Zootaxa 1555: 39–51 (2007)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

A new, toxic species of *Colostethus* (Anura: Dendrobatidae: Colostethinae) from the Cordillera Central of Colombia

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Abstract

A new species of *Colostethus* is described from cloud forest in the Cordillera Central of Colombia at approximately 2100–2500 m above sea level. It is a riparian species not known to occur more than a few meters from the water's edge. Specimens were collected in grassy vegetation and on and beneath rocks along streams and pools, in both primary forest and in or at the edge of forest clearings. Most specimens were collected during the day, but several were observed to be active at night. The new species differs from other species of *Colostethus* in lacking pale oblique lateral and ventrolateral stripes, possessing a pale dorsolateral stripe, lacking or having at most rudimentary toe webbing, and possessing a marbled or reticulated ventral color pattern. Adult males of the new species possess a swollen third finger and a gray or black throat. In life, the new species possesses bright lemon- or golden-yellow flash marks on the axilla, groin, belly, and concealed surfaces of the thigh and shank, and bluish-white ventral coloration, and it exudes a milky secretion from the skin. The aqueous extract of the skin is toxic, but additional samples are required to determine the nature of the toxic compound(s).

Key words: Taxonomy, systematics, Amphibia, Dendrobatoidea, South America, cloud forest, alkaloid, toxicity

Resumen

Se describe una nueva especie de *Colostethus* de bosque nublado en la Cordillera Central de Colombia, entre aproximadamente 2100–2500 m sobre el nivel del mar. La especie fue colectada en pastizales y sobre y por debajo de piedras en el borde de quebradas y pozos, tanto en bosque primario como en (o en el borde de) claros como potreros o zanjas de desagüe. La mayoría de los especímenes fueron colectados de día, pero algunos fueron observados activos por la noche. La nueva especie difiere de otras especies de *Colostethus* por la ausencia de líneas pálidas oblicua y ventrolaterales, la presencia de una línea pálida dorsolateral, la ausencia o casi ausencia de membrana podial, y la presencia en el vientre de un patrón marmoleado o reticulado. En machos adultos el tercer dedo de la mano está ensanchado y la garganta es de color gris o negro. La nueva especie posee marcas de coloración llamativa de color amarillo brillante en la axila, la ingle, el abdomen y las superficies ocultas del muslo y la tibia, coloración ventral blanco azuloso, y secreta una sustancia lechosa de la piel. El extracto acuoso es tóxico, pero se necesitan muestras adicionales para poder determinar la identidad de los compuestos tóxicos.

Palabras claves: Taxonomía, sistemática, Amphibia, Dendrobatoidea, Suramérica, bosque nublado, alcaloide, toxicidad

Introduction

Frogs of the dendrobatoid family Dendrobatidae are renowned for their toxicity and bright coloration. Nevertheless, within Dendrobatidae the genus *Colostethus* (Colostethinae) is generally considered to be composed

Accepted by M. Vences: 2 Jun. 2007; published: 20 Aug. 2007

of drab, non-toxic species. Although this is largely correct, many species of *Colostethus* possess some degree of bright coloration, and at least one, *C. panamensis*, is known to be toxic (Daly *et al.* 1994; reported as *C. inguinalis*; for taxonomy see Grant 2004). However, unlike other toxic dendrobatids whose skin toxins consist of lipophilic alkaloids, the toxicity of *C. panamensis* owes to the presence of the water-soluble alkaloid tetrodotoxin (TTX). *Colostethus panamensis* is the only species of dendrobatid previously reported to possess a water-soluble toxin.

As currently formulated, *Colostethus* includes 18 species (Grant *et al.* 2006). Most species are found on the Pacific versant and adjacent lowlands of Colombia and Ecuador, but three species occur in Middle America (*C. latinasus*, *C. panamensis*, and *C. pratti*), one reaches from the northern Chocó region of Colombia around the northern tip of the Cordillera Occidental and Cordillera Central south to the Magdalena Valley (*C. inguinalis*), one occurs in the Sierra Nevada de Santa Marta, Colombia (*C. ruthveni*), and one is found on the eastern slopes of the Andes in Ecuador (*C. fugax*). Only two nominal species (*C. fraterdanieli* and *C. thorntoni*) are known to occur in the Cordillera Central of Colombia, although a third, unnamed species has been known to me for over a decade and has been languishing in collections for much longer. Analysis of the biological activity of skin extracts show this to be the second toxic species of *Colostethus*. The purpose of this paper is to describe this new species of *Colostethus*.

Materials and methods

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 mean ± standard deviation. Relative lengths of Fingers I and II were determined following Kaplan (1997; see also Grant *et al.* 2006). Larval terminology follows Altig and McDiarmid (1999); staging follows Gosner (1960). Comparisons focus on closely related species and potentially sympatric species formerly placed in *Colostethus* and now placed in *Colostethus sensu stricto*, and *Hyloxalus*. Diagnostic characters follow Grant *et al.* (2006; see also Coloma 1995; Grant & Castro 1998; Grant & Rodríguez 2001). Institutional abbreviations are AMNH (American Museum of Natural History, New York), ICN (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá), KU (Natural History Museum and Biodiversity Research Center, The University of Kansas, Lawrence), NIH (National Institutes of Health, Bethesda), and UTACV (Collection of Vertebrates, University of Texas at Arlington, Arlington).

Results

***Colostethus ucumari*, new species**

Figs. 1–8

Holotype: ICN 28598 (field number JHR 2404), an adult male collected by Javier Bustos, Erika Nadachos K., Michael Alberico, and Jorge Humberto Restrepo at Colombia, Departamento de Risaralda, Parque Regional Natural Ucumarí, Campamento La Pastora, Quebrada La Pastora, 2500 m above sea level, approximately 4°42’N, 75°29’W, 15–17 February 1991.

FIGURE 1. *Colostethus ucumari* new species adult male AMNH 104369 in life, SVL = 24.0 mm. Photograph by Charles W. Myers.

Paratopotypes: ICN 28599–600.

Paratypes: All from Colombia. ICN 28551–52, 28556, 28575–76: Departamento de Risaralda, Parque Regional Natural Ucumarí, Campamento La Pastora, Quebrada La Pastora, 2490 m. ICN 15636: Departamento de Quindío, Hacienda El Carelia, ca. 8 km E Salento, 2410 m. ICN 38766–69: Departamento de Risaralda, Pijao, Vereda Guamal, Finca La Cristalina, 2152–2250 m. UTACV 39728–29: Departamento de Tolima, 20.3 mi WNW Cajamarca. KU 133306–13: Departamento de Caldas, 6 km ESE Villa María, 2130 m. AMNH 104369–74: Departamento de Caldas, 5.5–6 km by road southeastward from Villa María, 2320 m.

Etymology: The specific epithet, *ucumari*, is used as a noun in apposition and refers to the Parque Regional Natural Ucumarí, where the type locality of *Colostethus ucumari* is situated. Ucumarí, in turn, is the Quechua name for the spectacled bear, *Tremarctos ornatus*.

Diagnosis: A medium to large species of *Colostethus* (maximum SVL approximately 27 mm for adult males, approximately 30 mm for adult females); dorsal skin texture posteriorly granular; cloacal tubercles present; Finger I and Finger II subequal in length; adpressed Finger IV reaching beyond distal subarticular tubercle of Finger III, longer than Finger II; Finger III swollen in adult males; throat, chest, and anterior belly pale with dark marbling or reticulation in both sexes; throat darker in males than in females, ranging from gray to black; black arm band of adult males absent; testes white; toes conspicuously fringed, free of webbing or with at most basal webbing between Toes III–IV; pale dorsolateral stripe present; pale ventrolateral stripe absent; pale oblique lateral stripe absent; pale paracloacal marks absent; medial lingual process absent.

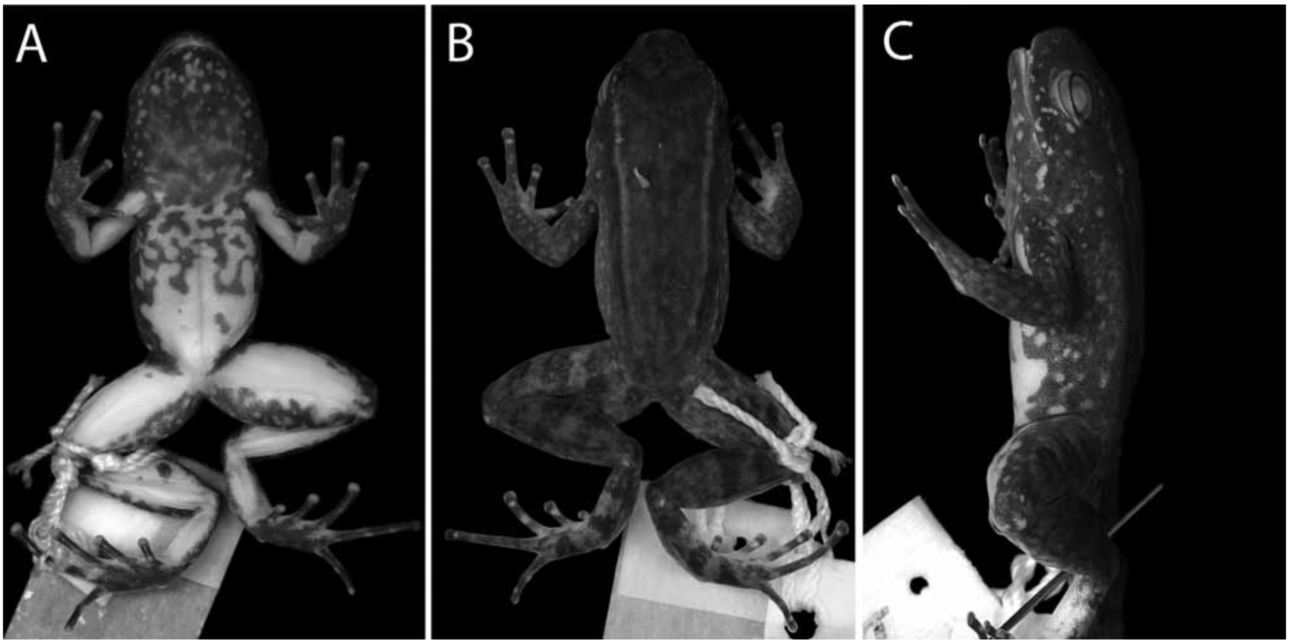

FIGURE 2. *Colostethus ucumari* new species adult male holotype ICN 28598, SVL = 22.1 mm. (A) Ventral view. (B) Dorsal view. (C) Lateral view.

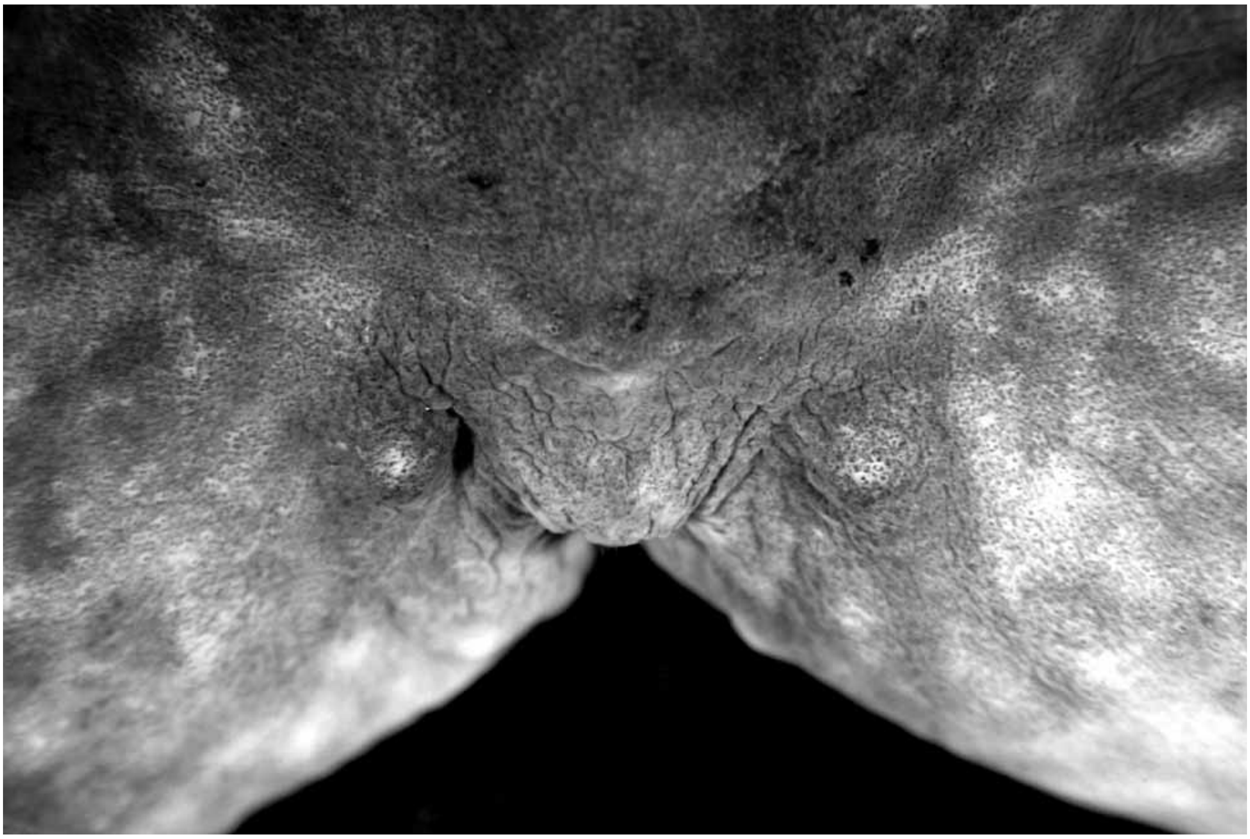

FIGURE 3. Cloacal tubercles of *Colostethus ucumari* new species (ICN 28600).

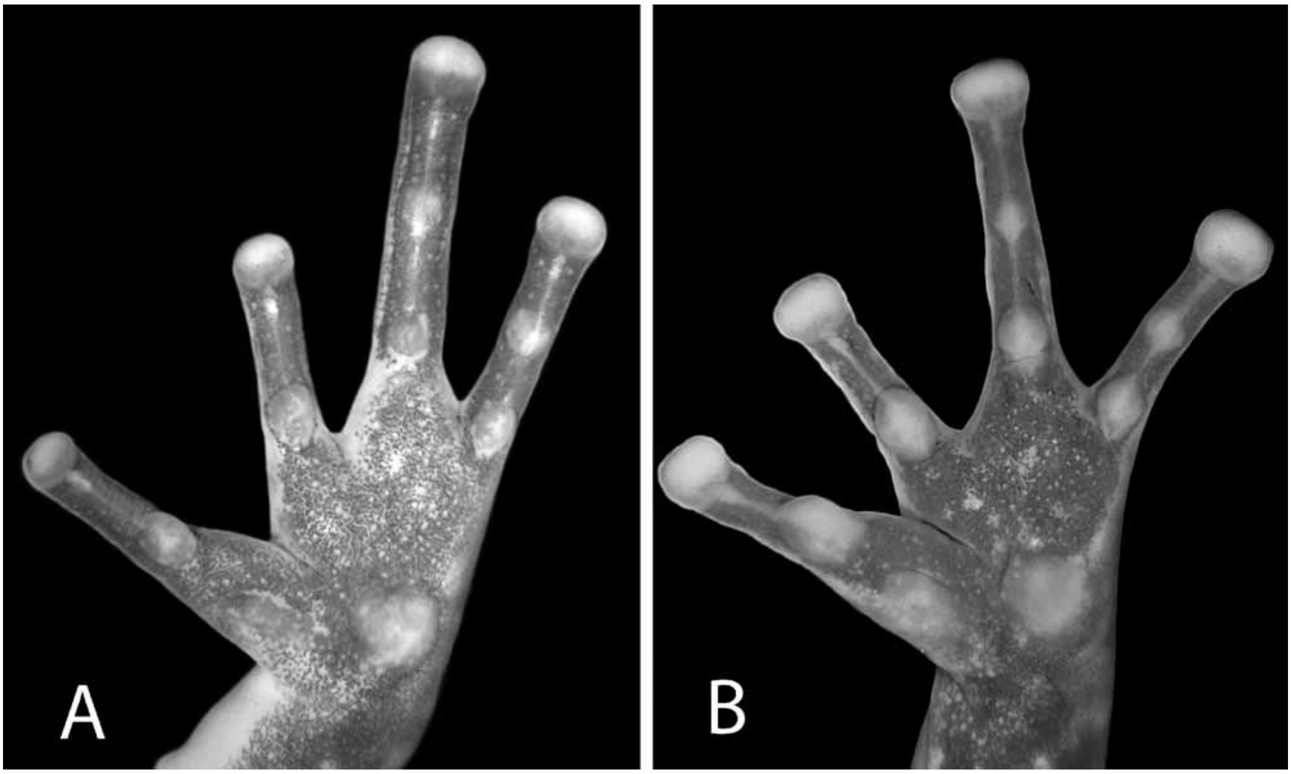

FIGURE 4. Hand morphology of *Colostethus ucumari* new species. (A) Left hand of adult male holotype ICN 28598. Hand length = 6.5 mm. Note the swelling along the preaxial side of Finger III. (B) Left hand of adult female paratype ICN 38766. Hand length = 7.7 mm. Finger III is not swollen.

Colostethus ucumari shares with *C. imbricolus* and *C. panamensis* the swelling of Finger III in adult males and the occurrence of conspicuous bright flash marks on the axilla, groin, belly, and concealed surfaces of the thigh and shank. It differs from both of those species in lacking a partial pale oblique lateral stripe and possessing a conspicuous pale dorsolateral stripe.

Colostethus ucumari differs from all other species of *Colostethus* except *C. ruthveni* and *C. thorntoni* in lacking a pale oblique lateral stripe (extending from groin to eye in *C. agilis*, *C. brachistriatus*, *C. dysprosium*, *C. fraterdanieli*, *C. fugax*, *C. jacobuspetersi*, *C. lynchi*, *C. mertensi*, and *C. yaguara*; extending from groin midway along flank in *C. furviventris*, *C. imbricolus*, *C. inguinalis*, *C. latinasus*, *C. panamensis*, and *C. pratti*). *Colostethus ucumari* differs from *C. ruthveni* in ventral coloration (marbled or reticulated ventral color pattern in *C. ucumari*, immaculate in *C. ruthveni*), and from *C. thorntoni* in the degree of webbing (toes free or with at most rudimentary webbing between Toes III–IV in *C. ucumari*; toes moderately webbed in *C. thorntoni*) and the possession of a pale dorsolateral stripe (absent in *C. thorntoni*). *Colostethus ucumari* further differs from *C. agilis*, *C. alacris*, *C. brachistriatus*, *C. dysprosium*, *C. fraterdanieli*, *C. fugax*, *C. imbricolus*, *C. inguinalis*, *C. jacobuspetersi*, *C. latinasus*, *C. lynchi*, *C. mertensi*, *C. panamensis*, *C. thorntoni*, and *C. yaguara* in possessing a pale dorsolateral stripe (absent in those species; present in *C. furviventris*, *C. pratti*, and *C. ruthveni*). *Colostethus ucumari* is also the only species of *Colostethus* known to possess cloacal tubercles (*sensu* Grant *et al.* 1997), although these structures are not always scored and may be lost as an artifact of preservation (Grant *et al.* 2006).

Among other dendrobatoids formerly placed in *Colostethus sensu lato* in the Colombian Andes, *Colostethus ucumari* most resembles *Hyloxalus abditaurantius*, another robust frog of similar size with which it shares conspicuous bright flash marks in life (yellow in *C. ucumari*, orange in *H. abditaurantius*), marbled or reticulated ventral coloration, a dark throat in adult males (due to presence of melanophores in *C. ucumari* and absence of iridophores in *H. abditaurantius*), cloacal tubercles, and the absence of a pale oblique lateral

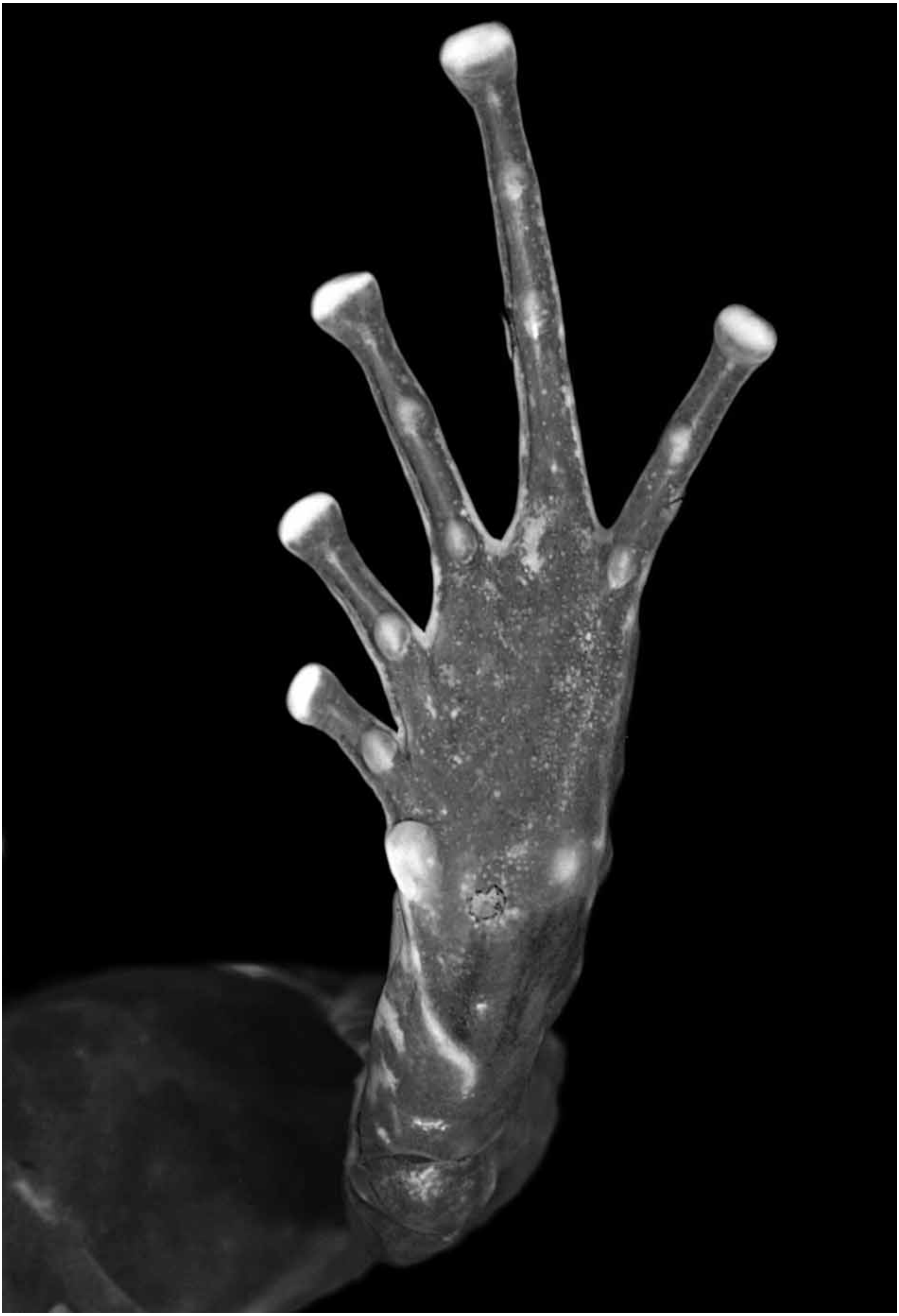

FIGURE 5. Foot morphology of *Colostethus ucumari* new species (ICN 38769). Foot length = 10.6 mm.

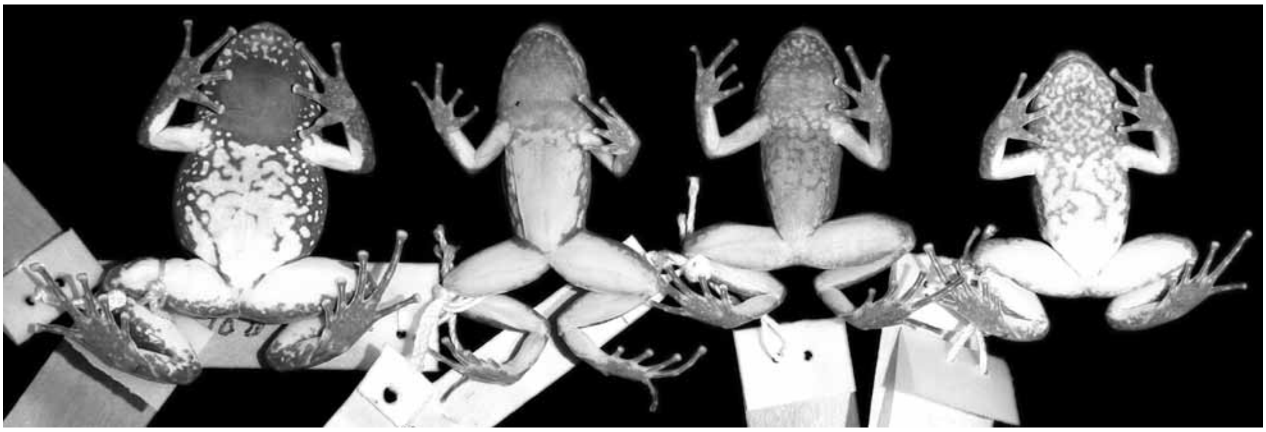

FIGURE 6. Variation in ventral coloration of male *Colostethus ucumari* new species. Left to right: ICN 38769 (SVL=27.0 mm), ICN 28556 (SVL=22.5 mm), ICN 28575 (SVL=22.1 mm), ICN 38768 (SVL=22.6 mm).

FIGURE 7. Variation in ventral coloration of female *Colostethus ucumari* new species. Left to right: ICN 15636 (SVL = 30.0 mm), ICN 38767 (SVL = 29.8 mm), ICN 28600 (SVL = 30.0 mm).

stripe (both possess small, irregular, pale dots scattered over the flanks). *Colostethus ucumari* differs most conspicuously from *H. abditaurantius* in possessing a pale dorsolateral stripe (absent in *H. abditaurantius*), having Finger III swollen in adult males (not swollen in *H. abditaurantius*), and lacking toe webbing or having at most basal webbing between Toes III–IV (toes extensively webbed in *H. abditaurantius*).

Measurements of holotype (Fig. 2): SVL 22.1 mm; forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow 5.1 mm; hand length from proximal edge of palmar tubercle to tip of Finger III 6.5 mm; shank length from outer edges of flexed knee to heel 10.0 mm; foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV 10.4 mm; head width between angle of jaws 8.0 mm; head length diagonally from corner of mouth to tip of snout 7.3 mm; eye length from posterior to anterior corner 3.1 mm; eye to naris distance from anterior corner of eye to center of naris 1.9 mm; distance between centers of nares 3.1 mm; snout length from anterior corner of eye to tip of snout 3.4 mm; interorbital distance 2.7 mm; diameter of tympanum 1.2 mm.

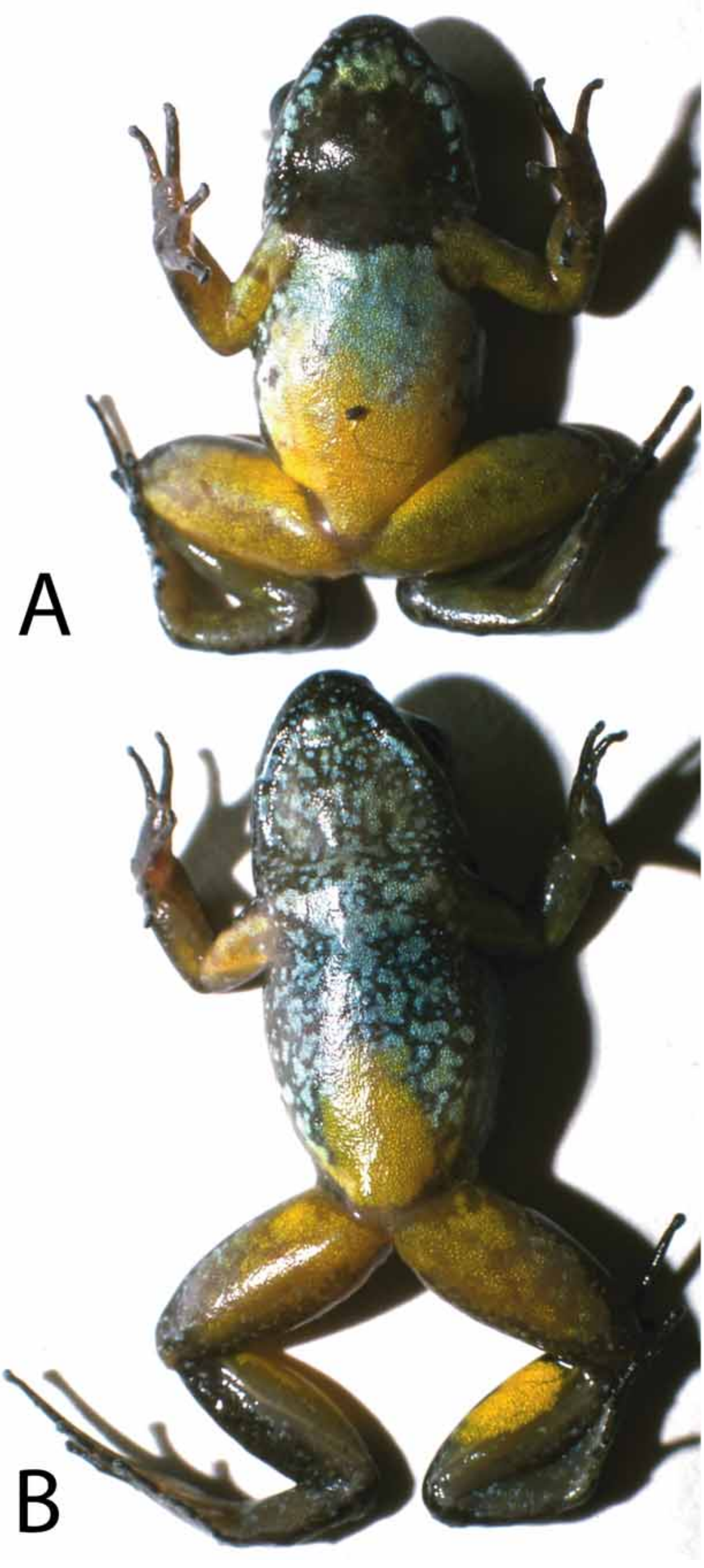

FIGURE 8. Ventral coloration of *Colostethus ucumari* new species in life. (A) Adult male AMNH 104369 (SVL = 24.0 mm). (B) Adult female AMNH 104371 (SVL = 25.4 mm). Photographs by Charles W. Myers.

Morphology: Adult males 22.1–27.0 mm SVL (*n* = 8; $\bar{x}$ = 24.06±2.06); testes unpigmented (white), testis length approximately 1/3–1/2 eye length. Adult females 24.4–30.0 mm SVL (*n* = 12; $\bar{x}$ = 27.27±2.08); mature oviducts unpigmented (white); mature ova approximately 2 mm in diameter, animal pole dark brown.

Ventral and lateral surfaces smooth. Dorsal surfaces with granules scattered irregularly in sacral region and (to a lesser degree) on thigh and shank. Well defined cloacal tubercles present (Fig. 3). Postrictal and preaxillary tubercles (one each) elongate. Head width between angle of jaws 31–39% SVL, 1.0–1.3 times head length. Interorbital distance 30–37% of head width. Canthus rostralis gently rounded. Loreal region flat or weakly concave, not sloping to lips. Eye length 39–48% of diagonal head length. Eye-naris distance 55–66% snout length and 55–74% 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. Diameter of tympanum 28–53% eye length. Teeth present on maxillary arch.

Hand length 26–31% of SVL and 1.2–1.3 times forearm length. Finger discs weakly to moderately expanded. Finger III of adult males swollen along preaxial side; postaxial swelling not detected (Fig. 4A); Finger III not swollen in adult females (Fig. 4B) 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 1–1–2–2. All tubercles strongly protuberant; subarticular and thenar tubercles elliptical; palmar tubercle subcircular.

Shank and foot length 40–47% and 40–51% of SVL, respectively. Relative lengths of appressed toes I < II < V < III < IV (Fig. 5). Toe III extended approximately midway between penultimate and ultimate subarticular tubercles of Toe IV; Toe V extended to distal edge of penultimate subarticular tubercle of Toe IV. Webbing absent or basal between Toes II–IV, lacking between others (formula **II** 2–3.5 **III** 2.5–4 **IV**). Fringes present on pre- and postaxial surfaces of all toes except Toe V, which lacks fringes. Discs weakly to moderately expanded. Tubercles strongly protuberant. Subarticular tubercles 1–1–2–3–2. Inner metatarsal tubercle elongate. Outer metatarsal tubercle subcircular, diameter roughly one 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 well defined, straight or weakly curved (weakly curved in holotype), not enlarged proximally to form tubercle-like structure, extending diagonally from inner metatarsal tubercle along distal one half of tarsus.

Color in preservative: Dorsum (Fig. 2A) dark brown or brown with dark brown blotches (as in holotype); granules dark brown. Pale dorsolateral stripe varying from pale brown to conspicuous cream or whitish gray, extending from tip of snout along canthus rostralis, outer edge of upper eyelid, and lateral edge of dorsum toward (but not reaching) tip of urostyle, not dropping toward base of thighs. Flank (Fig. 2C) dark brown with scattered pale (white or gray) flecks and dots. Pale ventrolateral and oblique lateral stripes absent. Otic region dark brown. Loreal region and snout dark brown; upper lip dark brown with white or gray dots.

Ventral coloration sexually dimorphic (Figs. 6–7). Both sexes marbled or reticulated anteriorly (extending posteriorly onto belly), but throat of adult males (i.e., region that becomes distended when vocal sac inflated) is darker, ranging from gray to black.

Dorsal, anterior, and posterior surfaces of arm brown with dark brown spots and blotches, often with small pale flecks and dots. Axilla lacking melanophores, forming flash mark. Ventral surfaces white or cream. Palmar surfaces brown; contact surfaces gray or lacking melanophores. Dorsally Fingers I and II proximally mostly white or gray with brown blotches, darker distally; Fingers III and IV mostly brown.

Dorsal surface of thigh gray or brown with diffuse darker brown transverse bands that align with bands on shank and foot of flexed limb. Anterior surface of thigh gray or brown with diffuse darker blotches; posterior surface gray or brown fading ventrally; pale paracloacal mark absent. Exposed surfaces of shank and foot gray or brown with dark blotches and diffuse transverse bands that align with those of dorsal surface of thigh. Ventral surface of thigh and concealed surfaces of shank and foot immaculate white or cream, forming flash marks. Plantar surfaces brown; contact surfaces gray or lacking melanophores. Dorsal surface of preaxial portion of foot and Toes I–III mostly cream or white; postaxial portion of foot and Toes IV–V mostly gray or brown.

Color in life (Figs. 1, 8): Charles W. Myers's field notes at AMNH report AMNH 104369–73 as brown with blackish brown interorbital and dorsal markings and a light but not sharply defined bronzy dorsolateral stripe. Sides of head and body brown with bluish-white dots (lacking on flank of female AMNH 104370). Posterior surface of thigh indistinctly mottled brown and black; ventral surface of thigh pale greenish gray. Iris bronze with black flecking or mottling. Adult male AMNH 104369 (Fig. 8A) with a gray throat and pale blue chest and lower lip margin. Females (e.g., AMNH 104371; Fig. 8B) and juveniles all with throat and chest pale blue with black or gray scribbling or blotching (i.e., throat not gray). All specimens with bright golden-yellow coloration on underside of arms and in axilla, on belly, and on concealed surfaces of shank.

John D. Lynch's field notes at ICN report ICN 15636 as brown with vague paler flecks and vague dorsolateral stripe. Throat and anterior venter pale blue with dark network. Lemon yellow patch in axilla, lowest groin, and behind knee. Iris dark brown. Posterior thighs dark gray-brown.

Toxicity: Charles W. Myers (field notes taken 2 December 1976, deposited at AMNH) observed that paratypes of *Colostethus ucumari* exuded a milky secretion along the sides of the body, posterior side of thighs, and concealed surfaces of shanks. In January 1977, John W. Daly analyzed extracts of the skin of AMNH 104371 for toxicity at NIH by injection into mice (John W. Daly *in litt.*, 20 December 2006; for procedures see Daly et al. 1994). Injection of the methanol extract caused some initial agitation and twitching, followed by normal activity. However, injection of the aqueous extract caused not only twitching, but also some gagging, followed by a period of inactivity. The identity of the water-soluble compound responsible for these toxic effects was not determined.

Mass spectral analysis in February 1977 showed the alkaloid fraction from the non-toxic methanol extract to contain small amounts of unknown compounds, none of which corresponded to any known dendrobatid alkaloids. The nature of these compounds could not be pursued at that time because of the limited quantities. Current reexamination using high resolution gas chromatographic mass spectral analysis of the thirty year old alkaloid fraction could only detect a trace amount of one of these compounds, which proved to be an artifact, namely 2-benzothazolyl-N,N-dimethyl dithiocarbamate (John W. Daly, *in litt.* 6 April 2006). The molecular ion was at m/z 254 $(C_{10}H_{10}N_2S_3)^+$ with the only major fragment ion at m/z 88 $(C_3H_6NS)^+$ (for presence of this compound in rubber-based vial closures see Kapp & Vetter 2006).

Larvae: The single stage 25 larva AMNH 104374 was taken from the back of male nurse frog AMNH 104369 (additional tadpoles were observed on this frog but were lost when catching it in dense grass). Body oval, slightly compressed anterior to intestine; length 4.1 mm; maximum width 2.9 mm; maximum height 2.0 mm. Eyes positioned dorsally, oriented dorsolaterally; interorbital distance 1.3 mm. Internarial distance 1.1 mm. Lateral line stitches absent. Spiracle sinistral. Vent tube dextral. Center of intestinal coil sinistral, ventrolateral. Tail tip broadly rounded; length 7.9 mm; maximum height 2.0 mm. Tail muscle width 0.9 mm and height 1.4 mm. Oral disc emarginate, positioned anteroventrally; width 1.0 mm. Anterior labium bearing broad dorsal gap. Marginal papillae of anterior and posterior labia uniserial, marginal papillae conical, short. Labial labial tooth row formula 1/3; only A-1 and P-1 with any degree of keratinization; A-1 complete (i.e., lacking gap), no additional anterior tooth ridges present. Upper and lower jaw sheaths serrated, narrowly keratinized upper jaw sheath gently curved, not pointed or notched. Tail (including both fins) and body with sparse, irregular brown stippling on cream ground, lacking conspicuous markings.

Distribution and natural history: *Colostethus ucumari* is known from cloud forest localities in the Cordillera Central at approximately 2100–2500 m above sea level. It is a riparian species not known to occur more than a few meters (<3 m) from the water's edge. Specimens were taken in grassy vegetation and on and beneath rocks along streams and pools, in both primary forest (i.e., unmodified forest of >20 m height) and in or at the edge of forest clearings, such as pastures and grassy roadside drainage ditches. Most specimens were taken during diurnal collecting, but the holotype and topoparatypes were recorded as being collected while active at night (specific time not reported, but collecting activities and other species obtained suggest it was nocturnal, not crepuscular).

Discussion

Colostethus ucumari is the second species of *Colostethus* demonstrated to possess skin toxins. Although the identity of the compound responsible for the toxicity was not determined, the fact that it was the aqueous extract that induced the significant response in mice indicates that a polar water-soluble compound caused the toxicity, perhaps TTX, as demonstrated for *C. panamensis* (Daly *et al.* 1994). Additional skin extracts are required to identify the compound responsible for the toxicity of *Colostethus ucumari*. No other dendrobatoid species is known to possess TTX or any other water-soluble toxin. Among other amphibians TTX and congeners have been reported for few but geographically and phylogenetically diverse taxa, including species of a number of salamandrid genera (*Cynops*, *Notophthalmus*, *Paramesotriton*, and *Taricha*), an ambystomatid (*Ambystoma tigrinum*), several species of the brachycephalid *Brachycephalus*, an unidentified species of rhacophorid (*Polypedates* sp.), and a number of species of the bufonid genus *Atelopus* (Daly 2004; Pires *et al.* 2005).

The origin of TTX and related compounds in *Colostethus* and other amphibians remains unknown. Daly *et al.* (1997) reported that captive-bred *Atelopus varius* lacked TTX (present in wild-caught specimens), which suggests TTX is obtained from the environment. Current hypotheses identify either diet (*cf*. lipophilic alkaloid-containing dendrobatids; Saporito *et al.* 2007) or endosymbiotic bacteria as potential origins; however, compelling evidence is lacking for either hypothesis (Daly 2004; Lehman *et al.* 2004). Further, it is clear from the distribution of TTX-containing species across the phylogeny of Amphibia (e.g., Frost *et al.* 2006) that the occurrence of TTX in skin secretions arose multiple times independently, suggesting the possibility of multiple, lineage-specific mechanisms. Lipophilic alkaloid sequestration also arose multiple times among frogs (for tabulation see Daly *et al.* 2005) and within Dendrobatidae (Santos *et al.* 2003; Vences *et al.* 2003) and is a synapomorphy of *Ameerega*, the sister group of *Colostethus* (Grant *et al.* 2006).

In addition to the synapomorphic occurrence of water-soluble skin toxins, *Colostethus panamensis* and *C. ucumari* share the bright yellow flash marks and bluish-white ventral coloration, which are suggestive of aposematic coloration. Similarly, *Colostethus imbricolus* possesses conspicuous bright orange flash marks and bluish-white ventral coloration, and Grant *et al*. (2006) found *C. panamensis* to be paraphyletic with respect to *C. imbricolus* (although the specific status of *C. imbricolus* is not in question), all of which suggests that it too may possess TTX or a TTX-like skin toxin. Daly *et al.* (1994) analyzed an aqueous extract of a single skin of *C. imbricolus* and failed to detect significant mouse toxicity or inhibition of [^{3}H]saxitoxin binding. However, extensive variation in levels of TTX was found in *C. panamensis* (for detailed accounts of variation in alkaloid profiles in other taxa see Saporito *et al*. 2006; Daly *et al.* 2007), and additional samples are required to adequately test the toxicity of *C. imbricolus*.

Given the small sample size (n = 1), the significance of the observed 1/3 labial tooth row formula is unclear. It was expected that this species would possess a 2(2)/3 formula, as is typical of other *Colostethus* larvae (including those in stage 25). The posterior-most tooth ridges lack keratinized teeth and are therefore difficult to observe, but there is no indication whatsoever of a second anterior tooth ridge. Consistent with A-1 of other dendrobatoids, the observed anterior tooth row lacks a median gap. Grant *et al.* (2006: 96) reported ontogenetic variation in the number of tooth rows in the colostethine *Ameerega hahneli*, and it is possible that a second anterior row, corresponding to A-2, may develop in later ontogenetic stages of *Colostethus ucumari*.

The last recorded observation of this species I am aware of owes to a photograph taken in 1996 by Wilmar Bolívar-G. of an uncollected specimen found near the bridge at El Cedral, near the beginning of the trail leading toward La Pastora in the Parque Regional Natural Ucumarí (coordinates at the bridge are 4°42.197'N, 32.199'W, 2120 m). In February 2004, I visited the area of the type locality and found *Colostethus fraterdanieli* to be abundant and calling from 1750 m, below the Santuario de Flora y Fauna Otún Quimbaya, up to approximately 2400 m, but I failed to detect any individuals of *C. ucumari*, despite having searched the same sites where specimens were secured previously. Nevertheless, conditions were fairly dry and searches of appropriate habitats were conducted over only two days, and Charles W. Myers noted in his 1976 field notes that *C. ucumari* was less common than *C. fraterdanieli*. *Colostethus fraterdanieli* has remained common at sites where other dendrobatid species that were previously common have undergone drastic declines (e.g., Finca San Pedro, a locality above El Queremal in the Department of Valle del Cauca, where *Hyloxalus abditaurantius*, *H. fascianiger*, and *H. lehmanni* appear to have disappeared; W. Bolívar-G., personal communication). Further investigation, including prolonged monitoring, is required to assess the status of C. ucumari (and other anurans) within the Parque Regional Natural Ucumarí.

Acknowledgments

G. Kattan (Fundación EcoAndina/Wildlife Conservation Society) first drew my attention to this species in 1994 while I was a student of F. Castro at the Universidad del Valle. I gratefully acknowledge the Corporación Autónoma Regional de Risaralda (CARDER) and Fundación EcoAndina for logistical support at the Santuario de Flora y Fauna Otún Quimbaya, managed by the Unidad de Parques Nacionales, and the Parque Regional Natural Ucumarí. For their assistance and hospitality I am grateful to W. Cardona, D. Correa, K. Fierro, G. Kattan, C. López, M. Rios, V. Rojas, and L. Valenzuela (all from Fundación EcoAndina/Wildlife Conservation Society). J. A. Campbell (UTACV), W. E. Duellman (KU), C. Franklin, (UTACV), J. D. Lynch (ICN), C. W. Myers (AMNH), and L. Trueb (KU) provided work space, specimen loans, unpublished data, and/or photographs. C. W. Myers examined the tadpole and provided a reassuring second opinion, and D. Sánchez (ICN) shared his data on dendrobatoid larvae generally. W. Bolívar-G. (Universidad del Valle) shared photographs and unpublished data. H. Martin Garraffo, T. F. Spande and J. W. Daly (NIH) made available unpublished data on toxicity of the aqueous fraction and the results of reanalysis of the alkaloid fraction of C. ucumari. I am grateful to S. Lötters and C. W. Myers for critical comments on the manuscript.

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