

## A NEW AMAZONIAN SPECIES OF *CRYPTOPHYLLOBATES* (ANURA: DENDROBATIDAE)

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**ABSTRACT:** A new genus, *Cryptophyllobates*, was recently described for a species of dendrobatid that was originally described as *Phyllobates azureiventris*. One of the distinguishing characters of this frog is the presence of dorsolateral stripes that end on the posterior back above the thighs. While conducting fieldwork in Acre, Brazil, I collected an unusual dendrobatid that transported all tadpoles in a clutch at one time; however, tadpoles of this species were more similar to *Dendrobates* than to *Epipedobates*. I subsequently discovered that this species is similar to *Cryptophyllobates azureiventris* and herein describe it as the second species in this genus. Molecular studies indicated that the new species and *C. azureiventris* are sister species and that they are closely related to some clades of *Colostethus*. Courtship of the new species was not observed, but tadpoles were found in a pool in a fallen tree, and adults were frequently seen in treefall gaps. Tadpoles are similar to those of *Dendrobates* in that they are predaceous, possibly as a result of convergence in behavior in response to development in similar restricted microhabitats.

**Key words:** Acre; Brazil; Amazon rainforest; *azureiventris*; Dendrobatid frogs; Poison frogs

GENERIC delimitations and relationships among dendrobatid frogs have been a source of confusion, partly because of convergence in color patterns and morphology of many species. Only three genera, *Colostethus*, *Phyllobates*, and *Dendrobates*, were recognized for many years. In 1987, Myers described two additional genera, *Epipedobates* and *Minyobates*, and since that time, five others have been described, four of which, *Aromobates*, *Mannophryne*, *Nephelobates*, and *Allobates* are generally accepted (La Marca, 1992; La Marca, 1994; Myers et al., 1991; Zimmerman and Zimmerman, 1988).

Recently, a new dendrobatid genus, *Cryptophyllobates*, was described for the Peruvian frog originally described as *Phyllobates azureiventris* (Kneller and Henle, 1985; Lötters et al., 2000). Only one species has been assigned to this genus to date. Since its original description, the affinities of this species have been uncertain, and the species has variously been assigned to *Dendrobates* (Myers and Burrowes, 1987) and to *Epipedobates* (Myers, 1987).

While conducting fieldwork in lowland Amazonian forest in the state of Acre in western Brazil in 1996, my field party and I discovered a frog with characteristics similar to

*C. azureiventris*. I recognized this frog as different from species of *Dendrobates* in that all tadpoles from a clutch are transported at once; however, other characteristics of the tadpoles are more similar to *Dendrobates* than to *Epipedobates*. Herein, I describe this species as the second species in the genus *Cryptophyllobates*.

### METHODS

Frogs were observed and/or captured during the course of a herpetological survey in lowland primary forest near Porto Walter, Acre, Brazil, a small village on the Rio Juruá accessible only by boat. The field site was located about 5 km W of Porto Walter (8° 16' S by 72° 46' W) (Fig. 1). Large treeholes were relatively rare in the forest; only two were found. Tadpoles were found in a pool formed in the trunk of a large fallen tree. The only disturbance of the forest at the time was the removal of selected large trees by the property owner; cutting these trees created gaps similar to natural treefalls. This area is no longer forested; it was converted to cattle pasture soon after our departure from the site. Additional details on the site and the effects of the artificially created treefall gaps are reported in Vitt et al. (1998) and in Caldwell and Oliveira (1999). The field party consisted of four people; fieldwork was carried out from 9 February to 18 April 1996. Our campsite was

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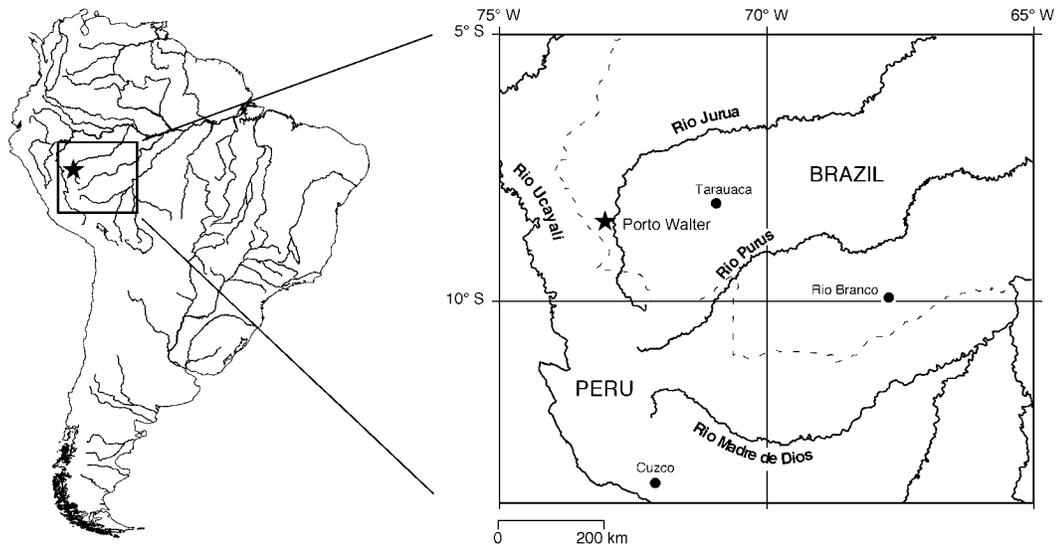


FIG. 1.—Map of South America with inset showing type locality near Porto Walter, Acre, Brazil.

constructed in minimally disturbed Amazonian lowland forest.

Eighteen specimens of the new species, including nine males, four females, and five juveniles, were captured during the course of the survey. We recorded habitat data on others that were not collected. Of the five juveniles collected, two were taken as tadpoles from a small pool in a fallen tree and allowed to metamorphose in the field laboratory prior to preservation. Specimens were initially fixed in 10% formalin and subsequently transferred to 70% ethanol for permanent storage.

Measurements (in mm) of preserved adult specimens were made with digital calipers or with a micrometer on a dissecting microscope, following Caldwell and Lima (2003): snout-vent length (SVL); head length from corner of mouth to tip of snout (HL); head width at level of angle of jaws (HW); snout length from anterior corner of eye to tip of snout (SL); eye to naris distance from anterior corner of eye to center of naris (EN); internarial distance (IN); eye length from anterior to posterior corner (EL); interorbital distance (IO); diameter of tympanum (TYM); forearm length from proximal edge of palmar tubercle to outer edge of flexed elbow (FAL); hand length from proximal edge of palmar tubercle to tip of Finger III (HAND); width disc on Finger III (WFD); tibia length from outer edge of flexed knee to

heel (TL); and foot length from proximal edge of outer metatarsal tubercle to tip of Toe IV (FL); width disc on Toe IV (WTD).

A total of 38 tadpoles in eight lots were collected. Five lots with a total of 34 tadpoles were taken from the backs of parent frogs; in addition, three lots with a total of four large tadpoles were free-living. Tadpoles were fixed and stored in 10% formalin. Tadpoles were staged according to Gosner (1960); measurements were made with digital calipers or with a micrometer on a dissecting microscope.

Photographs of preserved specimens were taken in the laboratory with a Canon EOS D-10 digital SLR camera outfitted with Canon autobellows and a 68-mm extension tube; a Leitz Summar 12-cm lens was used. Lighting was supplied by a Fostec fiberoptic ring. Images were transferred to a PowerMac computer using Canon RemoteCapture 1.0.

Specimens were deposited in the herpetology collections of the Museu Paraense Emílio Goeldi (MPEG) in Belém, Brazil, and the Sam Noble Oklahoma Museum of Natural History (OMNH). Color in life was taken from field notes of J. P. Caldwell. Additional specimens examined are from the Natural History Museum of The University of Kansas (KU). Specimens examined are listed in Appendix I. All measurements are in mm. Values given are means  $\pm$  SD.

## SPECIES DESCRIPTION

*Cryptophyllobates chlorocraspedus* sp. nov.  
(Fig. 2)

*Holotype*.—MPEG 12504 (original field no. JPC 13230), an adult male obtained on 1 March 1996 by Janalee P. Caldwell and Laurie J. Vitt from Brazil: Acre: ca. 5 km west of Porto Walter (8° 15' 31.2" S by 72° 46' 37.1" W), a small village on the Rio Juruá.

*Paratypes*.—OMNH 36169–77; MPEG 12505–12.

*Etymology*.—The species name, *chlorocraspedus*, is derived from the Greek *chloro* meaning green and the Greek *craspedus* meaning edge or border, in allusion to the bright lime green dorsolateral border that is continuous from the snout to the posterior dorsum.

*Definition and diagnosis*.—A medium-sized dendrobatid, SVL of largest male 27.3 and largest female 28.2 (Fig. 3). Body black with wide continuous stripe beginning on snout, extending onto back as dorsolateral stripes, and ending dorsally on posterior back. A labial stripe begins below eye and extends onto lip and upper forearm, ending at elbow. No stripe is present in groin or along side. Webbing is absent on fingers; toes have a trace of webbing between Toes II and III and between Toes III and IV. Males and females are not sexually dimorphic with respect to size of Finger III. Tadpole large, total length of largest tadpole at Stage 25 is 32.5 mm.

Molecular studies revealed that the two species of *Cryptophyllobates* are most closely related to mostly undescribed Ecuadorian and Peruvian *Colostethus* (unpublished data, J. C. Santos, L. A. Coloma, J. P. Caldwell, K. Summers, and D. C. Cannatella; see Discussion). Nevertheless, because color and pattern of the new species and some species of *Epipedobates* and *Phyllobates* are similar, I include comparisons among them in the diagnosis. Rodríguez and Myers (1993) noted that color in life provides good diagnostic characters for distinguishing morphologically similar species of *Epipedobates*; however, many other characters, including often neglected tadpole characters, distinguish most, if not all, dendrobatids. *Cryptophyllobates chlorocraspedus* differs from all species of *Colostethus* by being aposematically colored with brilliant lime green or yellow-green

dorsolateral stripes and other markings on a black ground color. It differs from all species of *Dendrobates* by having teeth present on the maxilla and premaxilla. It differs from similar and geographically proximal species of *Epipedobates* (including *E. bassleri*, *boulengeri*, *petersi*, *planipaleae*, *rubriventris*, *simulans*, and *smaragdinus*) in that these species have dorsolateral or lateral stripes (i.e., oblique lateral stripes) ending in the groin, not dorsally on the back above the thighs (Lötters et al., 1997; Morales and Velazco, 1998; Myers et al., 1998; Rodríguez and Myers, 1993; Silverstone, 1976). *Cryptophyllobates chlorocraspedus* differs from other species of *Epipedobates* (including *E. bilinguis*, *cainarachi*, *macero*, and *parvulus*) in that these species have deep red or brick red dorsa (Morales and Velazco, 1998; Rodríguez and Myers, 1993).

*Cryptophyllobates chlorocraspedus* is distinguished from *Phyllobates aurotaenia* in that the latter lacks a labial stripe and has a finely speckled pattern on the limbs and from *P. vittatus* by the presence (in *P. vittatus*) of a gold, orange, or red-orange dorsolateral stripe, a ventrolateral stripe extending from the groin to the arm insertion, and fine speckling on the limbs. *Cryptophyllobates chlorocraspedus* is distinguished from *C. azureiventris* by the lack of a lateral (i.e., oblique lateral) stripe (present in *C. azureiventris*), by the color of the stripes (bright lime or yellow-green in *C. chlorocraspedus*, bright yellow or orange in *C. azureiventris*), by the color pattern on the limbs (black with large, irregular lime green markings in *C. chlorocraspedus*, black with fine reticulations of blue, blue-green, or yellow-green in *C. azureiventris*), and by a trace of webbing between Toes II and III and between Toes III and IV in *C. chlorocraspedus* (absent in *C. azureiventris*).

*Description of the holotype*.—An adult male, head longer than wide, head width 92.5% of head length; head width between angles of jaws 33.1% of SVL. In dorsal view, snout truncated with slight rounding, bluntly rounded in lateral view, 52.9% of head length (Fig. 4). Nares opening posterolaterally, near tip of snout, internarial distance 43.6% of head width. Canthus rostralis rounded, loreal region flat. Eye–naris distance 67.0% of eye length; lower jaw with small medial knob that fits into upper jaw. Tympanum round, 44.2% of eye length,

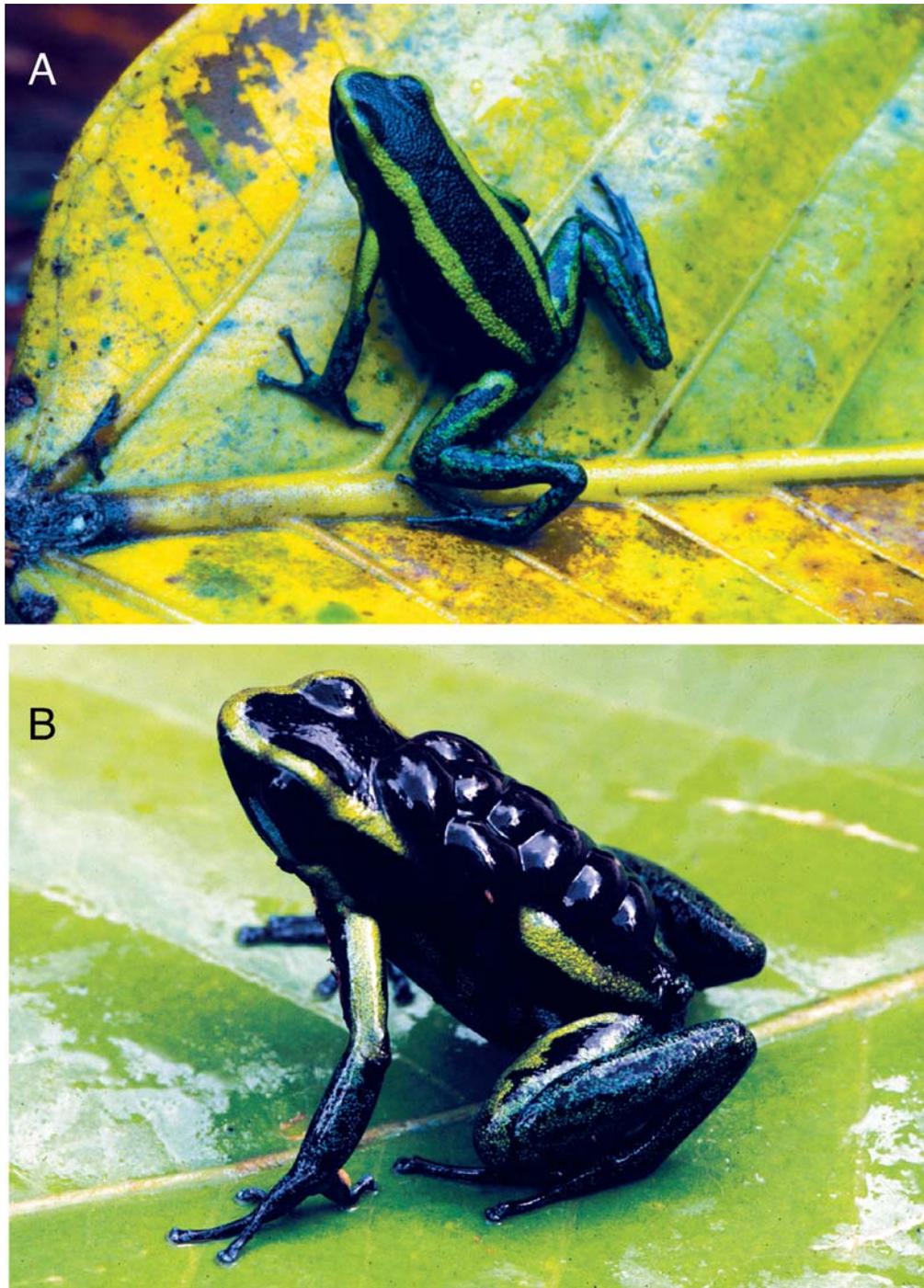


FIG. 2.—*Cryptophyllobates chlorocraspedus*. (A) Male, OMNH 36169, SVL 28.0 mm. (B) Male transporting 8 tadpoles, MPEG 12508, SVL 27.3 mm. Photographs by JPC.

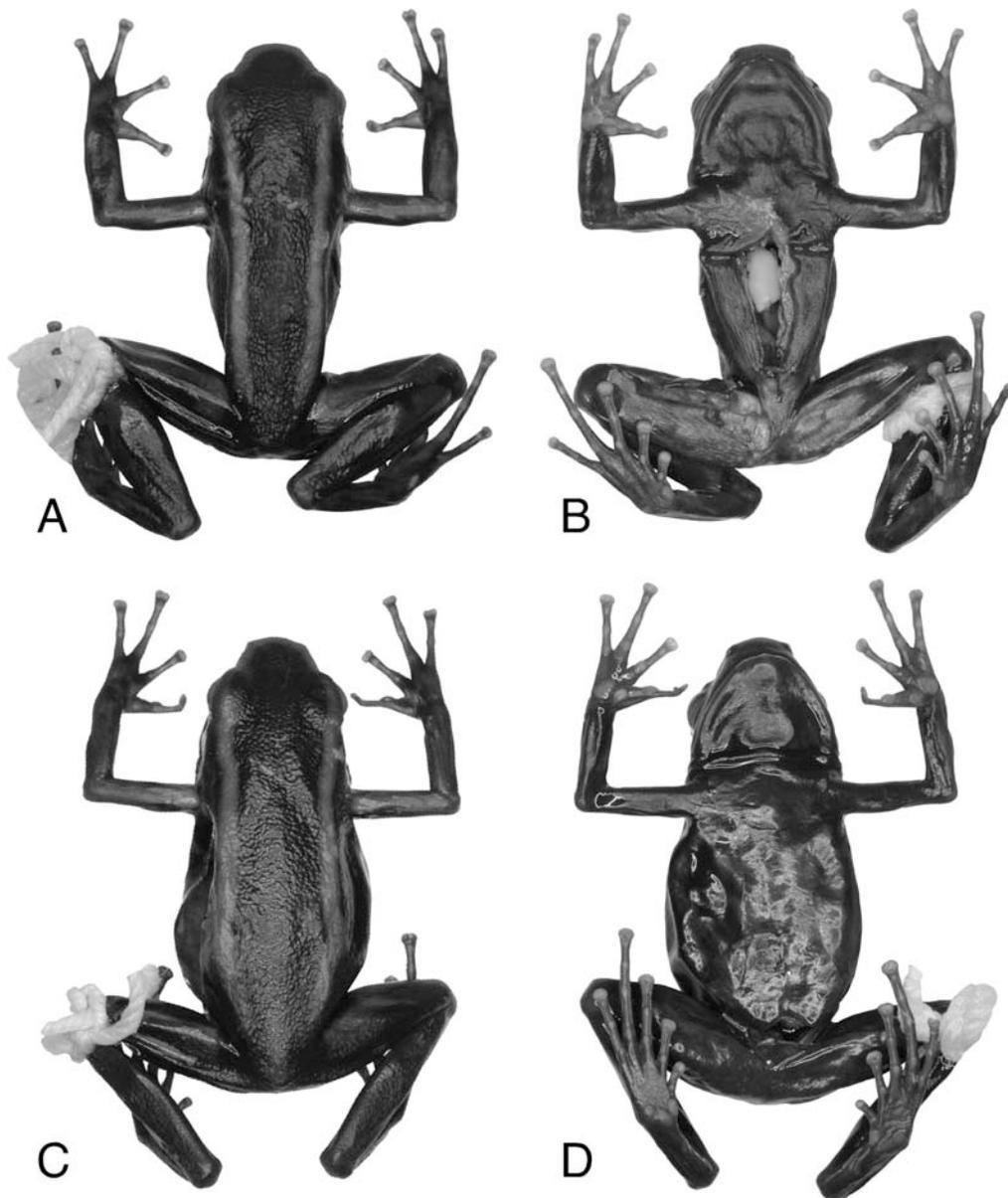


FIG. 3.—(A) Dorsal view of male holotype of *Cryptophyllobates chlorocraspedus*, MPEG 12504, SVL 24.1 mm. (B) Ventral view of holotype. (C) Dorsal view of female *Cryptophyllobates chlorocraspedus*, OMNH 36174, SVL 29.1 mm. (D) Ventral view of female.

directed posterolaterally. Posterodorsal margin of tympanum hidden by depressor muscle.

Tongue attached anteriorly; anterior margin squarish, median lingual process absent. Paired vocal slits elongate, extending nearly from corner of jaw to anterior tongue insertion. Small teeth present on maxilla and premaxilla.

Dorsal skin of head, body, and sides finely granular; skin on sides of head and dorsal surfaces of arms smooth. Skin on dorsal surfaces of legs barely granular. Skin on all ventral surfaces smooth. Anal flap absent; no anal tubercles. Dorsolateral stripe distinct, wide, continuous from around top of snout

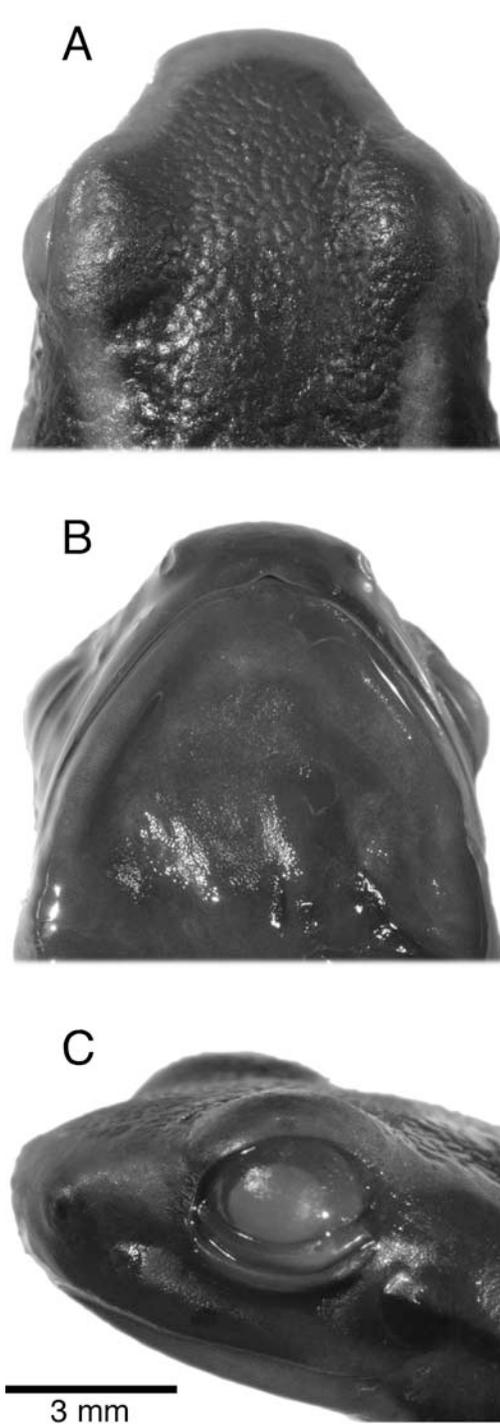


FIG. 4.—Head shape of holotype of *Cryptophyllobates chlorocraspedus*, MPEG 12504. (A) Dorsal view. (B) Ventral view. (C) Lateral view.

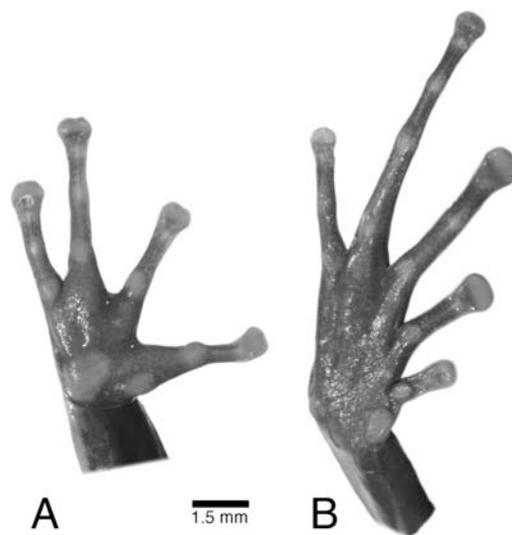


FIG. 5.—(A) Right hand of holotype *Cryptophyllobates chlorocraspedus*, MPEG 12504. (B) Right foot of holotype.

above eyes to terminate on posterior back above the thighs. Partial labial stripe begins below eye and extends along lip below tympanum onto upper arm, ending at elbow. Lateral stripe absent; three small diffuse spots present in groin on right side, one on left side.

Forelimb slender; hand length 29.3% of SVL; Finger I slightly shorter than Finger II when fingers appressed; Finger III > II > I > IV; Finger III not swollen (Fig. 5A). Palmar tubercle oval, 1.6 in diameter, 22.2% of hand length. Thenar tubercle oval, 0.93 in diameter. Tiny, white supernumerary tubercle on outer edge of both hands, located 0.2 from palmar tubercle on right hand. No fringes on fingers; no webbing between fingers. Subarticular tubercles present, one each on Finger I and II, two on Fingers III and IV. Basal subarticular tubercles large; distal subarticular tubercles of Fingers III and IV faint. Tips of digits somewhat expanded, disc width twice width of finger below disc; discs on all fingers with distinct paired dorsal scutes.

Hind limbs moderately slender. Tibia length 53.5% of SVL; foot length, 44.3% of SVL (Fig. 5B). Relative length of appressed toes IV > III > V > II > I. Toe discs not greatly expanded; fourth toe disc width slightly smaller than twice width of toe below it. Discs of Toes II, III, and IV wider than width of toes; discs of Toes I and V nearly same width as toe. Trace of

webbing between Toes II and III and between Toes III and IV. Inner metatarsal tubercle elliptical, 1.00 in length. Outer metatarsal tubercle small, round, 0.62 in diameter. Medial metatarsal tubercle absent. One subarticular tubercle on Toes I and II, two on Toes III and V, three on Toe IV. Basal subarticular tubercle on Toe IV offset laterally toward Toe V compared to other two subarticular tubercles. Toes faintly keeled. Faint outer metatarsal fold on outer edge of Toe V ends at level of outer metatarsal tubercle. No supernumerary tubercles on foot. Inner tarsal fold, 6.5, extends from proximal edge of inner metatarsal tubercle to about half length of tarsus and ends in small keel.

*Measurements of the holotype.*—SVL 24.1, HL, 8.6, HW 8.0, SL 3.8, EN 2.1, IN 3.5, EL 3.1, IO 5.5, TYM 1.4, FAL 5.8, HAND 7.1, WFD 0.97, TL 12.9, FL 10.7, WTD 1.01.

*Color of holotype in preservative.*—Dorsal surfaces black; dorsolateral and partial labial stripes whitish but distinct; pattern on limbs present but faint gray; ground color of undersurfaces black with gray reticulated pattern. Palms of hands lighter gray than undersurfaces of arms.

*Color of holotype in life.*—Color in life of MPEG 12504 (original field no. JPC 13230). Dorsum black, granular, with wide bright yellow-green dorsolateral stripes extending from snout above eyes to end dorsally above thighs on back. Dorsal surfaces of arms and legs with bright irregular linear markings of greenish-yellow. Bright greenish-yellow labial stripe begins below eye and extends onto upper arm ending at the elbow. All ventral surfaces black with deep sky blue reticulations. All ventral surfaces with same intensity of blue except ventral thighs; area around vent has grayish tinge. Flanks with a few yellow spots that become blue ventrally. Eyes black.

*Variation within type series.*—Nine adult males (including the holotype) had a mean SVL of  $25.0 \pm 1.1$  (range, 23.4–27.3). Four adult females had a mean SVL of  $28.2 \pm 1.1$  (range, 26.7–29.1). Two tadpoles that metamorphosed in the laboratory into juvenile females measured  $12.1 \pm 0.04$  (range, 12.06–12.11); three juvenile males collected in the forest measured  $14.1 \pm 2.6$  (range, 11.9–17.0). Variation of measurements of adults in the type series is given in Table 1.

TABLE 1.—Variation in adult male and female *Cryptophyllobates chlorocraspedus*. Values are means  $\pm$  SD; maximum and minimum values are in parentheses. Key to abbreviations is given in the methods.

Characters	Males (n = 9)	Females (n = 4)
HL	7.8 $\pm$ 0.3 (7.3–8.2)	8.6 $\pm$ 0.3 (8.3–9.1)
HW	8.1 $\pm$ 0.4 (7.5–9.0)	8.9 $\pm$ 0.3 (8.7–9.2)
SL	4.1 $\pm$ 0.2 (3.8–4.6)	4.4 $\pm$ 0.1 (4.3–4.6)
EN	2.3 $\pm$ 0.2 (2.1–2.6)	2.5 $\pm$ 0.2 (2.2–2.7)
IN	3.4 $\pm$ 0.1 (3.2–3.6)	3.8 $\pm$ 0.2 (3.6–3.9)
EL	3.2 $\pm$ 0.2 (2.8–3.4)	3.3 $\pm$ 0.1 (3.2–3.4)
IO	5.8 $\pm$ 0.3 (5.5–6.3)	6.2 $\pm$ 0.3 (5.9–6.5)
TYM	1.6 $\pm$ 0.2 (1.3–2.1)	1.7 $\pm$ 0.1 (1.5–1.8)
FAL	6.0 $\pm$ 0.4 (5.5–6.8)	6.5 $\pm$ 0.4 (6.2–7.0)
HAND	7.4 $\pm$ 0.3 (7.0–8.1)	7.9 $\pm$ 0.3 (7.4–8.3)
WFD	0.98 $\pm$ 0.09 (0.86–1.14)	1.06 $\pm$ 0.06 (0.97–1.12)
TL	12.9 $\pm$ 0.7 (12.0–14.5)	14.0 $\pm$ 0.7 (13.4–14.9)
FL	11.1 $\pm$ 0.7 (10.4–12.5)	11.5 $\pm$ 0.8 (10.4–12.2)
WTD	0.99 $\pm$ 0.09 (0.85–1.13)	1.10 $\pm$ 0.09 (0.99–1.17)

Variation of the remaining characters excludes the holotype. Dorsolateral stripe present, wide, and continuous in all adult specimens. In three of four adult females, the partial labial stripe begins beneath the center of the eye; in one specimen, the stripe begins near the level of the anterior edge of the eye. In eight adult males, the stripe begins at the posterior edge in two, in the center of the eye in two, and at the anterior edge in four. Although a distinct lateral stripe is absent, some frogs have small round or elongated diffuse spots in the groin. Of three females, one has a spot on the left side only, one has a single spot on both sides, and one has no spots in the groin. Seven males have from 0–3 spots on the right side and from 0–2 spots on the left side.

In some species of dendrobatids, the third finger of males is swollen compared to that in females; however, no indication of sexual dimorphism in this character is evident among the type series.

*Variation in color in life.*—Two females, OMNH 36169 and MPEG 12505, had a black dorsum with wide lime green dorsolateral stripes that began on the snout, continued above the eyes, and extended to the posterior back above the thighs. A lime green stripe began below the eye and extended along the lip below the tympanum and onto the upper arm to the elbow. In MPEG 12505, a diffuse green was present on the forearm and on the shank and tarsus; the inner half of the tarsus was

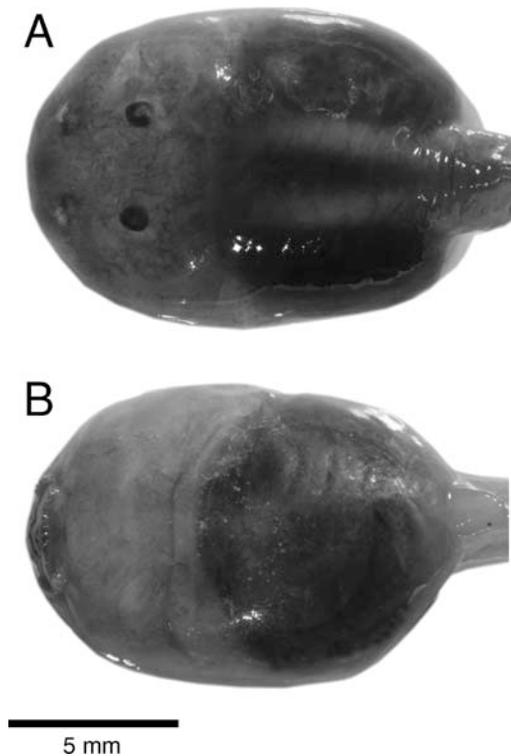


FIG. 6.—(A) Dorsal view of tadpole in stage 25, MPEG 12514, TL 32.5 mm, BL 13.5 mm. (B) Ventral view of tadpole.

diffuse blue, the outer half diffuse green. An irregular lime green stripe was present on the thigh. In OMNH 36169, the ventral surfaces were deep blue with black reticulations; the color was the same intensity on all ventral surfaces. In MPEG 12505, the ground color of the venter was black with irregular deep sky blue spots. The same color was present on the ventral sides of the limbs but was slightly brighter. Both specimens had black eyes.

A male, OMNH 36172, had a black, slightly granular dorsum, with brilliant lime green dorsolateral stripes. A stripe of the same color extended from below the eye to the elbow with a small break at insertion of the arm. The belly and undersurfaces of the limbs were black with wide, deep sky-blue reticulations. The chin was mostly black with a few irregular blue marks. The upper surfaces of the limbs had irregular lime green markings, except on the upper arm, which had a definite lime green stripe. The eye was black.

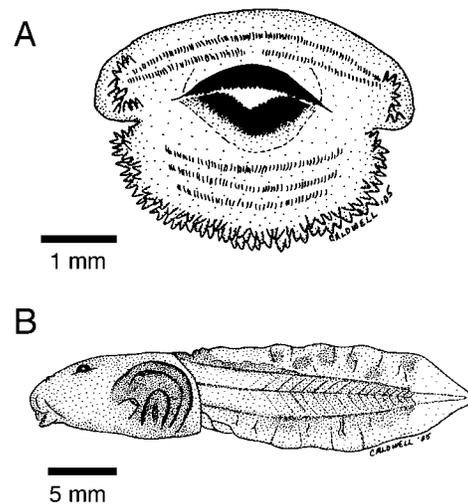


FIG. 7.—(A) Oral disc of tadpole of *Cryptophyllobates chlorocraspedus*, MPEG 12514. (B) Tadpole of *C. chlorocraspedus*, MPEG 12514.

A juvenile female, MPEG 12507, was collected on 26 Feb as a tadpole with large back legs and preserved on 11 Mar as a metamorph. After transformation, the ground color of the dorsum was black with iridescent green stripes from snout to sacrum. The belly was dark gray. Another juvenile female, OMNH 36173, was collected on 1 Mar as a tadpole with large back legs and preserved on 19 Mar. After transformation, the dorsum was black with brilliant green iridescent stripes. The upper arms and legs were black with irregular infusions of green to bluish green. The venter was dark gray with scattered small blue areas.

#### *Tadpole Description*

A large tadpole in Stage 25 was chosen for a detailed description. This tadpole is MPEG 12514 (original field number JPC 13204; Figs. 6, 7). Seven other lots of tadpoles were available for examination of variation. All tadpoles were in Stage 25, even though some were considerably larger than others.

*Description of tadpole.*—Total length 32.19, although end of tail regenerated; body length 12.94 (Fig. 7). Body depressed, maximum width, 8.62, maximum depth, 6.91. Snout broadly rounded in dorsal view, rounded in lateral view (Fig. 6). Nares small, directed

anterolaterally, located 1.51 anterior to eye, bordered above by a narrow unpigmented flap. Internarial distance 1.60. Eyes dorsal, small, 0.83 in length, interorbital distance from medial margins of orbits 2.25. Distance from eye to tip of snout 2.88.

Spiracle sinistral, not forming free tube, opening directed posterodorsally 7.80 from tip of snout; spiracle located 60.3% of body length from tip of snout, just below horizontal midline of body. Vent tube 1.65, opening dextral.

Caudal musculature deepest about midway length of tail. At deepest point, height of dorsal fin, 2.30, ventral fin 2.30, tail musculature 3.30. Dorsal fin originates at tail-body junction, gradually increasing until full height reached 5.50 posterior to tail-body junction. Regenerated length of tail, 4.00.

Oral disc ventral, 3.65 in transverse width, 42.3% of maximum body width (Fig. 7). Disc laterally emarginate, lower labium forming flap (free from body wall) with irregular double row of short, pointed papillae along the margin. Upper labium with short irregular row of papillae on outer margins, 12 on right side, 9 on left side. Most of upper labium, 2.45, 67.1% of transverse width of oral disc, continuous with snout and free of papillae. Lower jaw sheath broadly V-shaped, deeper than upper. Upper jaw sheath 1.80 in transverse width, 49.3% of disc width. Cutting edges of upper and lower jaw sheaths serrate, serrations not extending onto lateral processes of upper sheath.

Labial tooth row formula 2(2)/3. A-1 and A-2 same length, 3.00; A-1 complete; A-2 with small medial A-2 gap, 0.10, other gaps in A-2 created by missing labial teeth. P-1 and P-2 nearly same length, 2.55; P-3 shorter, 2.00, with slightly smaller labial teeth.

*Color in preservative.*—Upper body yellow-brown, skin slightly transparent, dark gray intestinal coils showing through sides of body. Ventral skin brown, transparent; gut showing through as dark gray. Tail musculature light yellow-brown, anterior one-third lightest; upper and lower fins transparent yellow-brown, upper with scattered irregular blotches, lower with slightly heavier pigmentation adjacent to tail musculature. End of tail regenerated, relatively clear. Eye black.

*Variation in tadpoles.*—Three additional large tadpoles collected from a pool in a fallen

tree, all in Stage 25, had a mean total length of  $28.2 \pm 6.6$  (range, 20.7–32.5) and a mean body length of  $11.4 \pm 2.9$  (range, 8.1–13.5). The tail was 59.8% of total length in these three tadpoles, although two of them had regenerated tails. In the single individual with an intact tail, the tail was 60.6% of total length. Width of the upper fin at its widest point,  $1.90 \pm 0.39$  (range, 1.65–2.35), was less than the width of the lower fin,  $2.30 \pm 0.33$  (range, 1.95–2.60). Tail musculature at its widest point was 2.58–0.72 (range, 1.75–3.05). Including the tadpole used for the description, the four large tadpoles had  $12.5 \pm 3.1$  (range, 10–17) short, pointed papillae on the right side of the upper labium and  $11.3 \pm 1.7$  (range, 9–13) papillae on the left upper labium.

Mean total length of 34 tadpoles being transported on the backs of male frogs was  $12.9 \pm 0.8$  (range, 10.7–14.3); all were in stage 25. For 33 back-riding tadpoles, the width of the upper fin at its widest point,  $0.50 \pm 0.07$  (range, 0.35–0.65) was slightly less than the width of the lower fin,  $0.65 \pm 0.15$  (range, 0.40–1.10). Tail musculature at this point was  $1.17 \pm 0.14$  (range, 0.85–1.40). Tail was 62.6% of total length in the 34 back-riding specimens. Larger back-riding tadpoles, total length  $13.1 \pm 0.6$  (range, 11.4–14.3;  $n = 31$ ) had well-developed jaw sheaths and labial tooth rows, although P-3 had not yet appeared in most of these specimens. Three smaller back-riding tadpoles from one male, total length  $11.4 \pm 0.7$  (range, 10.7–12.1;  $n = 3$ ) had barely developed jaw sheaths and no labial tooth rows. More yolk was present in the gut and the body was rounder than in the larger back-riding specimens.

*Color in life of tadpoles.*—Larger back-riding tadpoles (MPEG 12515) were gray dorsally, opaque ventrally. The tail musculature was lighter gray; tail fins were clear, and the upper fin had small gray reticulations. The eye was black with tiny yellowish or greenish flecks. One back-riding tadpole in MPEG 12513 had a grayish-brown body with evenly spaced chromatophores. Tail fins were clear. The eye was black with a few green chromatophores. A free-living tadpole (OMNH 36178, total length, 32.5) had a dark gray body with a bluish sheen. The tail musculature was lighter gray with an indistinct darker gray middorsal stripe. The tail fin was light gray

with a very narrow clear band around the edge. The eye was black.

#### *Natural History and Reproduction*

*Cryptophyllobates chlorocraspedus* was not abundant at this locality, which had eight other species of dendrobatids, all of which were encountered more frequently than *C. chlorocraspedus*. Courtship was not observed, but three gravid females were obtained on 17 Feb, 20 Feb, and 29 Mar; a nongravid female was obtained on 11 April. The largest ovarian egg found in one of the females was 2.3. Tadpoles of this species were found in a pool formed in the trunk of a fallen tree about 1.5 m above the ground. This area continually had one or two adults in the vicinity. At any one time, 4–5 tadpoles could be observed in the pool.

Of 17 specimens observed at the field site (not all collected), 12 were observed in treefalls, 5 were observed in primary forest, and one was observed in the vicinity of our camp (small open area in the forest). Of the 12 specimens in treefalls, 8 were on logs from 5 to 70 cm above the ground, 3 were in wood shavings on the ground, and one (the holotype transporting 10 tadpoles) was sleeping on a leaf at night. Kneller and Henle (1985) reported finding adults of *C. azureiventris* near a large, fallen tree trunk.

Of 38 tadpoles collected, 34 were back-riding tadpoles. All were being transported by males, presumably the parent frog. The mean number of tadpoles being transported was  $6.8 \pm 2.6$  (range, 3–10). Snout–vent length of the five males transporting tadpoles was  $25.4 \pm 1.2$  mm (range, 24.1–27.3). One of these five (the holotype) was encountered at night with 10 tadpoles on its back sleeping on a leaf overhung by other leaves 30 cm above a large fallen tree; one was in a small pool in low primary forest at noon during a rain; two were in small trenches placed in the forest to capture animals; data for one were not recorded. Males transporting tadpoles were captured from 17 Feb to 7 Apr.

One tadpole with a total length of 32.5 mm (in stage 25) was taken from the pool in a fallen tree and placed in a small cup with 200 ml of water; several smaller tadpoles of another species (not identified) taken from a nearby pond were placed with this tadpole. This

tadpole immediately attacked and consumed two of the small tadpoles. Another large tadpole of *C. chlorocraspedus* was placed in a cup with 200 ml of water and 15 small mosquito larvae; 24 hours later, 6 of the mosquito larvae were missing and presumed killed and eaten by the tadpole; I observed the tadpole capture and eat one of these mosquito larvae. A tadpole of *Epipedobates trivittatus* was placed with 15 mosquito larvae; none of these mosquito larvae was consumed.

#### DISCUSSION

Generic assignments for many species of dendrobatids have been problematic, primarily because of convergence of color patterns and morphology. Many species have been variously assigned to two or three different genera over the years; for example, *Cryptophyllobates azureiventris* was originally described as *Phyllobates* (Kneller and Henle, 1985), was transferred to *Epipedobates* by Myers (1987), and then was referred to *Dendrobates* by Myers and Burrowes (1987).

Recent molecular studies have revealed some surprising relationships among dendrobatid species and have shown a large degree of paraphyly among species once thought to be closely related. Vences et al. (2000), using 20 species of dendrobatids, showed that *Epipedobates* and *Colostethus* are paraphyletic and that *Epipedobates* (= *Cryptophyllobates*) *azureiventris* is most closely related to a species of *Colostethus*. Widmer et al. (2000) focused their molecular studies on relationships among the five species of *Phyllobates*, but also showed that *C. azureiventris* is not a member of this well-supported clade. Both of the most recent molecular studies agree in showing that *C. azureiventris* is most closely related to species of *Colostethus* occurring in the same general area (Santos et al., 2003; Vences et al., 2003). These latter molecular studies further reveal that clades of aposematic dendrobatids, once thought to be closely related and to have arisen from a basal nontoxic clade (*Colostethus*), have arisen independently multiple times (Santos et al., 2003, 57 species; Vences et al., 2003, 66 species).

Lötters et al. (2000) recognized that the species originally named as *Phyllobates azureiventris* had distinctive characters that

distinguished it from other currently known genera and proposed the new genus *Cryptophyllobates* for this species. The new species described herein is included in a greatly expanded data set of more than 100 species of dendrobatids; in that analysis, *C. chlorocraspedus* was sister to *C. azureiventris* and both were nested in a clade of Ecuadorian and Peruvian *Colostethus* (unpublished data, J. C. Santos, L. A. Coloma, J. P. Caldwell, K. Summers, and D. C. Cannatella).

A combination of characters was used by Lötters et al. (2000) to diagnose *Cryptophyllobates azureiventris*. *Cryptophyllobates chlorocraspedus* agrees with most of these, particularly in having distinct dorsolateral stripes that end posteriorly on top of the back above the thighs instead of in the groin as in most *Epipedobates*. *Cryptophyllobates azureiventris* and *C. chlorocraspedus* have morphologically similar tadpoles (Lötters et al., 2000; description of tadpole of *C. chlorocraspedus* herein). In both species all individuals in a clutch are transported at one time, in contrast to species of *Dendrobates*, which transports usually only one tadpole (but sometimes 2–3 tadpoles) at one time. Although Lötters et al. (2000) reported that tadpoles of *C. azureiventris* develop in pools that may have running water, I found tadpoles of *C. chlorocraspedus* developing in a pool formed in the trunk of a fallen tree. My observations on behavior of the tadpoles revealed that they are predaceous, readily attacking and consuming small tadpoles of other species and mosquito larvae. In this respect and in their size and shape, the tadpoles of *C. chlorocraspedus* are more similar to tadpoles of *Dendrobates* than to those of *Epipedobates*, and they are very different from tadpoles of *Colostethus*. Based on results of molecular studies cited above, the similarities between tadpoles of *Cryptophyllobates* and *Dendrobates* are a result of convergence, perhaps in response to developing in restricted microhabitats that harbor predators. Previous work has shown that tadpoles of *Dendrobates*, which usually develop in small phytotelmata, consume any small invertebrates that begin developing in their microhabitat, presumably as a mechanism to rid their space of predators before they grow large enough to consume the tadpole (Caldwell, 1993; Caldwell and Araújo, 1998).

The tadpoles of *C. chlorocraspedus* are unusual in reaching a large size before undergoing limb development. The three largest tadpoles in my sample averaged 32.0 mm and were still in stage 25. In comparison, tadpoles of *Dendrobates castaneoticus* were 14.9 mm in total length size at stage 25, and 28.3 mm in stage 35 (Caldwell and Myers, 1990).

Relationships among the various proposed genera (clades) will remain confused until additional species are included in molecular and morphological analyses. Tadpole behavior and morphology will also shed light on these relationships; however, mature tadpoles of dendrobatids are infrequently collected and very little is known about dendrobatid tadpole behavior. Descriptions of dendrobatid tadpoles often are based on back-riding tadpoles, which may not have key characters fully developed. Nevertheless, it is clear that the species described herein and *C. azureiventris* are allied and are distinguishable from other clades.

#### RESUMO

Um novo gênero, *Cryptophyllobates*, foi recentemente descrito para uma espécie de dendrobatídeo originalmente descrita como *Phyllobates azureiventris*. Uma das características diagnósticas é a presença de listras dorso-laterais que terminam na região posterior do dorso, na parte superior dos fêmures. Durante uma viagem a campo no estado do Acre, Brasil, coletei um dendrobatídeo diferente que transportava todos os girinos de uma ninhada de uma vez; entretanto, os girinos dessa espécie eram mais parecidos com *Dendrobates* do que com *Epipedobates*. Em seguida descobri que essa espécie era semelhante a *Cryptophyllobates azureiventris* e aqui a descrevo como a segunda espécie do gênero. Estudos moleculares mostraram que a nova espécie e *C. azureiventris* são táxons irmãos, e que o gênero está relacionado a alguns clados de *Colostethus*. Rituais de acasalamento não foram observados para a nova espécie, mas os girinos foram encontrados em uma poça formada em uma árvore caída e os adultos frequentemente observados em clareiras produzidas pela queda de árvores. Os girinos assemelham-se a *Dendrobates* por serem predadores, possivelmente uma convergência

no comportamento em resposta ao desenvolvimento em microhabitats restritos semelhantes.

*Acknowledgments.*—Field logistics for work in Acre, Brazil, were arranged by T. C. Avila-Pires of the Museu Paraense E. Goeldi and M. Scarcello of SOS Amazônia. Permits to conduct research and collect specimens in Brazil were issued by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Portaria MCT 170, de 28/09/94) and the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA, 073/94-DIFAS), respectively, under a research convenio between OMNH and MPEG. I thank my field companions, L. J. Vitt, T. C. Avila-Pires, and V. R. L. de Oliveira for help collecting specimens. L. J. Vitt provided comments on a draft of the paper and executed Figure 1. I thank R. J. Burkhalter, Collection Manager of the SNOMNH Division of Invertebrate Paleontology, for photographing the preserved specimens. I am grateful to M. S. Hoogmoed for his careful translation of the original description of *Phyllobates azureiventris* from German to English. A. A. Garda provided the Portuguese translation of the abstract, and C. A. Wolfe aided with manuscript preparation. W. E. Duellman suggested the combination of names for the new species. I thank L. Trueb and J. Simmons for the loan of specimens from the University of Kansas. This research was supported by National Science Foundation grants DEB-9200779 and DEB-9505518 to L. J. Vitt and JPC; additional funds were supplied by the Sam Noble Oklahoma Museum of Natural History.

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Accepted: 14 July 2005

Associate Editor: Joseph Mendelson

## APPENDIX I

### Specimens Examined

*Chryptophyllobates azureiventris* (2).—PERU: *San Martin*: Ponga de Shilcayo, ca 4 km NNW Tarapoto, 470 m, KU 211976–77.

*Cryptophyllobates chlorocraspedus* (18 and 8 lots tadpoles).—BRAZIL: *Acre*: Porto Walter, OMNH 36169–77, OMNH 36178–81 (tadpoles); MPEG 12504–12, MPEG 12513–16 (tadpoles).

*Epipedobates bassleri* (6).—PERU: *San Martin*: 20 km NE Tarapoto on road to Yurimaguas, KU 209399–401; 15 km NE Tarapoto, 800, KU 211978; 21.8 km NE Tarapoto, 970 m, KU 211979; *Llamas*: 14.8 km SW Zapatero, 1000 m, KU 211600.

*Epipedobates cainarachi* (3).—PERU: *San Martin*: 14 km ESE Shapaja, 360 m, KU 211973–75.

*Epipedobates espinosai* (4).—ECUADOR: *Pichincha*: 1 km E Mindo, 1400 m, KU 174543–44; km 62, Santo Domingo-Quito Road, KU 221631–32.

*Epipedobates petersi* (45).—PERU: *Pasco*: Oxapampa, Nevati, 275 m, KU 144344–46; Santa Isabella, 460 m, KU 144348–50; *Huanuco*: Finca Panguana, Rio Lullapichis, 4–5 km upstream from Rio Pac, KU 154963–67, KU 172118–42; S slope Serrania Sira, Casa de Campo, 690 m, KU 154968; *Loreto*: Rio Curanja, Balta, 300 m, KU 196748–52; *Ayacucho*: between Pataccoha and San Jose on Rio Santa Rosa, 1005 m, KU 196753–54; *Cuzco*: ca 40 km E Quince Mill on Puento Maldonado Road above Rio Marcapata, KU 196755.

*Epipedobates silverstonei* (5).—PERU: *Huanuco*: Divisoria en Cordillera Azul, 1600 m, KU 196763–64; Divisoria, 1600 m, KU 211610–12.

*Epipedobates trivittatus* (51 and 22 lots tadpoles).—BRAZIL: *Acre*: Porto Walter, OMNH 36109–33, OMNH 36134–44 (tadpoles); MPEG 12443–68, MPEG 12469–79 (tadpoles).

*Epipedobates zaparo* (9).—PERU: *Loreto*: San Jacinto, 175 m, KU 221840–42; 1.5 km N Teniente Lopez, 310 m, KU 221843–48.

*Epipedobates* sp. (undescribed, *E. petersi* group; 44 and 4 lots tadpoles).—BRAZIL: *Acre*: Porto Walter, OMNH 36145–66, OMNH 36167–68 (tadpoles); MPEG 12480–12501, MPEG 12502–03 (tadpoles).

*Herpetologica*, 61(4), 2005, 461–468

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## A NEW SPECIES OF *RIAMA* (SQUAMATA: GYMNOPHTHALMIDAE), ENDEMIC TO THE PENÍNSULA DE PARIA, VENEZUELA

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**ABSTRACT:** A new species of gymnophthalmid lizard is described from the montane forests of the Península de Paria in northeastern Venezuela. The new species is one of three gymnophthalmid species known to be endemic to the region, and the fourth species of *Riama* from Venezuela. It is likely the sister species to *R. shrevei* of Trinidad, but can be distinguished from the latter species by having a nasoloreal suture, fewer scale rows encircling the midbody, and by having a higher number of transverse dorsal scale rows.

**Key words:** Gymnophthalmidae; New species; Península de Paria; *Riama rhodogaster*; Squamata; Sucre state; Taxonomy; Venezuela

THE MOUNTAINOUS areas of the Península de Paria in northeastern Venezuela harbor a fascinating biological diversity, much of which continues to be discovered. Numerous plants and animals are endemic to Paria (Steyermark, 1973), but more interesting perhaps is the complex biogeography of this area. The differ-

ent species present in the humid forests of Paria above 600 m have their closest relatives in either the highlands of Trinidad, the coastal mountain ranges of Venezuela, or the Amazonian/Guianan region (Steyermark, 1974, 1979, 1982). cursory surveys of the herpetofauna of the montane forests of the Península de Paria have resulted in the discovery of several new species of amphibians and reptiles (Ayarza-

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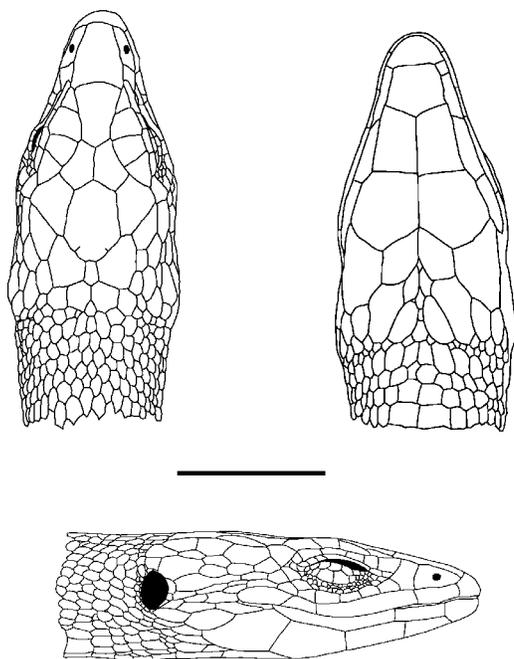


FIG. 1.—Head of the holotype of *Riama rhodogaster* (MHNLS 16645) in dorsal (top left), ventral (top right) and lateral (bottom) view. Scale bar = 5 mm.

güena and Señaris, 1997; Donoso-Barros, 1965; Mijares-Urrutia et al., 2000; Rivas et al., 1999; Schargel et al., 2005). Among these taxa are two recently described gymnophthalmid lizards: *Anadia pariaensis* (Rivas et al., 1999) and *Euspondylus monsfumus* (Mijares-Urrutia et al., 2000). Herein we describe yet another new gymnophthalmid lizard (genus *Riama*) from Península de Paria.

In an effort to establish a phylogenetic classification for the Cercosaurini tribe of gymnophthalmid lizards, Doan and Castoe (2005) resurrected the genus *Riama* to accommodate one of two recovered clades of the polyphyletic genus *Proctoporus*. *Proctoporus s.s.* is now restricted to five species from the central Andes of Peru and Bolivia; the remaining 24 species formerly belonging to *Proctoporus* have been allocated to *Riama*. Excluding the species herein described, three species of these secretive montane lizards occur in Venezuela: *R. achlyens* and *R. luctuosa* from the Cordillera de la Costa Central, and *R. inanis* from the Mérida Andes (Doan and Schargel, 2003). An additional species, *R. shrevei*, is known only from the

island of Trinidad, which is separated from the northeastern coast of Venezuela by a distance of 12 km. Donoso-Barros (1968) predicted that *R. shrevei* may eventually be collected from Paria. Recently, Rivas and Oliveros (1997) reported a specimen of *Riama* from Paria that they identified as *R. achlyens*. We since have obtained five additional specimens from this region, and have determined, instead, that they represent an undescribed species.

#### MATERIALS AND METHODS

To facilitate comparisons of standard diagnostic characters with other species of *Riama*, the definition and the description of the new species follows the format of Kizirian (1996). Specimens examined are listed in the appendix. Museum abbreviations follow Leviton et al. (1985) except for Museo de Historia Natural La Salle, Caracas (MHNLS). Sex was determined by everting the hemipenes in freshly killed specimens and confirmed in females by ventral dissection.

#### SPECIES ACCOUNT

##### *Riama rhodogaster* sp. nov.

*Proctoporus achlyens*: Rivas and Oliveros, 1997:69 [for EBRG 2741].

*Holotype*.—MHNLS 16645 (Fig. 1), an adult male, collected from a footpath between Las Melenas and Cerro Humo, approximately 650 m, Península de Paria, Sucre state, Venezuela; one of four specimens collected on 2 June 2002 by Gilson Rivas and Walter Schargel.

*Paratypes*.—MHNLS 15730–15731; UTA R-52896; three specimens with same collection data as holotype; UTA R-52895 from same locality, obtained by Jason Trujillo, Hinrich Kaiser, and Cesar L. Barrio on 5 September 2001.

*Referred specimens*.—EBRG 2741, a juvenile, collected from near Las Melenas, Península de Paria, Sucre, by Ramón Rivero on 15 August 1992.

*Diagnosis*.—(1) Frontonasal longer or equal in length to frontal; (2) nasoloreal suture present; (3) supraoculars four; (4) superciliary series complete, four; (5) supralabial-subocular fusion absent; (6) postoculars three; (7) postparietals 2–3; (8) supratympanic temporals

three or four, usually three; (9) genials two; (10) dorsals hexagonal, juxtaposed, most with rounded keel; (11) longitudinal dorsal scale rows 22–24; (12) transverse dorsal scale rows 42–44; (13) transverse ventral scale rows 19; (14) differentiated lateral scale rows absent; (15) femoral pores in males 28, in females 12–16, scales between femoral pores in males absent, in females one; (16) subdigital scales on Toe I 3–6; (17) limbs barely overlapping or not overlapping when adpressed against body in adults; (18) anterior cloacal plate scales absent or comprising one small scale; (19) hemipenis bilobed with several curved spinulate flounces; (20) dorsum brown with broken dorsolateral lines and poorly defined lateral ocelli.

*Riama rhodogaster* differs from all species in the genus, except *R. achlyens*, *R. inanis*, *R. laevis*, *R. luctuosa*, *R. oculata* and *R. shrevei* (all members of the phenetic *luctuosus* group; sensu Uzzell, 1958), by the absence of a narrow band of differentiated granular lateral scales. The new species differs from *R. laevis*, *R. luctuosa*, *R. inanis* and *R. oculata* by having hexagonal versus rectangular dorsal scales. It differs from *R. achlyens* (characters for *R. achlyens* in parentheses) by having 42–44 (37–40) transverse dorsal scale rows and by having in males a continuous row of femoral pores that is not separated by scales at the preanal region (femoral pores in males separated by two scales at preanal region). Additionally, the new species differs from all Venezuelan species of *Riama* by having a shallow, depressed head (head depth/head length = 0.36–0.40) versus having the head not noticeably depressed (0.45–0.56 in *R. achlyens*; 0.49–0.65 in *R. inanis*; 0.57 in *R. luctuosa*). *Riama rhodogaster* is most similar and presumably closely related to *R. shrevei* from Trinidad. Both species lack scales separating the medialmost femoral (= preanal) pores in males (Fig. 2), a condition which seems to be restricted to these two species among the *Riama* species that lack differentiated granular lateral scales. The new species differs from *R. shrevei* (characters for *R. shrevei* in parentheses) by having a nasoloreal suture (nasal and loreal fused), scales encircling midbody 28–30 (31–35) and transverse dorsal scale rows 42–44 (35–40).

*Description of holotype*.—Male, SVL 47.3 mm, tail length 61.8 mm (regenerated); head

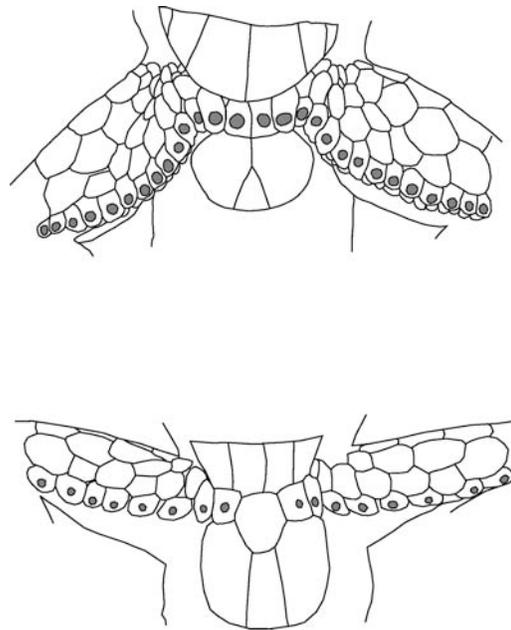


FIG. 2.—Ventral view of the pelvic region of a male (MHNLS 16645; holotype; top) and female (MHNLS 15730; bottom) *Riama rhodogaster* showing sexual dimorphism in the arrangement of femoral pores. Males of *R. shrevei* share the same femoral pore arrangement with males of *R. rhodogaster*.

scales smooth, glossy; rostral scale wider than long, higher than adjacent supralabials, in contact with frontonasal, nasal, and first supralabials posteriorly; frontonasal 1.3 times longer than wide, widest posteriorly, in contact with nasal, loreal, anteriormost superciliary, first supraocular, frontal posteriorly; nasoloreal suture complete (= loreal present); nasal quadrilateral; loreal pentagonal; prefrontals absent; frontal longer than wide, widest anteriorly, anterior suture convex, lateral sutures slightly concave, posterior suture angular with point directed posteriorly, not in contact with anteriormost superciliary anterolaterally, in contact with first and second supraocular laterally, frontoparietals posteriorly; frontoparietals roughly pentagonal, in contact with second, third and fourth supraocular, parietals and interparietal posteriorly; supraoculars four, none in contact with ciliaries; superciliary series complete, four, anterior superciliary lying between loreal, frontonasal, first and second supraoculars, second superciliary, and anteriormost ciliaries,

barely extending onto dorsal surface of head; palpebral disc divided into 3/4 large mostly unpigmented scales and many small pigmented or unpigmented scales; frenocular quadrilateral, in contact with loreal anteriorly; circumorbital scales between posteriormost supraocular and frenocular 6/6; postocular 3/2; interparietal heptagonal, longer than wide, in contact with parietals laterally, postparietals posteriorly and posterolaterally; parietals hexagonal, in contact with fourth supraocular anterolaterally, temporal scale posterolaterally, dorsalmost postocular laterally, postparietals posteriorly; postparietals three, lateral postparietals subhexagonal, medial postparietal narrow, pentagonal; temporals polygonal; supratympanic temporals 4/3; supralabials 4/5; infralabials 6/4; mental wider than long, in contact with the first infralabials, postmental posteriorly; postmental single, pentagonal, posterior suture angular, point directed posteriorly, in contact with first infralabial (right side) and first and second infralabials (left side); genials in two pairs, anterior pair quadrangular, in contact with second and third infralabials (left side) and second infralabial (right side); posterior genials pentagonal, in contact with second and third infralabials (right side) and with third and fourth infralabials (left side); gular scale rows 11; medialmost scales of four penultimate gular scale rows slightly broadened; gular fold bordered posteriorly by one to two rows of small granular scales; lateral neck scales rounded, smooth.

Dorsal scales hexagonal medially with tendency of becoming quadrangular laterally, longer than wide, juxtaposed, keeled medially with tendency of becoming smooth laterally, in 43 transverse rows; some middorsal scales irregularly arranged; longitudinal dorsal scale rows at fifth transverse ventral scale row 28 (granular scales included in count), at 10th transverse ventral scale row 23, at 15th transverse ventral scale row 24; differentiated lateral scales absent; granular scales replace dorsals toward insertion of limbs; complete transverse ventral scale rows 19; longitudinal ventral scale rows at midbody 6; cloacal plate divided in two large paired scales and small posterior triangular scale (Fig. 2); tail complete, regenerated at 44th subcaudal; scales on tail hexagonal, imbricate and keeled dorsally,

becoming rectangular, juxtaposed and smooth laterally; paired subcaudals rectangular, wider than long, smooth; left hemipenis incompletely everted, bilobate at tip; basalmost portion of organ naked, the remainder with finely spinulate, slightly curved flounces.

Limbs pentadactyl; digits clawed; forelimb reaching anteriorly to rictus of the mouth; dorsal and anterodorsal brachial scales polygonal, of varying sizes but mostly large, subimbricate, smooth; ventral and posterior brachial scales small, rounded, juxtaposed, smooth; antebrachial scales large polygonal, subimbricate, smooth; dorsal manus scales polygonal, subimbricate; palmar scales small, irregularly shaped, slightly domelike distally; thenar scales two, slightly keeled; dorsal scales on fingers smooth, quadrangular, covering dorsal half of digits, overhanging subdigital scales, three on I, four on II, five on III, six on IV, three on V; subdigital scales five on I, seven on II, nine on III, seven on IV, six on V; anterior thigh scales large, polygonal, becoming increasingly smaller ventrally; dorsal and anterodorsal thigh scales ovoid, juxtaposed, smooth; posterior thigh scales small, oval to granular, smooth, arranged irregularly; femoral pores 12/12, separated by 4 preanal pores, femoral and preanal scales together forming a continuous row; lateral and dorsal crus scales polygonal, subimbricate, weakly rugose, decreasing in size distally on lateral surface; scales on ventral surface flat, juxtaposed, larger than all other crus scales; scales on medial surface, subimbricate, smooth, slightly smaller than scales on ventral surface; dorsal pes scales smooth, polygonal; ventral pes scales elongately ovoid, weakly rugose; scales on dorsal surface of digits single, quadrangular, smooth, longer than wide, overhanging subdigital scales, two on I, five on II, eight on III, nine on IV, six on V; subdigital scales single, five on I, eight on II, eleven on III, 14 on IV, nine on V; limbs not overlapping by four dorsal scale lengths.

*Coloration of holotype.*—In preservative (70% ethanol), dorsal ground color cinnamon-brown, under magnification coloration composed of pale brown ground color with slightly darker mottling and scattered, black maculations; black, poorly defined, broken, dorsolateral line extending from neck to just beyond base of tail where it gradually fades

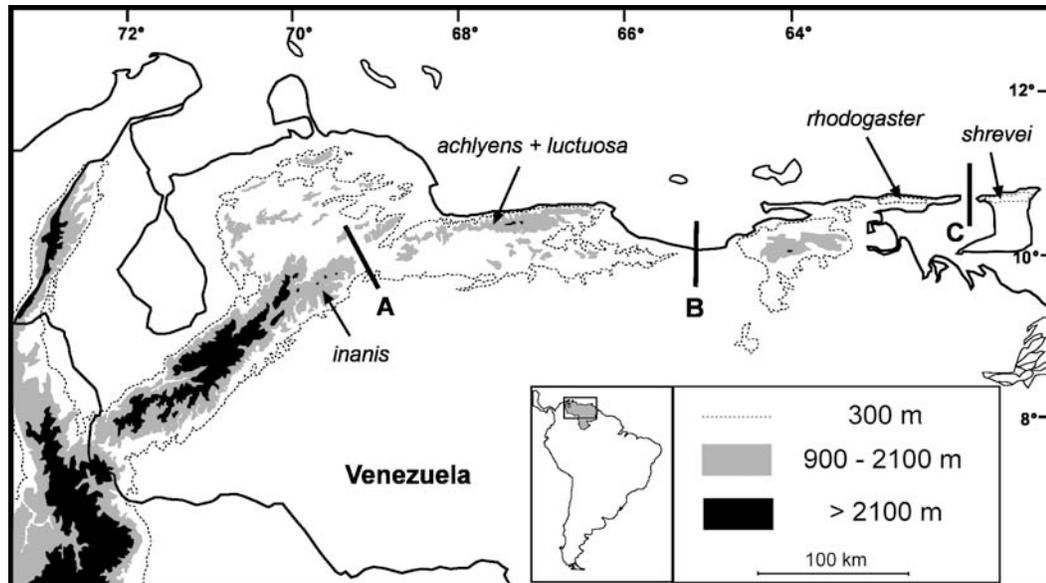


FIG. 3.—Map of northern Venezuela and Trinidad showing the distribution of the five species of *Riama* known from this region. Geographic barriers are identified as follows: A = Barquisimeto Depression; B = Unare Depression; C = Gulf of Paria.

into ground color; faint pale dorsolateral line bordering black line and extending from neck, disappearing just posterior to level of front limb insertion; posterior portion of scales on lateral surfaces of body and tail dark brown, forming indistinct transverse lines; approximately eight poorly defined lateral ocelli with black borders and cream centers, extending from neck to posterior two thirds of flank; limbs cinnamon-brown dorsally with small dark, scattered spots; dorsal surface of head cinnamon-brown with faint darker smudges, dark suffusion of pigment on supraocular scales; a faint, poorly defined, pale line edged by black extends from the posterior edge of the last superciliary to postparietals; lateral surface of head with two indistinct, short cream suborbital bars on labial scales, angled postero-ventrally; ventral surface of head, body, and limbs, cream; tail pale salmon, with brown mottling barely encroaching from lateral surfaces; dorsal and ventral surface of hands and feet dark brown. In life the coloration is essentially the same but the venter is pinkish red, being more intense posteriorly.

*Variation.*—The paratypes include one adult male (SVL: 39.6, MHLNS 15731), one juvenile male (SVL: 37.0, UTA R-52896), one

gravid adult female (SVL: 45.7, MHNLS 15730), and one juvenile female (SVL: 26.0, UTA R-52895). Meristic variation for the paratypes (in same order as above) is: longitudinal scale rows at midbody: 23, 24, 22, 23; longitudinal ventral rows 6 in all specimens; transverse dorsal scale rows 42, 44, 42, 43; transverse ventral scale rows 19 in all specimens; femoral pores (including preanals): 14/14, 14/14, 8/8, 6/6. Subdigital scales on fourth finger: 10, 9, 8, 9; Subdigital scales on fourth toe: 12, 14, 13, 13; Supralabial counts among paratypes range from 6 to 8. The condition of the cloacal plate seems to be sexually dimorphic. In males the cloacal plate is divided in two large paired scales and a small posterior scale, in females an anterior scale is also present precluding contact of the large paired scales and separating the medialmost femoral pores (Fig. 2).

Coloration in the paratypes is similar to the holotype with few noteworthy exceptions: extent and distinctiveness of the pale dorsolateral stripe is variable in the type series (MHNLS 15730 has a particularly distinct stripe that extends posteriorly to the level of the vent); in MHLNS 15730 and UTA R-52896 the lateral ocelli are not evident.

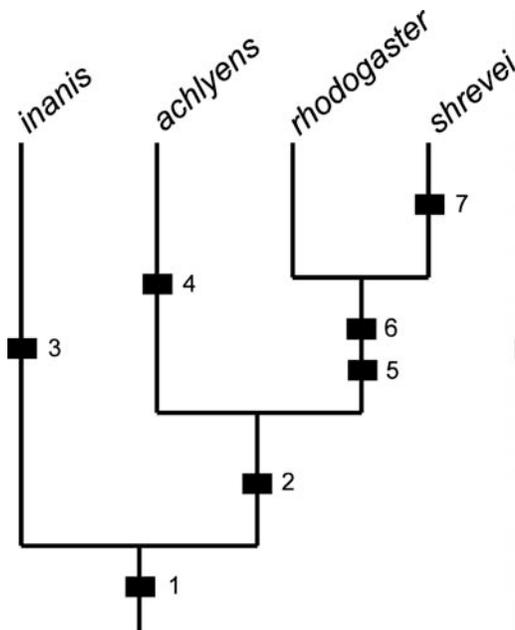


FIG. 4.—Suggested phylogenetic position of *Riama rhodogaster* on a subclade of the phylogeny obtained by Doan (2003). Characters mapped on the tree are: (1) Lateral scales absent. Although this character state is not unique to this clade it seems to be derived in *Riama*. Following Doan (2003) loss of lateral scales has occurred twice independently in *Riama*. (2) Hexagonal dorsal scales is a synapomorphy uniting *R. achlyens*, *R. rhodogaster*, and *R. shrevei* (3) Elongated second supralabial scale. This is a unique condition in *Riama* (Doan and Schargel, 2003). (4) Black blotches on cream venter. Within this clade all other species have a uniform venter. (5) No scales separating the medialmost femoral pores in males. This condition occurs in a few other species of *Riama* (Kizirian, 1996) but is unique to *R. rhodogaster* and *R. shrevei* within the *luctuosus* group. (6) Dorsoventrally compressed head. (7) Nasal and loreal fused. Whereas this condition occurs in other species of *Riama* (Kizirian, 1996) no species in the *luctuosus* group other than *R. shrevei* show this condition.

*Distribution and natural history.*—*Riama rhodogaster* is only known from the type locality at 650 m on the southern slope of the Península de Paria near Las Melenas (Fig. 3). This species is most likely endemic to the humid forest of the mountainous areas of the Península de Paria, given that similar habitat is isolated from this region by either dry lowlands or sea. All specimens except UTA R-52895 were collected under rocks in an area that had been recently clearcut. The intermediate elevation of the type-locality results in a transitional floral community between dense coastal forest and submontane deciduous forest (as

implied by Huber and Alarcón, 1998). UTA R-52895 was found crossing a trail through the forest during the day. MHNLS 15730 is an adult female with two oviductal eggs (eggs approximately 5 mm in length). In two trips to the region by one of us (GRF), in June and December of 2003, no specimens were collected despite a higher search effort lifting rocks in the same clearcut area, but it was noted that the soil was much dryer compared to the day the type specimens were collected. Other species of reptiles that have been collected at the same locality are: two arboreal gymnophthalmid lizards, *Anadia pariaensis* and *Euspondylus monsumus*, the diurnal gecko, *Gonatodes ceciliae* (also found under rocks), a skink, *Mabuya nigropunctata* and three species of snakes: *Bothrops venezuelensis*, *Liophis reginae* and *Taeniophallus nebularis*.

*Etymology.*—The species name is a noun in apposition, derived from the Greek *rhodon* (a rose, hence red) + *gaster* (belly); in allusion to the reddish venter observed in males of this species.

*Remarks.*—Doan (2003) presented evidence that Venezuelan (and Trinidad) *Riama* fall in at least two separate clades. One of these clades contains *R. achlyens* and *R. shrevei* with moderate support as sister taxa. We herein place *R. rhodogaster* in the context of the phylogenetic hypothesis presented by Doan (2003). Figure 4 shows the proposed phylogenetic arrangement with the distributions of some potential autapomorphic and synapomorphic characters. Although we have not performed a rigorous phylogenetic analysis, we consider that *R. rhodogaster* is most likely a member of the clade containing *R. achlyens* and *R. shrevei* because it shares with the aforementioned species the unique character of hexagonal dorsal scales (Doan, 2003). The sister species of *R. rhodogaster* is likely *R. shrevei*. These two species have a dorsoventrally compressed head and both lack scales separating the medialmost femoral (= preanal) pores in males. Both characters are regarded here as synapomorphies for this clade.

Our proposed phylogenetic placement for *Riama* suggests a pattern of speciation where cladogenetic events appear to have occurred in chronological order on a west-to-east axis. Moreover, all members of the clade examined

are allopatric and separated by geographic barriers that have been invoked by previous authors as playing an important role in the speciation of the montane biota of Venezuela (e.g., Duellman, 1979; Steyermark, 1979). These barriers are: (1) Barquisimeto Depression, separating the Cordillera de Mérida from the Cordillera de la Costa Central; (2) Unare Depression, separating the Cordillera de la Costa Central from the Cordillera de la Costa Oriental, and (3) Gulf of Paria, separating the easternmost extension (Paria) of the Cordillera de la Costa Oriental from the northern highlands of Trinidad (Fig. 3).

Whereas *R. rhodogaster* has its closest relative in Trinidad, the other two gymnophthalmids known from the humid forests of Paria, *Anadia pariaensis* and *Euspondylus monsfumus*, seem to be closely related to species in the Cordillera de la Costa Central. Moreover, neither *Anadia* nor *Euspondylus* are known to occur in Trinidad. Most other species of reptiles that occur in the humid forests of Paria are shared with either the Cordillera de la Costa Central or the highlands of Trinidad, and at least one species, *Taeniophallus nebularis*. (Schargel et al., 2005) supports a biogeographic connection with the Amazon lowlands. These findings further support the biogeographic complexity of Paria as first noted by Steyermark (1974, 1979, 1982).

#### RESUMEN

Se describe una nueva especie de lagartija (Gymnophthalmidae) proveniente de los bosques montañosos de la Península de Paria en el noreste de Venezuela. La nueva especie es una de las tres especies de gymnophthalmidos endémicas de la región y es la cuarta especie de *Riama* de Venezuela. Se trata probablemente de la especie hermana de *R. shrevei* de Trinidad, pero se distingue de esta especie por poseer sutura nasolorear, un menor número de escamas alrededor de la mitad del cuerpo, y por poseer una mayor número de hileras de escamas dorsales transversales.

*Acknowledgments.*—For allowing us to examine specimens under their care we are grateful to J. Dixon, J. García-Pérez, J. Hanken, J. Rosado, L. Trueb and K. Vaughan. Field work in Paria was partially supported by a Phi Sigma grant to WES that was generously matched by

the Department of Biology and the College of Science at The University of Texas at Arlington. Additional funds for work in Paria were provided to GRF by H. Kaiser. We thank R. Schargel for providing us with a vehicle while in the field. Travel expenses for GRF to work at UTA were generously provided by the Fundación La Salle de Ciencias Naturales, Caracas. C. Myers assisted with the etymology section and T. Castoe and T. Doan helped improve the manuscript with corrections and suggestions.

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Accepted: 26 May 2005

Associate Editor: Maureen Kearney

## APPENDIX I

### Specimens Examined

- Riama achlyens*: KU 133516–17, 167559, 182750, MCZ 53128, 66920, 100430, 109010, MHNLS 1278, 3075, 4924–25, 16170.
- Riama inanis*: MCNG 825–828 (type series).
- Riama luctuosa*: MCZ 100410, TCWC 59857.
- Riama shrevei*: MCZ 34273, 38659, 62506–07, 100466–71, 160065–67.
- Riama rhodogaster*: UTACV 52895–96 (paratypes), MHNLS 15730–31 (paratypes), MHNLS 16645 (holotype).

*Herpetologica*, 61(4), 2005, 468–477

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## A NEW SPECIES OF *HYDROPS* (SERPENTES: COLUBRIDAE: HYDROPSINI) FROM ARGENTINA, BRAZIL AND PARAGUAY

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**ABSTRACT:** A new species of *Hydrops* is described. The new species has a disjunct distribution with regard to other species in the genus, occupying subtropical to temperate areas of Paraná and Plata River basins (between 19° and 28° 30' S), from Pantanal in Mato Grosso do Sul, Brazil, through Paraguay and Paraná Rivers, with records in the Esteros de Iberá, Argentina. It differs from all congeners in the number of total ventral scales (ventrals plus subcaudals), number of dorsal scales and color pattern. Based on our data and those of previous authors, we present the variation in lepidosis and measurements, description of the hemipenes, and known distribution for the new species. Furthermore, a key for the identification of all taxa of the genus is presented.

**Key words:** Argentina; Brazil; *Hydrops*; New species; Paraguay

*HYDROPS* is a South American xenodontine genus closely related to *Helicops* and *Pseudoeuryx*, theoretically comprising a monophyletic group (see discussion in Vidal et al., 2002; Zaher, 1999). Seven taxa are currently recog-

nized: *Hydrops martii* (Wagler, 1824) and *Hydrops triangularis* (Wagler, 1824), with the latter including six subspecies. According to Albuquerque (2000), the *Hydrops triangularis* subspecies must be revised to insure their real status. These taxa are distributed in tropical areas, mainly in the Amazon Basin. *Hydrops*

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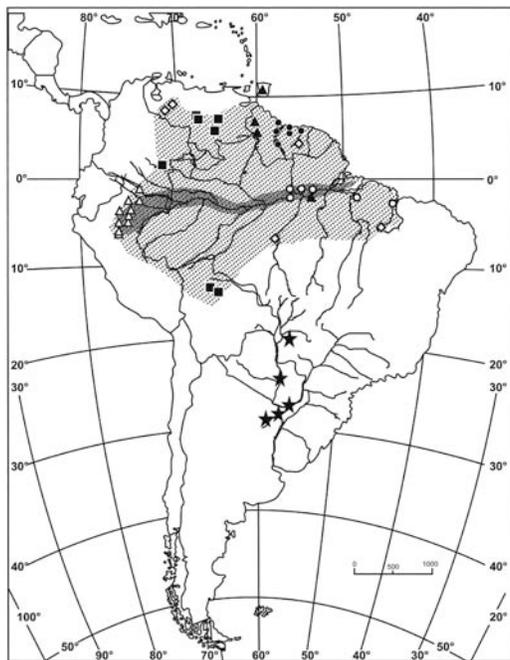


FIG. 1.—Geographic distribution of the genus *Hydrops*. The area of *Hydrops triangularis* (dots) and *H. martii* (vertical lines) was designed using the extreme records from Roze (1957b), Zaher and Caramaschi (1996), Yuki (1997), Rivas Fuenmayor and Fuentes (2000), Markezich (2001), Albuquerque (2001) and Guimarães et al. (2002). Precise localities are marked: stars, *Hydrops caesurus*; white triangles, *H. t. bassleri*; white squares, *H. t. bolivianus*; black circles, *H. t. fasciatus*; black triangles, *H. t. neglectus*; white circles, *H. t. triangularis*; black squares, *H. t. venezuelensis*; and white rhombus, *Hydrops triangularis* without subspecific assignment in the literature.

*martii* is restricted to the Amazonas River, where it is sympatric with *H. triangularis*. *Hydrops triangularis* ranges from 14° S, in rivers of the Bolivian Amazonas basin, up to 9° N in Venezuela, where the subspecies *H. t. venezuelensis* and *H. t. neglectus* reach the Orinoco River basin and even Trinidad and Tobago Islands (Fig. 4, in Roze, 1957b; Albuquerque, 2001; Markezich, 2001; Rivas Fuenmayor and Fuentes, 2000; Yuki, 1997; Zaher and Caramaschi, 1996). Roze (1957a) revised the genus, and described *Hydrops triangularis bassleri*, *H. t. bolivianus*, *H. t. neglectus* and *H. t. venezuelensis*; all species of the genus have no loreal; semi-divided nasal; only one rhombic or triangular prefrontal (character shared with *Helicops* and *Pseudoeryx*); small eyes with rounded pupils; narrow ventrals with rounded sides, and anal plate and subcaudals divided.

*Hydrops* differs from *Helicops* and *Pseudoeryx* in its smooth dorsal scales (keeled in *Helicops*) and in its maxillary diastema and color pattern with transverse bands (no diastema and longitudinal lines or dots in *Pseudoeryx*).

Williams and Couturier (1984) mentioned the genus for the first time from Argentina as *Hydrops triangularis bolivianus* Roze, 1957, although they concluded that the specimen did not completely match with any taxa previously described. Nevertheless the name was further used by other authors (Ceï, 1993; Williams and Francini, 1991; Williams and Scrocchi, 1994). Álvarez and Aguirre (1995) mentioned a new specimen they considered belong to the same taxon examined by Williams and Couturier (1984). The authors adopted a conservative position and named it as *Hydrops triangularis*. Buongermini and Waller (1998) recorded the same taxon from the Paraguay River. Finally, Giraud (2002) stated that there were no diagnostic characters to consider the Argentinian and Paraguayan specimens as *Hydrops triangularis bolivianus*.

We examined specimens of this taxon from several Argentinian collections, from the Museo de Historia Natural del Paraguay, and from the Universidade Federal de Mato Grosso do Sul, Campus de Corumbá, Brazil. Due to the lack of phylogenetic analysis for *Hydrops*, based on the morphological differences and disjunct distribution shown by the studied population (Fig. 1), we herein describe a new member of the genus.

#### MATERIALS AND METHODS

Snout-vent length (SVL) and tail length were measured with a meter stick to the nearest 1 mm. Other measurements were made with a dial caliper to the nearest 0.1 mm. A subcaudal incision was used to determine sex. To identify sexual dimorphism, we performed a parametric univariate statistical test (Student's *t*). The univariate normality assumptions of numerical characters were previously verified using a Shapiro-Wilks test, while homogeneity of variance was verified with the *F* test. We present a single value when counts from opposite sides of the same specimen were identical; a slash was used when opposite sides had different counts. The method of Dowling (1951) was used to count

ventral scales, and terminology for hemipenes follows Dowling and Savage (1960), Myers and Campbell (1981) and Zaher (1999).

Number of teeth was recorded from eight paratypes, and hemipenial features were examined "in situ", from semi-everted organs or from totally or semi-everted organs using the method of Pesantes and Abe (1994).

Except as noted, institutional abbreviations are those suggested by Leviton et al. (1985). The museum acronyms are: AMNH: American Museum of Natural History, New York, USA. CEUCH: Coleção Zoológica de Referência, Seção de Herpetologia, Universidade Federal do Mato Grosso do Sul, Campus de Corumbá, Corumbá, Mato Grosso do Sul, Brazil. MLP: Museo de Ciencias Naturales de La Plata, La Plata, Buenos Aires, Argentina. MNHNP: Museo Nacional de Historia Natural del Paraguay, Asunción, Paraguay. UFMT: Universidade Federal de Mato Grosso, Mato Grosso, Brazil. UNNEC: Colección Herpetológica de la Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina. UMNZ: Museum of Zoology, University of Michigan, Ann Arbor, USA.

#### SPECIES DESCRIPTION

##### *Hydrops caesurus* sp. nov.

##### *Cresonymy*

*Hydrops triangularis bolivianus*, Williams and Couturier, 1984 (not Roze, 1957).

*Hydrops triangularis bolivianus*, Williams and Francini, 1991 (not Roze, 1957).

*Hydrops triangularis bolivianus*, Cei, 1993 (not Roze, 1957).

*Hydrops triangularis bolivianus*, Williams and Scrocchi, 1994 (not Roze, 1957).

*Hydrops triangularis*, Álvarez and Aguirre, 1995 (not Wagler, 1824).

*Hydrops triangularis*, Aquino, Scott and Motte, 1996 (not Wagler, 1824).

*Hydrops triangularis*, Buonghermini and Waller, 1998 (not Wagler, 1824).

*Hydrops triangularis*, Giraudo, 2002 (not Wagler, 1824).

*Hydrops triangularis*, Álvarez et al., 2002 (not Wagler, 1824).

*Hydrops triangularis*, Álvarez et al., 2003a (not Wagler, 1824).

*Hydrops triangularis*, Álvarez et al., 2003b (not Wagler, 1824).

*Holotype*.—MNHNP 06698; (Collector number: MCZ Field Series Z-11689). An adult female from Departamento Itapúa; Isla Paloma, Canal de los Jesuitas, Paraguay. Collected by Consultora FORAGRO on 4 August 1994.

*Paratypes*.—CEUCH 027 (August 1997, skull); CEUCH 043 (October 1997, skull); CEUCH 077 (July 1998, skull and hemipenes): Ladário, Mato Grosso do Sul, Brazil. CEUCH 208 and CEUCH 279 (1 April 1999, skull); CEUCH 453 (3 August 1999); CEUCH 454–455 (skull)–456 (skull and hemipenes) and CEUCH 699 (2 August 1999): lagoa Negra, Ladário (18° 58' 15" S, 57° 33' 45" W), Mato Grosso do Sul, Brazil. MNHNP 4951: Departamento Itapúa; Complejo Isla Yacyreta. Paraguay. 3 August 1994. Consultora FORAGRO. 9 June 1994. Rescate de Fauna. MNHNP 04963: Departamento Itapúa; Complejo Isla Yacyreta. Paraguay. 3 August 1994. Consultora FORAGRO. MNHNP 06697: Departamento Itapúa; Isla Yacyreta and surroundings. Paraguay. 8 June 1994. Consultora FORAGRO. MNHNP 06700: Departamento Itapúa; Isla Yacyreta Isla Paloma, Canal de los Jesuitas, Complejo Isla Yacyreta. Paraguay. 9 June 1994. Consultora FORAGRO. MNHNP 06462: Departamento Pte. Hayes, Paraguay River; 14 km S from Puerto Rosario (24° 32' 22" S, 57° 10' 15" W). E. Buonghermini, R. Palacios, T. Waller and P. Micucci (skull and hemipenes). MNHNP 06699: Departamento Itapúa; Complejo Isla Yacyreta. Paraguay. MNHNP 09148: Departamento Itapúa; Complejo Isla Yacyreta. Paraguay. 9 June 1994. Rescate de Fauna ("in situ" hemipenis). MNHNP 09149: Departamento Itapúa; Isla Yacyreta. Paraguay. MNHNP 09151: Departamento Itapúa; Isla Yacyreta. Paraguay. MNHNP 09267: Paraguay. with no other specifications. MLP-JW 150: Bella Vista, Corrientes. Argentina. C. Baez. 4 May 1963. UNNEC 6725: Isla Yacyretá. Paraguay. 20 September 1994. L. Gniegting; mentioned by Álvarez and Aguirre (1995) as UNNEC 00409 (page 109) and UNNEC 00490 (page 111). UNNEC 7198–7589–93 (6 neonates): Puerto Carambola. Departamento San Miguel. Corrientes. Argentina. 12 December 1996. R. Aguirre and E. Schaefer.

*Diagnosis*.—Distinguished from all congeners by the presence of two longitudinal dorsal rows of transverse spots. The belly has trans-

verse black bands that extends up to the back, intercalating between the dorsal spots; all other taxa in the genus have transverse bands in the dorsum. Some specimens of *Hydrops triangularis fasciatus* have bands that do not reach the vertebral line, but this species has no dorsal spots. All specimens we examined have a cream spot in the sixth supralabial scale that can reach part of adjacent scales. *Hydrops caesurus* has the lowest total number of ventral counts (ventrals plus subcaudals) in the genus: 184–213 instead of 209–258 in other species. It differs from *Hydrops martii* (Wagler, 1830) in having 15 rows of dorsal scales instead of 17.

*Description of holotype*.—(Fig. 2a,b,c). Female; robust body, tail short (86 mm, 15.09% of SVL); total length 656 mm; SVL 570 mm; head length 22.8 mm (from snout tip to the mandible-quadrado joint).

Head depressed and a slightly distinct from the neck. Small eyes with round pupils; eye diameter 50% of the eye–nostril distance. Rostral scarcely visible dorsally, length of visible area less than 10% of frontal–rostral distance; prefrontals are twice as broad as the suture between them; one internasal slightly twice broader than long; nasals irregular twice broader than long; left nasal semidivided and the right divided; frontal pentagonal, length more than 60% of its width; one narrow supraocular, approximately twice longer than broad, wider behind the eye; parietals large maximum width slightly more than 50% of their; preocular small and subtriangular; two postoculars subequals; supralabials 8/8, only the fourth enters the orbit; first to fourth supralabials subequals approximately twice higher than broad; fifth supralabial slightly shorter than first to fourth; sixth and seventh are largest and the eighth is shorter than seventh. One plus one plus two temporals, the anterior is subrectangular and its length is two times its width; the posterior is irregular and its size is similar to the anterior; infralabials 8/9, first to fourth contact the first pair of chinshields; two pairs of chinshields, first 25% shorter than the second; four gulars separate the chinshields from two preventrals and 152 ventrals; anal plate divided; 33 divided subcaudals; terminal scale pointed; dorsal scales smooth in 15-15-15 rows, without reduction.

*Coloration in preservative*.—Dorsum dark brown, with black dorsal spots. Head dorsally

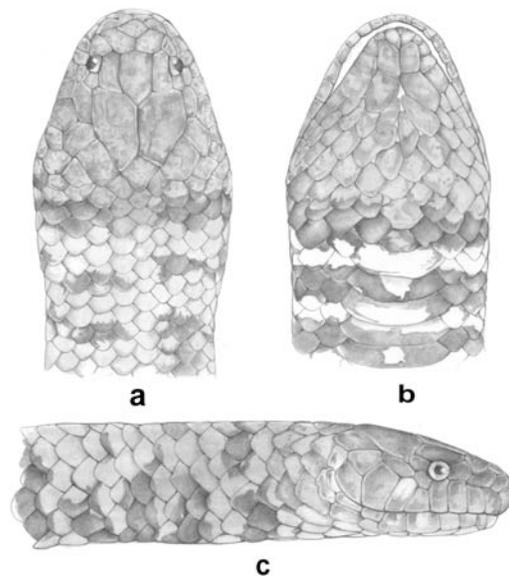


FIG. 2.—*Hydrops caesurus* Holotype (MNHN 06698). a: dorsal view of the head. b: ventral. c: lateral. Scale = 1 mm.

brown slightly darker than the rest of the dorsum; there is an inconspicuous black band at the end of the parietals and temporals. On the right side of the head, there is a light cream spot that covers almost all of the sixth supralabial, the inferior angle of the inferior postocular, the posterosuperior angle of the fifth supralabial and the posteroinferior angle of the seventh supralabial. On the left side of the head, the spot covers almost exclusively the superior half of the sixth supralabial; other supralabials have cream spots of different sizes. Ventral surface of the head with large cream spots, although the central area has a dark brownish color. First to seventh infralabials of both sides have a cream central area. Dorsally, posterior to the parietal band, there is a black ring one and a half to two scales width that is interrupted at the vertebral line. Behind the black ring, there are two series of black dorsal spots along the dorsum, 57 on the left side and 56 on the right side; they are approximately one scale width and extend from fourth to seventh rows. The dorsal spots continue on the tail, but they become irregular and smaller. Belly very dark and a pattern of black bands that continue as laterodorsal spots of the body can be noted. Bands are more conspicuous in the anterior and posterior

portions of the body, where 12 and 7 bands, can be counted, respectively. The edges of the black bands extend to the dorsum as laterodorsal spots intercalated between the dorsal spots. There are 57 laterodorsal spots on the left and 56 on the right side of the body, subtriangular and approximately one scale width at the fourth dorsal row and two to two and a half in the first dorsal row. They also occur on the tail, where the spots are smaller.

*Coloration in life.*—A photo of a single specimen from Serra do Amolar, Corumbá, Mato Grosso do Sul, shows a pattern very similar to the preserved specimens.

*Variation.*—The scale characters and coloration pattern of all the studied specimens are in Table 1. All the specimens have anal divided, eight supralabials with the fourth entering the eye, one preocular, two postoculars, and 1+1+2 temporals (except MNHNP 9267: 1+1+2/1+1+3).

The general color pattern of the paratypes is very similar to that of the holotype. The most remarkable variations are in the spots of the head, which have pale areas (probably light brown in life) that are not present in the holotype. These pale areas are very noticeable in the juveniles (Fig. 3a,b) that have the snout with a cream white band that occupies most of the first and second supralabials, nasals, anterior edge of prefrontals and anterior half of internasal. Behind the black band that covers the posterior edge of the parietals, there is a white band approximately 2 scales width, followed by a black band of the same width. The black band on the posterior edge of the parietals (divided in some exemplars) and the adjacent white band are always present with variable conspicuousness.

Ventral area of the head shows different proportions of light areas. The light and dark bands of the belly can be clearly observed in some specimens, particularly in the juveniles where the right and left halves do not correspond.

13+2 teeth (with diastema) in the maxilla (Table 2), two specimens have 12+2 and 14+2 in the right maxilla. Eight palatine teeth and frequently 17 to 19 in the pterygoid (three specimens have 20 or 21), the left pterygoid can be different from the right. 16 to 18 dentary teeth (one specimen has 15).

*Hemipenes.*—in situ, the hemipenis extends to the eighth subcaudal. Organ slightly bilobed and semicapitate (Fig. 4). Sulcus spermaticus centrolineal branches diverging at mid-length, between the bottom of hemipenial body and the point of bifurcation of the lobes, assuming a laterodistal position at the tip of the lobes. Peduncle naked and the basal area of hemipenial body with small spines. Both sides of the hemipenial body show scattered spines. Asulcate side with longitudinal folds. Laterally spines are larger than on the body. Proximal portion of the lobes with spinules and some unornamented calyces. The capitulate area of the asulcate side has naked folds.

The description of the hemipenes of *Hydrops caesurus* agrees with Roze (1957a), Zaher (1999) and Albuquerque (2002): unornamented calyces, semicapitate, and folds on the distal area of the hemipenial body.

*Sexual dimorphism.*—As Table 1 shows, a clear differentiation exists in the relationship between the snout-vent length and tail length. As in many other snakes, the males have a longer tail than the females: somewhat more than 24 to 34% in males ( $n = 14$ ;  $\bar{x} = 26.87$ ;  $SD = 3.15$ ) and from almost 14 to somewhat more than 20.5% in females ( $n = 10$ ;  $\bar{x} = 17.44$ ;  $SD = 2.10$ ). The subcaudal number is higher in males (51 to 62;  $n = 14$ ;  $\bar{x} = 56.7$ ;  $SD = 3.85$ ), without overlapping with the values of females (33 to 49;  $n = 10$ ;  $\bar{x} = 42.9$ ;  $SD = 5.4$ ). The ventrals showed significant statistical differences (test  $t = 3.26$ ,  $gl = 27$ ,  $P < 0.01$ ) with higher averages in the females (145–157,  $n = 13$ ;  $\bar{x} = 152$ ;  $SD = 3.3$ ) than the males (143–153,  $n = 16$ ;  $\bar{x} = 148.3$ ;  $SD = 2.70$ ).

*Distribution, habitat and natural history.*—*Hydrops caesurus* has a disjunct distribution with regard to the other species of the genus, occupying subtropical to temperate areas of the Paraná and Plata River basins (between 19° and 28° 30' S), from Pantanal in Mato Grosso do Sul, Brazil, through Paraguay and Paraná Rivers, with records in the Esteros de Iberá, old palaeoauce of the Paraná River in Argentina (Fig. 1).

*Hydrops caesurus* is mainly aquatic, as are all the other species of the genus, being frequently found in the floating vegetation of *Eichhornia crassipes* and *E. azurea* (Pontederiaceae) in the region of Corumbá and Ladário (Mato Grosso do Sul, Brazil). Within its



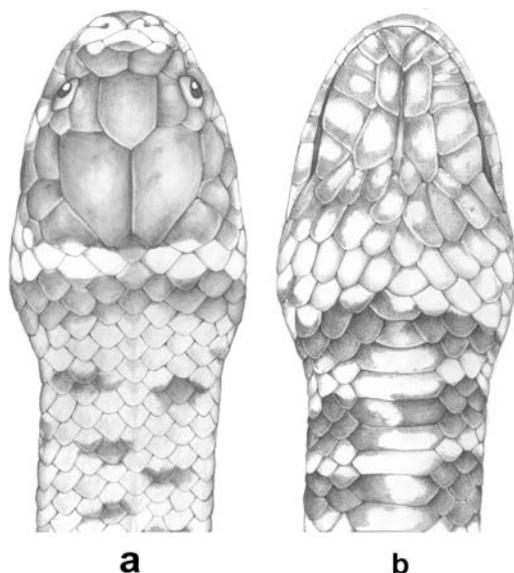


FIG. 3.—*Hydrops caesurus* Juvenile paratype (MNHNP 4951). a: dorsal view of the head and anterior portion of the body. b: ventral. Scale = 1 mm.

distribution, there is a wide availability of permanent, semipermanent and temporary aquatic habitats. The axis Pantanal – Paraguay River – Paraná River, constitutes one of the largest wetlands in South America, a very extensive and complex flooding plain with a variety of aquatic habitats: from lotics (rivers and streams of different intensities) to diverse lentic habitats formed by tidelands, lagoons, and hydromorphic savannas, all connected by periodical floods.

Some of the characteristic habitats of *H. caesurus* sp. nov. are similar through the whole region, including lentic habitats with little depth and an abundance of marshy macrophyts in the periphery (“pajonales” of *Panicum*

TABLE 2.—*Hydrops caesurus* dentition. Mx Maxilla, Pl palatine, Pt pterygoid, De dentary. A slash (“/”) is used to report right and left sides when they differ.

Museum number	Mx	Pl	Pt	De
CEUCH 027	15	8	18	17
CEUCH 043	15	8	18	16/17
CEUCH 077	15	8	17	15/17
CEUCH 208	15	8	21/20	16/17
CEUCH 279	15	8	20/18	18
CEUCH 455	15	/8	19	
CEUCH 456	16/15	8	19	16
MNHNP 6462	14/15	8	20	

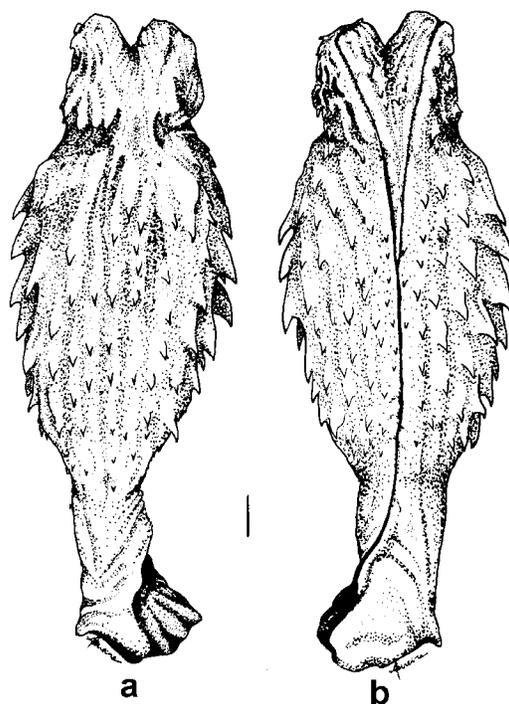


FIG. 4.—Asulcated and sulcated surfaces of the hemipenis of *Hydrops caesurus*. Paratype CEUCH 077. Scale = 1 mm.

spp., “juncales” of *Schoenoplectus californicus*, “totorales” of *Typha* spp., “pirizales” of *Cyperus giganteus*, “huajozales” of *Thalia* spp., and “carrizales” of *Panicum elephantipes* and *Polygonum* spp). Toward the center, in deeper sectors, there are floating communities of “camalotales” (*Eichhornia* spp., *Pontederia rotundifolia*, *Pistia stratiotes*) and submerged communities composed of *Ceratophyllum*, *Myriophyllum* and *Cabomba*, and others occur in the deepest areas. Another habitat in the Basin is the aquatic-marsh savannas with “palmars”, dense palm populations of *Copernicia* sp. with a herbaceous stratum, which is periodically flooded and acquires different characteristics depending of the quantity of water. More details on the geomorphologic, edaphic, climatic, and phytogeographic features of the region can be found in Merelles et al. (1992), Carnevali (1994), Adámoli and Pott (1999), and Neiff (2001).

*Hydrops caesurus* is an oviparous species. Six of the studied specimens (UNNEC 7198–7589–93) hatched in captivity from nine

elliptic eggs with coriaceous shell, collected on the banks of Carambolas stream, Corrientes, Argentina, in December 1999 (Alvarez et al., 2003 *a,b*). The measurements of 8 eggs (6 of them were measured after hatching) varied between 23.5 and 27 mm length ( $\bar{x}$  = 25.125, SD  $\pm$  1.382) and between 16 to 19 mm width ( $\bar{x}$  = 18, SD  $\pm$  1.035). Six males from Mato Grosso do Sul were studied, three of which (CEUCH 27, 400 SVL; CEUCH 77, 530 SVL, and CEUCH 455, ? SVL) showed the deferent duct rounded, indicating the passage of sperm. The smallest mature male (CEUCH 27) was 400 mm in SVL. The other males (CEUCH 453, 454 and 456) were immature (with translucent ducts) and measured between 319 and 353 mm SVL. Although it is frequently considered that the Hydropsini (Albuquerque, 2002; Zaher, 1999) are viviparous, Cunha and Nascimento (1981) registered viviparity and oviparity in different species of *Helicops* and mentioned the two reproductive modes in one specimen of *Pseudoeryx plicatilis mimeticus*. Rossman (1974) documented egg-laying in *Helicops angulatus*, and later (Rossman, 1984) documented live birth in the same species. We have no information of other reproductive data for the genus *Hydrops*.

The diet habits of *Hydrops caesurus* sp. nov. are unknown.

*Etymology*.—The specific epithet *caesurus* derives from the Latin *caesura*, meaning cut, pause. *Hydrops caesurus* is the only species in the genus that has no bands on the dorsum and the spots on it seem like an interrupted band.

*Remarks*.—The only subspecies previously described that has no entire bands on the dorsum is *Hydrops triangularis fasciatus* (see Roze, 1957a:Fig. 13b). Nevertheless, the bands on the back are an extension of those on the belly, whereas in *Hydrops caesurus* the ventral bands extend only up to the first dorsal rows, among which there are two series of dorsal spots.

Some of our results are in odds with those found by Roze (1957a). According to this, author the subspecies of *Hydrops triangularis* have 17 dorsal rows behind the head. However, in general, if a distance similar to the length of the head is considered, several specimens show 15 rows.

In the key showed by Roze (1957a), *Hydrops triangularis bassleri*, *H. triangularis bolivianus*

and *H. t. triangularis* have 51 subcaudals or less, when in fact they have 51 subcaudals or more. This problem was corrected by Peters and Orejas Miranda (1970). Considering these smaller corrections and including the new species described herein, a key for the species of the genus is presented:

KEY TO *HYDROPS* SPECIES AND SUBSPECIES  
(based on Albuquerque, 2000; Peters and Orejas Miranda, 1970; Roze, 1957a, and this paper)

- 1a.  
Dorsal scale rows at midbody 17 ..... *Hydrops martii*  
1b.  
Dorsal scale rows at midbody 15 ..... 2  
2a.  
Dorsal pattern of two longitudinal series of 53 to 62 dorsal spots that do not reach the vertebral line and two laterodorsal series of spots intercalated between the dorsal, that are an extension of the ventral bands. Total ventrals 184 to 206 in females and 194 to 213 in males ..... *Hydrops caesurus* sp. nov.  
2b.  
Dorsal pattern of 38 to 76 transverse bands on the dorsum. When the bands do not reach the vertebral line, they are an extension of the ventral bands and there are not two series of dorsal spots intercalated between them. 209 to 235 total ventrals ..... 3  
3a.  
Dorsal black bands narrow at the vertebral line or not reaching it ..... *Hydrops triangularis fasciatus*  
3b.  
Dorsal black bands laterally narrow, always complete, and broader in the vertebral line ..... 4  
4a.  
Posterior edge of dorsal black bands with irregular black projections; 69 subcaudals .....  
..... *Hydrops triangularis venezuelensis*  
4b.  
Posterior edge of dorsal black bands without irregular black projections. Fewer than 69 subcaudals 5  
5a.  
47 to 51 subcaudals; black bands of similar width and with irregular edges .....  
..... *Hydrops triangularis neglectus*  
5b.  
More than 51 subcaudals ..... 6  
6a.  
162 to 191 ventrals (169 to 191 in females) .....  
..... *Hydrops triangularis bassleri*  
6b.  
Ventrals 164 or fewer (fewer than 163 in females) ..... 7  
7a.  
Dorsal black bands narrow (one scale long) in the fourth dorsal scale row .....  
..... *Hydrops triangularis bolivianus*  
7b.  
Dorsal black bands of similar length (one and a half to two scales long) .....  
..... *Hydrops triangularis triangularis*

## RESUMEN

Se describe una especie nueva del género *Hydrops*. La nueva especie tiene la distribución más meridional del género (entre los 19° y 28° 30' de latitud sur) es disyunta con las otras especies y ocupa áreas subtropicales a templadas de la cuenca del río Paraná o del Plata, desde el Pantanal de Mato Grosso do Sul (Brasil) a través de los ríos Paraguay y Paraná, con registros en los esteros del Iberá, Argentina. Se diferencia de todas las otras especies del género por el número de escamas ventrales totales (suma de ventrales y subcaudales), por el número de hileras de escamas dorsales y por su coloración. Se presenta la variación de los caracteres, descripción de los hemipenes, distribución conocida y una clave para la identificación de todas las especies del género, basada en nuestros datos y autores anteriores.

*Acknowledgments.*—G. Schneider (UMNZ) sent us digital photos of the *H. triangularis bolivianus* holotype. R. A. K. Ribeiro sent us photos of a live specimen. A. de Figueredo Beda (UFMS) loaned the specimen from Miranda. The curators C. J. Cole (AMNH); B. B. Álvarez de Avanza and J. Céspedes (UNNEC) and J. Williams (MLP), kindly loaned the specimens under their care. J. Faivovich personally carried the specimens from AMNH. J. Oliveira Arruda and S. Sant'Anna de Souza helped us preparing skulls and hemipenes. N. K. de Pérez Carbajal rendered the illustrations, and M. Almazán the Fig. 1. M. Halloy kindly helped us with english version.

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Accepted: 5 May 2005

Associate Editor: Frank Burbrink

## APPENDIX I

### Specimens Examined

*Hydrops martii callostictus* (now *Hydrops martii* according to Albuquerque, 2000): AMNH R-54650. Perú. (Loreto): Río Itaya, Iquitos. Harvey Bassler. AMNH R-55494. Perú. (Loreto): Monte Carmelo, Requena (Uresti). Harvey Bassler.

*Hydrops martii martii* (now *Hydrops martii* according to Albuquerque, 2000): AMNH R-36161. Brasil: Manaus.

*Hydrops triangularis bassleri*: AMNH R-52354. Perú. (Loreto): Iquitos. Harvey Bassler. Paratype. AMNH R-52712. Perú. (Loreto): Iquitos. Harvey Bassler. Paratype.

*Hydrops triangularis bolivianus*: AMNH R-22449. Bolivia: Lago Rogoagua. N. E. Pearson. Paratype. UMNZ 56896. Bolivia: Puerto Sucre, Río Mamoré.

*Hydrops triangularis fasciatus*: AMNH R-14141. Guyana: (Mazaruni – Potaro): Kartabo 6° 21' N, 58° 41' W. May 1919. Tropical Research Expedition. AMNH R-18162. Guyana: Maripa, Essequibo R. W. Beebe.

*Hydrops triangularis neglectus*: AMNH R-25035. Guyana. H. R. Lang, W. J. La Varre. Paratype. AMNH R-25056. Guyana. Kamakusa. H. R. Lang, W. J. La Varre. Paratype.

*Hydrops caesurus*: CEUCH 3061. Brazil. Miranda (20° 14' S, 56° 22' W), Mato Grosso do Sul. Valdenir Correa. UFMT-R 1188, 1189 and 1192. Brazil. Fazenda Acurizal (17° 49' 51" S, 57° 33' 06" W), Serra do Amolar, Corumbá, Mato Grosso do Sul.