



Another new species of *Ranitomeya* (Anura: Dendrobatidae) from Amazonian Colombia

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Abstract

We describe a new species of *Ranitomeya* (family Dendrobatidae) which we discovered on a recent expedition to the Río Apaporis region in southeastern Colombia. This species had previously been referred to as *Dendrobates quinquevittatus* sensu Silverstone, based on a single specimen collected in the 1950s from the mouth of Río Apaporis. We found additional specimens from two sites in this region; near the town of La Pedrera (Departamento Amazonas), and on the lower Apaporis (Departamento Vaupés). We also found several *R. ventrimaculata*, and the two species are likely sympatric throughout much of this region. Although the new species and *R. ventrimaculata* have similar life-history attributes (such as using similar bromeliads for tadpole deposition), the two species clearly differ in color pattern and advertisement call parameters. Ongoing molecular studies indicate that the new species is not closely related to the sympatric *R. ventrimaculata*, but rather is sister to an apparently undescribed species of *Ranitomeya* from the upper Brazilian Amazon.

Key words: Anura, Apaporis, Caquetá, Colombia, Dendrobatidae, new species, poison frogs, *Ranitomeya defleri* sp. nov., *Ranitomeya ventrimaculata*, taxonomy

Resumen

Se describe una nueva especie de *Ranitomeya* (familia Dendrobatidae) que descubrimos en un expedición reciente al región del Río Apaporis en el suroriente del Colombia. Este especie se han referido a *Dendrobates quinquevittatus* sensu Silverstone, en base de una sola muestra cual fue coleccionado en los 1950s de la boca del Río Apaporis. Encontramos muestras adicionales en dos sitios en este región; cerca al pueblo de La Pedrera (Departamento Amazonas), y por el bajo Apaporis (Departamento Vaupés). También encontremos varios *R. ventrimaculata*, y es probable que las dos especies son simpátricos en mucho de este región. Aunque la nueva especie y *R. ventrimaculata* tienen atributos ecológicos similares (por ejemplo, el uso de bromelias similares por deposición de renacuajos), las dos especies son distintas con respecto a sus patrones y características de sus cantos. Estudios moleculares indican que la nueva especie no es cercanamente emparentada a los *R. ventrimaculata* simpátricos, más bien es hermana a una especie aparentemente indescrito de *Ranitomeya* de alto Amazonas Brasileiro.

Introduction

The genus *Ranitomeya* (family Dendrobatidae) represents 27 species of small, brightly colored poison frogs and reaches its highest diversity in Amazonian Peru and Andean Colombia (Lötters *et al.* 2007). Within this genus, two divergent clades can be recognized, each representing different geographic radiations. The *minuta* group comprises 12 species occurring in the Colombian Andes, the Chocó, and parts of Panama. The *ventrimaculata* group is composed of 15 species occurring throughout the Amazonian regions of Peru,

Ecuador, Colombia, and Brazil, and part of the Guiana Shield, and is thought to have originated within Amazonia approximately 5.4–8.7 MYA (Santos *et al.* 2009). Despite the exceptionally high diversity of the *ventrimaculata* group in Amazonian Peru, only one species of *Ranitomeya* is known from Amazonian Colombia, *R. ventrimaculata*. This is perhaps surprising, considering the Colombian Amazon covers an area of approximately 403,000 km², an area around half the size of the Peruvian Amazon (approximately 780,000 km²), which contains 15 species of *Ranitomeya*.

We expect that some of this apparent lack of *Ranitomeya* species from Amazonian Colombia can almost certainly be attributed to a sampling deficit rather than low diversity. Although some parts of Colombia have been relatively well-sampled (for example, the Chocó and parts of the Andes, see Silverstone 1975, Myers and Daly 1976), the Amazonian portion of the country has been virtually ignored. One of the few papers mentioning dendrobatids from the Colombian Amazon is Silverstone (1975), which contains records of *Dendrobates quinquevittatus* sensu Silverstone from three different localities: “Aserrío” (southwestern part of the country near the eastern base of the Andes), “mouth [of] Río Loretoyacu near Leticia” (likely Puerto Nariño, 66 km NW from Leticia), and “Río Apaporis” (roughly 320 km N from Leticia). However, *Dendrobates quinquevittatus* sensu Silverstone is thought to represent at least 11 different species (under current species definitions; see Lötters *et al.* 2007); therefore, determining the species identity of older specimens is problematic.

In examining Silverstone’s (1975) sketches, one frog in particular caught our interest: “Pattern F” from Figure 14, which is a sketch of the specimen from Río Apaporis. This frog possesses a dorsal pattern unlike any other known species of *Ranitomeya*, with three pairs of pale dorsolateral dashes and a thin U-shaped line on the snout. The Río Apaporis region is a remote area with a largely undocumented amphibian fauna. The Apaporis is a relatively large, blackwater river flowing southeast and joining Río Caquetá at the Brazilian border. The area near the confluence of these two rivers is interesting in that it contains several low hills which appear to be southern outliers of the sandstone plateaus farther north. The most notable of these is Cerro Yupatí, which rises to an elevation of 405 m near the town of La Pedrera. In 2008 we visited this area, spending a week around La Pedrera and the lower Apaporis. We were able to encounter four individuals strongly resembling Silverstone’s “Pattern F”, and herein describe this frog as a new species of *Ranitomeya*.

Materials and methods

The holotype of the new species is deposited in the herpetology collection of Harvard Museum of Comparative Zoology in Cambridge (MCZ), Massachusetts, U.S.A. Paratypes are preserved in 70% ethanol and deposited in the herpetology collection of the Pontificia Universidad Javeriana in Bogotá, Colombia (indicated with field number prefix JLB08). The following measurements were made with mechanical calipers and on standardized digital photos to the nearest 0.1 mm (nearest 0.01 mm for photo measurements), following Myers (1982) and Brown *et al.* (2006): snout-vent length (SVL), femur length from vent to lateral edge of knee (FL), tibia length from medial edge of heel to lateral edge of knee (TL), knee-knee distance with both legs extended straight (KK), foot length from proximal edge of metatarsal tubercle to tip of toe IV (FoL), hand length from proximal edge of metacarpal tubercle to tip of longest finger (HaL), head length from most exposed corner of occipitum to tip of snout (HL), head width between tympana (HW), body width under axillae (BW), upper eyelid width (UEW), interorbital distance (IOD), horizontal tympanum diameter (TD), horizontal eye diameter (ED), distance from outer corner of eye to tympanum (DET), length of finger I from proximal edge of median palmar tubercle to tip of finger disc (L1F), length of finger II from proximal edge of median palmar tubercle to tip of finger disc (L2F), width of disc of finger III (W3D), and width of finger III just below disc (W3F). Sex was determined by checking for presence/absence of vocal slits.

One free living tadpole was preserved in 70% ethanol for description and staged according to Gosner (1960). Mouthpart formulas follow McDiarmid and Altig (1999).

Advertisement calls of the new species and *Ranitomeya ventrimaculata* used in the analyses were

recorded with a Marantz PMD660 solid state digital recorder and a Sennheiser ME 66-K6 microphone. Calls were analyzed in Raven Pro 1.3 (Charif 2004) and compared to vocalizations of sympatric *Ranitomeya ventrimaculata*.

***Ranitomeya defleri* sp. nov.**

Figures 1–3

Dendrobates quinquevittatus (non Steindachner): Silverstone 1975 (partim) p. 20, Fig. 14, pattern F, (MCZ 28061)

Holotype. MCZ 28061, an adult male collected by I. Cabrera on 31 March 1952 at “Río Apaporis, Colombia”.

Paratypes. All from Colombia. Vaupés: JLB08-001, collected by J. Brown and E. Twomey, 6 August 2008, north bank of Mosiro Itájura (an oxbow lake off Río Apaporis, also known as ‘Lago Taraira’), 98 m elevation, 1° 4' 37.46" S, 69° 30' 51.34" W; approximately 0.2 km SW of Estación Biológica Caparú; JLB08-002, collected by J. Brown and E. Twomey, 7 August 2008, Departamento Vaupés, Colombia (same locality as JLB-001); JLB08-003, collected by J. Brown and E. Twomey, 8 August 2008 (same locality as JLB08-001). Amazonas: JLB08-004, collected by J. Brown and E. Twomey, 4 August 2008, north bank of Río Caquetá near Puerto Córdoba (a village 16.6 km NW from La Pedrera), 68 m elevation, 1° 16' 51.63" S, 69° 43' 10.36" W.

Etymology. The epithet is a patronym for Dr. Thomas Defler, an American primatologist who has worked for 32 years in Colombia. Dr. Defler founded Estación Biológica Caparú in 1983; since that time the station has served as an important outpost for biologists working in Amazonian Colombia.

Definition and diagnosis. Assigned to the genus *Ranitomeya* due to the combination of the following characteristics: small size (< 20 mm SVL), first finger distinctly shorter than second, dorsal coloration conspicuous and bright, dorsal skin smooth, toe webbing absent, maxillary and premaxillary teeth absent, pale limb reticulation present. *Ranitomeya defleri* is a relatively small species of *Ranitomeya*, adult SVL of approximately 15–18 mm. Dorsal body and head are black with irregular yellow markings; pale yellow-green vertebral stripe present on posterior two-thirds of dorsum. Limbs and venter are black with pale to bright blue reticulation forming round black spots on the limbs and irregular spots on the venter. Underside of head has a yellow ‘hourglass’ shape. Teeth absent; finger I shorter than finger II; disc of third finger 2.2–2.6 times wider than finger width. Tadpole gray, ovoid, with irregular yellow markings present from early in development.

Ranitomeya defleri can be distinguished from all other dendrobatids by its distinctive color pattern. Other species with which it could be confused include *R. flavovittata*, *R. vanzolinii*, and *R. ventrimaculata*. *Ranitomeya flavovittata* has highly variable dorsal markings consisting of yellow dots and dashes on a black ground color, similar to *R. defleri*. However, *R. flavovittata* lacks the large yellow blotches behind the eyes as in *R. defleri*. Also, the legs and venter of *R. flavovittata* have a pale blue or gray reticulum (vs. dark blue in *R. defleri*). *Ranitomeya vanzolinii* has a dorsum covered in small yellow spots which are sometimes fused forming dashes, but this species lacks a pale median stripe on the dorsum as found in *R. defleri*. Furthermore, *R. vanzolinii* has a yellow patch on the venter and lacks the yellow ‘hourglass’ found under the chin of *R. defleri*. Both *R. vanzolinii* and *R. flavovittata* share a similar call (a loud ‘trill’ similar to that of *R. imitator*) which differs from the buzz call of *R. defleri*. *Ranitomeya ventrimaculata* is a fairly variable species, but the form found throughout most of Amazonian Peru and Colombia (including near La Pedrera) can be described as having a yellow dorsum with a conspicuous black “Y” which starts at the rump and terminates above the eyelids. This species also lacks the pale median stripe found in *R. defleri* and has coarser black spotting on the limbs and venter. The only other species of *Ranitomeya* we found occurring near *R. defleri* was *R. ventrimaculata*. In addition to differences in color pattern, these two species can be differentiated on the basis of their advertisement calls (Table 1). *Ranitomeya ventrimaculata* has an advertisement call consisting of a series of buzz-like notes, each note 0.174 sec in duration, notes spaced 0.88 sec apart, notes pulsed at a rate of

143 pulses/sec. In *R. defleri*, notes are much longer (0.510 sec in duration), more spaced out (1.44 sec apart), and pulsed at a slower rate (98 pulses/sec).

TABLE 1. Comparison of advertisement call parameters for *Ranitomeya defleri* from type locality and *R. ventrimaculata*. Calls of *R. ventrimaculata* were chosen so there was one representative from the nearest population to *R. defleri* (Yupatí, Departamento Vaupés, Colombia), one representative from the Iquitos-French Guiana clade (Iquitos, Departamento Loreto, Peru), and one representative from the east-Andean versant clade (Shucushuyacu, Departamento Loreto, Peru). Measurements are based on mean values in a call series from a single individual.

Species	Locality	Temperature (°C)	Call parameters				Dominant frequency (Hz)
			Note duration (s)	Note spacing (s)	Pulses/note	Pulses/sec	
<i>R. defleri</i>	type locality	26	0.510	1.44	52.8	99.2	5357
<i>R. ventrimaculata</i>	Yupati	27	0.174	0.88	25.7	143.5	5368
<i>R. ventrimaculata</i>	Iquitos	26	0.230	0.91	19.3	83.9	4483
<i>R. ventrimaculata</i>	Shucushuyacu	25	0.184	1.00	17.0	92.2	5393



FIGURE 1. *Ranitomeya defleri* sp. nov. Male paratype (JLB08-004) in life from Puerto Córdoba, Amazonas, Colombia.

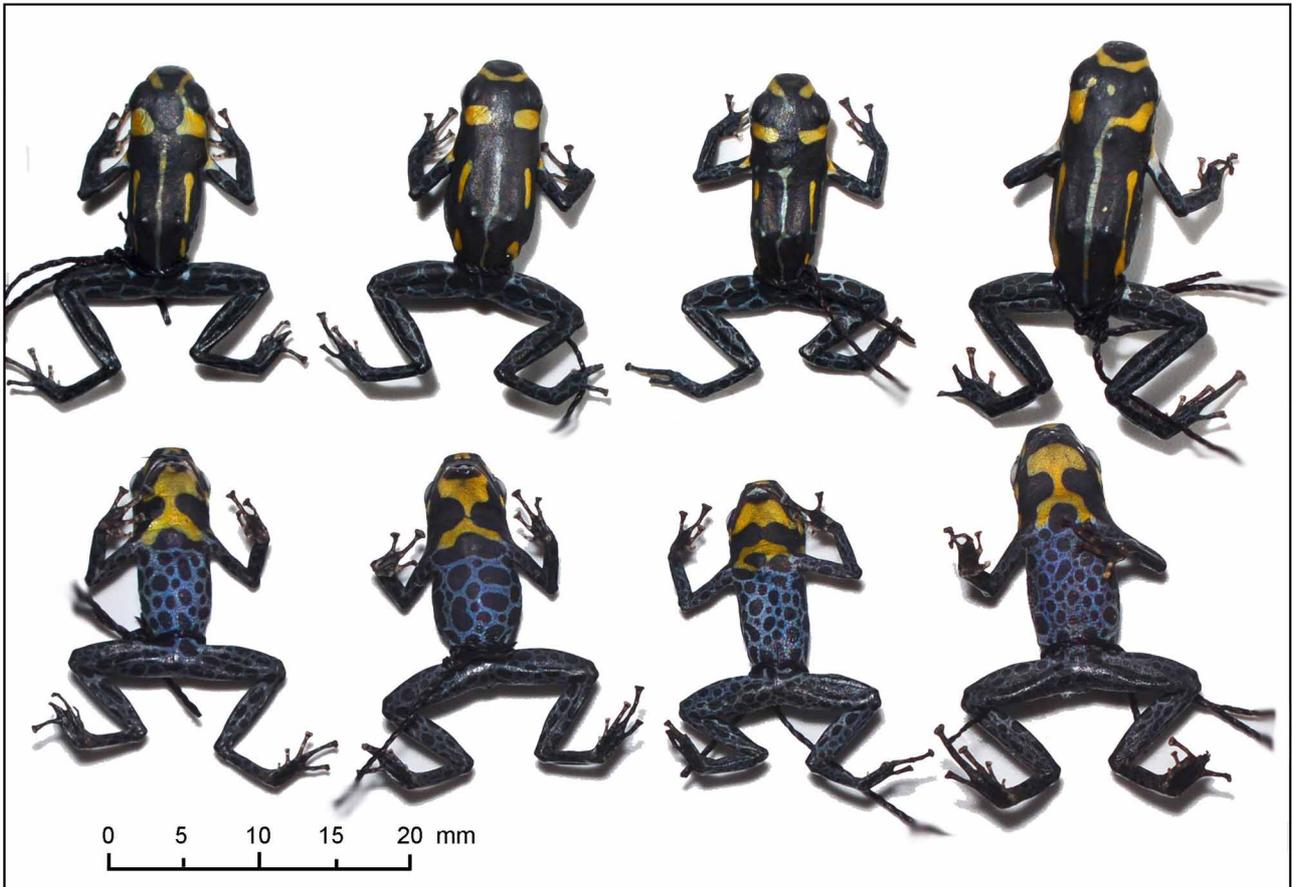


FIGURE 2. Paratypes of *Ranitomeya defleri* with corresponding ventral photos. Left to right, JLB08-001–JLB08-004.

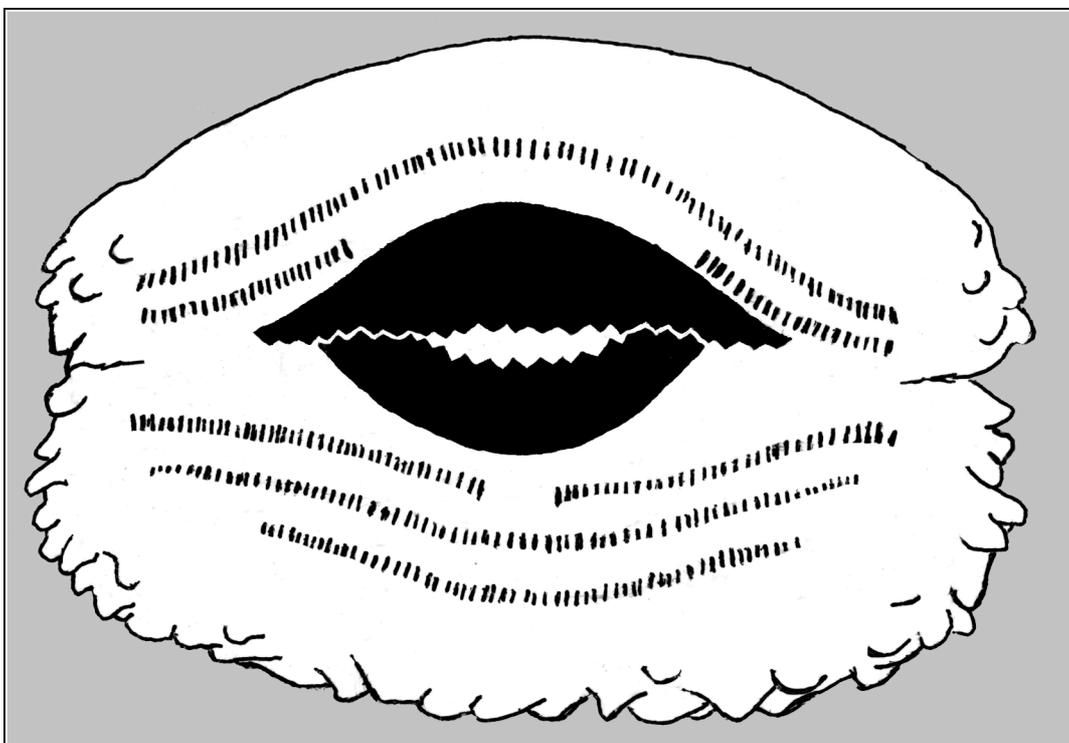


FIGURE 3. Drawing of the mouthparts of the tadpole of *R. defleri*, stage 29.

Measurements (in mm) of holotype. The male holotype has SVL 16.9; FL 7.0; TL 7.3; KK 14.2; FoL 6.3; HaL 4.5; HL 5.0; HW 5.2; BW 5.5; UEW 1.5; IOW 1.4; IND 1.5; TD 0.74; ED 1.26; DET 0.32; L1F 1.16; L2F 1.53; W3D 0.53; W3F 0.21. For paratype measurements see Table 2.

TABLE 2. Measurements (in mm) of *Ranitomeya defleri* type series (five males). Averages (with standard deviation) were calculated from the type series. For abbreviations of characters see Material and methods.

Character	MCZ 28061	JLB08 001	JLB08 002	JLB08 003	JLB08 004	Average
SVL	15.0	15.4	15.5	15.3	17.7	15.8 ± 1.1
FL	7.0	7.2	7.3	6.9	8.2	7.3 ± 0.5
TL	7.3	7.6	7.2	6.7	8.4	7.4 ± 0.6
KK	14.2	14.6	14.9	13.3	16.6	14.7 ± 1.2
FoL	6.3	5.6	6.6	6.0	7.5	6.4 ± 0.7
HaL	4.5	4.1	4.1	3.9	5.1	4.3 ± 0.5
HL	5.0	5.3	5.0	5.3	7.2	5.6 ± 0.9
HW	5.2	4.9	5.0	4.9	5.5	5.1 ± 0.3
BW	5.5	4.7	5.7	4.6	5.6	5.2 ± 0.5
UEW	1.5	2.8	2.6	2.1	3.0	2.4 ± 0.6
IOW	1.4	2.8	2.8	2.5	3.6	2.6 ± 0.8
IND	1.5	2.3	2.3	2.1	2.7	2.2 ± 0.4
TD	0.74	0.97	0.87	0.86	0.96	0.88 ± 0.09
ED	1.26	2.10	2.10	2.29	2.20	1.99 ± 0.42
DET	0.32	0.39	0.53	0.41	0.51	0.43 ± 0.07
L1F	1.16	1.82	1.81	1.67	2.00	1.69 ± 0.32
L2F	1.53	2.43	2.43	2.34	2.80	2.31 ± 0.47
W3D	0.53	0.98	0.80	0.81	0.86	0.80 ± 0.17
W3F	0.21	0.42	0.33	0.37	0.33	0.33 ± 0.08

Description of holotype. Widest part of head is at jaw articulations. Head slightly narrower than body. Tongue ovoid; teeth absent. The holotype is notable in that its pattern is approximately symmetrical on right and left halves. In preservative, the head is black with large, pale yellow dorsolateral spots behind each eye, snout is yellow anterior from orbits. On the snout, a black “U” connects nares through loreal region; creating a yellow spot on the tip of the snout and a thin yellow stripe just anterior to the eyes which crosses the head and terminates on the upper lips. Dorsum black with two yellow dorsolateral dashes on either side; thin, irregular yellowish-gray vertebral stripe extending from vent to approximately 2/3 distance towards eyes. There is a weakly-defined pale yellow spot on the dorsal surface of the axilla, extending partially onto the anterior flank; another yellow spot is present at the corner of the mouth. The arms, legs, and toes are covered in a pale gray reticulum (presumably blue in life) over a black ground color, creating round black spots; toes are gray. Underside of head yellowish-gray with lateral black gular spots, creating appearance of a pale hourglass. Lower lip color matches color of dorsolateral dashes. Venter black with discrete gray reticulation, creating black spots, much like the limbs. Iris black.

In preservative, skin texture nearly smooth on the dorsal surfaces of the body and head; limbs and rump weakly granular. Venter weakly granular on limbs and body, ventral surface of head nearly smooth. Snout sloping and rounded in lateral profile, round or slightly blunted in dorsal profile. Nares situated at tip of snout and directed laterally; both nares visible from ventral and anterior view but not from dorsal view. Canthus rostralis rounded, loreal region flat and nearly vertical. Upper eyelid approximately equal in width to

interorbital distance; internarial distance roughly equal to eye width. Tympanum round, partially concealed posterodorsally.

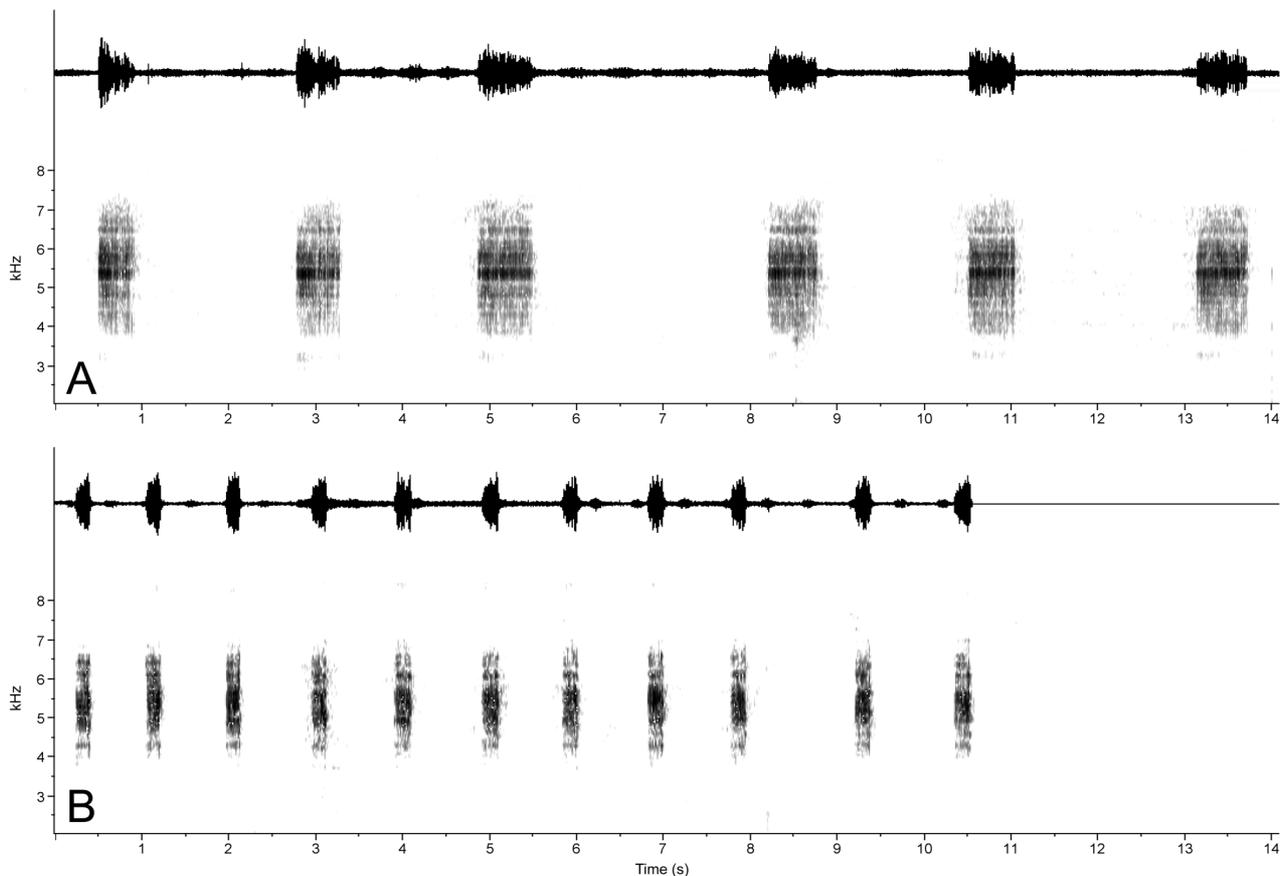


FIGURE 4. Advertisement calls of (A) *R. defleri* from type locality, recorded 8 August 2008 at 26° C. (B) Advertisement call of *R. ventrimaculata* from Cerro Yupatí, recorded 5 August 2008 at 27° C.

Hands relatively large, length 28.1 % of SVL. Relative length of appressed fingers III > IV > II > I; first finger 75.8 % length of second; finger discs moderately expanded, width of disc on finger III 2.5 times width of adjacent phalanx. An unpigmented median metacarpal tubercle is present on base of palm; inner metacarpal tubercle present near base of finger I; unpigmented proximal subarticular tubercles present on base of each digit, except on finger I, where tubercle is part-way up the digit; distal subarticular tubercle visible only on fingers III and IV. All tubercles raised above level of hands; scutes present on dorsal surface of fingers.

Hind limbs moderate length, with heel of appressed hind limbs reaching level of eye. Femur and tibia roughly equal in length, tibia 1.04 times length of femur; knee-knee distance 88.8 % of SVL. Relative lengths of appressed toes IV > III > V > II > I; first toe short with unexpanded disc; second toe with slightly expanded disc, discs on toes III–V moderately expanded. Two unpigmented metatarsal tubercles present on base of foot, one situated medially near base of toe I, the other situated laterally at the base of the fifth metatarsal. Proximal subarticular tubercles present at base of each toe but most notable on toes I and II due to their lack of pigmentation. Toes III and V with two subarticular tubercles, toe IV with three subarticular tubercles. A tarsal keel is present starting below the ankle and turning into the medial metatarsal tubercle at the foot. Tarsal tubercle absent; feet and hands lacking webbing and lateral fringing.

Variation. Adult males range from 15.3–17.7 mm SVL, females unknown. Head width 87–104 % of body width; head width 31–33 % of SVL. Tibia can be longer or shorter than femur; TL/FL ranges from 0.97 to 1.05. Knee-knee distance 87–96 % of SVL.

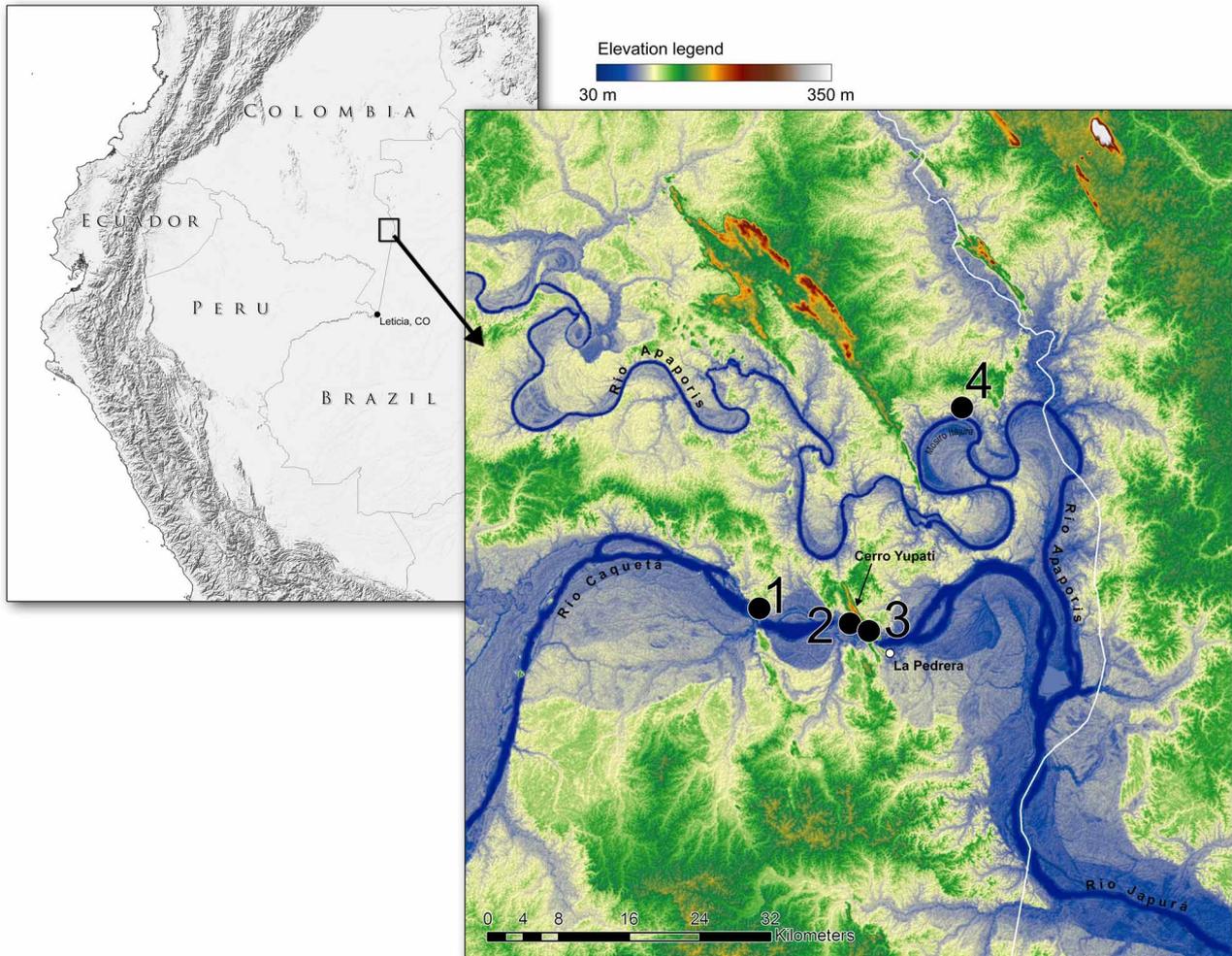


FIGURE 5. Map of study area. All localities in Colombia: (1) Puerto Córdoba, Departamento Amazonas, $1^{\circ} 16' 51.63''$ S, $69^{\circ} 43' 10.36''$ W, (*R. defleri*); (2) Angosturas, Departamento Amazonas, $1^{\circ} 17' 47.84''$ S, $69^{\circ} 37' 38.77''$ W, (*R. ventrimaculata* and putative *R. defleri* tadpoles); (3) Cerro Yupatí, Departamento Amazonas, $1^{\circ} 18' 15.59''$ S, $69^{\circ} 36' 30.28''$ W, (*R. ventrimaculata*); (4) Caparú, Departamento Vaupés, $1^{\circ} 4' 37.46''$ S, $69^{\circ} 30' 51.34''$ W (*R. defleri*). Two other dendrobatids were found in this region (*Ameerega trivittata* in Puerto Córdoba and Caparú, and *A. hahneli* in Puerto Córdoba).

The type series (Fig. 2) displays substantial variation in color pattern and most individuals are not as symmetrical as the holotype. For example, JLB08-004 has a vertebral stripe which connects to the right eyespot (vs. terminating mid-dorsum in the holotype), has only one elongate dorsolateral dash on either side (vs. two dashes in the holotype), and has whitish axillary spots (vs. yellow in the holotype). JLB08-001 lacks a defined “U” on the snout as in the holotype; rather, it has an irregular yellow blotch on the right side of the head which connects with the right eye spot. JLB08-003 also lacks a “U” on the snout, possesses irregular spots on the flanks (vs. regular and symmetrical dashes in the holotype), and has a vertebral stripe with small lateral branches (vs. branches absent in the holotype). We should note that the sketch of the holotype presented in Silverstone 1975 (p. 20, Fig. 14, pattern F) is drawn inaccurately; this was also mentioned by Myers (1982): “the Colombian frog [= MCZ 28061] is inaccurately drawn. The artist unfortunately omitted a pale vertebral line which was still conspicuous on the specimen when I saw it in 1980.” This pale vertebral line was still visible as of 2009.

Tadpole: A stage 29 tadpole was used for the description. This tadpole was collected on 4 August 2008 from the bromeliad in which one of the paratypes (JLB08-004) was calling. Total length 19.6 mm, body

length 7.1 mm, body width 4.4 mm. Snout rounded when viewed from above; body ovoid in dorsal view. Eyes black and conspicuous, dorsal, angled anterolaterally, pupils white in preservative. Nares not forming tube, situated half-way between eye and tip of snout, directed anterolaterally. Spiracle sinistral; vent dextral. Maximal tail height 2.9 mm measured half-way along tail length. Ventral tail fin begins at tail base, dorsal tail fin begins just posterior to plane of vent opening, ventral and dorsal fins relatively uniform in thickness throughout tail, tapering towards tip. Maximum musculature height 1.7 mm measured at tail base; height uniform throughout, tapering towards tip.

The mouth (Fig. 3) is directed anteroventrally. Oral disc emarginate, anterior and posterior labia forming flaps free from body wall, 1.5 mm in width. Marginal papillae absent on anterior labium except for lateral-most portion (4-6 papillae present), present on posterior labium in one row but with a distinct medial gap. Papillae white, conical; submarginal papillae absent. Jaw sheaths deep in longitudinal width, serrate, posterior sheath has a curved medial indentation. Lateral processes short, extending slightly past lower jaw. Labial tooth row formula is 2(2)/3(1). A-1 complete, A-2 with broad medial gap, same width as A-1. P-1 with small medial gap, P-2, and P-3 complete; P-1 and P-2 equal width, P-3 slightly shorter.

In preservative, pigmentation on the head and dorsum is mottled brown with a white ground color. This mottling is most dense on the vertebral region and head, less dense around the sides. Ventral coloration is almost entirely white, although small black melanophores are visible under a dissecting microscope. These melanophores cover the venter uniformly, with the exception of the mouthparts and vent tube, which lack any dark markings. The gut appears pale brown and is visible through the skin. Tail musculature pale brown, fins translucent white. The entire tail is covered with a faint reticulation of pale brown that is more dense around the musculature and less dense around the fins and the distal region of the tail. The tadpole had conspicuous dorsal markings in life, although these have faded in preservative. These markings were yellow in life; dorsal ground color in life was gray.

Vocalizations. On 6 August 2008 in Caparú we heard “a call that sounded like a *ventrimaculata* but quieter and longer with notes more spaced-out” (ET, field notes). This frog was collected and later designated a paratype. Although this individual ceased calling before we could obtain a recording, two days later we recorded another individual calling from the exact same spot. We were unable to capture this individual, but the call sounded similar to the call of the paratype. Furthermore, we are confident this call belongs to *R. defleri* (rather than *R. ventrimaculata*) because we witnessed the paratype from Puerto Córdoba making a similar call immediately prior to collection, and because we never found *R. ventrimaculata* in Caparú. The following call description is thus based on a recording of a single (uncollected) male; sample sizes refer to the number of individual notes (or spaces between notes) used for the analysis. Call data is reported as means, where *n* is the number of notes used to calculate the mean.

The advertisement call of *R. defleri* is a series of buzz-like notes (Fig. 4A) with the following parameters: mean note length 0.510 sec (*n* = 19); note spacing 1.44 sec (*n* = 15); dominant frequency 5357 Hz (*n* = 6); pulses per note 52.8 (*n* = 6); pulse rate 99.2 pulses/sec (*n* = 6). This species appears to call in weakly defined ‘bouts’ which consist of 3–8 regularly-spaced notes; pauses between bouts were typically 3 sec or more. Mean notes per bout 4.7 (*n* = 10 bouts); mean bout duration 8.31 sec (*n* = 10 bouts). Within a bout, notes are repeated at a mean rate of 1 note per 1.77 sec.

The call of *R. defleri* sounds similar to the call of *R. ventrimaculata*, but the latter species clearly differs in that notes are much shorter and more closely spaced. On 5 August 2008, we recorded a *R. ventrimaculata* from Cerro Yupatí, a 405 meter-high hill on the north bank of Río Caquetá just across the river from La Pedrera. This call is also a series of buzz-like notes (Fig. 4B); mean note length 0.174 sec (*n* = 23); note spacing 0.88 sec (*n* = 12); dominant frequency 5368 Hz (*n* = 9); pulses per note 25.7 (*n* = 9); pulse rate 143.5 pulses/sec (*n* = 9). This species also appears to call in weakly defined bouts consisting of 3–13 regularly-spaced notes; pauses between bouts are usually 6 sec or more. Mean notes per bout 7 (*n* = 6); mean bout duration 6.62 sec (*n* = 6). Within a bout, notes are repeated at a mean rate of 1 note per 0.95 sec. We have analyzed the calls of an additional 21 *R. ventrimaculata* individuals from throughout most of its range, and the overall mean note length for this species is 0.27 sec, roughly half the length of *R. defleri* notes.



FIGURE 6. Forest near Estación Biológica Caparú (6 August 2008).

Distribution and natural history. *Ranitomeya defleri* occurs in southeastern Colombia, where it is known from only two localities (Fig. 5) 32 km apart (Euclidean distance). This species likely occurs more widely throughout the Apaporis-Caquetá drainage (including in Brazil), although further sampling is needed to determine the extent of its distribution. Since much of the forest in the Apaporis region is seasonally flooded, this species may be absent from low-lying areas such as igapó forests. When we visited this region in August of 2008, nearly all of the forest south of the Caquetá was flooded several kilometers inland. It is possible that these large expanses of flooded forest may impose a southern limit to the distribution of this species, as we were unable to find *R. defleri* in La Pedrera (located on the south side of Caquetá) or in the forests around Leticia and Puerto Nariño. It does appear, however, that *R. defleri* occurs in very low-lying

forests, as the Puerto Córdoba locality was just a few meters above the flood zone.

The sites where we found *R. defleri* were generally undisturbed, primary forests. These forests are located in the “Caquetá Moist Forest” (Millikin 2008), one of the world’s eco-regions as defined by the World Wildlife Fund. Caparú has a mean annual temperature of 25.1° C (Defler 1996), with a mean annual rainfall of 3836 mm (Defler and Defler 1996). There is little seasonal variation in rainfall, with the driest month (September) receiving 258 mm rainfall on average, compared to an average monthly precipitation of 319 mm (Defler and Defler 1996). Forests along Río Apaporis and near La Pedrera appear to have had little or no impact from humans. Caparú is one of the most pristine examples of lowland rainforest we have seen, with many large trees and a relatively sparse understory with little light penetration (Fig. 6). The canopy in the sites where the frogs were found is dominated by trees of the families Fabaceae (legumes), Moraceae (figs), Euphorbiaceae (spurges), and Arecaceae (palms) (Defler and Defler 1996). The understory consists mostly of large palms and tree saplings, and the ground is covered by a thick, wet leaf litter. Most woody surfaces in the understory are covered with moss, yet very few bromeliads can be found despite these wet conditions. The most common bromeliads are a slender, spiny species which grow on the sides of trees, forming small clumps of 2–4 plants. These bromeliads are small, approximately 8 inches tall by 6 inches in diameter, but contain a substantial volume of water in their central axil (mean = 32 ml, range = 20–42 ml, $n = 4$). In Caparú, we were unable to find tadpoles of *R. defleri*, but we did find an *R. defleri* tadpole in Puerto Córdoba in one of these bromeliads. Additionally, we found tadpoles in a site at the western foot of Yupatí (Angosturas in Fig. 5), which may belong to *R. defleri* based on color pattern. These tadpoles were found in the central axil of a similarly-shaped bromeliad which was growing terrestrially. Small egg clutches (2–4 eggs) were also found in these bromeliads, although we do not know whether these belonged to *R. defleri* or *R. ventrimaculata*. Adults were found at different heights in the forest. Two of the specimens from Caparú were found at the base of trees, while the third was found amidst low-growing shrubs growing on a stream-bank. The single specimen from Puerto Córdoba was found in a bromeliad at roughly 3 meters from the ground, where it was courting a female. We heard males calling in the morning (9 h) and evening (18 h), although the call is faint and easily missed. Population densities of *R. defleri* appear to be low in the areas we searched. In Caparú, we were able to find only three individuals in three full days of searching, and only found one during three days around La Pedrera. In Caparú, we met two Colombian biologists that had been conducting a herpetological survey for the past month, consisting of daily surveys, and found only a single *R. defleri*.

Conservation status. Following the IUCN Red List criteria (IUCN 2001), we suggest this species be listed as Least Concern (LC). Although the area of occupancy for this species is unknown, the Apaporis region has experienced minimal habitat loss due to deforestation. Few people live in this area, and those that do rely primarily on fishing rather than agriculture for subsistence. As such, there is little risk of significant habitat loss in the near future.

Discussion

During the past three decades, there has been a steady rise in the number of species teased apart from *Dendrobates quinquevittatus* sensu Silverstone (1975) as new data has become available. Under current species definitions, Silverstone’s definition of *D. quinquevittatus* included specimens of *Adelphobates quinquevittatus* sensu stricto (Caldwell and Myers 1990), *Excidobates captivus* (Myers 1982), *Ranitomeya amazonica* (Schulte 1999), *R. benedicta* (Brown *et al.* 2008), *R. defleri* (this paper), *R. fantastica* (Myers 1982), *R. lamasi* (Morales 1992), *R. summersi* (Brown *et al.* 2008), *R. vanzolinii* (Myers 1982), *R. ventrimaculata* (Caldwell and Myers 1990), and an undescribed species of *Ranitomeya* from Brazil (see “Ventrimaculatus Clade 3” in Fig. 1 and individual E in Fig. 2 in Brown *et al.* 2006; herein referred to as *Ranitomeya* sp. B). Undoubtedly, additional species in this group remain to be described, as large tracts of upper-Amazonian rainforest remain virtually unstudied (e.g., Amazonian Colombia, northern Peru, and nearly the entire Peru/Brazil border).

Based on an unpublished molecular phylogeny (including 202 individuals representing 25 species of *Ranitomeya* using 12s, 16s, and cyt-b), *R. defleri* (Genbank accession numbers GU062190–GU062192) is sister to *Ranitomeya* sp. B, although the two species display substantial morphological and genetic divergence (greater than 7 % genetic distance in the aforementioned phylogeny) (unpubl. data). We have examined specimens of *Ranitomeya* sp. B from several localities in Brazil, and there appears to be minimal morphological variation in this species even over large geographic areas. This species is superficially similar in dorsal color and pattern to *Adelphobates quinquevittatus* (see Caldwell and Myers 1990, Fig. 11, individual A) and *R. biolat*, with three thin, complete longitudinal stripes which are yellow in life (T. Grant *in litt.*, 27 February 2009).

The marked difference in call parameters between *R. ventrimaculata* and *R. defleri* in sympatry may be relevant to maintenance of species boundaries, as the two species appear to utilize similar breeding resources. Previous authors have shown that temporal aspects of calls may be important for species recognition. For example, pulse rate has been shown to be important for interspecific recognition in several species of hylid frogs (see Wells 2007 for a review). In the case of *R. ventrimaculata* and *R. defleri*, temporal differences in calls may be especially important since the two species share similar frequency domains (buzz-like calls with a dominant frequency of approximately 5300 Hz). Although we do not know whether *R. defleri* displays call variation in other parts of its range, *R. ventrimaculata* displays substantial variation throughout its range with respect to note repetition rate and pulse rate. The elevated pulse rate of *R. ventrimaculata* in the Apaporis region may aid its ability to distinguish from *R. defleri* calls.

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