.

Distribution and natural history.—*Allobates niputidea* inhabits wet tropical forests of the foothills of the western slopes of the Cordillera Oriental (Boyacá and Santander) and eastern slopes of the Cordillera Central (Caldas and Antioquia; Fig. 6). The forests at these localities are no taller than 20 m. The mean temperature of the region is 28 C and annual precipitation is greater than 2,000 mm, with one rainy season in April–June and a second season of greater precipitation in September–November.

Allobates niputidea is diurnal. All postmetamorphic specimens were collected between 0700–1100 hrs, active and calling in forest leaf litter. All specimens were taken within forest at considerable distances (>3 m) from permanent streams. Adults were observed scattered throughout the forest from September–November, whereas juveniles were taken around isolated pools in the forest interior.

The type locality was sampled in early September 2003 (just prior to the onset of winter rains) and March, April, July, and August 2004, but, although sampling protocols did not differ appreciably, *Allobates niputidea* was not detected until the beginning of the rain in September 2004.

Etymology.—The specific epithet is a noun in apposition and is the name commonly applied by Colombian herpetologists to this and other small, brown frogs of unknown identity.

Discussion

With 46 currently recognized species, *Allobates* is one of the two large and poorly understood genera extracted from the former *Colostethus sensu lato*, which was recognized as a heterogeneous and non-monophyletic mess for decades (Grant et al., 2006). The other large clade is *Hyloxalus*, which includes 57 species (other genera that include species of the former *Colostethus* are *Anomaloglossus*, *Aromobates*, *Colostethus sensu stricto*, *Epipedobates*, and *Silverstoneia*). Recent studies have added to our knowledge of *Allobates* and *Hyloxalus* (Duellman, 2004; La Marca et al., 2004; Caldwell, 2005; Kok et al., 2006; Lima et al., 2007), but much more work is required to fully document and explain their diversity. Despite the distant relationship between these genera (Grant et al., 2006), they

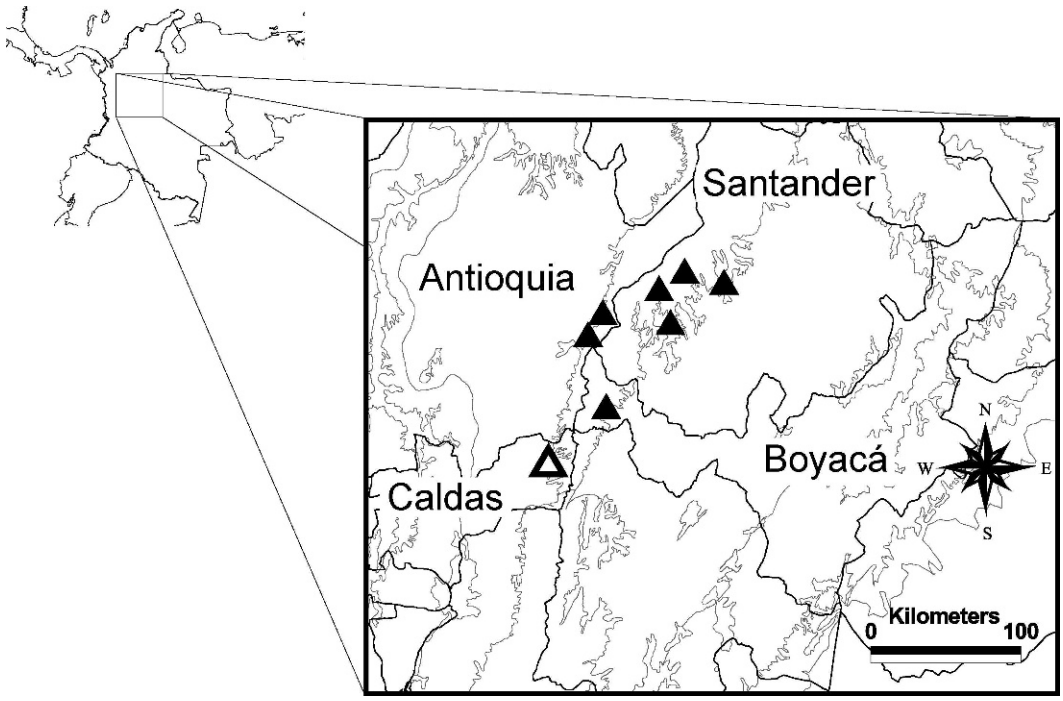

Fig. 6. Map of central Colombia (see upper left for context) showing the known localities (triangles) of *Allobates niputidea*. Gray lines indicate 500 m contour. Black lines indicate departmental borders; names are given for departments that include *A. niputidea* localities. All localities occur below 350 m in the Magdalena Valley. The open triangle indicates the type locality.

present remarkable convergences. For example, the *Allobates femoralis* group and *Hyloxalus azureiventris* group are both incapable of sequestering lipophilic alkaloids (Grant et al., 2006) but are brightly colored and appear to mimic toxic dendrobatids (Darst et al., 2006).

Allobates niputidea and *A. talamancae* appear to be the only species of aromobatids with exclusively female nurse frogs, although this claim must be tempered by the small sample sizes and occurrence of biparental transport in several species of *Allobates* (Grant et al., 2006). *Allobates niputidea* and *A. talamancae* are also the only known *trans*-Andean species of *Allobates* (Fig. 7). In addition to the evidence provided by Grant et al. (2006) in support of their phylogenetic

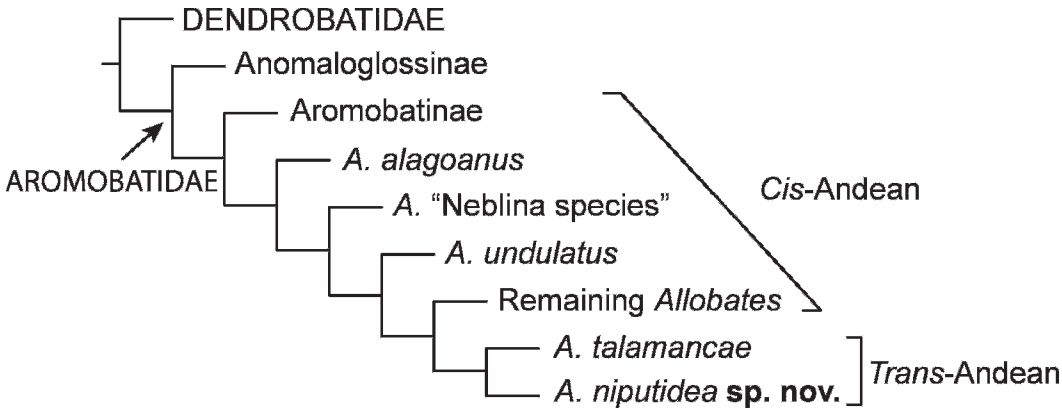

Fig. 7. Summary of the phylogeny proposed by Grant et al. (2006) and the distribution of *Allobates* and its sister group (Aromobatinae) in relation to the Andes. Dendrobatidae and Anomaloglossinae occur on both sides of the Andes.

position, the resemblance of these species to each other and to Amazonian species of *Allobates* (e.g., *A. melanolaemus*) is undeniable. This pattern of a predominantly Amazonian group with a small radiation across the Andes is shared with several other groups of frogs, including *Dendrobates* (Dendrobatidae), *Rhinella* (Bufonidae), *Ceratophrys* (Ceratophryidae), *Trachycephalus* (Hylidae), and the *Scinax rostratus* group (Hylidae). Although the Cordillera Oriental currently represents a formidable barrier, it was no more that 40% of its modern elevation until 4 million years ago (Ma), and the current elevation was not achieved until around 2.7 Ma (Gregory-Wodzicki, 2000). Consequently, it is conceivable that these groups were all divided by the rapid Andean uplift in the Pliocene.

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