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A NEW SPECIES OF MARSUPIAL FROG (HYLIDAE: *GASTROTHECA*) FROM THE ANDES OF SOUTHERN COLOMBIA

By

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Marsupial frogs of the genus *Gastrotheca* are widespread and diverse in the Andes of Colombia, Ecuador, and Peru. Most of the species in the high Andes of Colombia and Ecuador produce eggs that hatch as tadpoles, but two species—*G. orophylax* and *plumbea*—have eggs that develop directly into froglets (Duellman and Pyles, 1980). The other high Andean species include *G. argenteovirens* and *G. aureomaculata* in Colombia and *G. cavia, lojana, monticola,* and *psychrophila* in Ecuador, a complex of species in southern Colombia and Ecuador referred to *G. riobambae.*

In 1979 Pedro M. Ruíz-C. of the Instituto de Ciencias Naturales in Bogotá showed Duellman a series of *Gastrotheca* from the Valle de Sibundoy in the Cordillera Oriental in southern Colombia. Subsequent study of these specimens revealed that they represented an undescribed species. In 1984 we worked in the Valle de Sibundoy and obtained additional specimens. One of these provided tadpoles, some of which were raised through metamorphosis and are now small adults living in the laboratory.

Pedro M. Ruíz-C., Director of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, has shared his knowledge of Colombian *Gastrotheca* with, and provided many specimens to, the senior author. We acknowledge Ruíz's helpfulness and contributions to a knowledge of Colombian anurans by associating his name with the new species.

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Gastrotheca ruizi new species

Holotype.—KU 200000, an adult female from Santiago, Municipio de Mocoa, Intendencia de Putumayo, Colombia (77°00′ W, 01°05′ N, elevation 2250 m), obtained on 25 February 1984 by Patricia A. Burrowes.

Paratypes.—KU 200001–05, 200303 collected with the holotype; ICN 1633–34, 1637, 1641, 2611, 4736–37, KU 196267–68 from Sibundoy, Municipio de Mocoa, Departamento de Putumayo, Colombia, elevation 2220 m, collected in April 1975 by M. Fajardo.

Referred Specimens.—ICN 2891–92 (young), KU 196269 (skeleton) from Sibundoy; KU 200006–14 (tadpoles), 200015 (young).

Diagnosis.—A large member of the *Gastrotheca riobambae* complex; males attaining a snout-vent length of 67.4 mm, females 78.0 mm, with an acuminate snout in dorsal view and anteroventrally inclined snout in profile; length of first finger slightly longer than second; dorsum dark green or dark brown medially and pale green or tan laterally; flanks and hidden surfaces of thighs uniformly dark brown with a tint of bronze on the flanks and of blue in the groin and on the limbs; dorsal coloration separated or not from flanks by narrow bronze line; tympanum bronze; skin on dorsum smooth.

Gastrotheca ruizi can be distinguished from all other members of the genus by the pointed, sloping snout, and from other species in the high Andes of Colombia and northern Ecuador by having the first finger longer than the second, instead of shorter or equal in length. Of the two other species in the Andes of southern Colombia, *G. argenteovirens* has a truncate snout in profile (Fig. 1) and finely granular skin on the dorsum, especially on the head; the dorsum is uniformly green or brown with a narrow bronze dorsolateral line, and the groin and hidden surfaces of the hind limbs are blue mottled with black. The other species, *G. riobambae,* has a rounded snout in profile and smooth to pustular skin on the dorsum; the dorsum is green or tan with dark green or brown irregular spots usually arranged in two longitudinal rows, and the groin and hidden surfaces of the hind limbs are gray or pale blue. The bronze tympanum of *G. ruizi* is similar to the gold tympanum of *G. aureomaculata,* a species of similar size but with a blunt snout and a dorsal color pattern varying from uniform green to black with bluish yellow flecks. *Gastrotheca cavia* from Lago Cuicocha, Ecuador, has a round snout, smooth skin on the dorsum, black mottling on the flanks, and black flecks on the dorsum. Two species having direct development, *G. orophylax* and *G. plumbea,* have weakly granular skin on the dorsum and rounded snouts, the flanks are brown in *G. plumbea.*

Description.—Body robust; mean snout-vent length considerably greater in females (69.8 ± 3.62 mm) than in males (59.3 ± 1.34 mm); snout acuminate in dorsal view, in lateral profile continuously inclined from nostrils to tip of snout (Fig. 1); canthus rostralis angular; loreal region slightly concave; lips thin, rounded; top of head concave between elevated lateral edges of frontoparietals; interorbital distance slightly

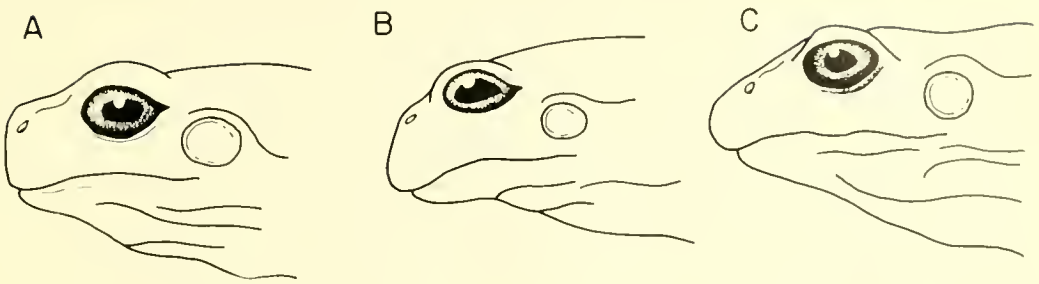

Fig. 1. Lateral views of the heads of *Gastrotheca* showing shapes of the snouts. A. *G. argenteovirens*, KU 181190. B. *G. riobambae*, KU 179720. C. *G. ruizi*, KU 200004.

greater than width of eyelid and of internarial distance; internarial area slightly concave; nostrils barely protuberant, directed dorsolaterally at point below anterior terminus of canthus rostralis; diameter of eye slightly greater than distance from eye to nostril; tympanum vertically ovoid, separated from eye by distance twice length of tympanum; tympanic annulus distinct, smooth; supratympanic fold moderately heavy, extending from posterior corner of eye to point above axilla.

Arms robust; axillary membrane absent; hands large; fingers long, unwebbed; discs small, round; diameter of discs slightly smaller than length of tympanum; relative length of fingers $2<1<4<3$; subarticular tubercles small, round, moderately low; supernumerary tubercles few, small, present only on proximal segments of fingers; palmar tubercle bifid; prepollical tubercle large, elongated, ovoid, bearing brown nuptial excrescences medially on thumb in males. Hind limbs moderately short, robust, about 44% of snout-vent length; foot length slightly greater than tibia length; calcar, outer metatarsal tubercle, and tarsal folds absent; inner metatarsal tubercle moderately large, ovoid, visible from above; toes long, bearing discs slightly smaller than those on fingers; relative length of toes $1<2<3<5<4$; toes about two fifths webbed; webbing formula $I2^{-}$–$2^{+}II2^{-}$–$3III2$–$3^{+}IV3$–$2V$; subarticular tubercles small, round; supernumerary tubercles small, ovoid, present only on proximal segments.

Skin on dorsum of head, body, and limbs smooth; eyelid tubercles absent, skin on flanks areolate; skin on belly and ventral surfaces of thighs granular. Anal opening directed posteriorly at upper level of thighs; anal sheath short; anal folds and tubercles absent; pouch opening U-shaped with anterior border at level of sacrum.

Vomerine odontophores small, transversely ovoid, widely separated medially at level of posterior margins of small quadrangular choanae (in one specimen bearing 5 teeth on each process). Tongue cordiform, free posteriorly for about one fifth of its length. Vocal slit extending from midlateral base of tongue to angle of jaw. Vocal sac single, median, subgular.

Color in preservative: In most specimens dorsum dark bluish gray with narrow middorsal and broad dorsolateral pale bluish gray stripes. Flanks, anterior and posterior surfaces of thighs, and feet dark gray to dark brown.

One female (KU 200303) having dorsum and flanks dull tan; upper flanks finely mottled with black.

Color in life: KU 200000—dorsum dark green medially and pale green laterally; top of head and loreal region pale green; tympanum bronze; dorsal surfaces of thighs greenish brown; posterior surfaces of thighs grayish brown with tint of dark blue; throat yellow; belly dull cream; ventral surfaces of limbs creamy gray; iris dull greenish bronze with fine black reticulations. KU 200001, 200003–05—same coloration but with a narrow bronze line separating dorsal color from flanks; groin and anterior and posterior surfaces of thighs pale blue. KU 200002—dorsum dark brown with bronze middorsal and dorsolateral lines; lateral part of dorsum pale green (Fig. 2). KU 200303—dorsum greenish tan with diffuse brown dorsolateral area; irregular bronze dorsolateral line extending to groin; flanks mottled bronze-tan and brown; limbs brown; venter grayish cream with blue suffusion in axilla and groin.

Measurements.—The measurements (in mm) of the adult female holotype are: snout-vent length 78.0, tibia length 33.2, foot length 33.5, head length 24.5, head width 26.1, diameter of eye 5.0, diameter of tympanum 4.0, eye-nostril 5.4. The measurements of the type series are summarized in Table 1.

Tadpoles.—One female (KU 200303) gave birth to 134 tadpoles on 7 March 1984. These were preserved at intervals until metamorphosis occurred on 17 June 1984. The ages and sizes of the tadpoles are given in Table 2.

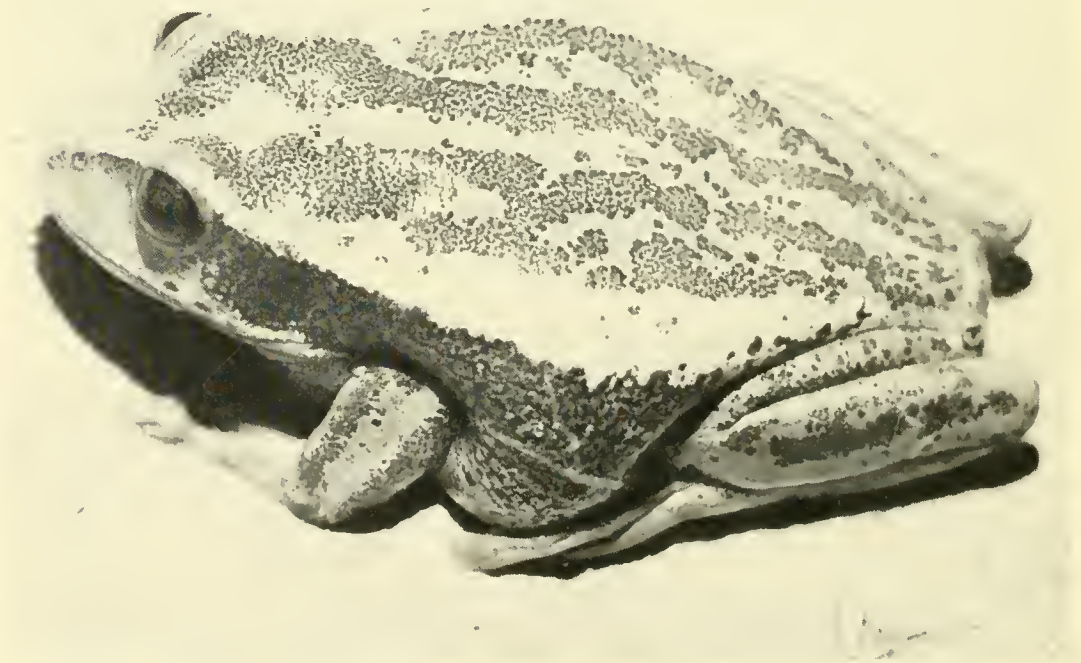

Fig. 2. *Gastrotheca ruizi*, adult male, snout-vent length 63 mm.

Table 1.—Measurements of *Gastrotheca ruizi*
First line is mean and standard error; second line is range.
Significant differences between sexes: ** $p = 0.01$, * $p = 0.05$, Brown-Forsythe f-test (Dixon, 1981).

Character	Males ($n = 11$)	Females ($n = 4$)
Snout-vent length**	59.3 ± 1.34	69.8 ± 3.62
	53.5–67.4	62.1–78.0
Tibia length**	26.8 ± 0.44	30.7 ± 0.93
	24.9–30.0	28.8–33.2
Foot length**	28.2 ± 0.55	32.0 ± 0.56
	25.8–32.7	30.9–33.5
Head length	20.0 ± 0.35	24.1 ± 2.11
	18.4–21.6	20.9–29.9
Head width*	20.4 ± 0.31	22.8 ± 1.20
	18.8–21.8	20.4–26.1
Interorbital distance	5.1 ± 0.15	5.6 ± 0.39
	4.4–5.8	4.6–6.3
Diameter of eye	5.3 ± 0.23	5.6 ± 0.23
	4.4–7.0	5.0–6.1
Diameter of tympanum	3.9 ± 0.24	3.9 ± 0.22
	2.7–5.0	3.2–4.2
Eye-nostril	4.6 ± 0.13	5.3 ± 0.17
	4.1–5.4	4.8–5.5

Body in dorsal view ovoid, half again as wide as deep; in profile snout sloping from nostrils to tip of snout; eyes small, directed dorsolaterally; interorbital distance one third width of body; nostrils slightly closer to eyes than to tip of snout, directed anterolaterally. Spiracle sinistral, ventrolateral, at about midlength of body; anal tube sinistral. Caudal musculature moderately deep, tapering to a point just short of tip of rounded fin; fins moderately deep; anteriorly, ventral fin slightly deeper than dorsal fin; depth of each fin about equal to depth of caudal musculature at midlength of tail; dorsal fin not extending onto body.

Mouth small, anteroventral, about half greatest width of body; lips barely infolded laterally; median part of upper lip bare; elsewhere lip bordered by single row of small, blunt papillae; a few additional papillae in lateral fold. Two upper and three lower rows of denticles, all of about equal length in larger tadpoles; first lower row narrowly interrupted medially; upper beak a broad shallow arch; lower beak V-shaped; both beaks finely serrate.

A tadpole in State 32 has a brown body and grayish tan venter; the caudal musculature and fins have minute brown flecks and a dark line on either side of the base of the dorsal fin. A tadpole in Stage 38 has the

Table 2.—Development of Tadpoles of *Gastrotheca ruizi*
Mean is in parentheses below range.

Age (days)	*N*	Stage	Body length	Total length
0	10	29–30	6.8–7.5 (7.2 ± 0.14)	14.5–17.5 (16.1 ± 0.36)
1	2	30–31	7.8–8.0 (7.9)	18.0–20.5 (19.3)
3	2	31	8.0–8.4 (8.2)	20.4–21.0 (20.7)
5	2	31	8.1–8.5 (8.3)	20.8–21.0 (20.9)
7	2	32	8.6–9.0 (8.8)	21.6–22.0 (21.8)
9	2	32	9.0	22.5
11	2	32	10.0–11.0 (10.5)	25.0–28.0 (26.5)
14	1	32	10.0	25.0
89	1	38	24.0	66.5
102	1	46	28.0	—

pigment on the tail concentrated into a longitudinal row of distinct spots on the dorsal and ventral fin; a dark dorsolateral stripe is present on the caudal musculature, and there is a dark midlateral line on the proximal one third of the musculature. A newly metamorphosed young (KU 200015) is colored much like the adults, except that the green color is more intense. The shanks and feet are bronze-brown with a green longitudinal stripe on the foot. The lower flanks are cream with a bronze-brown tint, and the upper flanks are dark brown. The venter is creamy white, and the labial stripe is white. The iris is coppery bronze.

Distribution and Ecology.—Gastrotheca ruizi is known only from the Valle de Sibundoy in the Cordillera Oriental (Fig. 3). The valley lies at an elevation of 2200–2250 m and is about 6 km wide and 18 km long west to east. According to the ecological map of Colombia by the Instituto Geográfico "Agustín Codazzi" (1977), the valley lies in the very wet low montane forest life zone. However, the entire valley is in crops or pasture. The valley is drained by the Río Sibundoy, which flows into the Río Putumayo in the Amazon lowlands.

The village of Santiago, the type locality, is 53 km east of Pasto on the road to Puerto Asís; the only other locality, the village of Sibundoy, is 13 km farther east on the same road.

On 25 February 1984, *G. ruizi* were calling from drainage ditches bordering fields just south of a small bridge over the Río Sibundoy at the southern edge of Santiago. The ditches are 1–1.5 m deep with water about 0.5 m deep. Males were calling from branches of small bushes 1–2 m

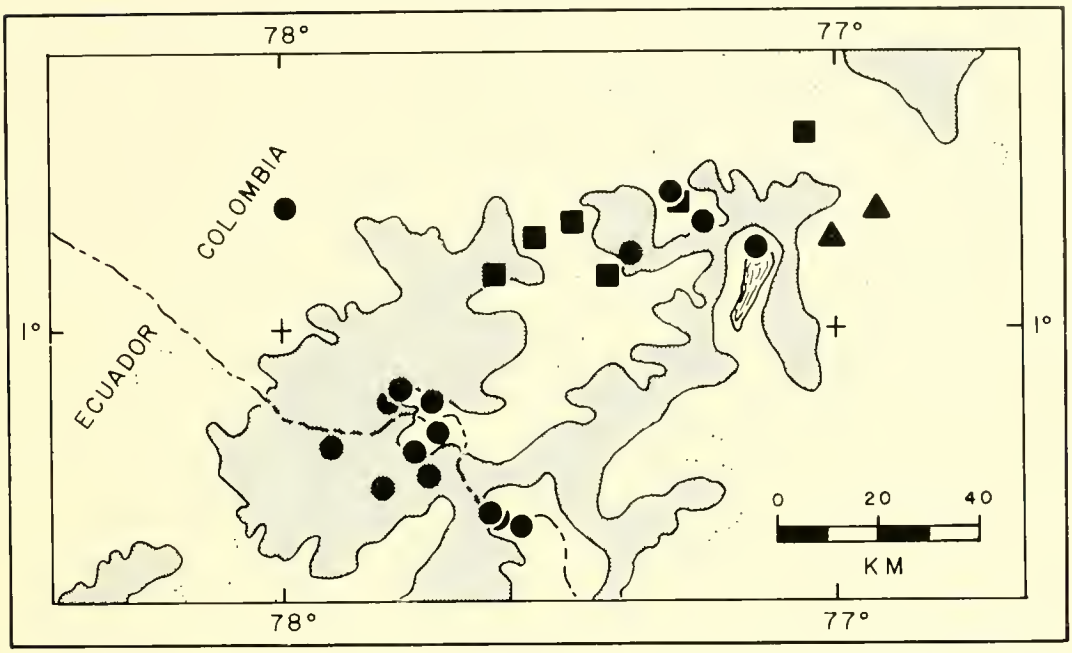

Fig. 3. Andean region of southern Colombia and northern Ecuador. The dotted line is the 2000-meter contour; the area above 3000 meters is shaded. Dots are localities for *Gastrotheca riobambae;* squares are *G. argenteovirens,* and triangles are *G. ruizi.*

above the water. The call consists of a single primary note "wraack" usually followed by two or three secondary notes "ack-ack-ack." Two brooding females were on dense masses of leaves above the ditches.

DISCUSSION

The complex topography in southern Colombia and adjacent Ecuador apparently is responsible for the patterns of distribution of the species of *Gastrotheca* in that region (Fig. 3). The distributions of tadpole-producing species of *Gastrotheca* in the Andes are essentially allopatric, but tadpole-producing species do occur sympatrically with species having direct development. In the region under consideration, the tadpole-producing *G. riobambae* is sympatric with the direct-developing *G. orophylax* in the area of El Carmelo–Santa Bárbara in extreme northern Ecuador.

In southern Colombia and northern Ecuador there are three tadpole-producing species of *Gastrotheca:* (1) *G. argenteovirens* at elevations of 2050 to 3050 m on the western slopes of the Cordillera Central in central Colombia southward to the Nudo de Pasto and also on the western slopes of the Cordillera Occidental in southern Colombia; (2) *G. riobambae* at elevations of 2500 to 4000 m in the Cordillera Oriental, intermontane basins, and Cordillera Occidental from central Ecuador to extreme southern Colombia; (3) *G. ruizi* at elevations of 2220 to 2250 m in the Valle de Sibundoy on the eastern slopes of the Cordillera Oriental in southern Colombia.

Gastrotheca ruizi is allopatric to the other species. In southern

Colombia, its range is separated from the ranges of *G. argenteovirens* and *G. riobambae* by the crest of the Cordillera Oriental, which is at an elevation of more than 3200 m between the Valle de Sibundoy and Lago de la Cocha at 2970 m, the closest known locality for *G. riobambae.* The latter is unknown from the eastern slopes of the Cordillera Oriental in Colombia, but it is known from localities of 2360 to 3400 m on the eastern slopes in Ecuador. The Valle de Sibundoy is separated from these localities by eastern spurs of the Andes, notably the cordilleras Patascoy, Pax, and Tigre.

Gastrotheca argenteovirens inhabits cloud forest and subparamo on the western slopes of the Cordillera Central. It is known from Pasto and several other localities on the western slopes of that Cordillera in southern Colombia. There the Cordillera Central is separated from the northern terminus of the Cordillera Occidental of Ecuador and southern Colombia by the deep, subhumid valley of the Río Guaitaría, a tributary of the Río Patía, which flows into the Pacific Ocean and separates the principal Cordillera Occidental of western Colombia from the western cordilleras of southern Colombia and Ecuador. *Gastrotheca argenteovirens* occurs on both sides of the valley of the Río Guaitaría; it is known from Guaitarillo and Túquerres at elevations of 2650 and 3050 m, respectively, in the Cordillera Occidental.

Gastrotheca riobambae is widespread at elevations above 2500 m in northern Ecuador, but there are few records of the species in southern Colombia. It is known from Cuaspud and Cumbal at elevations of 3200 and 3030 m, respectively, in the Cordillera Occidental west of the Río Guaitaría; a record for Ricuarte, elevation 1180 m (ANSP 25316) is considered to be in error. To the east of the Río Guaitaría in the Cordillera Central, the species has been collected at Pasto, 7.5 km east of Pasto, two localities south of Pasto, and Lago de la Cocha; all of these are at elevations of 2530 to 3400 m.

The ranges of *G. argenteovirens* and *G. riobambae* overlap in the vicinity of Pasto; specimens of both species are known from Pasto. In attempting to explain the allopatric distributions of the tadpole-producing species *G. marsupiata* and *G. peruana* in Peru, Duellman and Fritts (1972) suggested that the scarcity of ponds for the development of tadpoles might restrict the distributions of those species. However, aquatic sites (permanent and temporary ponds and man-made ditches) are numerous in southern Colombia. Although the tadpoles of *Colostethus* sometimes are found in ditches with tadpoles of *Gastrotheca,* usually only tadpoles of *Gastrotheca* are found in these aquatic sites. The only other tadpoles in this region are those of *Atelopus ignescens* and *Centrolenella buckleyi,* both of which together with most of those of *Colostethus* are found in streams.

The tadpoles of *G. argenteovirens* and *G. riobambae* have been found in similar microhabitats and agree with other *Gastrotheca* tadpoles in being dietary generalists as indicated by their oral morphology (Wassersug and Duellman, 1984). However, there are slight morphological differences among the tadpoles and seemingly some major developmental differences.

The tadpoles of *G. argenteovirens* hatch at a more advanced stage than the others. Three lots of tadpoles of *G. argenteovirens* were hatched and raised in the laboratory in Bogotá by Pedro M. Ruíz C. There were 20, 29, and 55 tadpoles born to three females. The tadpoles hatched at stages 33–37 (Gosner, 1960) at body lengths of 9.8–12.4 mm (mean 10.9 mm, $n = 6$) and total lengths of 24.2–32.4 mm (mean 27.4 mm, $n = 6$). Larvae metamorphosed in 19–43 days with snout-vent lengths of 11.0–12.4 mm (mean 11.7, $n = 4$).

Embryonic development in *G. riobambae* was summarized by del Pino and Escobar (1981), who noted that clutches consist of an average of 128 eggs. A brood hatched from a female from 7 km north of Latacunga, Provincia de Cotopaxi, Ecuador, was raised in the laboratory at 20°C. Four hatchlings in stages 30–31 have body lengths of 6.0–6.5 mm (mean 6.1) and total lengths of 14.0–15.5 mm (mean 14.5); tadpoles in this lot began to metamorphose in 59 days. A single juvenile preserved at metamorphosis has a snout-vent length of 27.0 mm.

Thus, *G. riobambae* and *G. ruizi* are alike in having tadpoles that hatch at stages 29–31, require two months or more for development and metamorphose into froglets having snout-vent lengths of more than 25 mm. Both species have clutches in excess of 100 eggs. On the other hand, clutch size is less than 60 in *G. argenteovirens;* the hatchlings are at a more advanced stage (33–37), and these metamorphose in 19–43 days into froglets having snout-vent lengths of less than 13 mm. The latter species seems to have a different life-history strategy than the other species; it has fewer, but larger, tadpoles that develop faster into smaller froglets. Therefore, it seems likely that individual tadpoles of *G. argenteovirens* utilize a smaller quantity of aquatic resources (and for a shorter period of time) than the other species. Possibly in this way the tadpoles of *G. argenteovirens* and *G. riobambae* may be able to coexist.

The skulls of *G. argenteovirens* and *G. riobambae* are alike in having the frontoparietals expanded laterally and forming a pointed postorbital process, whereas the skull of *G. ruizi* has a small postorbital projection, and the lateral edges of the frontoparietals are greatly elevated. The nasals, frontoparietals, squamosals, and facial processes of the maxillae are deeply exostosed in *G. argenteovirens* and *G. ruizi* and slightly, if at all, exostosed in *G. riobambae.* The posterior angle of the alary processes of the premaxillae is about 20° in *G. argenteovirens*, 30° in *G. riobambae*, and 45° in *G. ruizi;* the acute angle of these processes accounts for the sloping snout in *G. ruizi.*

The relationships of *G. ruizi* certainly are with the tadpole-producing species in the northern Andes. More precise placement must await the completion of analyses of osteological, developmental, and electrophoretic data now in progress.

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RESUMEN

Se describe una nueva especies, *Gastrotheca ruizi*, que se encuentra en el Valle de Sibundoy en la Cordillera Oriental del sur de Colombia. Esta especie se distingue de todas las otras especies de *Gastrotheca* por tener un hocico puntiagudo, y de otras especies de altitud elevada en los Andes de Colombia y el norte de Ecuador por tener el primer dedo de la mano más largo que el segundo. *Gastrotheca ruizi* tiene un patrón de color distintivo, con la parte dorsal media verde ó marrón oscura (interrumpida en el centro por una línea verde pálida en algunos especímenes), línea ancha dorsolateral de color verde pálida y flancos marrón oscuro separados ó no del dorso por una línea estrecha de color bronce.

Una hembra de *G. ruizi* produjo 134 renacuajos; las larvas en el momento de la eclosión estaban en etapas de desarrollo 29 y 30. Algunas completáron su metamórfosis en 102 dias con un largo de 28 mm. En los Andes del sur de Colombia, y Ecuador adyacente, tres especies de *Gastrotheca* producen renacuajos. De estas, *G. ruizi* es la única especie que se conoce del Valle de Sibundoy en la vertiente este de la Cordillera Oriental. *Gastrotheca argenteovirens* y *G. riobambae* son en la mayor parte alopátridas, pero en los alrededores de Pasto, Colombia, la distribución de estas dos especies se sobrepone.

SPECIMENS EXAMINED

In addition to the specimens of *G. ruizi* listed in the description, the following material was used in this study:

Gastrotheca argenteovirens.—COLOMBIA: *Nariño:* Cacería San Rafael, 12 km from Conzacá, 2050 m, ICN 12206; Guaitarillo, 2650 m, FMNH 54793–843; Pasto, 2530 m, ICN 3407, 4743; Resguardo Indígena Aponte (Municipio de Tablón), INDERENA (2); Tangua, 2400 m, UV 28783; Túquerres, 3050 m, FMNH 54844–45.

Gastrotheca riobambae.—COLOMBIA: *Nariño:* Cuaspud, 3200 m, TNHC 40564–65; Cumbal, 3030 m, ANSP 25317–21; 4 km SSW

Cumbal, 3260 m, 12208–09; Hacienda La Marquesa, 23 km S Pasto, 3400 m, ICN 12207; Lago de la Cocha (N shore), 2790 m, KU 169401–02; Pasto, 2530 m, LACM 50172; Represa del Río Bobo, 6 km S, 11 km W Pasto, ICN 12210–16; ?Ricuarte, 1180 m, ANSP 25316; Vereda de San Fernando, 7.5 km E Pasto, 2800 m, KU 200016 (tadpoles). ECUADOR: *Carchí:* El Carmelo, 2710 m, KU 178558; 4.3 km SE El Carmelo, 2640 m, KU 180343–44 (tadpoles); Quebrada de Piedras, 20 km S Tulcán, 3400 m, KU 118120; 10 km W Tufiño, 3400 m, KU 203540 (tadpoles); Tulcán, 2950 m, KU 117978–79, 118119 (tadpoles), 178555–57, 179719–20, 180338 (tadpoles), 180339 (young); 14 km SW Tulcán, 3340 m, KU 166185 (tadpoles); 30 km SW Tulcán, 3140 m, KU 203541–42 (tadpoles). *Napo:* Santa Bárbara, 2650 m, KU 190032–33, 190034 (tadpoles); Río Chingual, 3.9 km W Santa Bárbara, 2360 m, KU 203439–40.

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