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A SYSTEMATIC REVIEW OF THE MARSUPIAL
FROGS (HYLIDAE: *GASTROTHECA*)
OF THE ANDES OF ECUADOR

By

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Many species of marsupial frogs, genus *Gastrotheca*, occur in the Andes and associated cordilleras from western Venezuela southward to northern Argentina. Because of the paucity of specimens of many of the named taxa and confusing variation exhibited by some species, the taxonomy of the marsupial frogs has been chaotic. Duellman and Fritts (1972) reviewed the species occurring in the Andes to the south of the Huancabamba Depression in northern Perú and delimited seven species there as members of the *Gastrotheca marsupiata* group. These frogs differ in cranial characters from the species in the Huancabamba Depression and northward, all of which were referred to the *Gastrotheca argenteovirens* group by Duellman and Fritts (1972).

The Ecuadorian species included in the latter group were: *G. lojana* Parker, 1932; *G. monticola* Barbour and Noble, 1920; *G. plumbea* (Boulenger, 1882); and *G. riobambae* (Fowler, 1913). Colombian and Venezuelan species assumed to belong to the same group were: *G. argenteovirens* (Boettger, 1892); *G. aureomaculata* Cochran and Goin, 1970; *G. helenae* Dunn, 1944; *G. medemi* Cochran and Goin, 1970; *G. mertensi* Cochran and Goin, 1970; and *G. nicefori* Gaige, 1933. It now seems apparent that these frogs are treated best as two distinct species groups. The Ecuadorian species listed above and two species named in this paper can be referred to as the *Gastrotheca plumbea* group, and the Colombian and Venezuelan species, as the *Gastrotheca argenteovirens* group. When better known, *G. williamsoni* Gaige, 1922, and an unnamed species related to *G. plumbea* from Antioquia and Cundinamarca, Colombia,

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may be referable to the *Gastrotheca argenteovirens* and *plumbea* groups, respectively.

Thus, this paper is a review of the *Gastrotheca plumbea* group. The purpose of the present paper is to provide a synthesis of accumulated information and in so doing, 1) define the species, 2) assign names to taxonomically recognizable populations, and 3) summarize data on geographic variation, distribution, ecology, and life history. The results presented here, together with the synthesis of the southern Andean frogs by Duellman and Fritts (1972), will provide a basis for a future systematic assessment of the *Gastrotheca argenteovirens* group.

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MATERIALS AND METHODS

I have examined 1125 preserved frogs (including type specimens of all taxa), 24 skeletons, and 50 lots of tadpoles referable to the species discussed in this paper, and I have studied each of the species in the field. Terminology follows that of Duellman (1970), except for two additional measurements: length of third finger is the distance from the proximal edge of the palmar tubercle to the tip of the finger; length of thumb is the distance from the proximal edge of the prepollical tubercle to the tip of the thumb. Throughout the text, specimens are listed by their catalogue numbers preceded by the appropriate museum abbreviations, as follows:

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
BMNH	British Museum (Natural History)
CAS	California Academy of Sciences
CAS-SU	Stanford University Collection (in California Academy of Sciences)
FMNH	Field Museum of Natural History
FSM	Florida State Museum
KU	University of Kansas Museum of Natural History
MCZ	Museum of Comparative Zoology, Harvard University
MJP	Museo Javier Prado, Lima, Perú
MNCN	Museo Nacional de Ciencias Naturales, Madrid
MNHN	Museum National d'Histoire Naturelle, Paris
NHMW	Naturhistorisches Museum, Wien
NIHRM	Naturhistoriska Riksmuseet, Stockholm
SMF	Senckenbergische Museum, Frankfurt
TNHC	Texas Natural History Collection
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum
UZM	Universitets Zoölogiske Museum, Copenhagen
ZMB	Zoölogisches Museum, Berlin

THE *GASTROTHECA PLUMBEA* GROUP

Species comprising this group have short to moderately long legs, narrow to moderately wide heads, relatively large hands, moderate to extensive exostosis of the dermal roofing bones, broad frontoparietals expanded into lateral flanges, the frontoparietal fontanelle covered by the frontoparietals, and a long cultriform process of the parasphenoid. All species have aquatic tadpoles.

In contrast, members of the *Gastrotheca argenteovirens* group have long legs, broad heads, large hands, extensive exostosis of the dermal roofing bones and in some species co-ossification and casquing, and at least in some species a short cultriform process. Insofar as known, all species in this group have aquatic tadpoles, but at least in *G. argenteovirens*, the tadpoles hatch at an advanced stage, and the larval period is short. Members of the *Gastrotheca marsupiata* group have short legs, narrow heads, small hands, no exostosis of the dermal roofing bones, small narrow frontoparietals not roofing the frontoparietal fontanelle, and a long cultriform process. Three species have aquatic tadpoles; in the other four development is completed in the maternal pouch.

ACCOUNTS OF SPECIES

In the following accounts, each taxon is diagnosed; the variation is discussed, and the distribution of each species is annotated. Pertinent measurements and proportions are given in Table 1, and the frogs are illustrated in figures 1 and 2. Maximum snout-vent lengths are given in the diagnoses.

TABLE 1. Measurements and proportions of Andean *Gastrothoecca*.
(First line, mean \pm 1 SD \bar{x} ; second line, range)

Species and Sex	N	Snout-Vent Length (SVL)	Tibia Length/SVL	Foot Length/SVL	Interorbital/Head Width	Eyes-Nostril/Head Length	Tympanum/Eye
<i>G. caucia</i>	♂ 6	54.4 \pm 4.435	0.414 \pm 0.013	0.462 \pm 0.26	0.290 \pm 0.016	0.265 \pm 0.015	0.539 \pm 0.055
		46.2—58.5	0.401—0.435	0.427—0.491	0.276—0.316	0.246—0.278	0.481—0.632
♀ 14	♀ 14	63.3 \pm 2.940	0.415 \pm 0.017	0.474 \pm 0.023	0.286 \pm 0.012	0.256 \pm 0.013	0.621 \pm 0.042
		57.5—67.2	0.392—0.452	0.440—0.509	0.265—0.309	0.223—0.281	0.561—0.695
<i>G. lojana</i>	♂ 5	53.4 \pm 2.230	0.479 \pm 0.012	0.450 \pm 0.011	0.351 \pm 0.022	0.303 \pm 0.010	0.609 \pm 0.020
		50.5—56.0	0.469—0.500	0.437—0.464	0.333—0.377	0.294—0.315	0.587—0.636
♀ 3	♀ 3	58.5	0.511	0.466	0.396	0.297	0.501
		50.7—67.4	0.497—0.522	0.454—0.479	0.390—0.406	0.263—0.319	0.480—0.530
<i>G. monticola</i>	♂ 4	55.0	0.468	0.458	0.285	0.267	0.594
		46.0—60.0	0.446—0.527	0.432—0.500	0.273—0.294	0.247—0.280	0.540—0.682
♀ 4	♀ 4	66.8	0.505	0.455	0.418	0.302	0.695
		61.6—77.0	0.468—0.529	0.434—0.475	0.387—0.435	0.278—0.323	0.564—0.759
<i>G. phumbea</i>	♂ 9	57.4 \pm 3.150	0.478 \pm 0.012	0.470 \pm 0.010	0.313 \pm 0.013	0.301 \pm 0.014	0.630 \pm 0.026
		52.2—62.3	0.457—0.492	0.452—0.483	0.294—0.337	0.280—0.321	0.600—0.667
♀ 3	♀ 3	64.5	0.497	0.476	0.348	0.296	0.634
		59.7—68.0	0.489—0.509	0.456—0.510	0.305—0.403	0.279—0.308	0.568—0.691
<i>G. psychrophila</i>	♂ 8	49.6 \pm 1.769	0.492 \pm 0.020	0.467 \pm 0.022	0.353 \pm 0.011	0.263 \pm 0.008	0.650 \pm 0.037
		46.0—51.5	0.472—0.524	0.442—0.493	0.341—0.374	0.246—0.272	0.579—0.700
♀ 2	♀ 2	60.9	0.509	0.510	0.362	0.248	0.707
		60.8—61.0	0.502—0.515	0.505—0.515	0.358—0.365	0.244—0.252	0.704—0.709
<i>G. riobamba</i>	♂ 15	43.4 \pm 3.043	0.383 \pm 0.021	0.416 \pm 0.021	0.259 \pm 0.010	0.239 \pm 0.016	0.577 \pm 0.039
		38.8—48.7	0.357—0.410	0.362—0.434	0.245—0.283	0.213—0.272	0.532—0.644
♀ 9	♀ 9	47.8 \pm 3.429	0.412 \pm 0.016	0.442 \pm 0.017	0.308 \pm 0.013	0.285 \pm 0.012	0.567 \pm 0.031
		41.0—51.2	0.373—0.434	0.416—0.478	0.241—0.275	0.218—0.268	0.549—0.739

Gastrotheca cavia new species

Holotype.—KU 148532, an adult female, 64.0 mm, from Isla Pequeña, Laguna Cuicocha, Provincia Imbabura, Ecuador, 2890 m; one of a series collected on 31 October 1971 by William E. Duellman and John E. Simmons.

Paratopotypes.—KU 138216-20, 24 July 1970, Thomas H. and Patricia R. Fritts; 139137-9, 30 January 1971, William E. Duellman; 143094, 148530-1, 148533-36, 31 October 1971, William E. Duellman and John E. Simmons; 148537-40, 30 January 1971, William E. Duellman.

Diagnosis.—1) Body robust, 58.5 mm in males, 67.2 in females; 2) snout round in dorsal view, rounded above and anteroventrally inclined in profile; 3) canthus rounded; 4) loreal region shallowly concave; 5) tympanum vertically elliptical; 6) supratympanic fold moderately heavy; 7) subarticular tubercles on hand large, round; 8) supernumerary tubercles on hand low, round; 9) palmar tubercle bifid; 10) fingers not webbed; 11) toes one-third webbed; 12) tarsal fold low, extending one-third length of tarsus; 13) inner metatarsal tubercle low, ovoid, visible from above; 14) outer metatarsal tubercle low, flat; 15) subarticular tubercles on foot large, round; 16) supernumerary tubercles on foot small, low; 17) discs round; 18) dorsal skin shagreened, tubercular in tympanic region; 19) dorsum green or tan with or without small irregular black spots; narrow bronze dorsolateral stripe usually present; 20) facial area uniform green or tan; canthal and labial stripes absent; 21) flanks tan with numerous small black spots; 22) dorsal surfaces of limbs plain or with small black spots; 23) posterior surfaces of thighs cream with black mottling; 24) venter cream with black mottling; 25) squamosal exostosed, in broad contact with maxillary; 26) temporal arcade complete in large individuals; 27) prevomers abutted medially; 28) transverse processes on eighth presacral vertebra slightly inclined anteriorly.

Gastrotheca cavia resembles *G. riobambae* in having short legs, a narrow interorbital distance, and a short snout. It differs from *G. riobambae* in having a distinct dorsolateral light stripe, small black flecks on the flanks, and dorsal markings comprised of small black spots. *Gastrotheca riobambae* lacks a dorsolateral light stripe and has large dark spots on the flanks and a dorsal pattern consisting of paired elongate dark marks; the dorsal pattern is shared with *G. lojana* and *monticola*. *Gastrotheca plumbea* and *psychrophila* have unmarked dorsal surfaces and uniformly dark flanks and venters. The venter in *G. cavia* is cream with small dark spots.

Variation.—Whereas some individuals have only a few black flecks on the posterior part of the dorsum, others have more flecks over the entire dorsum; in more heavily flecked specimens, flecks on the shank tend to form transverse bars. In life, adults are green;

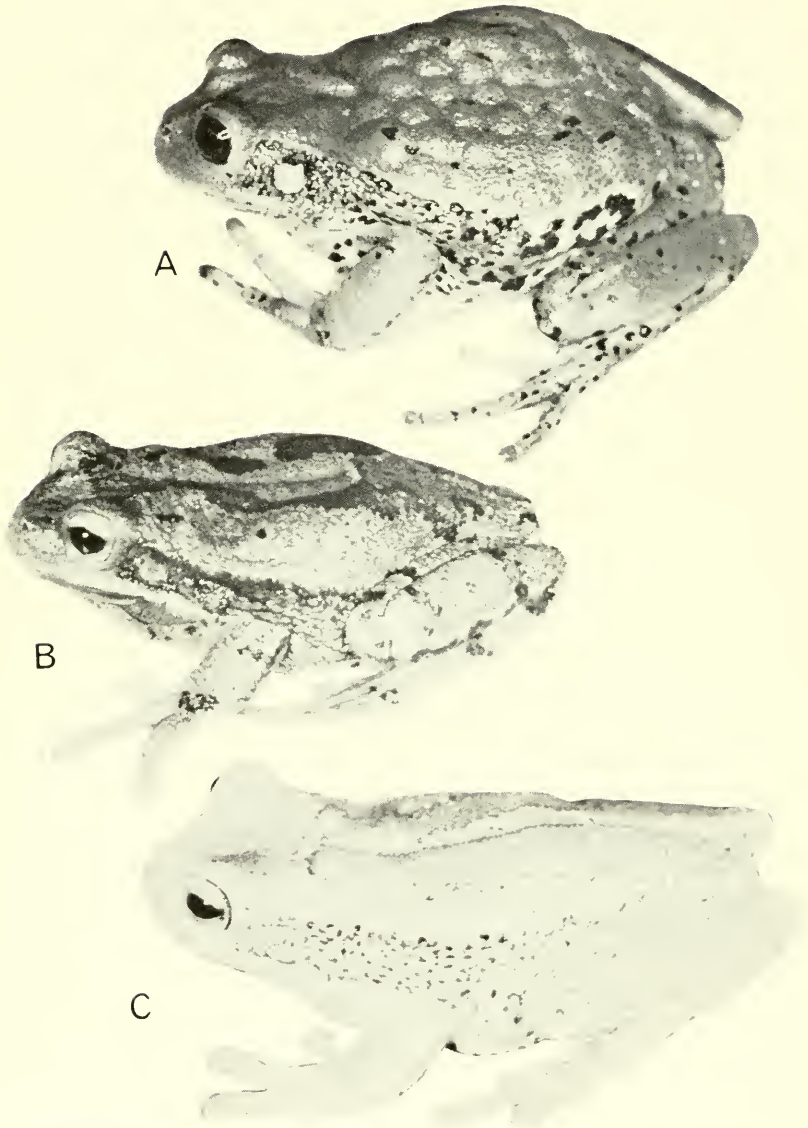


FIG. 1. A. *Gastrotheca cavia*, ♀, SVL 60.0 mm, KU 139139. B. *G. lojana*, ♂, SVL 56.5 mm, KU 148549. C. *G. monticola*, ♀, 65.0 mm, KU 148568.

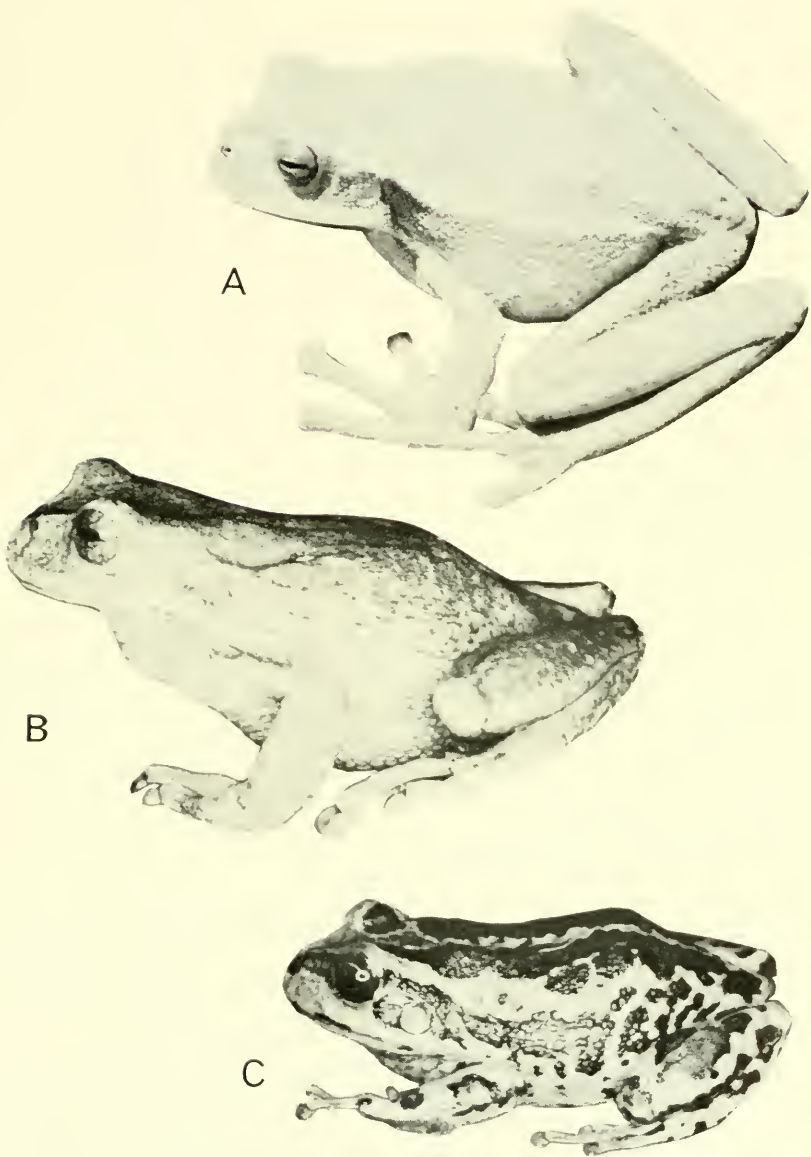


FIG. 2. A. *Gastrotheca plumbea*, ♂, SVL 55.3 mm, KU 142614. B. *G. psychrophila*, ♀, SVL 61.0 mm, KU 120650. C. *G. riobambae*, ♂, 46.5 mm, KU 120725.

the flanks are cream or bronze with black flecks, fused into reticulations in some individuals. The groin and posterior surfaces of the thighs are pale blue with black flecks. The dorsolateral stripe, extending from the posterior edge of the eye to the groin, usually is bronze and distinct. In some individuals, the stripe is narrow and fragmented by black flecks; in others it is cream, and in one female it is absent. The throat is pale yellow; the rest of the venter is dull grayish white with small black spots. The iris is dull bronze, heavily marked with brown spots and black flecks. Juveniles are pale green or bronze-tan; the flanks and hidden surfaces of the limbs are pale greenish yellow with black spots, and the venter is pale yellow with or without black reticulations. Although most males and all females are green, three males are tan.

Distribution.—This species is known definitely from only two localities in the Cordillera Occidental in northwestern Ecuador (Fig. 3). The species is abundant on two rocky islands in a crater lake, Laguna Cuicocha, at an elevation of 2890 m on the south slope of Volcán Cotacachi. The other locality, Hacienda San Nicolas is at an elevation of 2000 m on the Pacific slope of the Cordillera Occidental. Two specimens from "Western Ecuador" (BMNH 1860.6.16.124-125) and one from Ibarra (?) (BMNH 1898.4.28.156) are referred to this species.

Remarks.—Many adults were found in large terrestrial bromeliads in July, 1970, January and October, 1971. At the time of the last two visits, some adults were found beneath rocks. Brooding females were obtained in January and July, but not in October. Tadpoles were found in the lake surrounding the island in January, and at the same time two metamorphosing young were observed on reeds in the lake. Tadpoles have two upper and three lower rows of denticles.

Superficially, *Gastrotheca cavia* resembles *G. argenteovirens* Boëtger; I have examined the type of the latter (SMF 2676) and have compared living and preserved specimens of *argenteovirens* with *cavia*. In comparison with *G. cavia*, *G. argenteovirens* has proportionately longer legs (ratio of tibia length to snout-vent length 0.488-0.514, $\bar{x} = 0.498 \pm 0.010$, $N = 5 \delta \delta$; 0.486-0.514, $\bar{x} = 0.501 \pm 0.012$, $N = 4 \text{♀} \text{♀}$) and broader interorbital distance (ratio of interorbital distance to head width 0.335-0.371 ± 0.014 , $\bar{x} = 0.358$, $N = 5 \delta \delta$; 0.369-0.395 $\bar{x} = 0.383 \pm 0.011$, $N = 4 \text{♀} \text{♀}$). The flanks and posterior surfaces of the thigh are mottled with dark blue, and the dorsum lacks black flecks. Furthermore, the cultriform process of the parasphenoid is short, and in large individuals there is integumentary-cranial co-ossification.

Etymology.—The specific name is the same as the generic name for the guinea pig (Caviidae), called *cui* in Quechua the domi-



FIG. 3. Distributions of *Gastrotheca cavia* (triangles), *G. monticola* (hexagons), *G. plumbea* (inverted triangles), and *G. psychrophila* (circles).

nant Indian language in the Ecuadorian Andes. *Cuicocha* means lake of the guinea pig.

Gastrotheca lojana Parker New combination

Gastrotheca marsupiata lojana Parker, 1932:25 [Holotype.—BMNH 1931.2.12.4 (RR 1947.2.31.13) from Loja, Provincia Loja, Ecuador; C. Carrion collector].

Diagnosis.—1) Body depressed, 56.0 mm in males, 60.0 in females; 2) snout round in dorsal aspect and in profile; 3) canthus rounded; 4) loreal region barely concave; 5) tympanum vertically elliptical; 6) supratympanic fold moderately heavy, angled posteroventrally behind tympanum; 7) subarticular tubercles on hand

large, round; 8) supernumerary tubercles on hand small, subconical; 9) palmar tubercle bifid; 10) fingers not webbed; 11) toes one-half webbed; 12) tarsal fold low, extending one-half length of tarsus; 13) inner metatarsal tubercle low, elliptical, visible from above; 14) outer metatarsal tubercle low, round; 15) subarticular tubercles on foot large, round; 16) supernumerary tubercles on foot low, round; 17) discs round; 18) dorsal skin shagreened; 19) dorsum tan or green, with or without pair of elongate dark markings; narrow bronze or cream dorsolateral stripe present; 20) facial area green or tan; bronze canthal stripe and cream labial stripe present; 21) flanks dark brown with cream spots ventrally; 22) dorsal surfaces of limbs green or tan, with or without narrow brown transverse bars; 23) posterior surfaces of thighs heavily mottled with bluish purple; 24) chin and chest gray; belly pinkish bronze; 25) squamosal exostosed, in narrow contact with maxillary; 26) temporal arcade complete; 27) prevomers narrowly separated medially; 28) transverse processes on eighth presacral vertebra transverse.

Gastrotheca lojana resembles *G. monticola* and *riobambae* in usually having a pair of elongate dorsal markings. It differs from *G. riobambae* in having fine pale reticulations laterally or dark flanks, nearly uniformly dark posterior surfaces of the thighs, and a dorsolateral light stripe; *G. riobambae* has large spots on the flanks, mottled posterior surfaces of the thighs, and lacks a dorsolateral light stripe. *Gastrotheca monticola* has mottled posterior surface of the thighs and further differs from *G. lojana* in having a wider dorsolateral stripe and a cream venter with dark spots, whereas the venter in *G. lojana* is dark brown with creamy-white spots. The other Andean *Gastrotheca* in Ecuador lack paired dorsal markings.

Variation.—Variation in coloration can best be described by the following accounts of topotypic adult males (colors in life):

KU 148549.—Tan above with greenish suffusion dorsolaterally; dorsolateral and labial stripes bronze; flanks and dorsal markings dark brown; upper surfaces of thighs bronze-tan; upper surfaces of shanks and posterior surfaces of thighs dull green; anterior surfaces of thighs dark brown; throat brown; belly brown with white spots; ventral surfaces of thighs pinkish brown; ventral surfaces of shanks bluish white.

KU 148550.—Tan above with brown markings; face mask and anterior flanks dark brown; labial stripe creamy bronze; anterior and posterior surfaces of thighs mottled dark brown and blue; throat gray-brown; belly brown with white spots.

KU 148551.—Dorsum dull green with dark brown markings; flanks are dark brown; anterior and posterior surfaces of thighs and inner surfaces of shanks mottled dull blue and dark brown; throat dark bronze brown; belly brown with cream spots.

KU 126073.—Dorsum pale greenish brown with dark brown markings; labial and dorsolateral stripes cream; flanks gray-brown; groin and posterior surfaces of thighs creamy brown with green flecks.

KU 142603.—Dorsum dull leaf green with no distinct markings; canthal, labial, and dorsolateral stripes bronze; flanks bronze-brown; groin and anterior and posterior surfaces of thighs purplish brown; throat pinkish bronze; belly same, becoming darker brown posteriorly, with white spots.

In all specimens the iris is bronze. Four specimens from Chachapoyas, Departamento Amazonas, Perú (KU 138238-41) are colored somewhat differently: "Adults with leaf green dorsum; one with thin beige stripe from nostril through eye to inguinal region and beige spots on flanks; all with white supralabial border; posterior thigh light leaf green; anterior thigh pale leaf green with few black flecks; venter yellow-beige; iris metallic orange. Juvenile with white patch at anus; dorsum tan with light brown blotches edged with dark brown; blotch between eyes and inverted U on body with few scattered small spots posteriorly; broad rich light brown stripe from eye to midflank; groin gray-white with small black blotches; posterior thigh flesh-pink, leaf green distally; supralabial area beige-white" (T. H. Fritts, field notes, 1 May 1970).

The dorsal markings are highly variable. Some individuals lack markings except for a few scattered spots. In most individuals a pair of broad longitudinal marks extend from the scapular region to the groin. In some individuals the marks are fragmented into anterior and posterior components, whereas in others the marks are confluent anteriorly. If an interorbital mark is present, it may or may not be connected to the body markings.

Distribution.—This species occurs at moderate elevations in the Huancabamba Depression and associated interandean valleys in northern Perú and southern Ecuador, where it has been found from elevations of 2100 to 2350 m in both Atlantic and Pacific drainages (Fig. 4). A record from Zamora, Ecuador, at an elevation of 1000 m on the Amazonian slopes is highly questionable; the specimen (BMNH 1933.6.24.45) is *G. lojana*, but the locality data probably are erroneous.

Remarks.—In the Loja valley in southern Ecuador this species is found most frequently in large *Agave*, where the frogs seek shelter at the bases of the leaves by day and call by night. Individuals also have been found under rocks and in marshy meadows. At Chachapoyas, Perú, they were beneath rocks and clods of earth in a cultivated field. Tadpoles were found in a grassy irrigation ditch. They are uniformly black and have two upper and three lower rows of denticles.

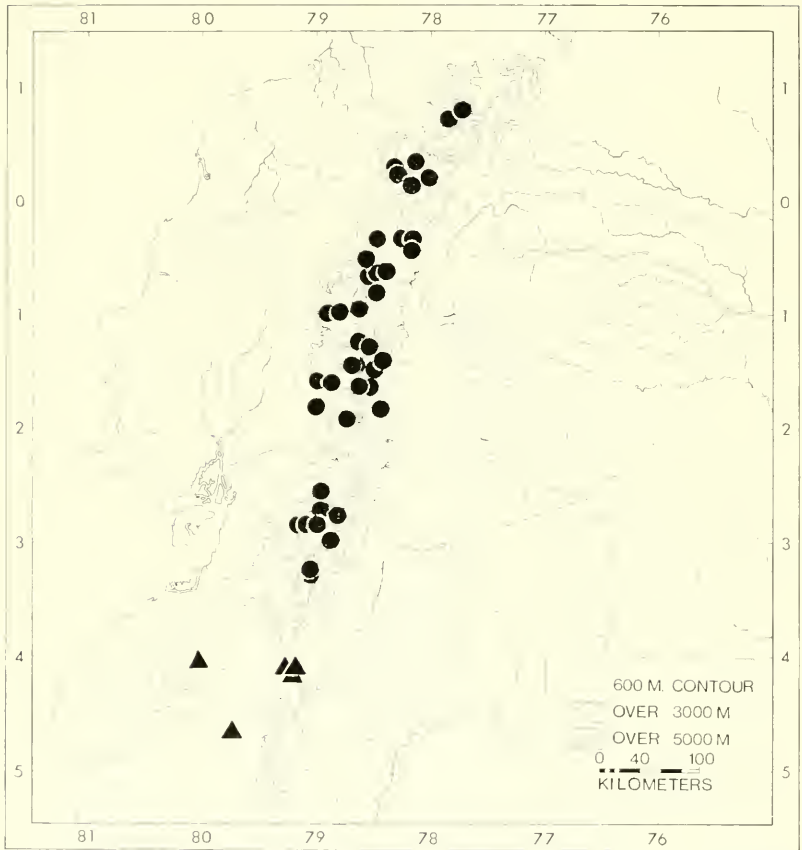


FIG. 4. Distributions of *Gastrotheca lojana* (triangles) and *G. riobambae* (circles).

One specimen (FSM 30080, an adult male having a snout-vent length of 48.5 mm) from 24 km WSW of Leimebamba, Departamento Amazonas, Perú, 3370 m tentatively is referred to *G. lojana*. This individual differs from all other *G. lojana* by having a dark brown dorsum with tan middorsal and dorsolateral stripes; the venter is mottled with dark gray. Furthermore, the locality is 1000 m higher than any other recorded for *G. lojana*.

Parker (1932:25) named *lojana* as a subspecies of *Gastrotheca marsupiata*, a name which he applied to populations now known as *G. riobambae*. As noted in the foregoing diagnosis, *G. lojana* differs from *G. riobambae* in a number of characters; there is no evidence for gene flow between the southern populations of *G. riobambae* and *G. lojana*.

Gastrotheca monticola Barbour and Noble

Gastrotheca monticola Barbour and Noble, 1920:426 [Holotype.—MCZ 5290 from Huancabamba, Departamento Piura, Perú; G. K. Noble collector].

Gastrotheca marsupiata monticola—Parker, 1932:25.

Gastrotheca monticola monticola—Vellard, 1957:39.

Diagnosis.—1) Body robust, 60.0 mm in males, 77.0 mm in females; 2) snout round in dorsal view and profile; 3) canthus rounded; 4) loreal region barely concave; 5) tympanum nearly round, slightly higher than wide; 6) supratympanic fold moderately heavy, curved posteroventrally behind tympanum; 7) subarticular tubercles on hand large, round; 8) supernumerary tubercles on hand large, conical; 9) palmar tubercle bifid; 10) fingers not webbed; 11) toes one-half webbed; 12) tarsal fold tubercular, extending full length of tarsus; 13) inner metatarsal tubercle elongate, visible from above; 14) outer metatarsal tubercle absent; 15) subarticular tubercles on feet large, round; 16) supernumerary tubercles on hands small, round, flat; 17) discs round; 18) dorsal skin shagreened; 19) dorsum green or tan, usually with paired elongate dark markings; creamy bronze dorsolateral stripe present; 20) facial area green or tan; creamy bronze canthal stripe present; 21) flanks brown with cream and black flecks; groin blue; 22) dorsal surfaces of limbs green or tan with or without darker transverse bands; 23) posterior surfaces of thighs blue; 24) throat gray; chest and belly creamy gray with gray spots; 25) squamosal weakly exostosed, in moderately broad contact with maxillary; 26) temporal arcade complete in large individuals; 27) prevomers narrowly separated medially; 28) transverse processes on eighth presacral vertebra barely inclined anteriorly.

Gastrotheca monticola differs from *G. plumbea* and *psychrophila* in having a pale venter with black spots, instead of a uniformly dark venter. *Gastrotheca cavia* resembles *G. monticola* in having a broad dorsolateral stripe and mottled posterior surfaces of the thighs, but *G. cavia* lacks paired longitudinal dark marks on the dorsum, characteristic of *G. monticola*, *lojana*, and *riobambae*. The latter species differs from *G. monticola* in having large dark spots, instead of fine reticulations, on the flanks, and in lacking a dorsolateral stripe. *Gastrotheca monticola* is most like *G. lojana*, from which it differs in having a pale venter with dark spots (dark with white spots in *lojana*), broader dorsolateral stripe, and more mottling on the flanks and thighs.

Variation.—The dorsum is green with paired longitudinal dark markings on the body; a large dark spot on the head, including the eyelids, is present in some individuals. The longitudinal marks extend from the eyelids or occipital region to the groin. In some individuals the marks are confluent anteriorly. The marks are green, usually darker than the dorsal ground color, and outlined

with brown. The flanks are brown with or without bronze flecks. The dorsolateral and labial stripes are bronze-tan to metallic cream. The groin and hidden surfaces of the thighs vary from pale green to blue with cream and black mottling. The venter is creamy tan to creamy yellow with brown flecks; the vocal sac is gray. The iris is pale bronze.

Comparison of specimens from Saraguro, Ecuador, with the type series from Huancabamba, Perú, revealed slight differences. The Peruvian specimens have less ventral spotting and more dark pigment on the posterior surfaces of the thighs. One Peruvian specimen (UMMZ 57747A), a male, has a highly fragmented dorsal pattern.

Distribution.—*Gastrotheca monticola* occurs at elevations of 1600-2500 m on the Pacific slopes and associated intermontane valleys in northern Perú and southern Ecuador (Fig. 3). The Cordillera Occidental in that region is dissected by many broad, dry valleys, so it is unlikely that the distribution of *G. monticola* is continuous.

Remarks.—At Saraguro, Ecuador, adults were found beneath rocks in a pasture and in and along a vegetation-choked drainage ditch. At Girón, Ecuador, adults were in *Agave* plants by day. Tadpoles were found in the ditch at Saraguro. The body is dull green above and greenish silver below; the tail is tan with green lichenous markings. The tadpoles have two upper and three lower rows of denticles.

Parker (1932:25) considered *G. monticola* to be a subspecies of *G. marsupiata* (= *riobambae*). The differences noted in the diagnosis obviate such an arrangement in the absence of evidence indicating genetic interchange. Cochran and Goin (1970:185) used the combination *Gastrotheca monticola argenteovirens*. Boettger named *argenteovirens* in 1892, whereas the name *monticola* dates from Barbour and Noble (1920). Moreover, the two taxa are considerably different and certainly not conspecific.

Gastrotheca plumbea (Boulenger)

Nototrema plumbeum Boulenger, 1882:417 [Holotype.—BMNH 78.1.25.22 (RR 1947.2.31.19) from Intac, Provincia Pichincha, Ecuador; Mr. Buckley collector].

Gastrotheca plumbeum—Peters, 1955:346.

Diagnosis.—1) Body robust, 62.3 mm in males, 68.0 mm in females; 2) snout round in dorsal view, angular above and inclined anteroventrally in profile; 3) canthus rounded; 4) loreal region barely concave; 5) tympanum vertically elliptical; 6) supratympanic fold weak; 7) subarticular tubercles on hand moderate, round; 8) supernumerary tubercles on hand small, round; 9) palmar tubercle bifid; 10) fingers webbed basally; 11) toes one-half webbed; 12) tarsal

fold round, extending one-third length of tarsus; 13) inner metatarsal tubercle elliptical, visible from above; 14) outer metatarsal tubercle absent; 15) subarticular tubercles on foot moderate, round; 16) supernumerary tubercles on foot small, conical; 17) discs round; 18) dorsal skin shagreened; 19) dorsum green with narrow bronze dorsolateral stripe; 20) facial area green with bronze canthal and labial stripes; 21) flanks brown; 22) dorsal surfaces of limbs green, mottled or not with tan; 23) posterior surfaces of thighs bronze-tan; 24) venter greenish yellow; 25) squamosal not exostosed, in moderately broad contact with maxillary; 26) temporal arcade incomplete; 27) prevomers abutted medially; 28) transverse processes on eighth presacral vertebra strongly inclined anteriorly.

Gastrotheca plumbea differs from all other Andean *Gastrotheca*, except *G. psychrophila*, in having a uniformly pigmented venter and a green iris. Like *G. psychrophila*, it also lacks dorsal markings, but it differs from *G. psychrophila* in having paler venter, a dorsolateral light stripe, a green, instead of brown dorsum, and a green, instead of copper, iris.

Variation.—The dorsum invariably is unmarked bright green to tannish green. The canthal, labial, dorsolateral, and anal stripes are yellow. The loreal region, flanks, and posterior surfaces of the thighs are bronze, and the dorsal surfaces of the limbs are greenish bronze. The venter is yellowish tan with a greenish tint on the throat, and the ventral surfaces of the shanks are blue. A diffuse blue spot is present in the grain; the iris is green.

Distribution.—*Gastrotheca plumbea* is known from moderate elevations (1300-2350 m) on the Pacific slopes of the Cordillera Occidental in Ecuador (Fig. 3). Although the range of the species may extend northward into Colombia, it is doubtful if the species ranges into Perú; the dry valleys of the Huancabamba Depression probably are a barrier to southward dispersal.

Remarks.—At Pilaló, Provincia Cotopaxi, Ecuador, where there are remnants of cloud forest, individuals were found in bromeliads in trees and on a cliff by day; males called from bromeliads at night.

Gastrotheca psychrophila new species

Holotype.—KU 120760, an adult female, 61.0 mm, from the ridge between Loja and Zamora, 2850 m, 13-14 km E (by road) of Loja, Provincia Zamora-Chinchipec, Ecuador; obtained on 10 June 1968 by John D. Lynch.

Paratopotypes.—KU 120761, 10 June 1968, John D. Lynch; 141586, 21 May 1971, Richard R. Montanucci; 142631-7, 21-23 July 1971, William E. Duellman.

Diagnosis.—1) body depressed, 51.5 mm in males, 61.0 mm in

females; 2) snout pointed with vertical rostral keel, in profile rounded above and anteroventrally inclined; 3) canthus angular; 4) loreal region flat; 5) tympanum slightly higher than wide; 6) supratympanic fold heavy, curved downward behind tympanum; 7) subarticular tubercles on hand large, round; 8) supernumerary tubercles on hand large, round; 9) palmar tubercle trifid; 10) fingers webbed basally; 11) toes slightly less than one-half webbed; 12) tarsal fold curved, two-thirds length of tarsus; 13) inner metatarsal tubercle elliptical, visible from above; 14) outer metatarsal tubercle low, round; 15) subarticular tubercles on foot large, round; 16) supernumerary tubercles on foot large, conical; 17) discs round; 18) dorsal skin shagreened; 19) dorsum uniform dark brown to grayish tan or dull green; 20) facial area colored like dorsum; bronze labial stripe in females; 21) flanks bluish black; 22) dorsal surfaces of limbs dark brown to grayish tan; 23) posterior surfaces of thighs bluish black; 24) venter grayish brown; 25) squamosal exostosed, in broad contact with maxillary; 26) temporal arcade incomplete; 27) prevomers abutted medially; 28) transverse processes on eighth presacral vertebra strongly inclined anteriorly.

Gastrotheca psychrophila differs from all other Andean *Gastrotheca*, except *G. plumbea*, in having a dark venter. It also is like *G. plumbea* in lacking dorsal blotches, but *G. psychrophila* differs from *G. plumbea* in lacking a dorsolateral light stripe and in having a darker venter, usually a primarily brown dorsum (green in *G. plumbea*) and a copper iris (green in *G. plumbea*).

Variation.—Individuals of this species are capable of considerable metachrosis. When frogs were found in bromeliads they were dark brownish black above and below; the flanks and posterior surfaces of the thighs were dark bluish black. Later the dorsum changed to copper or bronze-tan with or without diffuse pale green blotches or streaks. The flanks are orange-brown or dark brown. The axilla, groin, and hidden surfaces of the limbs are bluish gray or bluish purple. The lips are dull bronze, and the iris is copper with black flecks.

Distribution.—This species is known only from the ridge between Loja and Zamora, Ecuador (Fig. 3). Most individuals have been found on the upper eastern slope between 2750 m and the crest at 2850 m.

Remarks.—The Loja-Zamora ridge is exceedingly wet; cold winds blow from the east. The vegetation near the crest consists of grasses and dense bushes. Large bromeliads are abundant on the ground and in the bushes. Adult *G. psychrophila* were found in the bromeliads and under rocks. Tadpoles were obtained from a grassy pond on the west side of the ridge. The tadpoles are black and have two upper and three lower rows of denticles.

Etymology.—The specific name is from the Greek *psychros*,

meaning cold, and *philos*, meaning having an affinity for; the name is used in allusion to the climate at the type locality.

Gastrotheca riobambae (Fowler)

Hyla riobambae Fowler, 1913:157 [Holotype.—ANSP 16161 from Riobamba, Provincia Chimborazo, Ecuador; S. N. Rhoads collector].

Hyla quitoe Fowler, 1913:159 [Holotype ANSP 18238 from Quito, Provincia Pinchincha, Ecuador; S. N. Rhoads collector].

Chorophilus olivaceus Andersson, 1945:85 [Holotype.—NHRM 1965 from "Rio Napo, 400 m." (= ? Baños, Provincia Tungurahua), Ecuador; William-Clarke Machtyre collector].

Gastrotheca marsupiatata *ecuadoriensis* Vellard, 1957:43 [*Nomen nudum*].

Gastrotheca riobambae—Duellman and Fritts, 1972:11.

Diagnosis.—1) Body robust, 48.7 mm in males, 51.2 in females; 2) snout rounded in dorsal view and in profile; 3) canthus rounded; 4) loreal region shallowly concave; 5) tympanum round; 6) supratympanic fold weak, curved posteroventrally behind tympanum; 7) subarticular tubercles on hand large, round; 8) supernumerary tubercles on hand small, subconical; 9) palmar tubercle bifid; 10) fingers not webbed; 11) toes one-fourth webbed; 12) tarsal fold curved, extending full length of tarsus; 13) inner metatarsal tubercle elliptical, visible from above; 14) outer metatarsal tubercle absent; 15) subarticular tubercles on foot large, subconical; 16) supernumerary tubercles on foot small, round; 17) discs round; 18) dorsal skin shagreened, with scattered pustules, tubercular in tympanic region; 19) dorsum green or tan, usually with pair of large elongate dark spots; 20) facial area green or brown; canthal and labial stripes absent; 21) flanks green, blue, or tan with dark brown or black spots; 22) dorsal surfaces of limbs green or tan, usually with elongate dark mark on thigh and irregular blotches or transverse bars on shank; 23) posterior surfaces of thighs dark brown with cream flecks; 24) venter cream with brown or gray mottling on chest and belly; 25) squamosal exostosed in large individuals, in moderately broad contact with maxillary; 26) temporal arcade incomplete; 27) prevomers abutted or narrowly separated medially; 28) transverse processes on eighth presacral vertebra transverse or slightly inclined anteriorly.

Gastrotheca riobambae is like *G. cavia* in having short legs, a short snout, and a narrow interorbital distance, but it differs from *G. cavia* by having paired longitudinal dorsal marks, large spots on the flanks, and no dorsolateral light stripe. The dorsal color patterns of *G. lojana* and *monticola* are similar to that of *G. riobambae*, but both *G. lojana* and *G. monticola* have reticulated or plain flanks and dorsolateral light stripes. *Gastrotheca plumbea* and *psychrophila* have no dorsal markings and uniformly colored flanks; the former has a dorsolateral light stripe.

Variation.—The preceding diagnosis is based principally on

topotypic material. Considerable variation, especially in coloration, obtains in this species. Five aspects of coloration are worthy of discussion (Table 2):

1. Dorsal ground color: The dorsum is either green or brown, varying to grayish tan in some individuals. The proportions of green to brown individuals is highly variable in local samples. At Papallacta on the high Amazonian slopes of the Cordillera Oriental, all individuals are green. The same is true at Guaranda on the Pacific slopes of the Cordillera Occidental. Approximately one-half of the frogs from the Cuenca Basin are green. At Riobamba, in the upper reaches of the Río Pastaza drainage, 97 percent of the frogs are brown; at Baños, lower in the Río Pastaza valley, 89 percent are brown.

2. Dorsal markings: Most specimens have dark dorsal blotches. In green frogs these are usually darker green, but in some the blotches are brown. The same variation occurs in brown frogs, with the addition of green blotches that are dark brown peripherally and bordered or not by cream. The blotches usually are in the form of a pair of broad, irregular marks extending from the eyelid or occiput to the rump. In a few individuals the blotches are fragmented into a row of spots; in others they are expanded so as to cover most of the dorsum. With the exception of the series from Riobamba, all large samples contain some individuals lacking dorsal blotches. Plain individuals make up less than one-third of each sample, except that from Guaranda, in which one-half of the specimens lack blotches. Most *Gastrotheca riobambae* lack definite dorsolateral light stripes, but these stripes are present in some specimens from Guaranda and the Cuenca Basin.

3. Thigh coloration: In most samples the posterior surfaces of the thighs are brown, gray, or tan (frequently with a green suffusion) with black flecks or small spots. In specimens from Riobamba and Guano the posterior surfaces of the thighs are tan or green with small cream flecks. The thighs are uniform dull blue in specimens from Papallacta and Biblian, bluish green from Cuenca, and blue with black flecks from Mulaló and Guaranda.

4. Flank coloration: The flanks are tan, green, gray, or blue, usually with black or dark brown spots. In specimens from Papallacta and Biblian the flanks are uniform blue.

5. Ventral coloration: Specimens from Papallacta are uniformly gray below. In all other samples the belly is cream; the belly is marked with black, gray, or dark brown flecks, spots, blotches, or reticulations in all other samples, except those from the Cuenca Basin, in which the belly is uniformly cream.

In all specimens the iris is deep bronze to copper with black reticulations; males in all samples have dark brown to gray vocal sacs.

TABLE 2. Geographic variation in *Gastrotheca riobambae*.

Locality	N ♂; ♀	Green: Blotched: Brown Plain	Posterior Thighs	Flanks	Belly	Max. SVL (mm) ♂; ♀
Imbabura:						
Otovalo-Quiroga	23:8	12:19 23:8	Tan-green; black flecks	Blue gray; black spots	Black blotches	50;49
Pichincha:						
Quito	7:10	3:14 15:2	Brown-green; black flecks or plain	Blue-green; black spots	Small black spots	52;57
Napo:						
Papallacta	13:2	15:0 12:3	Blue	Blue	Gray	53;63
Cotopaxi:						
Mulaló	6:10	8:8 12:4	Blue; black flecks	Blue; black flecks	Small black flecks	42;47
Tungurahua:						
Baños	39:13	6:46 50:2	Gray-green; black spots	Gray-green; black spots	Black spots	49;56
Tungurahua:						
Mochla	15:2	5:12 15:2	Green	Green; black flecks	Black flecks	47;52
Chimborazo:						
Riobamba-Guano	48:14	2:60 62:0	Tan-green; cream flecks	Blue-green; black spots	Black reticulations	50;55
Bolivar:						
Guaranda	6:6	12:0 6:6	Blue; black flecks	Blue; black flecks	Black flecks	50:57
Canar:						
Biblián	5:4	5:4 7:2	Blue	Blue	Cream	54;58
Azuay:						
Cuenca	26:7	16:17 25:8	Blue-green	Blue-green	Cream	55;58

There are some correlations between some of the aspects of coloration. Only three of the 37 plain specimens incorporated in table 2 are brown. The color of the flanks generally is the same as the dorsum in green frogs, but in many brown frogs the flanks are green. Apparently the development of blue color on the flanks (most prevalent in the groin) is independent of dorsal color, but uniformly blue flanks are most prevalent in green frogs. The color of the flanks and posterior surfaces of the thighs usually are the same, but the markings on these surfaces are not necessarily the same.

When the variation in coloration is examined with respect to geography, two things are evident: 1) Samples containing only green frogs are from the outer slopes of the Andes (Papallacta and Guaranda); all samples from the inner slopes and interandean valleys contain both green and brown frogs. 2) Samples from the Cuenca Basin (Cuenca and Biblian) lack spots on the flanks, thighs, and venter. Other samples are more alike than any is to the four mentioned above. Because the population in the Cuenca Basin may be isolated genetically from more northern populations, it may represent a distinct taxon. Likewise, the populations on the outer Andean slopes may be isolated genetically from those in the interandean valleys. The populations at Guaranda and Papallacta are widely separated topographically with different phenons occurring in the intervening area.

If the variation in *Gastrotheca riobambae* is examined with respect to genetic polymorphism, it can be conjectured that the polymorphs at any given locality represent a balanced polymorphism resulting from selection for fitness to a particular environment (Levins, 1968). Data from the samples incorporated in Table 2 were analyzed with respect to climatic variables (mean annual temperature, mean annual rainfall, minimum and maximum monthly rainfall, and number of rainy days). Comparisons of percentages of green versus brown frogs, plain versus blotched frogs, and blue versus non-blue flanks and thighs with each of the climatic variables resulted in no correlations.

Jameson and Pequegnat (1971) demonstrated that similar color polymorphism in *Hyla regilla* is correlated with seasonal and microecological differences in vegetation color. The samples of *G. riobambae* containing only green frogs are from areas where the vegetation is in leaf and green throughout the year. The population containing the highest percentage of brown frogs (Riobamba) is from an area having sparse deciduous vegetation. At these and other localities, there was no planned sampling at different seasons; at those localities sampled at different seasons there is no significant difference in the frequency of different morphs in the samples.

Distribution.—*Gastrotheca riobambae* has a broad geographic

and altitudinal range in Ecuador (Fig. 4). It occurs on the upper Pacific slopes of the Cordillera Occidental (> 2600 m) and Amazonian slopes of the Cordillera Oriental (> 1800 m), and in interandean valleys (> 2300 m) as far south as the slopes of Cerro Tinajillas in Provincia Azuay. The species occurs at elevations of 3860 m in the Páramo de Apagua, 3960 m at Paso de Guamani, and 4135 m on Volcán Antisana. The species occurs in extreme southern Colombia, but specimens resembling *G. riobambae* from Bogotá, Departamento Cundinamarca, and San Pedro, Departamento Antioquia, apparently are not conspecific.

Remarks.—*Gastrotheca riobambae* occurs in a variety of habitats ranging from wet montane meadows to dry rocky hillsides. The species frequents ruderal situations—drainage and irrigation ditches, *Agave*, and corn fields. On cloudy or rainy days individuals are active, and males commonly call by day. Despite low temperatures (as low as $2-4^{\circ}$ C), adults are most active at night. Tadpoles develop in still water. In large ponds the tadpoles aggregate in shallow water, but upon the slightest disturbance, they rapidly flee to deep water.

As noted in the preceding discussion of variation, some populations currently assigned to *Gastrotheca riobambae* may be specifically distinct. I suggest that biochemical and karyological investigations might be fruitful approaches to the taxonomy of this complex.

DISCUSSION

Apparent evolutionary trends in the Andean marsupial frogs are confusing. Members of the *Gastrotheca marsupiata* group are the most terrestrial and live in what seem to be suboptimal environmental conditions—dry interandean valleys. On the other hand, members of the *Gastrotheca argenteovirens* group and some members of the *Gastrotheca plumbea* group are arboreal and live in what seem to be more optimal anuran environments—cloud forest and wet páramo.

Within the *Gastrotheca plumbea* group, two species (*plumbea* and *psychrophila*) inhabit cool moist environments. *Gastrotheca plumbea* lives in arboreal and terrestrial bromeliads in cloud forest, and *G. psychrophila* inhabits terrestrial bromeliads in wind-swept subparamo (Fig. 5). The other species in the *Gastrotheca plumbea* group principally inhabit drier interandean valleys and Pacific slopes of the Andes. In these areas the frogs live in páramo, *Agave*, and cultivated fields; *G. cavia* inhabits bromeliads in scrubby subparamo (Fig. 6).

Among the members of the *Gastrotheca plumbea* group, *G. riobambae* is most like members of the *Gastrotheca marsupiata*



FIG. 5. Type locality of *Gastrotheca psychrophila*, ridge east of Loja Ecuador. Note terrestrial bromeliads in foreground.

group in having a relatively narrow head, least developed lateral flanges on the frontoparietals, and relatively small hands. The color pattern of *G. riobambae* is similar to that of *G. peruana*, the northernmost species in the *Gastrotheca marsupiata* group. I consider the *Gastrotheca plumbea* group to have been derived from the *Gastrotheca marsupiata* group and *G. riobambae* to be the most primitive member of the *Gastrotheca plumbea* group. All other members of the group have more extensive cranial ossification and exostosis.

The major phyletic line in the *Gastrotheca plumbea* group has dorsolateral light stripes and moderately long snouts. Two members (*G. lojana* and *monticola*) of this line retain the paired dorsal blotches of *G. riobambae*, whereas the dorsum is plain in *G. plumbea*, a species most like members of the Colombian *Gastrotheca argenteovirens* group. The nearly unicolor *G. psychrophila* and the flecked *G. cavia*, each apparently represent independent derivatives from a *G. riobambae*-like stock.

Vuilleumier (1971) documented Pleistocene changes in the flora and avifauna in the Andes. Her summary of geological, climatic, and biogeographic evidence demonstrates two glaciations in the Ecuadorian Andes. During glacial periods snow line was lowered as much as 700 m, and temperatures were depressed 4-11° C. The patterns of speciation and distribution of the *Gastrotheca plumbea* group are compatible with Vuilleumier's paleobiogeographic hy-



FIG. 6. Type locality of *Gastrotheca cavia*, Isla Pequeña, Laguna Cuicocha, Provincia Imbabura, Ecuador. Note bromeliads in scrubby trees in middle of picture.

pothesis. *Gastrotheca lojana* and *monticola* are relictual populations of warm-dry interglacial periods now isolated in lower and drier areas than other members of the group. During climatic depression in glacial periods, populations were isolated in interandean basins and the outer slopes of the Andes; thus, *G. riobambae*, *plumbea*, and *psychrophila* differentiated in the intermontane valleys, Pacific slopes, and Amazonian slopes, respectively. A *riobambae*-like stock apparently was isolated from more southern populations by uninhabitable environments in the Nudo de Mojanda during a glacial period and differentiated into *G. cavia*. Conceivably, the differentiation of the six species occurred at the time of the first glacial period. If so, the differentiation within *G. riobambae* and southward migration of *G. lojana* and *monticola* into northern Perú could be coincidental with the second glaciation. This proposed speciation model is similar to that suggested by Montanucci (1973) for the Andean microteiid genus *Pholidobolus*, a group of lizards inhabiting the same areas as *Gastrotheca*.

SUMMARY

The marsupial frogs of the genus *Gastrotheca* inhabiting the Andes and interandean valleys of Ecuador form a phylogenetic unit (*Gastrotheca plumbea* group) that is intermediate between the more southern *Gastrotheca marsupiata* group and the more

northern *Gastrotheca argenteovirens* group. The *Gastrotheca plumbea* group is characterized by a supraorbital flange on the frontoparietals and extensive exostosis, but no co-ossification, of the cranial roofing bones. Apparently all species in the group have free-swimming tadpoles.

The *Gastrotheca plumbea* group contains six species: *G. lojana* Parker, *G. monticola* Barbour and Noble, *G. plumbea* (Boulenger) and *G. riobambae* (Fowler). In addition, two new species are named herein: *G. cavia* from Laguna Cuicocha, Provincia Imbabura, Ecuador, and *G. psychrophila* from the ridge east of Loja, Ecuador. *Gastrotheca riobambae* is highly variable; some populations may represent distinct species.

The *Gastrotheca plumbea* group seems to have been derived from the *Gastrotheca marsupiata* group, and *G. riobambae* probably is the most primitive member of the group. Speciation within the group evidently occurred through isolation of populations due to climatic fluctuation during the Pleistocene.

RESUMEN

Las ranas marsupiales del género *Gastrotheca* que habitan los Andes y valles interandinos del Ecuador forman una unidad filogenética (el grupo *Gastrotheca plumbea*) que es un grupo inter-mediano entre el grupo *Gastrotheca marsupiata* del sur y el grupo *Gastrotheca argenteovirens* del norte. El grupo *Gastrotheca plumbea* se caracteriza por tener una protuberancia supraorbital en los frontoparietales y prominencias extensas pero no co-ossificación de los huesos que forman la cubierta craneal. Parece que todas las especies del grupo tienen renacuajos acuáticos.

El grupo *Gastrotheca plumbea* tiene seis especies: *G. lojana* Parker, *G. monticola* Barbour and Noble, *G. plumbea* (Boulenger), y *G. riobambae* (Fowler). Además dos especies nuevas son nombradas aquí: *G. cavia* de la Laguna Cuicocha, Provincia Imbabura, Ecuador, y *G. psychrophila* de la cordillera al este de Loja, Ecuador. *Gastrotheca riobambae* es muy variable; algunas poblaciones pueden representar especies distintas.

El grupo *Gastrotheca plumbea* parece derivarse del grupo *Gastrotheca marsupiata*, y probablemente *G. riobambae* es la especie más primitiva de este grupo. La diferenciación en el grupo ocurre evidentemente como resultado del aislamiento de poblaciones debido las fluctuaciones climáticas durante el Pleistoceno.

SPECIMENS EXAMINED

Gastrotheca cavia

"Western Ecuador," BMNH 1860.6.16.124-125. Imbabura: Hacienda San Nicolas, 2000 m, UMMZ 92269, 92278-9, 92289-98; Ibarra, 2300 m, BMNH

(898.4.28.156; locality?); Laguna Cuicocha, 2890 m, KU 138216-20, 139136-9, 139439 (tadpoles), 139440 (young), 143094, 143537 (tadpoles), 148530-42, 148543-4 (skeletons), 148545-7 (tadpoles), 148548 (young).

Gastrotheca lojana

Loja: Celica, 2130 m, BMNH 1931.11.3.3-4; Loja, 2150 m, BMNH 1931.2.12.10-13, 1933.6.24.18-44, 1935.11.3.26-32, 1947.2.31.6-18, KU 120673-4; 2 km N Loja, 2100 m, KU 142846 (tadpoles); 5 km N Loja, 2150 m, 138235-6, 138237 (skeleton); 2 km E Loja, 220 m, KU 120675; 9 km E Loja, 2660 m, KU 121387 (tadpoles); 2 km S Loja, CAS 93898; 3 km W Loja, 2150 m, KU 138233; 5.5 km W Loja, 2330 m, KU 142603-8, 148549-51; 10 km W Loja, 2500 m, KU 138234.

Zamora-Chinchipec: Zamora, 1000 m, BMNH 1933.624.45 (locality?).

PERÚ: *Amazonas*: Chachapoyas, 2340 m, KU 138238-41; 24 km WSW Leimebamba, 3370 m, FSM 47216 (1D?). *Cajamarca*: Cajamarca, MJP 204. *Piura*: Ayabaca, MJP 702 (2).

Gastrotheca monticola

Azuay: Girón, 2240-2500 m, KU 138401-3. *Loja*: Saraguro, 2500 m, KU 138404-9, 138410 (skeleton), 138769 (tadpoles), 141565, 142609-13, 142847 (tadpoles), 148563-8, 148569-70 (skeletons), 148571 (tadpoles).

PERÚ: *Cajamarca*: Bellavista, BMNH 1947.2.22.47-8, 1947.2.25.77-8; Quericotilla, MCZ 5328-20. *Piura*: Huancabamba, AMNH 7551, MCZ 5290-3, 5296-7, 5299-300, 5302, 5304-7, 5309, 5312-15, 5317, 5319, 5328-30, SMF 2677, UMMZ 55747.

Gastrotheca plumbea

Azuay: Molleturo, 2350 m, ZMB 30057. *Carchi*: Atal, near San Gabriel, UMMZ 83655. *Cotopaxi*: Pílaló, 2320 m, KU 132413-22, 132423 (skeleton), 142614. *Pichincha*: Intac, 1200 m, BMNH 1947.2.31.19.

Gastrotheca psychrophila

Loja: 10 km E Loja, 2570 m, KU 142855 (tadpoles). *Zamora-Chinchipec*: 13-15 km E. Loja, KU 120760-2, 141585 (skeleton), 141586, 141595, 142631-7.

Gastrotheca riobambae

Province Unknown: No specific locality, MNHN 965, 6227-9 (8), 9595; Andes, BMNH 58.7.25.21, 58.7.25.23, 58.7.25.25, 58.7.25.27-8, 58.7.25.31-3; Western Ecuador, BMNH 60.6.16.17, 60.6.16.127. *Azuay*: Bestion, AMNH 13967; Cuenca, 2540 m, CAS 85172, KU 120676-723, 129797-8, SMF 2669-75, USNM 61757-60, USNM-JAP 2345, 2347-8, 2350; 6 km N Cuenca, AMNH 71588-600; 9 km N Cuenca, CAS S5339-40, 93884-94; 18 km N Cuenca, CAS-SU 21851; 4 km E Cuenca, 2540 m, KU 138587-613, 138622-3 (skeletons), 138773 (tadpoles); 8 km SW Cuenca, AMNH 71601-2; 8.8 km NW Cuenca, 2620 m, KU 141583-4, 141594 (tadpoles); 9 km S Cumbe, 3300 m, KU 132536 (tadpoles); 10 km S Cumbe, 3350 m, KU 132392; 28.6 km S Cumbe, 3190 m, KU 142853 (tadpoles); 0.8 km S Cutchil, 2535 m, KU 141582; 2.1 km S Cutchil, 2720 m, KU 141572; 3.5 km S Cutchil, 2785 m, KU 141579-81; 8.5 km S Cutchil, KU 141577-8; Lago de Sarogucho, 20 km W Cuenca, CAS 94114; Laguna de Zurucuchu, 3200 m, KU 121388 (tadpoles); Narihuina, MNHN 06-283; Río Matadero, 8 km E. Cuenca, CAS-SU 21845-6; Río Matadero, 9 km E Cuenca, CAS 94217 (tadpoles). 94218-22, CAS-SU 21847-8; Río Matadero, 12 km E Cuenca, KU 129779-96; Sinicay, 2560 m, AMNH 17451-7, 17459-63, 17465-8, 17552, 17567. *Bolívar*: Guaranda, 2640 m, KU 132403-12, 132531 (tadpoles), 132540 (young); 27.3 km

E Guaranda, 3800 m, KU 142850 (tadpoles); 2.5 km S Guaranda, 2650 m, KU 142616-9, 142851 (tadpoles), 142852, 148573; Guaranda-Riobamba road at Chimborazo border, 3700 m, KU 132541, 132542 (young). *Cañar*: 3 km S Azogues, 2500 m, KU 138624-7, 138774 (tadpoles); Biblian, 2620 m, KU 141570-1, 141573, 142620-4, 147113; 8 km NW Biblian, 3420 m, KU 132537 (tadpoles); Cañar, NHMW 6476, 6480, 2.8 km S Cañar, 3150 m, KU 141574-6; km 94, Guayaquil-Cuenca railroad, CAS 93899-900. *Carchi*: El Carmelo (El Pun), 2750 m, USNM-JAP 4946-7; Quebrada de Piedras, 20 km S Tulcan, 3400 m, KU 118120 (tadpoles); Tulcan, 3000 m, KU 117978-9, 118119 (tadpoles). *Chimborazo*: No specific locality, BMNH 1932.10.2.86; Guamote, USNM 33863; 1 km S Guano, 2500 m, KU 132354-89, 148581, 148582-4 (skeletons); 148592; Hacienda Alao, 15 km SE Pungala, 3100 m, KU 132543 (tadpoles); Laguna de Colta, 15 km SE Riobamba, 3400 m, NSNM-JAP 1728, 1730-3; Riobamba, 2780 m, ANSP 16161, KU 120732, MNHN 02-62(2), 02-350(2); 10 km N Riobamba, 2730 m, KU 138547-73, 138574-6 (skeletons); 15 km E Riobamba, 2600 m, KU 120725-31, 120758-9, 121389 (tadpoles); Rosario, NHMW 6485; San Juan, 3160 m, KU 142615; 10 km W San Juan, 3160 m, KU 120724; 20 km SW Santa Rosa, 3700 m, KU 132348-9; Urbina Railroad Station, 3609 m, KU 132350-3; Volcán Chimborazo, USNM 103268-74. *Cotopaxi*: El Porvenir, 2 km W Campamento Mariscal Sucre, 3620 m, KU 124167 (tadpoles); Guilo, 8 km E Pilaló, 3500 m, KU 132538 (tadpoles); Laguna de Limpios, N base Volcán Cotopaxi, 3890 m, KU 122593; 4 km S Latacunga, USNM 164337; 6 km S, 7 km E Latacunga, 2750 m, KU 127082-4; Mulaló, 2980 m, KU 141566, 146263-4, 146749-61, 146762-3 (skeletons); Páramo de Apagua, 3860 m, KU 132390-1, 132535 (tadpoles); 24.3 km E Pilaló, 3750 m, KU 142848 (tadpoles); 11.3 km W Pujili, 3500 m, KU 141567; 38.3 km W Pujili, 3350 m, KU 142849 (tadpoles); Río Pita, N base Cerro Ingaloma, 3780 m, KU 122594-9. *Imbabura*: Ibarra, 2300 m, AMNH 10569-71, BMNH 98.4.28.152-4, NHMW 6482-6; N slope Nudo de Mojanda, 3650 m, KU 132393; Nudo de Mojanda, 4 km S San Pablo, 3050 m, KU 132394; Otovalo, 2550 m, KU 68708, 138587-613, MNCN 333; Quebrada San Miguel, 1 km N Otovalo, 2560 m, KU 117980; Quiroga, 2500 m, KU 1138577-86, 148585-6 (tadpoles). *Napo*: Laguna Papallacta, 3350 m, KU 109169 (tadpoles); Papallacta, 3130 m, KU 143095-102, 143538-40 (tadpoles), 143541, 148574-7; Río Napo, 400 m, MNRM 1965 (locality?); Santa Barbara, 2625 m, USNM-JAP 4479, 4507; 1 km NW Santa Barbara, 2625 m, USNM-JAP 4487, 4491-3; 1 km SW Santa Barbara, 2625 m, USNM-JAP 4567; Volcán Antisana, 4135 m, AMNH 20127. *Pastaza*: Mera, 1140 m, AMNH 52852 (locality?). *Pichincha*: Intac, 1200 m, BMNH 78.1.25.20, FMNH 3607, NHMW 6481 (6) (locality?); Llave Pongo, AMNH 20140; Machachi, 2950 m, SMF 2667-8, UMMZ 47216; Paso de Guamani, 20 km E Pifo, 3960 m, KU 111626, 112316-7 (tadpoles), 127081, 127134 (tadpoles); W slope Paso de Guamani, 3940 m, KU 109170 (tadpoles), 109334-5; Quito, 2840 m, AMNH 20438-41, 20447-50, 20471-90, 60631; ANSP 18235, CAS-SU 2274, 11436-7, KU 94403, 111613-25, 112313-5 (tadpoles), 148416-28, 148578-80, 148587-91 (tadpoles), 148593-9, NMCN 156 (2), 158 (6), MNHN 31 (2), 1662 (2), 4878 (4), USNM 57804, USNM-JAP 1570-2, 1574, 1576-7, 1579, 1584, 1586-7, 1593, 1595, 1620-4, 1666, 1669, 1686, 2248-50, 22514, 2487, 2506-8; UZM 1474, 1477-8, 14424-93; between Río Arturo and Taldadas, NE Cayambe, 3450 m, CAS-SU 8281; Río Chiche, Valle de los Chillos, 2535 m, KU 152147-8; Santo Domingo de los Colorados, 500 m, AMNH 20147 (locality?). *Tungurahua*: Ambato, 2700 m, KU 120733-40, 121390 (tadpoles), USNM 164302; Baños, 1800 m, CAS-SU 5082, FMNH 28091-2, 173661-80, KU 99123, 99124-9 (skeletons), 99130-84, UIMNH 65539-675, USNM-JAP 5834-6, 6010-12, 6014, 6019-20; Chambo Grande, 7.6 km SE Pelileo, 2340 m, KU 141568-9, 142625-6, 146261-2; 10 km W Cotaló, 3300 m, KU 132400-2; 1 km W Juan Benigno Vela, 3080 m,

KU 132395-6; Llanganati, near Río Jorge, 3000 m, CAS-SU 17426-7; 4 km N Mocha, 3140 m, KU 120757; 10 km SW Mocha, 3700 m, KU 120741-56; Pelileo, 2600 m, MNHN 03/211; 3 km SSW San Miguelito, 2620 m, KU 132399; 12 km SW Santa Rosa, 3400 m, KU 132397-8.

COLOMBIA: *Cundinamarca*: Bogotá, BMNH 1919.3.6.37 (locality?). *Narino*: Cuaspud, TNHC 40564-5.

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