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MARSUPIAL FROGS (ANURA: HYLIDAE: *GASTROTHECA*) OF THE ECUADORIAN ANDES: RESOLUTION OF TAXONOMIC PROBLEMS AND PHYLOGENETIC RELATIONSHIPS

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ABSTRACT: Analyses of data on allozymes, morphometrics, structural characters, and coloration resulted in the definition of nine species of *Gastrotheca* in the Andes of Ecuador and southern Colombia. Some populations that previously were referred to *G. riobambae* are recognized as new species: *G. espeletia* from the páramos of southern Colombia and northern Ecuador, *G. litonedis* from the Cuenca Basin in Ecuador, and *G. pseustes* from the Andean cordilleras south to the Loja Basin. The range of *G. riobambae* is restricted to elevations mostly below 3000 m from the Río Chonta south to the Riobamba Basin. *Gastrotheca marsupiata lojana* Parker, 1932 is placed in the synonymy of *G. monticola* Barbour and Noble, 1920, and *G. cavia* Duellman, 1974 is placed in the synonymy of *G. riobambae* (Fowler, 1913).

A phylogeny based on shared derived electromorphs shows *G. pseustes* to be grouped with *G. griswoldi* and *marsupiata* from the Andes of Peru. Among all of the other species from the Andes of Ecuador, the two species having direct development (*G. orophylax* and *plumbea*) are most closely related to *G. litonedis, monticola,* and *psychrophila* from southern Ecuador; these five species together are related to *G. espeletia, riobambae,* and *ruizi* from northern Ecuador and southern Colombia.

Key words: Anura; *Gastrotheca*; Andes; Allozyme electrophoresis; Phylogenetics

THE marsupial frogs of the genus *Gastrotheca* in the Andes of South America have been confused taxonomically for many years. Subsequent to Duméril and Bibron's (1841) description of *Hyla marsupiata* from Cuzco, Peru, the species became the type of *Gastrotheca* (Fitzinger, 1843). Although other species were named from the Andes (e.g., *Nototrema plumbeum* Boulenger, 1882, *Nototrema bolivianum* Steindachner, 1892, *Hyla argenteovirens* Boettger, 1892, and *Nototrema peruanum* Boulenger, 1900), most Andean specimens were referred to *Gastrotheca marsupiata* until the 1970's.

Duellman and Fritts (1972) reviewed the marsupial frogs in the Andes of Peru, Bolivia, and Argentina, and they concluded that Ecuadorian populations formerly referred to *G. marsupiata* were a distinct species, for which *Hyla riobambae* Fowler, 1913 was the earliest available name. Duellman (1974) summarized the data on marsupial frogs from the Andes of Ecuador and (1) discussed variation in *G. riobambae,* (2) recognized *G. lojana* Parker, 1932, *G. monticola* Barbour and Noble, 1920, and *G. plumbea* (Boulenger, 1882) as distinct species, and (3) described two new species—*G. cavia* and *G. psychrophila*. Duellman and Pyles (1980) named *G. orophylax* from Ecuador, and Duellman and Burrowes (1986) named *G. ruizi* from Colombia.

The taxonomic status of different populations of *G. riobambae* was questioned by Scanlan et al. (1980), who noted that some populations of *G. riobambae* were

immunologically closer to *G. marsupiata* than to other populations of *G. riobambae*. This observation led to a critical reexamination of specimens of *Gastrotheca* from the Andes of southern Colombia and Ecuador and the collection of additional material, including tissues for electrophoretic analysis of allozymes.

The purposes of this paper are to present the results of our analyses, to name three new species, to place two names in synonymy, and to provide an hypothesis of phylogenetic relationships among Andean marsupial frogs. Details of intraspecific variation, ecology, and life history, as well as locality records for all specimens examined, are reserved for a monographic treatment of the genus in preparation by the senior author.

Material and Methods

A total of 1465 adult and subadult frogs, 33 skeletons, 130 lots of tadpoles, and 26 lots of young of *Gastrotheca* representing populations of the nominal taxa in the high Andes of Ecuador, northern Peru, and southern Colombia was examined. Sixteen morphological measurements were obtained to the nearest 0.1 mm with needle-tipped dial calipers from 556 well-preserved adults, as follows: snout–vent length (SVL), tibia length, foot length, head length, greatest head width, eye diameter, tympanum diameter, interorbital distance, internarial distance, eyelid width, snout length, orbit–jaw distance, naris–jaw distance, thumb length, third finger length, and width of disc on third finger. See Duellman (1970) and Duellman and Pyles (1980) for methods of taking measurements.

A total of 25 external, descriptive characters was assayed and recorded in a dichotomous manner: i.e., presence or absence of a character state. Data obtained in this manner enable the application of multivariate statistical techniques (Blackith and Reyment, 1971). All statistical analyses were accomplished through the use of Biomedical Computer Programs (Dixon, 1981).

Analyses of morphometric data were performed only on adults, and the sexes were analyzed separately; if no significant differences existed between the sexes, they were combined. Univariate statistics and one-way analyses of variance (α = 0.05) were obtained on all morphometric data. A stepwise discriminant analysis (BMDP7M) and a principal components analysis (BMDP4M) were used in an attempt to determine group separation. In those species represented by several samples from throughout a broad geographic range, the descriptive data for individual populations were analyzed separately and together after they were determined to represent a single taxon.

Tissue samples were obtained from populations of *Gastrotheca* from throughout the Andes of Ecuador and southern Colombia and from populations of *G. griswoldi* and *G. marsupiata* in Peru. Samples of liver and skeletal muscles were removed and frozen immediately in liquid nitrogen for transport to the laboratory where they were maintained at −80 C until use (none longer than 1 yr). All voucher specimens were preserved and deposited in the herpetological collection in the Museum of Natural History, The University of Kansas (see Appendix I).

Tissues were ground with a teflon homogenizer and diluted 1:1 (muscle) or 1:3 (liver) with 0.01 M tris–0.001 M EDTA–0.001 M β-mercaptoethanol, pH 7.5. Homogenates were centrifuged at 15,000 rpm for 5 min; supernatants were refrozen at −80 C prior to use. Procedures for horizontal starch gel electrophoresis followed Selander et al. (1971). Three buffer systems were used: (1) TC 6.7; electrode: 0.223 M tris–0.086 M citric acid, pH 6.3; gel: 0.008 M tris–0.003 M citric acid, pH 6.7; NADP added to gel (8 mg/400 ml) and cathodal electrode tray (10 mg/400 ml). (2) TBE 8.0; electrode: 0.50 M tris–0.65 M boric acid–0.02 M EDTA, pH 8.0; gel: 1:9 dilution of electrode buffer; NADP added to gel (8 mg/400 ml) and cathodal electrode tray (10 mg/400 ml). (3) TBE 9.1; electrode and gel: 175.0 mM tris–17.5 mM boric acid–2.75 mM EDTA, pH 9.1; NAD added to gel (100 mg/400 ml) and cathodal electrode tray (60 mg/400 ml).

Gels were prepared from 50% Con-

TABLE 1.—Enzyme loci examined, abbreviations used, Enzyme Commission (E.C.) numbers (Commission on Biochemical Nomenclature, 1984), associated buffer systems, and tissues used.

Enzyme	No. loci	Abbreviation	E.C. No.	Buffer system	Tissue
Acid phosphatase	3	ACP	3.1.3.2	TC 6.7	liver
Adenosine deaminase	1	ADA	3.5.4.4	TBE 8.0	muscle
Alcohol dehydrogenase	1	ADH	1.1.1.1	TBE 9.1	liver
Catalase	1	CAT	1.11.1.6	TC 6.7	liver
Fumarate hydratase	1	FUM	4.2.1.2	TBE 9.1	liver
Glucose-6-phosphate dehydrogenase	1	G-6-PD	1.1.1.49	TBE 8.0	muscle
Glucose phosphate isomerase	1	GPI	5.3.1.9	TBE 9.1	liver
β-Glucuronidase	1	β-GUR	3.2.1.31	TBE 9.1	liver
Glutamate-oxaloacetate transaminase	2	GOT	2.6.1.1	TBE 9.1	liver
Glyceraldehyde-3-phosphate dehydrogenase	1	G-3-PD	1.2.1.12	TBE 9.1	liver
α-Glycerophosphate dehydrogenase	1	α-GPD	1.1.1.8	TBE 9.1	liver
3-Hydroxyisobutyrate dehydrogenase	1	HDH	1.1.1.31	TBE 9.1	liver
Isocitrate dehydrogenase	1	IDH	1.1.1.42	TBE 9.1	liver
Lactate dehydrogenase	2	LDH	1.1.1.27	TBE 8.0	muscle
				TBE 9.1	liver
Malate dehydrogenase	2	MDH	1.1.1.37	TC 6.7	liver
				TBE 9.1	liver
Mannosephosphate isomerase	1	MPI	5.3.1.8	TBE 8.0	muscle
α-Mannosidase	1	α-MAN	3.2.1.24	TC 6.7	liver
6-Phosphogluconate dehydrogenase	1	6-PGD	1.1.1.44	TC 6.7	liver
Phosphoglucomutase	1	PGM	2.7.5.1	TBE 8.0	muscle
Sorbitol dehydrogenase	1	SDH	1.1.1.14	TBE 9.1	liver
Superoxide dismutase	2	SOD	1.15.1.1	TBE 9.1	liver
Triosephosphate isomerase	1	TPI	5.3.1.1	TBE 9.1	liver
Xanthine dehydrogenase	1	XDH	1.1.1.37	TBE 9.1	liver

naught starch (lot 370-1) and 50% Otto Hiller Electrostarch (lot 392). Gels were 12% starch for all buffer systems. Two drops of β-mercaptoethanol were added to the gel buffer mixture after boiling and degassing. Gels were electrophoresed under the following conditions: buffer system 1: 6.25 V/cm for 10 h; buffer system 2: 5.0 V/cm for 11 h; and buffer system 3: 12.5 V/cm for 11 h. All gels were maintained at 4 C during electrophoresis.

Each gel was sliced into 1-mm-thick slabs for staining. The loci examined and buffer conditions used are listed in Table 1. Multiple loci were numbered from cathode to anode. Electromorphs were assigned letters according to their mobility, again beginning with the electromorph closest to the cathode. Procedures for staining were those described by Selander et al. (1971), Harris and Hopkinson (1976), and Siciliano and Shaw (1976). Phosphorescent stains (acid phosphatase, β-glucuronidase, and α-mannosidase) were viewed and photographed under 375-nm UV light.

Tissues were obtained from tadpoles and adults. Electrophoretic comparison of tissues obtained from tadpoles and adults from the same population revealed no differences. Thus, we pooled data derived from both tadpoles and adults.

Modified Nei's genetic distances and identities (Hillis, 1984) were calculated for all pairwise combinations of species examined. These distances were used to construct a UPGMA phenogram (Sneath and Sokal, 1973) to assess average genetic divergence among the species. In order to reconstruct the phylogeny of the species, the most parsimonious cladogram was constructed by standard phylogenetic methods (Wiley, 1981). Electromorphs found in both the ingroup and the outgroup (*G. testudinea* and *G. weinlandii*) were considered to be primitive. Electromorphs were ordered into transformation series following the taxonomic outgroup and functional outgroup criteria of Watrous and Wheeler (1981), as expanded by Farris (1982).

Tadpoles were staged according to Gos-

TABLE 2.—Genetic distances (above diagonal) and genetic identities (below diagonal) of 14 taxa of *Gastrotheca*.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. *G. espeletia*	—	0.111	0.111	0.330	0.595	0.623	0.878	0.969	0.819	1.424	1.905	1.981	2.674	1.981
2. *G. riobambae*	0.895	—	0.001	0.252	0.535	0.561	0.725	0.883	0.733	1.172	1.905	1.758	2.658	1.751
3. *G. "cavia"*	0.895	0.999	—	0.251	0.535	0.562	0.724	0.882	0.733	1.172	1.905	1.758	2.674	1.758
4. *G. ruizi*	0.719	0.777	0.778	—	0.728	0.761	0.948	0.969	0.908	1.467	2.168	2.269	2.674	2.269
5. *G. orophylax*	0.552	0.586	0.586	0.483	—	0.150	0.691	0.728	0.633	1.576	1.981	1.576	2.674	1.981
6. *G. plumbea*	0.536	0.570	0.570	0.467	0.861	—	0.673	0.669	0.607	1.517	1.758	1.443	2.751	2.019
7. *G. psychrophila*	0.416	0.484	0.485	0.388	0.501	0.510	—	0.680	0.742	0.831	1.611	1.349	3.367	1.981
8. *G. monticola*	0.379	0.413	0.414	0.379	0.483	0.512	0.506	—	0.407	1.767	2.674	1.981	2.674	2.269
9. *G. litonedis*	0.441	0.480	0.481	0.403	0.531	0.545	0.476	0.665	—	1.953	2.411	2.042	2.674	2.217
10. *G. pseustes*	0.241	0.310	0.310	0.231	0.207	0.219	0.436	0.171	0.142	—	0.467	0.305	2.260	1.383
11. *G. marsupiata*	0.149	0.149	0.149	0.114	0.138	0.172	0.200	0.069	0.090	0.627	—	0.426	2.674	2.269
12. *G. griswoldi*	0.138	0.172	0.172	0.103	0.207	0.236	0.259	0.138	0.130	0.737	0.653	—	2.269	1.576
13. *G. weinlandii*	0.069	0.070	0.069	0.069	0.069	0.064	0.034	0.069	0.069	0.104	0.069	0.103	—	1.170
14. *G. testudinea*	0.138	0.174	0.172	0.103	0.138	0.133	0.138	0.103	0.109	0.251	0.103	0.207	0.310	—

ner (1960), and their specific identities were determined by means of electrophoretic comparisons with adults, obtaining tadpoles from a known parent, and/or raising some individuals of a lot through metamorphosis. Other lots of tadpoles were identified by comparison with those of known identity.

Minor osteological differences among the species have been noted. A discussion of these has been reserved for a comprehensive account of the genus.

RESULTS

The results of the analyses of allozyme electrophoresis, morphometrics, descriptive characters, and tadpoles are presented separately.

Allozyme Electrophoresis

Among the enzymatic products of the 29 loci examined, 185 electromorphs were identified among the species of *Gastrotheca* included in the study (Appendix II). The average number of alleles per locus ranged from 1.0 (*G. espeletia, griswoldi, monticola,* and *testudinea*) to 1.66 (*G. pseustes*). Average heterozygosity values are not presented, because highly variable enzymes, such as esterases and peptidases, were not examined; these loci often are too variable to be informative phylogenetically in a group of diverse taxa.

Genetic identities and distances are presented in Table 2. The distances were used to construct a UPGMA phenogram (Fig. 1). All of the currently recognized species show considerable genetic divergence with the exception of *G. cavia,* which is indistinguishable allozymically from *G. riobambae*. In addition, the allozymic data show that three previously unrecognized species of *Gastrotheca* exist in the Andes of Ecuador and southern Colombia (*G. espeletia, litonedis,* and *pseustes*).

Morphometrics

Despite various statistical machinations of the morphometric data, no clear-cut morphometric distinctions exist among the species (Table 3). Minor differences exist in disc size and tibia length (small discs

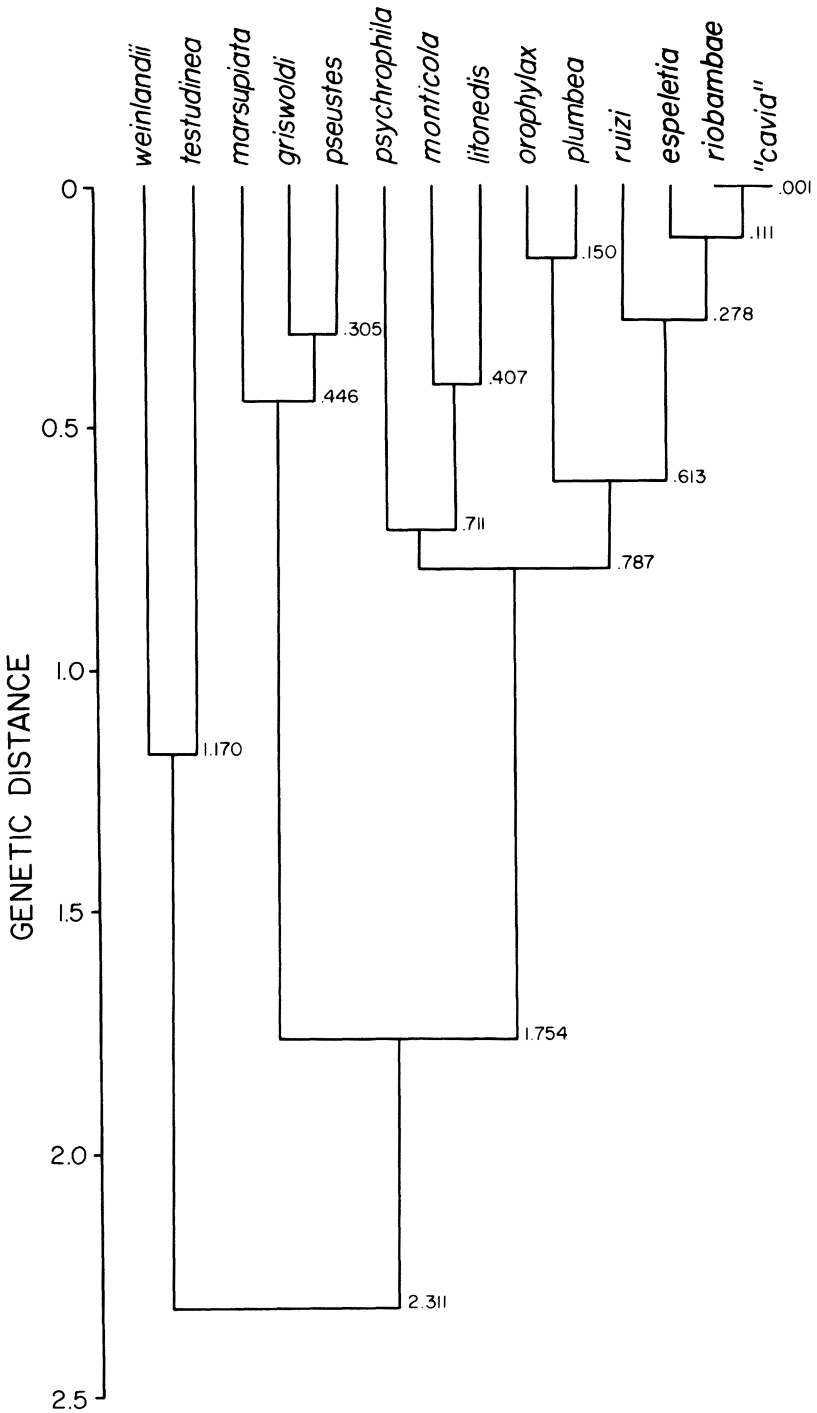

FIG. 1.—Phenogram of modified Nei genetic distances (Hillis, 1984) among 14 nominal taxa of *Gastrotheca*.

TABLE 3.—Measurements of seven species of *Gastrotheca*. First line is range; second line is mean and 1 SD; measurements of *G. orophylax* and *G. plumbea* were given by Duellman and Pyles (1980).

Character, *n*, sex	*G. espeletia* 3♂♂ 6♀♀	*G. litonedis* 9♂♂ 15♀♀	*G. monticola* 33♂♂ 48♀♀	*G. pseustes* 69♂♂ 69♀♀	*G. psychrophila* 3♂♂ 9♀♀	*G. riobambae* 11♂♂ 4♀♀	*G. ruizi* 11♂♂ 4♀♀
Snout–vent length							
♂♂	47.0–52.6 49.4 ± 2.87	42.3–52.5 47.9 ± 3.18	40.6–58.6 52.6 ± 3.72	38.3–54.4 46.4 ± 3.68	45.8–49.9 47.7 ± 2.06	34.1–56.8 43.0 ± 4.87	48.0–65.0 56.3 ± 6.04
♀♀	44.3–51.9 47.5 ± 3.50	48.2–62.4 53.1 ± 3.21	46.3–73.0 59.4 ± 5.72	36.0–62.4 49.6 ± 5.69	43.9–63.5 52.5 ± 6.61	33.3–66.4 48.6 ± 7.58	45.8–65.6 56.0 ± 9.37
Tibia length							
♂♂	16.6–21.4 19.5 ± 2.55	19.2–22.5 21.1 ± 1.19	22.7–31.1 27.3 ± 1.88	16.6–23.9 20.4 ± 1.69	23.4–24.6 24.0 ± 0.60	14.2–24.1 17.5 ± 2.02	22.5–28.0 25.8 ± 1.90
♀♀	16.7–19.8 17.5 ± 1.18	20.7–25.5 23.2 ± 1.56	24.1–38.2 29.8 ± 3.21	15.6–32.5 22.5 ± 3.40	23.5–30.7 26.2 ± 3.21	13.9–27.8 20.0 ± 3.14	21.9–30.0 26.2 ± 3.85
Foot length							
♂♂	18.8–24.1 22.1 ± 2.86	20.2–22.9 21.8 ± 0.88	18.8–26.8 23.7 ± 1.85	17.9–25.8 21.7 ± 1.89	21.3–24.0 22.7 ± 1.36	14.6–26.3 18.5 ± 2.45	23.4–29.6 26.7 ± 2.28
♀♀	18.7–23.0 20.2 ± 1.70	21.4–27.0 24.2 ± 1.67	21.2–39.4 27.6 ± 3.48	16.2–28.5 23.2 ± 2.63	20.0–31.8 25.2 ± 4.54	14.7–31.9 21.8 ± 3.81	21.1–35.0 29.6 ± 5.96
Head length							
♂♂	15.2–17.4 16.2 ± 1.11	13.6–16.9 15.3 ± 0.98	14.1–21.7 17.8 ± 1.31	12.3–17.5 14.6 ± 1.18	16.3–16.7 16.5 ± 0.21	11.2–17.8 14.0 ± 1.40	17.2–21.5 19.5 ± 1.54
♀♀	14.9–17.3 15.9 ± 0.93	15.2–19.1 17.0 ± 1.14	14.7–22.7 18.8 ± 1.78	11.6–19.4 15.5 ± 1.71	15.8–20.5 17.5 ± 1.93	11.1–23.2 15.9 ± 2.17	16.7–21.0 19.0 ± 2.25
Head width							
♂♂	16.4–19.2 17.8 ± 1.40	14.9–18.3 16.8 ± 1.19	15.5–28.3 20.2 ± 2.41	13.6–19.9 16.3 ± 1.30	18.1–19.0 18.6 ± 0.47	12.7–19.9 15.7 ± 1.47	17.7–21.5 19.7 ± 1.39
♀♀	16.5–19.3 17.7 ± 1.07	16.5–20.2 18.4 ± 1.21	16.4–29.8 21.5 ± 2.36	13.3–22.7 17.4 ± 2.07	18.1–22.8 19.7 ± 2.02	12.1–31.5 17.6 ± 2.72	16.7–22.1 19.4 ± 2.37
Interorbital distance							
♂♂	3.6–4.9 4.3 ± 0.65	4.0–5.0 4.5 ± 0.31	5.1–8.0 6.9 ± 0.74	3.2–6.9 4.2 ± 0.50	5.5–6.0 5.8 ± 0.27	3.2–5.3 3.9 ± 0.46	4.5–5.8 5.3 ± 0.40
♀♀	3.6–4.3 3.9 ± 0.28	4.6–6.0 5.3 ± 0.47	5.0–10.0 7.4 ± 1.24	3.1–8.3 4.8 ± 1.16	5.7–7.3 6.3 ± 0.65	3.1–6.9 4.4 ± 0.79	4.5–6.3 5.5 ± 0.85
Internarial distance							
♂♂	2.5–3.0 2.8 ± 0.27	2.5–3.0 2.8 ± 0.18	3.0–4.2 3.6 ± 0.30	2.5–3.7 2.9 ± 0.25	2.3–2.7 2.5 ± 0.20	1.7–3.6 2.4 ± 0.39	3.4–4.7 4.1 ± 0.43
♀♀	2.6–3.2 2.9 ± 0.21	2.7–3.5 3.1 ± 0.25	3.2–4.6 3.9 ± 0.36	2.4–3.9 3.1 ± 0.34	2.4–3.5 2.8 ± 0.39	1.5–4.0 2.8 ± 0.50	3.8–4.4 4.0 ± 0.29
Eye–nostril distance							
♂♂	3.2–4.0 3.5 ± 0.44	3.0–4.1 3.6 ± 0.32	4.2–5.7 4.9 ± 0.36	2.9–4.6 3.5 ± 0.32	4.3–4.8 4.5 ± 0.25	2.5–4.5 3.3 ± 0.42	4.2–5.4 4.7 ± 0.46
♀♀	3.2–3.8 3.5 ± 0.25	3.5–4.6 4.1 ± 0.28	4.4–6.5 5.2 ± 0.56	2.8–5.9 3.9 ± 0.64	4.1–5.4 4.6 ± 0.42	2.7–4.9 3.7 ± 0.47	4.4–5.5 5.0 ± 0.56
Diameter of eye							
♂♂	4.4–4.6 4.5 ± 0.12	3.9–4.8 4.4 ± 0.34	4.3–5.8 5.1 ± 0.41	2.7–5.3 4.3 ± 0.36	3.9–4.6 4.4 ± 0.23	3.1–5.4 4.0 ± 0.46	5.3–7.0 5.8 ± 0.59
♀♀	3.7–4.5 4.1 ± 0.28	4.3–5.4 4.8 ± 0.31	3.9–6.8 5.5 ± 0.54	3.1–5.9 5.6 ± 0.62	3.7–4.8 4.4 ± 0.34	3.5–6.1 4.4 ± 0.63	5.0–6.1 5.6 ± 0.46
Diameter of tympanum							
♂♂	1.8–2.5 2.2 ± 0.36	1.9–2.8 2.2 ± 0.27	2.2–3.8 2.8 ± 0.37	1.7–3.0 2.3 ± 0.27	2.4–2.7 2.6 ± 0.15	1.7–3.0 2.2 ± 0.27	3.9–5.0 4.4 ± 0.41
♀♀	2.2–2.7 2.5 ± 0.19	2.2–3.1 2.6 ± 0.30	2.3–3.8 3.0 ± 0.39	1.7–3.5 2.4 ± 0.43	2.2–3.2 2.7 ± 0.30	1.6–3.5 2.5 ± 0.42	3.6–4.2 4.0 ± 0.25

TABLE 3.—Continued.

Character n, sex	G. espeletia 3♂♂ 6♀♀	G. litonedis 9♂♂ 15♀♀	G. monticola 33♂♂ 48♀♀	G. pseustes 69♂♂ 69♀♀	G. psychrophila 3♂♂ 9♀♀	G. riobambae 11♂♂ 4♀♀	G. ruizi 11♂♂ 4♀♀
Width of eyelid							
♂♂	3.5–4.1 3.7 ± 0.32	3.4–4.2 3.8 ± 0.32	2.9–5.1 4.1 ± 0.45	2.9–4.8 3.8 ± 0.40	2.7–3.6 3.3 ± 0.52	2.6–4.2 3.3 ± 0.37	3.5–5.1 4.1 ± 0.49
♀♀	3.2–4.2 3.6 ± 0.36	3.4–4.5 3.8 ± 0.34	3.0–5.1 4.2 ± 0.45	2.8–4.7 3.8 ± 0.41	2.6–4.2 3.7 ± 0.50	2.6–5.2 3.6 ± 0.47	3.6–4.7 4.0 ± 0.51
Orbit–jaw distance							
♂♂	2.7–3.1 2.8 ± 0.23	1.6–2.5 2.3 ± 0.28	1.8–2.8 2.5 ± 0.20	1.5–2.6 2.0 ± 0.22	2.4–2.9 2.6 ± 0.27	1.7–3.2 2.3 ± 0.35	3.0–4.0 3.6 ± 0.36
♀♀	2.3–3.1 2.7 ± 0.32	2.3–2.9 2.6 ± 0.20	2.1–3.7 2.8 ± 0.35	1.6–2.9 2.2 ± 0.34	2.3–3.2 2.7 ± 0.35	1.5–3.6 2.6 ± 0.47	3.1–4.0 3.5 ± 0.42
Nostril–jaw distance							
♂♂	3.3–3.9 3.6 ± 0.31	2.9–3.6 3.3 ± 0.24	2.6–3.9 3.4 ± 0.35	2.5–3.7 3.0 ± 0.27	3.1–3.9 3.5 ± 0.40	2.3–4.0 2.9 ± 0.37	3.7–5.0 4.2 ± 0.15
♀♀	2.8–4.1 3.4 ± 0.42	3.1–4.2 3.6 ± 0.30	2.6–4.8 3.9 ± 0.47	2.3–4.2 3.20 ± 0.41	3.2–4.8 3.8 ± 0.54	2.1–4.8 3.3 ± 0.58	3.7–4.8 4.2 ± 0.56
Thumb length							
♂♂	8.1–10.3 9.5 ± 1.22	8.2–9.6 8.8 ± 0.54	7.4–11.2 9.5 ± 0.87	6.5–9.9 8.5 ± 0.77	8.2–8.8 8.6 ± 0.35	5.9–12.1 7.9 ± 1.13	9.2–11.9 10.5 ± 1.04
♀♀	7.5–10.4 8.9 ± 1.02	8.4–10.7 10.0 ± 0.76	8.5–13.3 10.8 ± 1.27	6.5–11.6 9.2 ± 1.13	7.2–11.5 9.4 ± 1.63	5.9–19.6 9.3 ± 1.92	9.0–13.7 11.5 ± 2.47
Third finger							
♂♂	13.2–18.0 16.0 ± 2.48	13.8–15.9 14.7 ± 0.67	14.2–19.5 17.0 ± 1.35	12.2–18.6 15.0 ± 1.26	15.9–16.9 16.5 ± 0.53	9.9–19.8 13.3 ± 1.86	16.2–20.4 18.7 ± 1.41
♀♀	13.4–16.3 14.8 ± 1.20	14.5–18.8 16.6 ± 1.35	15.3–24.4 19.3 ± 2.06	9.2–19.6 15.9 ± 1.94	14.7–21.0 16.9 ± 2.57	10.3–23.4 15.4 ± 2.90	15.5–21.1 18.4 ± 2.68
Diameter of disc							
♂♂	1.7–2.1 1.9 ± 0.21	0.0–2.6 1.9 ± 0.75	2.1–3.8 2.9 ± 0.32	1.2–2.9 2.0 ± 0.34	2.5–2.9 2.7 ± 0.21	1.0–3.1 1.8 ± 0.37	2.0–2.7 2.2 ± 1.10
♀♀	1.6–2.3 1.9 ± 0.27	1.8–2.7 2.4 ± 0.24	2.3–4.2 3.1 ± 0.42	1.4–3.1 2.2 ± 0.36	2.3–3.5 2.8 ± 0.45	1.3–3.3 2.0 ± 0.44	1.8–3.2 2.3 ± 0.62

and short tibia characterize *G. espeletia*, *pseustes*, and *riobambae*). Geographical variation in *G. riobambae* and *pseustes* is greater than the differences among some of the species.

A principal components analysis showed that Component I is strictly size related, whereas other components incorporated shape factors—Component II primarily being orbit–jaw distance versus disc size, and Component III primarily being internarial distance versus disc size (Fig. 2).

With the exception of obviously larger species (e.g., *G. monticola* and *orophylax*) differing from obviously smaller species (e.g., *G. espeletia*), measurements and proportions are of little use in differentiating the species.

Structural Characters

Distinctive differences in snout shape (especially in profile) characterize some of the species; for example, the snout is long and sloping in *G. ruizi* and truncate in *G. orophylax* and *plumbea*. In some of the other species, subtle differences exist in snout shape (Fig. 3).

The extent of the webbing on the toes was coded as to the place of the distal terminus of the web with respect to the discs and subarticular tubercles on the fourth and fifth toes. Most of the species are alike in the extent of interspecific variation in toe webbing. However, *G. riobambae* has more webbing than the similar species *G. espeletia* and *pseustes* (Fig. 4).

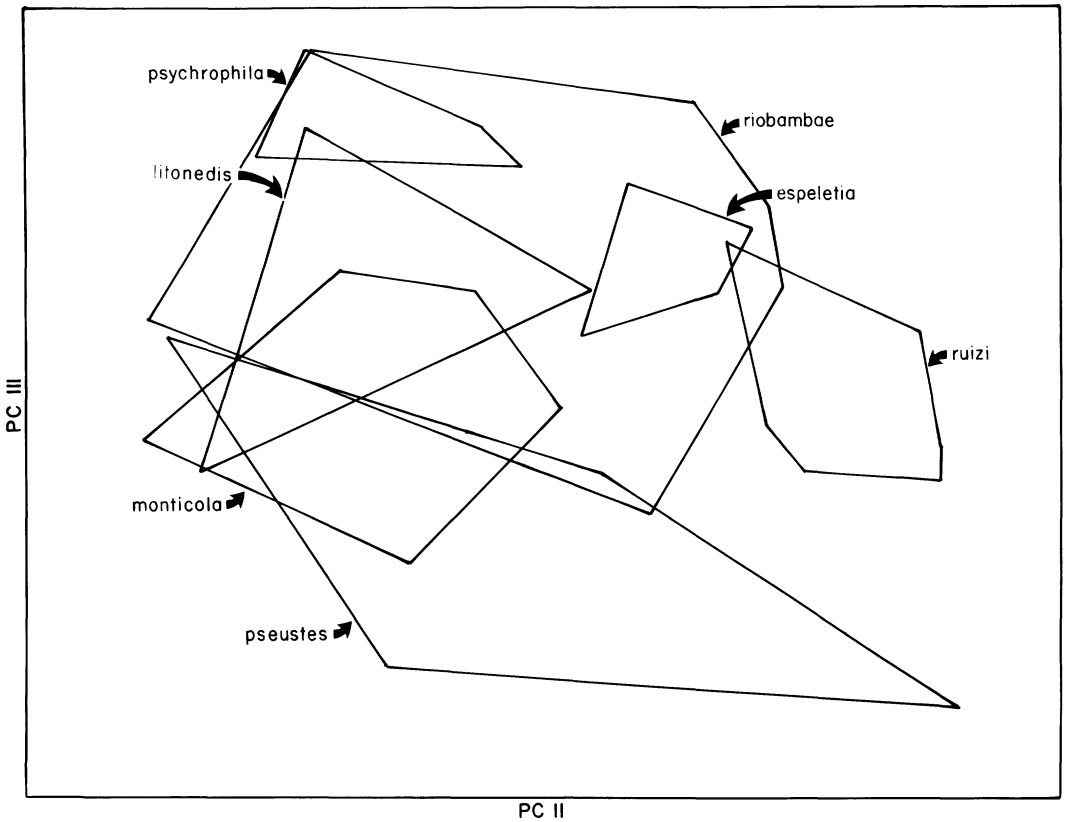

FIG. 2.—Results of a principal components (PC) analysis of morphometric data (16 measurements of 556 specimens) of seven species of *Gastrotheca*. Axis II is PC II; axis III is PC III.

The texture of the dorsal skin was coded as smooth, areolate, granular, or pustular. Smooth skin is characteristic of *G. ruizi*, but in the other species, skin texture is variable. The variation in some cases may be an artifact of preservation. Few individuals, if any, of most species are pustular, except *G. pseustes* in which 25% of the specimens have this condition.

Coloration

The dorsal coloration of all of these species of *Gastrotheca* consists of a green or brown ground color with or without darker green or brown markings. If dorsal markings are present, they usually are in the form of a dark longitudinal paravertebral mark or series of spots beginning in the occipital region and continuing to the sacrum or beyond. In *G. ruizi*, the middorsal and dorsolateral surfaces are brown, and the paravertebral areas are pale green. The entire dorsum is uniform green in *G. orophylax* and *plumbea*, and the former has uniform green flanks. Dorsally, *G. psychrophila* is dark grayish brown. The dorsal coloration of the other species is highly variable and is not useful in identifying the species.

Three kinds of pale cream or bronze stripes may be present. The presence of a labial stripe is variable in all species. A dorsolateral stripe separating the dorsal color from that of the flank is consistently absent in *G. espeletia* and *psychrophila*, always present in *plumbea*, and variable in the other species. A transverse supraanal stripe is absent in all specimens of *G. espeletia*, *psychrophila*, and *ruizi* and variably present in the other species. A dark canthal stripe is variable in most species but consistently absent in *G. psychrophila*, *plumbea*, and *ruizi*.

The flanks are uniformly dark brown in

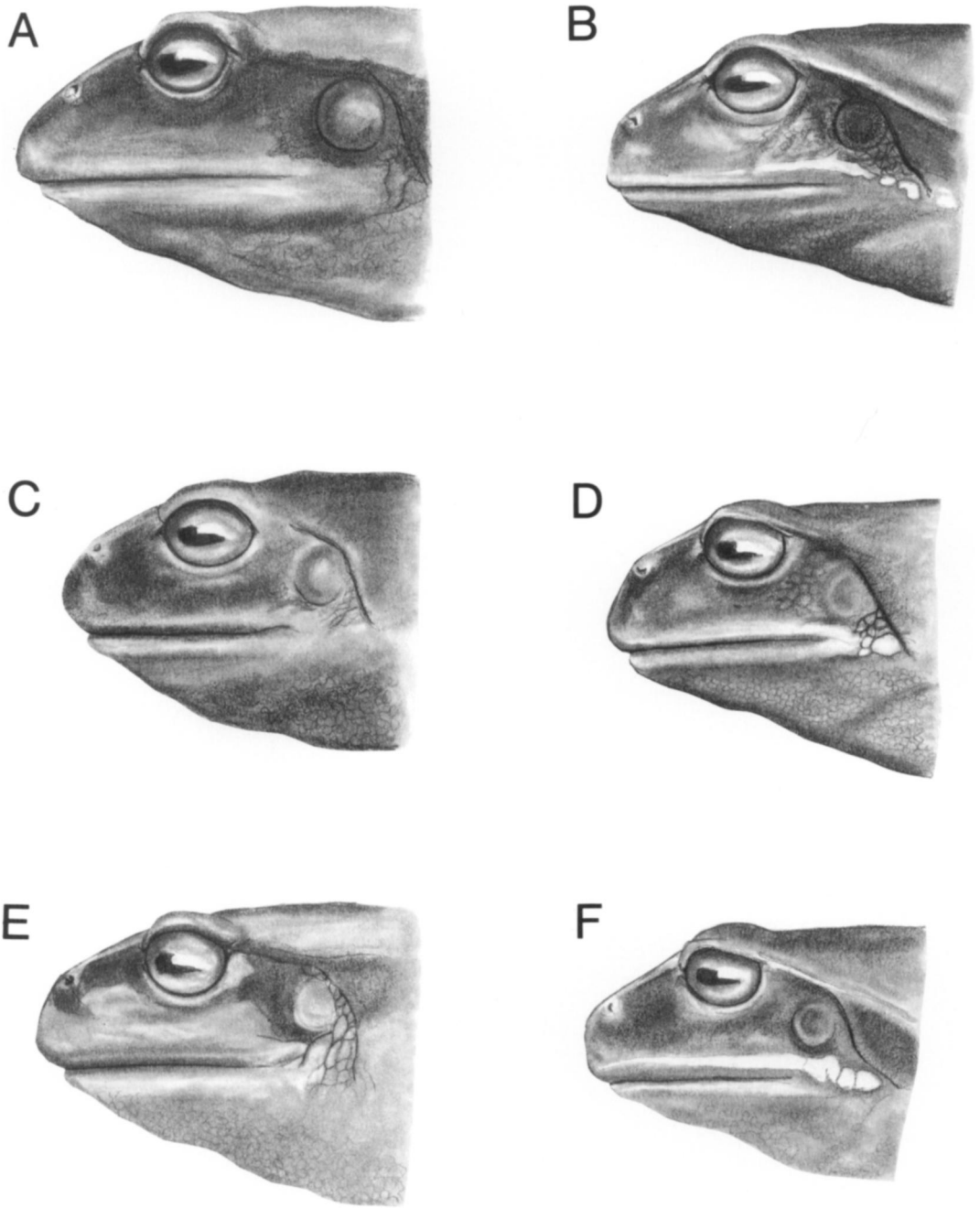

FIG. 3.—Lateral view of heads of *Gastrotheca*: (A) *G. ruizi*, KU 200004, (B) *G. pseustes*, KU 203448, (C) *G. espeletia*, KU 169401, (D) *G. litonedis*, KU 203441, (E) *G. riobambae*, KU 120730, (F) *G. monticola*, KU 138235.

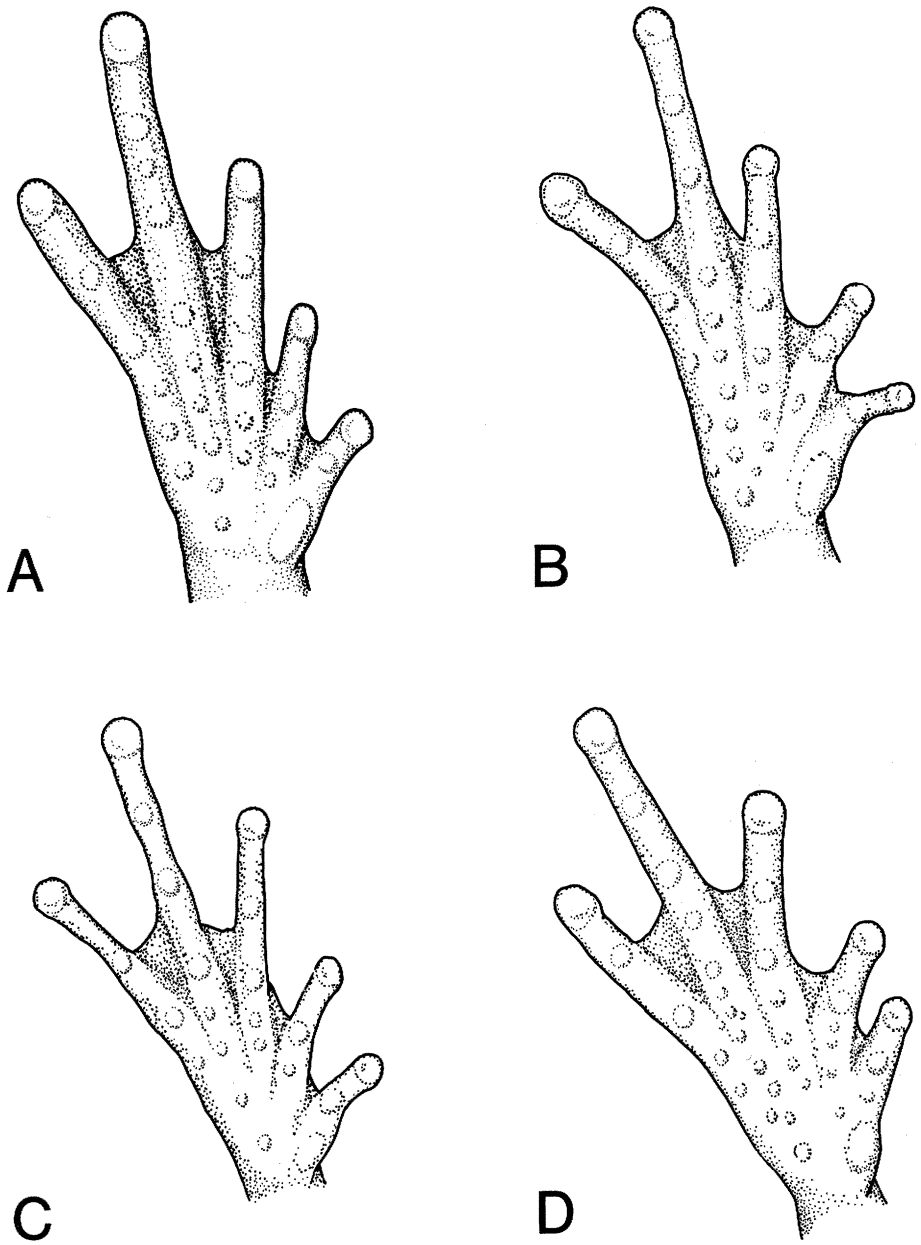

FIG. 4.—Plantar views of right feet of *Gastrotheca*: (A) *G. espeletia*, KU 169401, (B) *G. riobambae*, KU 120730, (C) *G. pseustes*, KU 203448, (D) *G. litonedis*, KU 203441.

G. plumbea and *ruizi*; in the other species, they are pale cream or pale blue with black spots or mottling, or they are dark brown with pale spots. The belly is uniformly cream or pale gray in *G. litonedis*, *orophylax*, *plumbea*, and *ruizi* and cream or gray with dark brown or black flecks, spots, or mottling in the other species. The interspecific differences in ventral pattern are especially subtle. For example, individuals of *G. riobambae* have distinct flecks, spots, or mottling on the belly and ventral surface of the shank, whereas the belly in *G. pseustes* has diffuse dark spots,

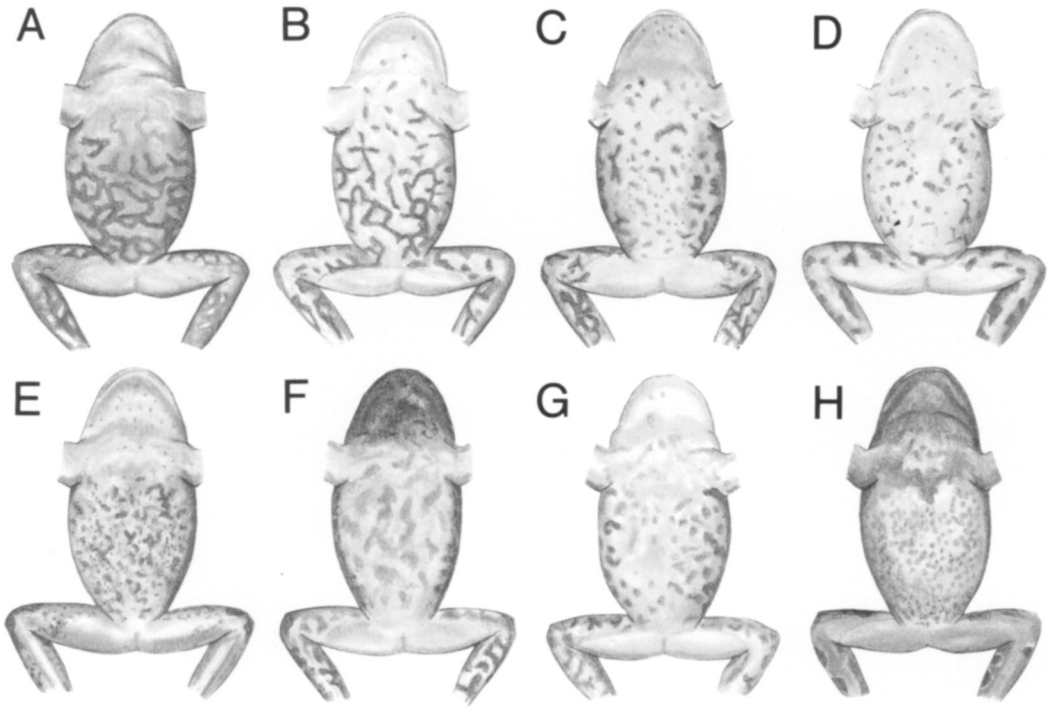

FIG. 5.—Ventral color patterns in *Gastrotheca*: (A) *G. riobambae* from Guano, Provincia Chimborazo, Ecuador, KU 138568, (B) *G. riobambae* from Otavalo, Provincia Imbabura, Ecuador, KU 138606, (C) *G. riobambae* from Laguna Cuicocha, Provincia Imbabura, Ecuador, KU 138219, (D) *G. riobambae* from Quito, Provincia Pichincha, Ecuador, KU 148422, (E) *G. pseustes* from Saraguro, Provincia Loja, Ecuador, KU 142613, (F) *G. pseustes* from Cuenca, Provincia Azuay, Ecuador, KU 120715, (G) *G. espeletia* from Tulcán, Provincia Carchi, Ecuador, KU 117979, (H) *G. espeletia* from Tulcán, Provincia Carchi, Ecuador, KU 178555.

which may be fused into a dark suffusion (Fig. 5).

Tadpoles

The larvae of all species of *Gastrotheca* are generalized, large (up to 80 mm total length) pond-type tadpoles with two upper and three lower rows of denticles. Minor differences were found among the species, but many of these differences are not consistent. In the descriptions of tadpoles in the following accounts of the species, the modal condition is described. Consequently, relative proportions of the body and tail may vary from sample to sample, or within samples. The characters found to be useful in distinguishing the tadpoles of the different species are as follows.

1. Shape of the snout: This is truncate in dorsal view in *G. monticola* and rounded in the other species. In profile, the snout varies from a gradual incline from the nostrils to the tip in *G. ruizi* to round in *G. riobambae*.

2. Interorbital distance: This measurement varies interspecifically from about 25–50% of the width of the head at the level of the orbits.

3. In lateral view, the throat is slightly concave in *G. riobambae* and convex in the other species.

4. The cloacal (anal) tube is median, sinistral, or dextral to the ventral fin, and the opening is transverse or diagonal.

5. The dorsal fin begins abruptly (forming a definite hump) in *G. espeletia* and *psychrophila* and gradually (with no hump) in the other species.

6. The labial papillae are in two alternating rows laterally and ventrally in all species except *G. espeletia* (single row

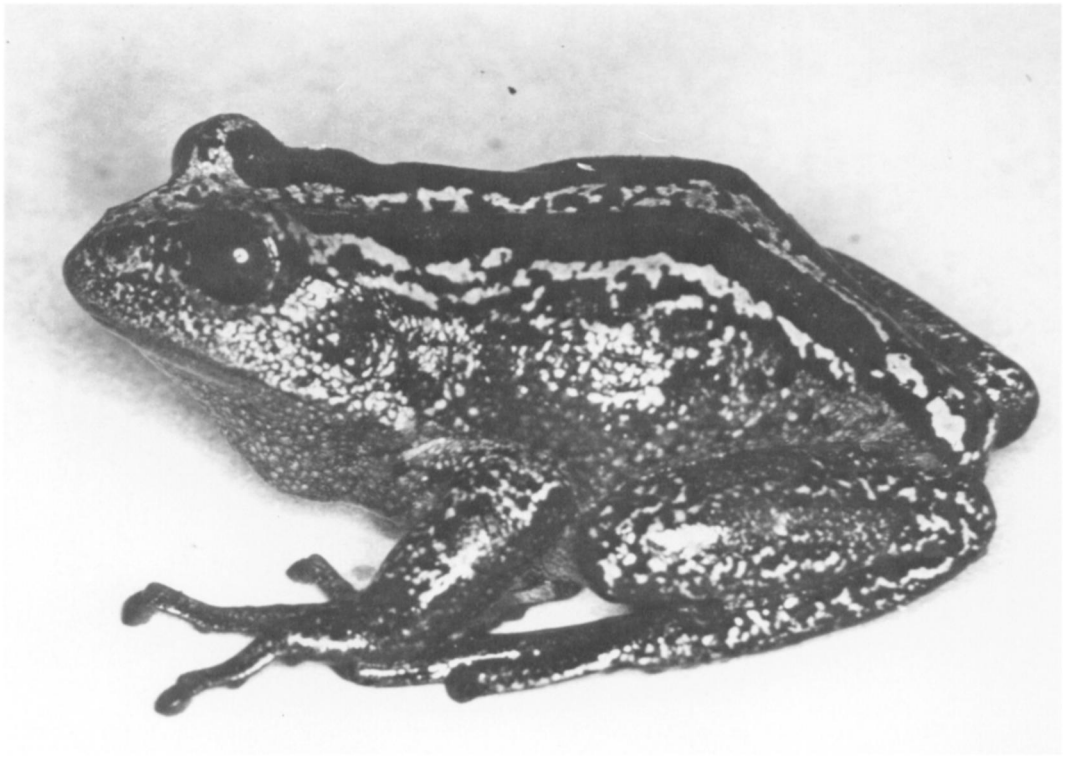

FIG. 6.—Holotype of *Gastrotheca espeletia*, adult male, 52.6 mm SVL, KU 169401.

ventromedially) and *G. ruizi* (single row throughout).

Advertisement Call

All of the species of *Gastrotheca* in the high Andes of Ecuador and southern Colombia have a call consisting of a moderately long note, followed or not by two or three shorter notes: "wraaack-ack-ack." Too few recordings are available for meaningful comparisons, so no attempt has been made to utilize call characters.

ACCOUNTS OF THE SPECIES

In the following accounts of species, "key" diagnostic characters are presented in a uniform numbered sequence followed by statements about how to distinguish the species from others. The percentage of individuals having a given character state is given in the diagnoses; the absence of a percentage indicates that the condition is constant within the sample. Descriptions of holotypes are given for the new species.

Gastrotheca ***espeletia*** sp. nov.
Figure 6

Holotype.—KU 169401, an adult male, from the north shore of Lago de la Cocha, 2790 m (01°08′ N, 77°07′ W), Departamento Nariño, Colombia, one of a series collected on 24 September 1974 by William E. Duellman.

Paratopotype.—KU 169402, an adult male, collected with the holotype.

Diagnosis.—(1) SVL to 52 mm in males, 51 mm in females; (2) head width equal to head length; (3) snout in dorsal view acutely rounded, in profile rounded with tip projecting well beyond, and nostrils posterior to level of, anterior margin of lower jaw; (4) interorbital distance 110% of width of eyelid; (5) eye 125% of eye–nostril distance; (6) tibia length 38% of SVL, less than foot length; (7) skin on dor-

sum smooth; (8) first finger longer than second; (9) discs on fingers only slightly wider than digits; (10) webbing extending to penultimate tubercle on fourth toe, to distal tubercle on fifth toe; (11) pale labial stripe absent (78%); (12) dark canthal stripe present (78%); (13) tympanum brown in life; (14) dorsum dark gray to tan with darker longitudinal, paravertebral markings on body and usually dark spots on shanks; (15) pale dorsolateral stripe absent; (16) pale supra-anal stripe absent; (17) flanks gray or tan, with dark spots in 78%; (18) anterior and posterior surfaces of thighs gray with black spots or mottling; (19) ventral surfaces of body and shanks dull cream with heavy black mottling or flecks, or dark gray; vocal sac dark gray; (20) tadpoles having the snout bluntly rounded in dorsal view, angular from level of nostrils to truncate terminus in profile; throat convex in profile; eyes small, directed laterally; interorbital distance greater than one-third width of head; dorsal fin rising abruptly from posterior edge of body; cloacal tube median; labial papillae in single row ventromedially, in two alternating rows ventrolaterally.

Gastrotheca espeletia is like *pseustes* and *riobambae* in having short limbs and small digital discs. It differs from *pseustes* in having bold spots or mottling (or uniform dark gray) ventrally, as contrasted with diffuse gray spots or a pale venter in *pseustes*; furthermore, the snout is narrower in *espeletia* than in *pseustes*. In *pseustes* and *riobambae*, the first and second fingers are equal in length, whereas the first finger is longer than the second in *espeletia*, the webbing on the feet is more extensive in *riobambae*. The tadpoles of *espeletia* differ from those of both species and are like those of *psychrophila* in having the dorsal fin arising abruptly from the body; the labial papillae are in a single row ventromedially and two alternating rows ventrolaterally in *espeletia*, whereas they are in two alternating rows along the entire ventral lip in the others.

Description of holotype.—An adult male with a SVL of 52.6 mm; body robust; snout acutely rounded in dorsal view, in lateral profile rounded, protruding well beyond margin of jaws; canthus rostralis angular; loreal region slightly concave; lips rounded; top of head concave; interorbital distance slightly greater than width of eyelid; internarial area slightly depressed; nostrils slightly protuberant, directed dorsolaterally at point just behind anterior margin of lower jaw and below anterior terminus of canthus rostralis; diameter of eye slightly less than distance from eye to nostril; tympanum vertically ovoid, separated from eye by distance 1.5 times length of tympanum; tympanic annulus distinct, smooth; supratympanic fold weak, extending from posterior corner of eye to point above insertion of forelimb.

Arms robust; axillary membrane absent; hands large; fingers unwebbed; discs small, round; diameter of discs about 60% length of tympanum; relative length of fingers $2 < 1 < 4 < 3$; subarticular tubercles small, subconical, nonbifid; supernumerary tubercles few, minute, present only on proximal segments of fingers; palmar tubercle bifid; prepollical tubercle elongately ovoid, bearing brown nuptial excrescences medially. Hind limbs moderately short, robust, 40.7% of SVL; foot length 43.1% of SVL; calcar and tarsal folds absent; outer tarsal tubercle minute; inner metatarsal tubercle ovoid, not visible from above; toes long, bearing discs slightly smaller than those on fingers; relative length of toes $1 < 2 < 3 = 5 < 4$; toes about one-third webbed; webbing formula I 2—2^+ II 2^-—3 III 2—3 IV 3—2^- V; subarticular tubercles small; supernumerary tubercles minute, 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.

Vomerine odontophores inclined posteromedially, separated medially between posterior margins of small ovoid choanae, bearing 4-4 teeth. Tongue cordiform, shallowly notched posteriorly, free behind for about one-fourth of its length. Vocal

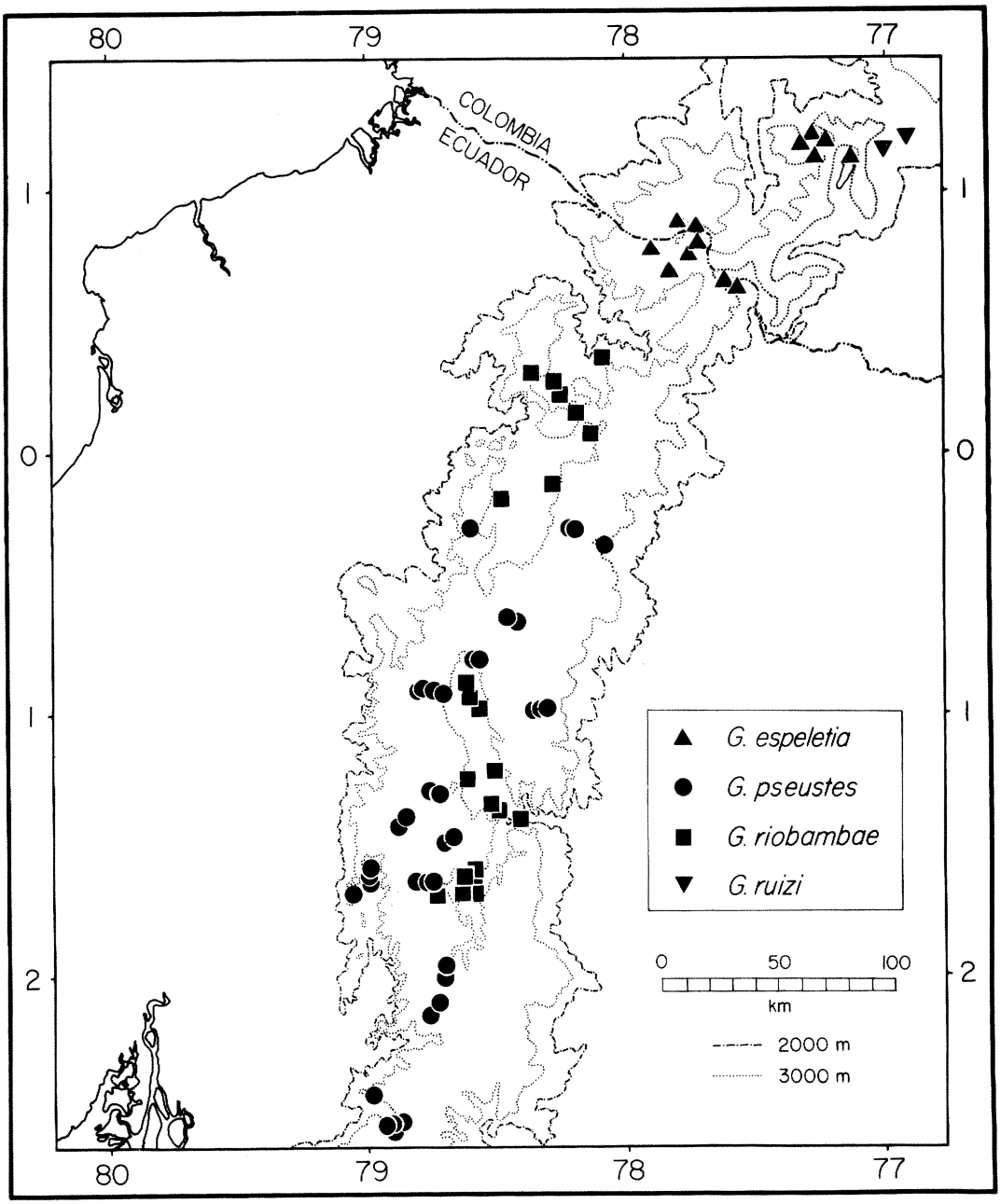

FIG. 7.—Map of northern Ecuador and southern Colombia showing localities for species of *Gastrotheca*.

slit extending along inner margin of mandible from midlateral base of tongue to angle of jaw. Vocal sac single, median, subgular.

Color in preservative: Dorsum and venter dull gray with pale gray flecks on posterolateral surfaces of body.

Color in life: Dorsum metallic bronze-brown with pale green flecks dorsolaterally; axilla, groin, anterior and posterior surfaces of thighs, and inner surfaces of shanks greenish blue; vocal sac gray; rest of venter dull bluish gray; iris reddish brown with fine black reticulations.

Measurements: SVL 52.6, tibia length 21.4, foot length 24.1, head width 19.2,

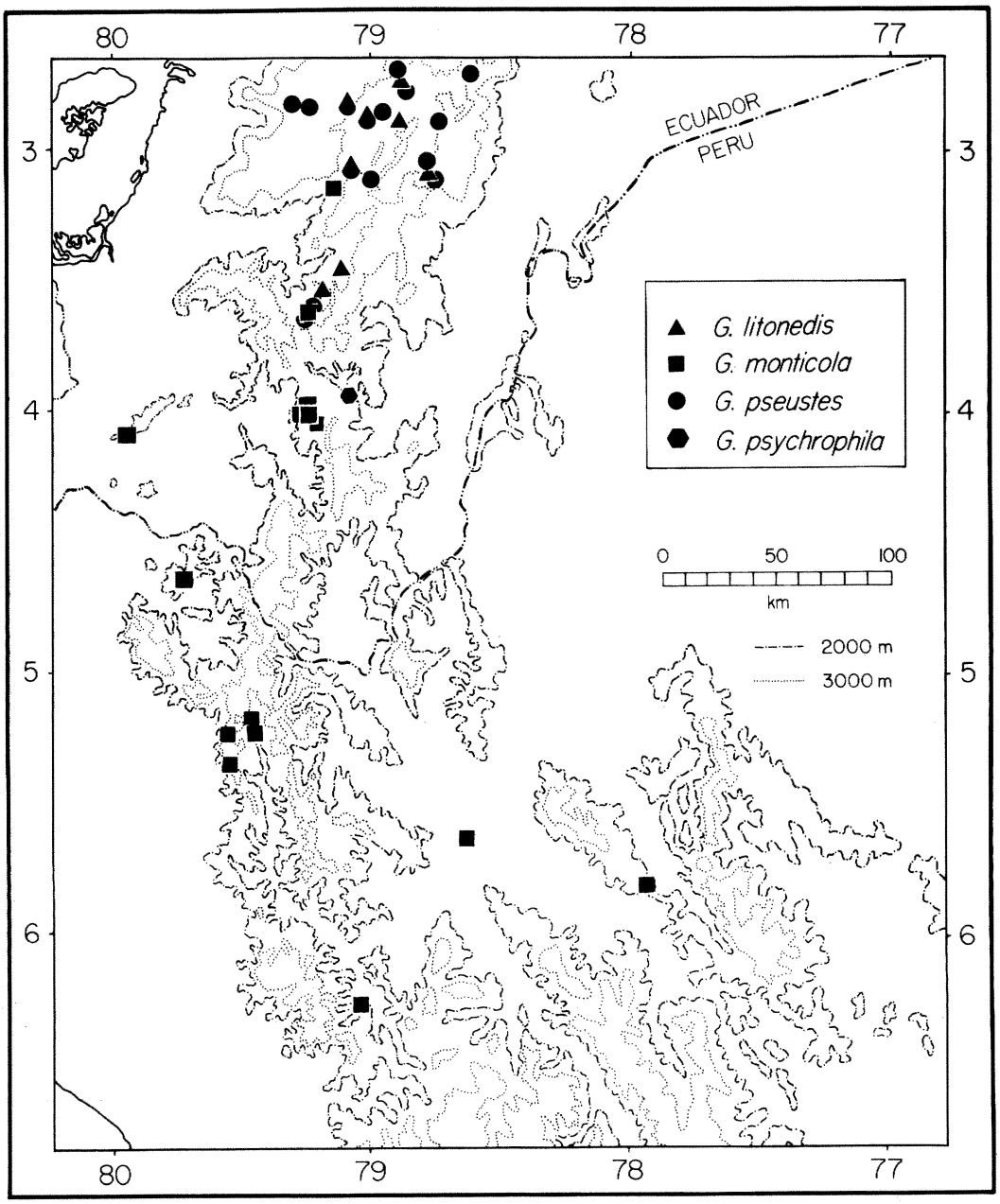

FIG. 8.—Map of southern Ecuador and northern Peru showing localities for species of *Gastrotheca*.

head length 17.4, interorbital distance 4.9, width of eyelid 4.1, diameter of eye 4.6, diameter of tympanum 2.5 mm.

Distribution.—*Gastrotheca espeletia* occurs at elevations of 2530–3400 m in the southern part of the Cordillera Central in Colombia and in the Nudo de Pasto in southern Colombia and northern Ecuador (Fig. 7).

Etymology.—The specific epithet, *espeletia*, is a noun in apposition referring to the composite *Espeletia* characteristic of the páramos inhabited by the frogs.

Gastrotheca ***litonedis*** sp. nov.
Figure 9

Holotype.—KU 202690, an adult female, from 10 km (by road) northeast of

FIG. 9.—Holotype of *Gastrotheca litonedis*, adult female, 62.4 mm SVL, KU 202690.

Girón, 2750 m (03°05′ S, 79°06′ W), Provincia Azuay, Ecuador, obtained on 7 March 1984 by William E. Duellman.

Diagnosis.—(1) SVL to 53 mm in males, 59 mm in females; (2) head width slightly greater than head length; (3) snout in dorsal view rounded, in profile bluntly rounded with nostrils at anterior margin of lower jaw; (4) interorbital distance 131% of width of eyelid; (5) eye 119% of eye–nostril distance; (6) tibia length 44% of SVL, about equal to foot length; (7) skin on dorsum areolate (50%), smooth (21%), granular (21%), or pustular (8%); (8) first finger about equal in length to second; (9) discs on fingers about twice width of digit; (10) webbing extending to penultimate tubercle on fourth toe, to distal tubercle on fifth toe; (11) pale labial stripe present (96%); (12) dark canthal stripe absent (96%); (13) tympanum brown in life; (14) dorsum of body uniform tan or green (38%) or with dark brown or green markings, usually (54%) with longitudinal paravertebral marks; shank uniform (46%) or marked with dark spots (42%) or bars (12%); (15) pale dorsolateral stripe absent (79%); (16) pale supra-anal stripe absent; (17) flanks uniform pale brown (68%) or with dark (25%) or light (8%) spots; (18) anterior and posterior surfaces of thighs uniform tan or gray (96%) or with spots (4%); (19) ventral surfaces uniform pale cream (96%) or with small flecks (4%); vocal sac pale gray; (20) tadpoles having the snout bluntly rounded in dorsal view, inclined from nostrils to tip in profile; throat convex in profile; eyes large, directed dorsolaterally; interorbital distance about one-fourth width of head; dorsal fin arising gradually from posterior edge of body; cloacal tube dextral; labial papillae in single row ventrally.

Gastrotheca litonedis is most like its sympatric congener, *G. pseustes*, from which it differs in having a wider head,

blunter snout, slightly more webbing on the feet, larger digital discs, and a uniformly pale venter. The tadpoles of *litonedis* have a single row of labial papillae ventrally and a dextral cloacal tube (two alternating rows of papillae and a median tube in *pseustes*). From its closest relatives (*G. monticola* and *psychrophila*), *G. litonedis* differs by having proportionately shorter hind limbs and usually pale flanks with dark spots, whereas the flanks are dark in the others (with pale spots in *G. monticola*). Also, *G. litonedis* differs from *G. monticola* by lacking a dark canthal stripe, pale supra-anal and dorsolateral stripes, and dark spots on the venter. From *G. psychrophila*, *G. litonedis* also differs by having the first finger about equal in length to the second (shorter than the second in *psychrophila*) and dark markings usually present on the dorsum.

Description of holotype.—An adult female having a SVL of 62.4 mm; body moderately robust; snout rounded in dorsal view, in lateral profile bluntly rounded; canthus rostralis angular; loreal region barely concave; lips rounded; top of head slightly concave; interorbital distance nearly twice width of eyelid; internarial area flat; nostrils barely protuberant, directed laterally at level of anterior margin of lower lip and at terminus of canthus rostralis; diameter of eye slightly less than distance from eye to nostril; tympanum vertically ovoid, separated from eye by distance slightly greater than length of tympanum; tympanic annulus distinct, smooth; supratympanic fold moderate, extending from posterior corner of eye to point above insertion of forelimb.

Arms moderately robust; axillary membrane absent; hands large; fingers unwebbed; discs small, round; diameter of discs equal to length of tympanum; relative length of fingers 1 = 2 < 4 < 3; subarticular tubercles moderately large, round; supernumerary tubercles few, small, present only on proximal segments of fingers; palmar tubercle not bifid; prepollical tubercle elongate, ovoid. Hind limbs moderately short, robust, 48.2% of SVL; foot length 47.1% of SVL; calcar, outer metatarsal tubercle, and outer tarsal fold absent; inner tarsal fold weak, present on distal half of tarsus; inner metatarsal tubercle large, flat, ovoid, not visible from above; toes long, bearing discs slightly smaller than those on fingers; relative length of toes 1 < 2 < 3 = 5 < 4; toes about one-third webbed; no web between first and second toes; webbing formula for other toes II 1½—3 III 2—3$^+$ IV 3—2$^-$ V; subarticular tubercles moderately small, round; supernumerary tubercles small, present only on proximal segments.

Skin on dorsum of head, body, and limbs, and on flanks smooth; eyelid tubercles absent; 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 V-shaped with anterior border at level of sacrum.

Vomerine odontophores slightly inclined posteromedially, narrowly separated medially, between small, round choanae, bearing 7-7 teeth. Tongue broadly ovoid, shallowly notched anteriorly, barely free posteriorly.

Color in preservative: Dorsum bluish gray; flanks and narrow canthal stripe dark brown; groin and anterior surfaces of thighs dark brown with cream flecks; posterior surfaces of thighs dark brown; margin of lip from point below eye to angle of jaw white; venter dull gray.

Color in life: Dorsum uniform green; flanks bronze-brown; axilla, groin, and hidden surfaces of thighs pale blue; throat greenish bronze; venter creamy gray; iris deep bronze with black reticulations.

Measurements: SVL 62.4, tibia length 30.1, foot length 29.4, head width 21.7, head length 20.5, interorbital distance 8.5, width of eyelid 4.6, diameter of eye 5.9, diameter of tympanum 4.2 mm.

Distribution.—This species is confined to intermontane basins in southern Ecuador (Fig. 8). It is widely distributed in the Cuenca Basin, where it occurs principally at elevations of 2500–2750 m in subpáramo and subhumid pastureland. It ascends the eastern slopes of the Cordillera Occidental to elevations of 3820 m, where it occurs in grassy páramo.

Etymology.—The specific name is de-

rived from the Greek *litos* meaning plain and the Greek *nedys* meaning belly; the name is applicable to this species that characteristically has an unmarked venter.

Gastrotheca monticola Barbour and Noble

Gastrotheca monticola Barbour and Noble, 1920:426.—Holotype: MCZ 5290 from Huancabamba, Departamento Piura, Peru.

Gastrotheca marsupiata lojana Parker, 1932:25.—Holotype: BMNH 1947.2. 31.13 from Loja, Provincia Loja, Ecuador. New synonym.

Diagnosis.—(1) SVL to 53 mm in males, 59 mm in females; (2) head width greater than head length; (3) snout in dorsal view rounded, in profile bluntly rounded with nostrils at level of anterior margin of lower jaw; (4) interorbital distance 173% of width of eyelid; (5) eye 105% of eye–nostril distance; (6) tibia length 51% of SVL, greater than foot length; (7) skin on dorsum areolate (95%) or smooth (5%); (8) first finger about equal in length to second; (9) discs on fingers twice width of digits; (10) webbing extending to penultimate tubercle (85%) or slightly beyond (15%) on fourth toe, and to distal tubercle (73%), between distal tubercle and disc (25%), or to disc (2%) on fifth toe; (11) pale labial stripe present (74%); (12) dark canthal stripe present (62%); (13) tympanum green or brown in life; (14) dorsum of body uniform green (29%) or with dark markings (blotches 48%, longitudinal paravertebral markings 36%, and/or middorsal dark mark 51%); shanks uniform green (40%) or with dark bars (60%); (15) pale dorsolateral stripe present (74%); (16) pale supra-anal stripe present (76%); (17) flanks dark brown or dark green with pale spots (71%); (18) anterior and posterior surfaces of thighs dull bluish gray with black spots (85%); (19) ventral surfaces of body and shanks pale cream with dark spots (96%); vocal sac dark gray; (20) tadpoles having the snout truncate in dorsal view, curved from nostrils to tip in profile; throat convex in profile; eyes large, directed dorsolaterally; interorbital distance about one-third width of head; dorsal fin arising gradually from posterior edge of body; cloacal tube sinistral; labial papillae in two alternating rows ventrally.

Gastrotheca monticola differs from the other species of *Gastrotheca* by its large size and broad head with a broad interorbital region; its green dorsum with pale dorsolateral and supra-anal stripes resembles the pattern of *plumbea*, a species having a uniformly pale venter, as contrasted with the usually spotted venter in *monticola*. The tadpoles of *monticola* differ from those of the other species by having a truncate snout in dorsal view.

Distribution.—*Gastrotheca monticola* is widely distributed in the Huancabamba Depression in northern Peru and extreme southern Ecuador, and in the Cordillera Occidental in southern Ecuador at elevations of 1000–3350 m (Fig. 8).

Remarks.—Heretofore, *G. lojana* has been recognized as a species distinct from *G. monticola* (e.g., Duellman, 1974; Duellman and Fritts, 1972). Moreover, Duellman (1972) referred all specimens from Saraguro, Ecuador, to *G. monticola*, whereas it now is evident that most of the specimens from Saraguro are *G. pseustes*. Series of specimens from Huancabamba (type locality of *G. monticola*), the mountains to the west of Huancabamba, and from Pomacochas in the Cordillera Oriental in Peru are indistinguishable morphometrically and in structural characters and coloration. In a discriminant functions analysis of morphometric data from these specimens (grouped as *G. monticola*) compared with data from specimens from the vicinity of Loja, Ecuador (type locality of *G. lojana*), the dispersion of *G. lojana* was completely incorporated within that of *G. monticola*. Furthermore, no consistent differences could be found in structural characters or coloration to distinguish the species.

Electrophoretic data are available only from the sample from Loja, but immunological data from specimens from Loja, Pomacochas, and Huancabamba reveal no differences between the populations (Linda R. Maxson, personal communication).

Because populations inhabiting the type localities of the two nominal taxa cannot be distinguished morphologically or immunologically, *Gastrotheca marsupiata lojana* Parker, 1932 is placed in the synonymy of *Gastrotheca monticola* Barbour and Noble, 1920.

Gastrotheca orophylax Duellman and Pyles

Gastrotheca orophylax Duellman and Pyles, 1980:5.—Holotype: KU 164243 from 11 km (by road) east-southeast of Papallacta, 2660 m, Provincia Napo, Ecuador.

Diagnosis.—(1) SVL to 59 mm in males, 74 mm in females; (2) head width greater than head length; (3) snout in dorsal view bluntly rounded, in profile truncate with nostrils at level of anterior margin of lower jaw; (4) interorbital distance nearly twice width of eyelid; (5) eye slightly smaller than eye–nostril distance; (6) tibia length 51% of SVL, longer than foot length; (7) skin on dorsum smooth (68%) or areolate (32%); (8) first finger shorter than second; (9) discs on fingers twice as wide as digits; (10) webbing extending to penultimate tubercle (89%) or slightly beyond on fourth toe, to distal tubercle (59%) or slightly beyond on fifth toe; (11) pale labial stripe absent; (12) dark canthal stripe absent; (13) tympanum bronze in life; (14) dorsum of body and limbs uniform green; (15) pale dorsolateral stripe absent; (16) pale supra-anal stripe absent; (17) flanks uniform green; (18) anterior and posterior surfaces of thighs uniform bluish green; (19) ventral surfaces pale creamy gray; vocal sac grayish green; (20) development direct.

Gastrotheca orophylax is unique in being a uniformly green frog except for a short bronze supratympanic stripe and bronze tympanum. In size and structure it is like *monticola* and *plumbea*, both of which commonly have pale dorsolateral, labial, and supra-anal stripes. Furthermore, most specimens of *monticola* have dark markings dorsally and black spots ventrally, and *plumbea* has dark brown flanks.

Distribution.—This species is known from elevations of 2620–2910 m in cloud forests on the Amazonian slopes of the Cordillera Oriental of the Andes in northern Ecuador and extreme southern Colombia.

Gastrotheca plumbea (Boulenger)

Nototrema plumbeum Boulenger, 1882: 417.—Holotype: BMNH 1947.2.31.19 from Intac, Provincia Imbabura, Ecuador.

Gastrotheca plumbeum.—Peters, 1955: 346.

Diagnosis.—(1) SVL to 61 mm in males, 73 mm in females; (2) head width slightly greater than head length; (3) snout in dorsal view bluntly rounded, in profile steeply inclined from nostrils (at level of anterior margin of lower jaw) to tip; (4) interorbital distance equal to or slightly greater than width of eyelid; (5) eye slightly larger than eye–nostril distance; (6) tibia length 49% of SVL, longer than foot length; (7) skin on dorsum smooth (64%) or areolate (36%); (8) first finger shorter than second; (9) discs on fingers twice width of digits; (10) webbing extending to penultimate tubercle on fourth toe, to distal tubercle (76%) or point between distal tubercle and disc (24%) on fifth toe; (11) pale labial stripe present (96%); (12) dark canthal stripe absent; (13) tympanum green or brown in life; (14) dorsum of body and limbs uniform green; (15) pale dorsolateral stripe present; (16) pale supra-anal stripe absent (70%); (17) flanks uniform brown; (18) anterior and posterior surfaces of thighs uniform dark brown; (19) ventral surfaces uniform cream; vocal sac pale gray; (20) development direct.

Gastrotheca plumbea has a pattern like that in some specimens of *pseustes*, but it differs from that species by having the first finger shorter than the second and by having larger digital discs. The presence of pale labial, dorsolateral, and supra-anal stripes separates *plumbea* from *orophylax*, and the uniformly pale venter distinguishes it from *monticola*, which usually has a spotted venter.

Distribution.—This species is restricted to cloud forests at elevations of 1300–2350 m on the Pacific slopes of the Cordillera Occidental in Ecuador.

Gastrotheca ***pseustes*** sp. nov.
Figure 10

Holotype.—KU 203443, an adult female, from 7.1 km by road north of San Lucas, 2940 m (03°41′ S, 79°15′ W), Provincia Loja, Ecuador, obtained on 8 March 1984 by William E. Duellman.

Diagnosis.—(1) SVL to 54 mm in males, 62 mm in females; (2) head width slightly greater than head length; (3) snout in dorsal view round, in profile inclined from nostrils (at level of anterior margin of lower jaw) to tip; (4) interorbital distance 118% of width of eyelid; (5) eye 133% of eye–nostril distance; (6) tibia length 44% of SVL, barely longer than foot length; (7) skin on dorsum granular (34%), areolate (33%), pustular (25%), or smooth (8%); (8) first finger equal in length to second; (9) discs on fingers small, slightly wider than digits; (10) webbing extending to a point between antepenultimate and penultimate tubercles (82%) or to penultimate tubercle (18%) on fourth toe, to distal tubercle on fifth toe; (11) pale labial stripe present (92%); (12) dark canthal stripe present (83%); (13) tympanum brown or green in life; (14) dorsum of body uniform green or tan (20%) or with dark green or brown markings (paravertebral longitudinal markings in 55% and middorsal mark in 4%); shanks uniform (28%) or marked with dark spots (27%) or bars (45%); (15) pale dorsolateral stripe absent (75%); (16) pale supra-anal stripe absent (82%); (17) flanks uniform tan or gray (37%), dark with pale spots (26%), or pale with dark spots (37%); (18) anterior and posterior surfaces of thighs uniform blue or bluish brown (68%) or with black spots (32%); (19) ventral surfaces uniform gray (40%) or gray with diffuse dark spots (60%); vocal sac pale gray with dark flecks; ventral surfaces of shanks uniform gray; (20) tadpole having the snout bluntly rounded in dorsal view, inclined from nostrils to bluntly rounded tip in profile; throat convex in profile; eyes large, directed dorsolaterally; interorbital distance slightly less than half width of head; dorsal fin arising gradually from posterior edge of body; cloacal tube median; labial papillae conical, in two alternating rows ventrally.

Gastrotheca pseustes is like *espeletia* and *riobambae* in having short limbs and small digital discs. It differs from *espeletia* in having the first and second fingers of equal length and by having a broader, more blunt snout. It differs from *riobambae* by having less webbing on the feet, a more truncate snout, and the absence of bold black spots or mottling on the ventral surface of the shank. Both *litonedis* and *plumbea* have color patterns like that exhibited by some specimens of *pseustes,* but both of these species have larger digital discs and uniformly pale venters, as contrasted with the usually diffusely gray spotted venter in *pseustes.* The presence of two alternating rows of labial papillae ventrally in tadpoles of *pseustes* distinguishes them from tadpoles of *espeletia* and *litonedis,* which have a single row, at least ventromedially. The tadpoles of *riobambae* differ by having the throat concave in profile. From its relatives (members of the *G. marsupiata* group), *G. pseustes* differs in being larger than any species except *G. peruana.* From that species, *G. pseustes* differs by having a round instead of an acuminate snout in dorsal view, more webbing on the feet, and in coloration. In *G. pseustes* the venter is gray with or without diffuse dark spots, and the posterior surfaces of the thighs are pale brown or blue with or without dark spots. In *G. peruana* the venter is creamy white, and the posterior surfaces of the thighs are brown with or without pale spots.

Description of holotype.—An adult female having a SVL of 55.2 mm; body moderately robust; snout rounded in dorsal view, in lateral profile inclined from nostrils to tip; canthus rostralis angular; loreal region slightly concave; lips rounded; top of head slightly concave; interorbital distance slightly greater than width of eyelid; internarial area flat; nostrils slightly protuberant, directed laterally at

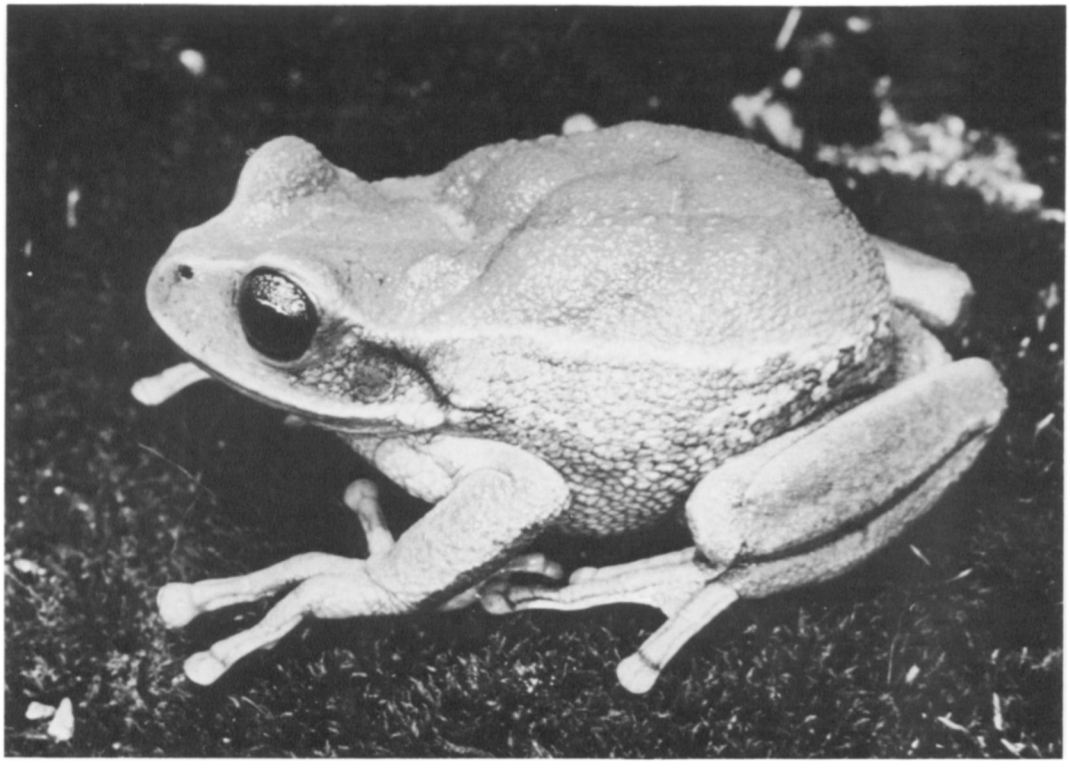

FIG. 10.—Holotype of *Gastrotheca pseustes*, adult female, 55.2 mm SVL, KU 103443.

level of anterior margin of lower jaw and at terminus of canthus rostralis; diameter of eye about equal to distance from eye to nostril; tympanum vertically ovoid, separated from eye by distance equal to length of tympanum; tympanic annulus distinct, smooth; supratympanic fold moderately heavy, extending from posterior corner of eye to point above insertion of arm.

Arms moderately robust; axillary membrane absent; hands large; fingers long, unwebbed; discs small, round; diameter of discs equal to length of tympanum; relative length of fingers 1 = 2 < 4 < 3; subarticular tubercles moderately small, round, none bifid; supernumerary tubercles few, small, round, present only on proximal segments of fingers; palmar tubercle bifid; prepollical tubercle elongate, flattened. Hind limbs moderately short, robust, 45.6% of SVL; foot length 45.7% of SVL; calcar absent; inner tarsal fold low, on distal third of tarsus; outer metatarsal tubercle small, subconical; inner metatarsal tubercle ovoid, flat, not visible from above; toes long, bearing discs slightly smaller than those on fingers; relative length of toes 1 < 2 < 3 = 5 < 4; toes about one-third webbed; webbing formula I 2^+—2^+ II 2—2^+ III 2^+—3^+ IV 3^+—2 V; subarticular tubercles small, round; supernumerary tubercles small, round, present only on proximal segments.

Skin on dorsum of head, body, and limbs granular; 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 transverse ridges, narrowly separated medially, between small round choanae, bearing 7-7

teeth. Tongue narrowly cordiform, shallowly notched anteriorly and posteriorly, barely free behind.

Color in preservative: Dorsum of head, body, forelimbs, shanks, feet, and distal parts of digits, and loreal region bluish gray. Labial stripe, supra-anal stripe, dorsal surfaces of proximal parts of hands, upper arms, and thighs creamy tan; creamy canthal stripe bordered below by narrow brown line extending from tip of snout through nostril and along outer edge of eyelid and continuous with dorsolateral line along supratympanic fold to groin; tympanum and anterior flanks brown; posterior flanks, groin, and anterior surfaces of thighs brown with cream flecks; posterior surfaces of thighs brown; venter uniform dull gray.

Color in life: Dorsum of head, body, forelimbs, shanks, and loreal region lime green; flanks, hidden surfaces of thighs, and canthal stripe brown; dorsal border of canthal stripe, dorsolateral stripe, supra-anal stripe, dorsal edges of shanks, and feet pale bronze; labial stripe and spots in groin and on anterior surfaces of thigh cream; venter creamy gray; iris dull bronze with black reticulations.

Measurements: SVL 55.2, tibia length 25.2, foot length 26.2, head width 19.5, head length 18.3, interorbital distance 6.5, width of eyelid 5.4, diameter of eye 5.9, diameter of tympanum 4.0 mm.

Distribution.—This species is widely distributed in the Cordillera Oriental and Cordillera Occidental south of the Equator to the high elevations north of the Loja Valley in southern Ecuador (Figs. 7, 8), where it occurs at elevations of 2200–4000 m. In the northern part of the range it seems to be confined to elevations above 3000 m, whereas in the south it ranges from 2200–3800 m.

Etymology.—The specific name *pseustes* is Greek meaning liar; the name is used in reference to the phenotypic similarity of this species to *G. riobambae*, with which it has been confused previously.

Gastrotheca psychrophila Duellman

Gastrotheca psychrophila Duellman, 1974:15.—Holotype: KU 120760 from ridge between Loja and Zamora, 2850 m, 13–14 km (by road) east of Loja, Provincia Loja, Ecuador.

Diagnosis.—(1) SVL to 50 mm in males, 63 mm in females; (2) head width greater than head length; (3) snout in dorsal view broadly rounded, in profile bluntly rounded, with nostrils at level posterior to anterior margin of lower jaw; (4) interorbital distance 171% of width of eyelid; (5) eye 97% of eye–nostril distance; (6) tibia length 50% of SVL, barely longer than foot length; (7) skin on dorsum areolate (71%) or smooth (29%); (8) first finger slightly shorter than second; (9) discs on fingers twice width of digits; (10) webbing extending to penultimate tubercle (86%) or only to point between antepenultimate and penultimate tubercles (14%) on fourth toe, to distal tubercle on fifth toe; (11) pale labial stripe present (71%); (12) dark canthal stripe absent; (13) tympanum dull brown or dark gray in life; (14) dorsum of body and limbs uniformly dark gray or greenish brown (86%), with dark spots (7%), or dark middorsal mark (7%); (15) pale dorsolateral stripe absent; (16) pale supra-anal stripe absent; (17) flanks uniformly dark gray or brown (86%), or with pale spots (14%); (18) anterior and posterior surfaces of thighs uniform dark bluish gray; (19) ventral surfaces uniform pale creamy gray; vocal sac dark gray; (20) tadpoles having the snout bluntly rounded in dorsal view, inclined from nostrils to round tip in profile; throat convex in profile; eyes small, directed dorsolaterally; interorbital distance greater than half width of head; dorsal fin arising abruptly from posterior edge of body; cloacal tube median; labial papillae in two alternating rows ventrally.

Gastrotheca psychrophila superficially resembles *ruizi*, which differs by having an acuminate snout, pale green paravertebral marks, and first and second fingers equal in length. The tadpoles of *psychrophila* differ from those of the other species (except *espeletia*) by having the dorsal fin arising abruptly from the body; the tadpoles of *espeletia* have only a single row of labial papillae ventromedially, whereas

there are two alternating rows in *psychrophila*.

Distribution.—This species is known from a limited area at an elevation of 2750–2850 m on a ridge, the Abra de Zamora, between Loja and Zamora, in the Cordillera Oriental in southern Ecuador (Fig. 8).

Gastrotheca riobambae (Fowler)

Hyla riobambae Fowler, 1913:157.—Holotype: ANSP 16161 from Riobamba, Provincia Chimborazo, Ecuador.

Hyla quitoe Fowler, 1913:159.—Holotype: ANSP 18238 from Quito, Provincia Pichincha, Ecuador. Synonymy fide Duellman and Fritts, 1972:11.

Chlorophilus olivaceus Andersson, 1945: 85.—Holotype: NHRM 1965 from "Río Napo, 400 m" (? = Baños, Provincia Tungurahua, Ecuador). Synonymy fide Duellman and Fritts, 1972:11.

Gastrotheca marsupiata ecuatoriensis Vellard, 1957:43 (nomen nudum). Synonymy fide Duellman and Fritts, 1972: 11.

Gastrotheca riobambae.—Duellman and Fritts, 1972:11.

Gastrotheca cavia Duellman, 1974:5.—Holotype: KU 148532 from Isla Pequeña, Laguna Cuicocha, 2890 m, Provincia Imbabura, Ecuador. New synonym.

Diagnosis.—(1) SVL to 57 mm in males, 66 mm in females; (2) head width slightly greater than head length; (3) snout in dorsal view round, in profile acutely rounded, protruding beyond jaw, with nostrils at level posterior to margin of lower jaw; (4) interorbital distance 120% of width of eyelid; (5) eye 120% of eye–nostril distance; (6) tibia length 41% of SVL, slightly less than foot length; (7) skin on dorsum areolate (50%), smooth (45%), or granular (5%); (8) first finger equal in length to second; (9) discs on fingers small, slightly wider than digits; (10) webbing extending to distal tubercle (55%), point midway between penultimate and distal tubercles (42%) or penultimate tubercle (3%), on fourth toe, to distal tubercle (95%) or between penultimate and distal tubercles (5%) on fifth toe; (11) pale labial stripe absent (88%); (12) dark canthal stripe present (88%); (13) tympanum brown or green in life; (14) dorsum of body uniform tan or green (19%) or with dark brown or green longitudinal paravertebral markings (81%); shanks uniform (3%) or with dark spots (98%); (15) pale dorsolateral stripe absent (73%); (16) pale supra-anal stripe present (62%); (17) flanks pale with dark spots (98%); (18) anterior surfaces of thighs pale tan or bluish tan with dark mottling; posterior surfaces uniform pale (37%) or with dark spots (63%); (19) ventral surfaces uniform cream (3%) or with dark spots, flecks, or mottling (97%); vocal sac gray; ventral surfaces of shanks cream with dark spots or mottling; (20) tadpoles having the snout round in dorsal view, bluntly rounded in profile; throat concave in profile; eyes large, directed dorsolaterally; interorbital distance about one-third width of head; dorsal fin arising gradually from posterior edge of body; cloacal tube median; labial papillae in two alternating rows ventrally.

Gastrotheca riobambae is like *espeletia* and *pseustes* in having short limbs and small digital discs. It differs from both in having more extensive webbing on the feet and by having bold, dark spots or mottling on the ventral surfaces of the shank. Furthermore, the snout is more rounded in *riobambae* than in *pseustes* and less protruding than in *espeletia*. The tadpoles of *riobambae* differ from those of the other species by having the throat concave in profile.

Distribution.—This species is widely distributed in the inter-Andean basins in central and northern Ecuador from the Riobamba Basin in the south to Otavalo and Ibarra in the north (Fig. 7). In these basins, it occurs at elevations of 2500–2900 m. From the Ambato Basin, it descends the valley of the Río Pastaza to a point below Baños at an elevation of 1590 m. South of Riobamba it occurs in a valley at an elevation of 3220 m, and at Machachi it is found at 3120 m; in the northern part of its range, it occurs at Laguna Cuicocha at an elevation of 3070 m.

Remarks.—Duellman (1974) recog-

nized specimens from the islands in Laguna Cuicocha as a distinct species, *G. cavia*. These frogs differ from other populations of *G. riobambae* in (1) average larger size, (2) presence of a pale labial stripe, (3) absence of a dark canthal stripe, and (4) groin and anterior surfaces of thighs blue with black spots. Furthermore, all frogs from this population have areolate dorsal skin, no anal stripe, and scattered dark flecks on the dorsum (absent in seven of 33 specimens); these characters are variable in other populations.

The morphological differences exhibited by specimens from the islands in Laguna Cuicocha possibly are indicative of incipient speciation. However, no allozymic differences exist between samples from Cuicocha and other populations referred to *G. riobambae* among the enzymatic products of the 29 loci examined, nor were allozymic differences found between specimens from the islands and the shore of the lake. In the absence of measurable allozymic differentiation of the population from Cuicocha, the nominal species *G. cavia* Duellman, 1974, is considered to be a junior synonym of *G. riobambae* (Fowler, 1913).

Gastrotheca ruizi Duellman and Burrowes

Gastrotheca ruizi Duellman and Burrowes, 1986:1.—Holotype: KU 200000 from Santiago, 2250 m, Municipio de Mocoa, Intendencia de Putumayo, Colombia.

Diagnosis.—(1) SVL to 65 mm in males and females; (2) head width about equal to head length; (3) snout in dorsal view acuminate, in profile inclined from nostrils (well behind anterior margin of lower jaw) to tip protruding well beyond margin of lower jaw; (4) interorbital distance 131% of width of eyelid; (5) eye 120% of eye–nostril distance; (6) tibia length 46% of SVL, barely less than foot length; (7) skin on dorsum smooth; (8) first finger equal in length to second; (9) discs on fingers twice width of digits; (10) webbing extending to penultimate tubercle on fourth toe, to point between distal tubercle and disc on fifth toe; (11) pale labial stripe absent (92%); (12) dark canthal stripe absent; (13) tympanum bronze in life; (14) dorsum of body dark green or brown with pale green paravertebral longitudinal marks; shanks uniform green or brown; (15) pale dorsolateral stripe absent (67%); (16) pale supra-anal stripe absent; (17) flanks uniform dark brown; (18) anterior and posterior surfaces of thighs uniform dark brown; (19) ventral surfaces uniform creamy gray (92%) or with dark spots (8%); (20) tadpoles having the snout round in dorsal view, inclined from nostrils to tip in profile; throat convex in profile; eyes large, directed dorsolaterally; interorbital distance less than one-third width of head; dorsal fin arising gradually from posterior edge of body; cloacal tube median; labial papillae in single row ventrally.

Gastrotheca ruizi is distinctive in having an acuminate, protruding snout and a dark dorsum with pale green longitudinal paravertebral marks. It is like *orophylax* in having a bronze tympanum, but otherwise *orophylax* is uniform green and has a truncate snout. Superficially, *ruizi* resembles *psychrophila*, which has a rounded snout and lacks paravertebral green marks. The tadpoles of *ruizi* differ from those of the other species by having a narrow interorbital region, inclined snout, and single row of labial papillae ventrally.

Distribution.—This species is known from only two localities at elevations of 2220 and 2250 m in the Valle de Sibundoy in the Cordillera Oriental in southern Colombia (Fig. 7).

Phylogeny

In attempting to reconstruct the phylogeny of the *Gastrotheca* in the high Andes of Ecuador and southern Colombia, we have relied primarily on allozymic data. Two species of the *Gastrotheca marsupiata* group from the Andes of Peru (*G. griswoldi* and *marsupiata*) were incorporated into the data set, and two species of the *Gastrotheca ovifera* group (*G. testudinea* and *weinlandii*) from lower montane forests were used as the outgroup.

Thirteen alleles were identified as primitive based on their presence in both

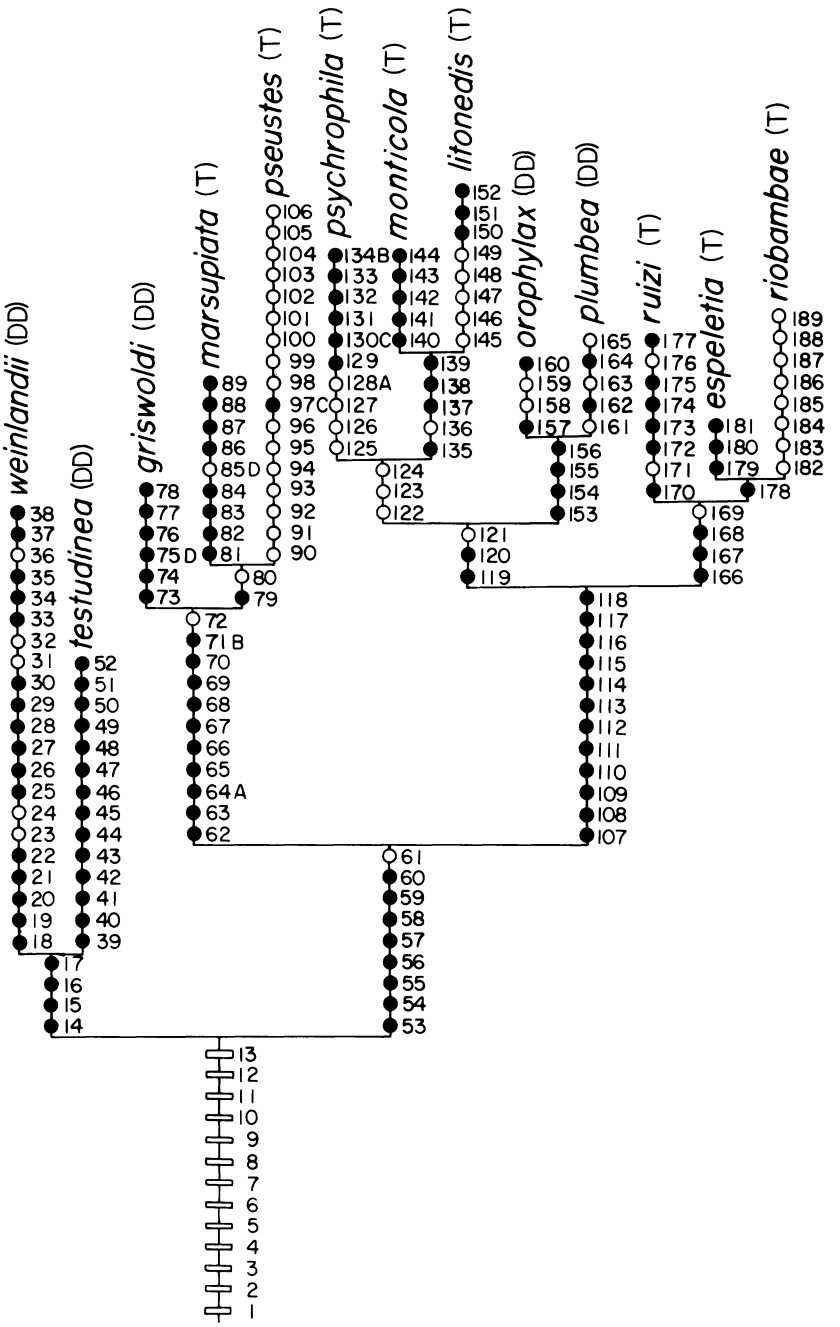

FIG. 11.—Cladogram of hypothesized phylogenetic relationships among 13 species of *Gastrotheca* based on allozymic data. Each of 189 allelic changes is numbered; these hypothesized transitions are listed in Appendix III. Rectangles denote alleles that are primitive for the entire group; open circles indicate the retention of the primitive allele in addition to the derived allele, and solid circles indicate the fixation of the derived allele. Four homoplasies are noted by letters A–D. Reproductive mode for each species is indicated by DD (= direct development) or T (= tadpoles).

the ingroup and outgroup (Fig. 11). Nine alleles support the monophyly of the ingroup. Two distinct clades of species in the ingroup correspond to the *G. marsupiata* group (Duellman and Fritts, 1972) and the *G. plumbea* group (Duellman, 1974). One of the previously undescribed species, *G. pseustes*, which has been universally confused with *G. riobambae* of the *G. plumbea* group, is clearly a member of the *G. marsupiata* group. This association was first suggested by immunological data presented by Scanlan et al. (1980). *Gastrotheca pseustes* is the only member of the *G. marsupiata* group that occurs in the Andes to the north of the Huancabamba Depression, which is the southern boundary of the *G. plumbea* group.

Only four homoplasies need to be postulated for the electrophoretic data (Fig. 11). Three of these (GPI^{f}, G-3-PD^{f}, and SDH^{d}) occur as convergences between the *G. marsupiata* group (specifically *G. pseustes*) and *G. psychrophila*. The congruence of these convergences by chance is unlikely; it is more probable that several alleles of *G. pseustes* were incorporated into the genome of *G. psychrophila* as a result of a past period of hybridization. At the present time, *G. psychrophila* occurs only in a restricted area in the Cordillera Oriental in southern Ecuador, whereas *G. pseustes* is widespread in the cordilleras and inter-Andean basins in southern Ecuador but does not occur sympatrically with *G. psychrophila*. The three convergent electromorphs present in *G. pseustes* and *G. psychrophila* suggest past sympatric interaction and hybridization between these two species, with the eventual extinction of the population of *G. pseustes* in that part of the Cordillera Oriental inhabited by *G. psychrophila*.

The fourth homoplasy (GOT-2^{f}) is interpreted as a convergence in *G. griswoldi* and *marsupiata*.

A phylogenetic analysis of the allozymic data (Fig. 11) provides a strongly supported phylogeny of northern Andean *Gastrotheca*. Within the *G. plumbea* group, there is a primary dichotomy between the species of southern Colombia and northern Ecuador (*G. espeletia, riobambae*, and *ruizi*) and those of southern Ecuador and the cloud forests on the Andean slopes (*G. litonedis, monticola, orophylax, plumbea*, and *psychrophila*). Within the last group, the two species inhabiting cloud forests (*G. orophylax* and *plumbea*) form a subgroup distinct from the remaining three taxa. The close phylogenetic relationships of these two species indicated by allozymic data are supported by their morphological similarities and mode of life history—direct development of eggs into froglets.

The morphological data on adults and tadpoles do not refute the proposed phylogeny, nor do they lend support. Most of the morphological characters are highly variable (e.g., morphometrics) and/or of unknown polarity (e.g., coloration). The position of *G. ruizi* on the cladogram is supported by its morphological similarities with *G. espeletia* and *riobambae*, and its cranial ridges and acuminate snout are derived autapomorphies. On the other hand, the similarities in morphology and coloration of *G. riobambae* and *pseustes* belie their relationships as indicated by allozymic and immunological data.

Frogs of the genus *Gastrotheca* carry eggs in a dorsal pouch; in some species in the *G. marsupiata* and *G. plumbea* groups, the eggs hatch as tadpoles which complete their development in ponds, whereas in other species of these groups and in all species in the groups inhabiting the lowlands and lower montane forests, the eggs undergo direct development into froglet in the pouch. The only members of the *G. plumbea* group that exhibit direct development are *G. orophylax* and *G. plumbea*. These two species form a subgroup within the southern Ecuadorian group of species (Fig. 11).

Assuming that our phylogenetic arrangement based on allozymic data is correct, direct development is characteristic of all members of the outgroup and of only some members of the ingroup. As noted by Wassersug and Duellman (1984), who reviewed the oral features of *Gastrotheca* tadpoles and embryos, the generally accepted trend in anuran development is

from aquatic tadpoles to direct development. However, this trend seems to be contradicted in *Gastrotheca*. Direct development is characteristic of all species groups of *Gastrotheca* in the lowlands and lower montane forests, as well as the related genera *Cryptobatrachus*, *Stefania*, and *Hemiphractus*. Tadpole production through developmental arrest may have occurred in the lineage giving rise to the Andean *Gastrotheca*. If this is correct, reversals to direct development must be postulated in the lineage that gave rise to *G. orophylax* and *G. plumbea* and in the lineage (if indeed there is only one) to the various species in the *G. marsupiata* group that have direct development (Fig. 11).

Resumen

Ocho especies pertenecientes al género *Gastrotheca* se hallaban identificados en los Andes de Ecuador y en el extremo sur de Colombia. *Gastrotheca cavia, lojana, monticola, psychrophila, riobambae,* y *ruizi* se caracterizan por poseer huevos que eclosionan en estadios larvarios, mientras que *G. orophylax* y *plumbea* poseen huevos con desarrollo directo, en el cual todas las etapas larvarias ocurren dentro del huevo y en el momento de eclosión nacen individuos totalamente metamorfoseados.

Productos enzimáticos correspondientes a 29 loci fueron examinados electroforéticamente. Un total de 185 electromorfos fueron identificados para las especies de *Gastrotheca* de los Andes de Ecuador, y para 4 especies habitantes de otras regiones, *G. griswoldi* y *marsupiata* de los Andes del Peru y *G. testudinea* y *weinlandii* del bosque húmedo de premontaña en Ecuador.

El resultado del análisis electroforético fue complementado con análisis morfométricos (16 medidas tomadas en 556 especímenes), de caracteres estructurales (forma de rostro, textura de la piel, desarrollo de membranes palmares) y de coloración. Estos análisis revelaron la existencia de tres nuevas especies entre las muestras previamente identificados como *G. riobambae*. Las nuevas especies son: *G. espeletia* habitante de los páramos del sur de Colombia y norte de Ecuador, *G. litonedis* de la Hoya de Cuenca en Ecuador, y *G. pseustes* de las cordilleras andinas desde latitudes al sur de la línea ecuatorial hasta la Hoya de Loja. La distribución de *G. riobambae* se halla restricta a las hoyas interandinas desde el Río Chonta hacia el sur hasta la Hoya de Riobamba a alturas no mayores de 3000 m.

Gastrotheca marsupiata lojana Parker, 1932 es ubicada en la sinonímia de *G. monticola* Barbour y Noble, 1920, y *G. cavia* Duellman, 1974 pasa a la sinonímia de *G. riobambae* (Fowler, 1913).

La reconstrucción filogenética basada en electromorfos sinapomórficos muestra a *G. pseustes* agrupada con *G. griswoldi* y *marsupiata*, especies de los Andes del Peru. Entre todas las otras especies de los Andes de Ecuador, dos especies poseen desarrollo directo (*G. orophylax* y *plumbea*), y sus electromorfos las indican cercanamente relacionadas con *G. litonedis, monticola,* y *psychrophila* del sur de Ecuador; estas cinco especies se hallan relacionadas a *G. espeletia, riobambae,* y *ruizi* del norte de Ecuador y Colombia.

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Appendix I

Specimens of *Gastrotheca* examined electrophoretically. All specimens are in the Museum of Natural History, University of Kansas (KU) and are from Ecuador unless noted otherwise.

Gastrotheca espeletia.—Carchi: 30 km SW Tulcán, 3140 m, 203542. Napo: Río Chingual, 3.9 km W Santa Bárbara, 2360 m, 203439–40.

Gastrotheca griswoldi.—PERU: Junín: 27 km S Junín, 4060 m, 204001–02.

Gastrotheca litonedis.—Azuay: Cuenca, 2600 m, 203442; 10 km NW Girón, 2750 m, 202690; Laguna de Zurucuchu, 16 km NW Cuenca, 3200 m, 203441; 12.9 km SW La Paz, 2720 m, 203545 (2 tadpoles). Loja: 16.8 km NNE Urdaneta, 2910 m, 203546 (2 tadpoles).

Gastrotheca marsupiata.—PERU: Cuzco: San Jerónimo, 3150 m, 204007–08.

Gastrotheca monticola.—Loja: 5.2 km W Loja, 2310 m, 202688, 203547 (tadpoles).

Gastrotheca orophylax.—Napo: 1 km E Santa Bárbara, 2520 m, 202693–94.

Gastrotheca plumbea.—Cotopaxi: Pilaló, 2320 m, 202695–99.

Gastrotheca pseustes.—Azuay: Cuenca, 2600 m, 203465; 34.1 km NW Cuenca, 3820 m, 203550 (2 tadpoles); 42.8 km NW Cuenca, 3820 m, 203469; 11.5 km SE Gualaceo, 2940 m, 203459; 10 km NW Girón, 2750 m, 202691–92; Laguna de Zurucuchu, 16 km NW Cuenca, 3200 m, 203461–64; 5.7 km SW La Paz, 3000 m, 203549 (2 tadpoles); 2 km SSE Palmas, 2340 m, 203470–73. Cañar: 3 km S Cañar, 3450 m, 203474–76; Ingapirca, 3140 m, 203477–80; 4 km N Zhud, 3040 m, 203537–39 (now skeletons). Chimborazo: 4.7 km NE Tixán, 3150 m, 203558 (2 tadpoles). Cotopaxi: 3.5 km W Mulaló, 2730 m, 203534–36; 14 km NW Pujilí, 3350 m, 203483; 15.6 km NW Pulijí, 3450 m, 203484–91. Loja: 7.1 km N San Lucas, 2940 m, 203443; 3.7 km S Saraguro, 2800 m, 203444–48, 203457–58. Napo: 29.5 km E San Miguel de Salcedo, 3610 m, 203501; 38.3 km E San Miguel de Salcedo, 3530 m, 203502; 43.4 km E San Miguel de Salcedo, 3390 m, 203559 (2 tadpoles); east slope Paso de Guamaní, 3720 m, 203564 (2 tadpoles). Pichincha: 1.8 km SSE San Juan, 3420 m, 203565 (2 tadpoles).

Gastrotheca psychrophila.—Loja, Abra de Zamora, 15 km E Loja, 2800 m, 203596–99.

Gastrotheca riobambae.—Chimborazo: Cunuc-Pogyo, 2.2 km NE Cajambamba, 3220 m, 203519–23; 3.1 km N Riobamba, 203515; 6.7 km E Riobamba, 2550 m, 203516–18. Cotopaxi: 7 km N Latacunga, 2800 m, 204033–34. Imbabura: Laguna Cuicocha, Isla Grande, 3070 m, 202680–83; Laguna Cuicocha, south shore, 3070 m, 202684–85. Pichincha: Santa Clara, 2900 m, 203503–07. Tungurahua: 1.1 km SW Pelileo, 2520 m, 203527–29.

Gastrotheca ruizi.—COLOMBIA: Putumayo: Santiago, 2250 m, 200003–05, 200303.

Gastrotheca testudinea.—Morona-Santiago: 18.6 km WSW Plan de Milagro, 2275 m, 202701.

Gastrotheca weinlandii.—Morona-Santiago: 8.8 km WSW Plan de Milagro, 2370 m, 202702.

APPENDIX II

Frequencies of electromorphs observed among 14 nominal taxa of *Gastrotheca*.

Locus	Allele	*G. espeletia*	*G. riobambae*	*G. cavia*	*G. ruizi*	*G. orophylax*	*G. plumbea*	*G. psychrophila*	*G. monticola*	*G. litonedis*	*G. pseustes*	*G. marsupiata*	*G. griswoldi*	*G. weinlandii*	*G. testudinea*
ACP-1	a	—	0.13	—	—	—	—	—	—	—	—	—	—	—	—
	b	1.0	0.87	1.0	1.0	1.0	1.0	1.0	1.0	1.0	—	—	—	—	—
	c	—	—	—	—	—	—	—	—	—	—	—	—	1.0	1.0
	d	—	—	—	—	—	—	—	—	—	0.07	—	—	—	—
	e	—	—	—	—	—	—	—	—	—	0.93	1.0	1.0	—	—
ACP-2	a	—	—	—	—	—	—	—	1.0	1.0	—	—	—	—	—
	b	1.0	1.0	1.0	1.0	1.0	1.0	1.0	—	—	—	—	—	—	—
	c	—	—	—	—	—	—	—	—	—	1.0	—	1.0	—	1.0
	d	—	—	—	—	—	—	—	—	—	—	1.0	—	—	—
	e	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
ACP-3	a	—	—	—	—	—	—	—	—	0.07	—	—	—	—	—
	b	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.93	—	—	—	—	—
	c	—	—	—	—	—	—	—	—	—	1.0	1.0	1.0	1.0	1.0
ADA	a	—	—	—	—	—	—	0.12	—	—	—	—	—	—	—
	b	—	—	—	—	—	—	—	—	—	0.05	—	—	—	—
	c	—	—	—	—	—	—	0.63	—	—	—	—	—	—	—
	d	—	—	—	—	—	—	—	—	—	0.82	1.0	—	—	—
	e	1.0	0.97	1.0	1.0	1.0	1.0	0.25	1.0	0.93	—	—	—	—	—
	f	—	0.03	—	—	—	—	—	—	—	—	—	—	—	—
	g	—	—	—	—	—	—	—	—	—	—	—	—	1.0	1.0
	h	—	—	—	—	—	—	—	—	—	0.13	—	—	—	—
	i	—	—	—	—	—	—	—	—	0.07	—	—	—	—	—
	j	—	—	—	—	—	—	—	—	—	—	—	1.0	—	—

APPENDIX II
Continued.

Locus	Allele	*G. espeletia*	*G. riobambae*	*G. cavia*	*G. ruizi*	*G. orophylax*	*G. plumbea*	*G. psychrophila*	*G. monticola*	*G. litonedis*	*G. pseustes*	*G. marsupiata*	*G. griswoldi*	*G. weinlandii*	*G. testudinea*
ADH	a	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
	b	1.0	1.0	0.83	—	1.0	1.0	—	—	0.21	—	—	—	—	—
	c	—	—	—	1.0	—	—	—	—	—	—	—	—	—	—
	d	—	—	—	—	—	—	—	—	—	0.98	1.0	1.0	—	—
	e	—	—	—	—	—	—	—	—	—	0.02	—	—	—	—
	f	—	—	0.17	—	—	—	—	—	—	—	—	—	—	—
	g	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
	h	—	—	—	—	—	—	1.0	1.0	0.79	—	—	—	—	—
CAT	a	—	—	—	—	—	—	—	—	—	—	1.0	—	—	—
	b	—	—	—	—	—	—	—	—	—	—	—	1.0	—	—
	c	—	—	—	—	1.0	1.0	—	—	—	—	—	—	—	—
	d	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—
	e	—	1.0	1.0	0.50	—	—	1.0	—	1.0	1.0	—	—	—	—
	f	—	—	—	—	—	—	—	1.0	—	—	—	—	—	—
	g	—	—	—	0.50	—	—	—	—	—	—	—	—	—	—
	h	—	—	—	—	—	—	—	—	—	—	—	—	1.0	1.0
FUM	a	—	—	—	—	1.0	1.0	1.0	1.0	1.0	—	—	—	—	—
	b	1.0	1.0	1.0	1.0	—	—	—	—	—	1.0	1.0	1.0	—	—
	c	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
	d	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
G-6-PD	a	—	—	—	—	—	0.38	—	—	—	—	—	—	—	—
	b	1.0	1.0	1.0	1.0	—	—	—	—	—	—	—	—	—	—
	c	—	—	—	—	1.0	0.62	1.0	1.0	1.0	1.0	—	1.0	1.0	1.0
	d	—	—	—	—	—	—	—	—	—	—	1.0	—	—	—
GPI	a	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
	b	—	—	—	—	—	—	0.62	—	—	—	—	—	—	—
	c	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
	d	1.0	1.0	1.0	1.0	1.0	1.0	—	—	1.0	—	—	—	—	—
	e	—	—	—	—	—	—	—	—	—	0.01	—	—	—	—
	f	—	—	—	—	—	—	0.38	—	—	0.99	1.0	1.0	—	—
	g	—	—	—	—	—	—	—	1.0	—	—	—	—	—	—
β-GUR	a	—	—	—	—	—	—	1.0	—	—	—	—	—	—	—
	b	—	—	—	—	—	—	—	—	—	1.0	1.0	1.0	—	—
	c	1.0	1.0	1.0	1.0	1.0	1.0	—	1.0	1.0	—	—	—	1.0	1.0
GOT-1	a	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
	b	—	1.0	1.0	—	1.0	1.0	1.0	1.0	0.14	1.0	—	1.0	—	1.0
	c	—	—	—	—	—	—	—	—	0.86	—	—	—	—	—
	d	—	—	—	—	—	—	—	—	—	—	1.0	—	—	—
	e	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—
	f	—	—	—	1.0	—	—	—	—	—	—	—	—	—	—
GOT-2	a	—	—	—	—	—	—	—	—	—	—	—	—	1.0	1.0
	b	—	—	—	—	—	—	—	—	—	0.02	—	—	—	—
	c	—	—	—	—	1.0	1.0	—	—	—	—	—	—	—	—
	d	—	—	—	—	—	—	—	—	—	0.15	—	—	—	—
	e	—	—	—	—	—	—	0.38	1.0	1.0	—	—	—	—	—
	f	—	—	—	—	—	—	—	—	—	—	0.75	1.0	—	—
	g	1.0	1.0	1.0	1.0	—	—	0.62	—	—	0.83	0.25	—	—	—
G-3-PD	a	—	—	—	—	—	—	—	1.0	0.57	—	—	—	—	—
	b	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
	c	—	—	—	—	—	—	—	—	—	—	—	—	0.50	—
	d	—	—	—	1.0	—	—	—	—	—	—	—	—	—	—
	e	1.0	1.0	1.0	—	1.0	1.0	—	—	0.43	—	1.0	1.0	—	—
	f	—	—	—	—	—	—	1.0	—	—	1.0	—	—	—	—
	g	—	—	—	—	—	—	—	—	—	—	—	—	0.50	—

APPENDIX II
Continued.

Locus	Allele	*G. espeletia*	*G. riobambae*	*G. cavia*	*G. ruizi*	*G. orophylax*	*G. plumbea*	*G. psychrophila*	*G. monticola*	*G. litonedis*	*G. pseustes*	*G. marsupiata*	*G. griswoldi*	*G. weinlandii*	*G. testudinea*
α-GPD	a	—	—	—	—	—	—	—	—	—	0.93	1.0	1.0	1.0	—
	b	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
	c	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	—	—	—	—	—
	d	—	—	—	—	—	—	—	—	—	0.07	—	—	—	—
HDH	a	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
	b	—	—	—	—	—	—	—	—	—	1.0	1.0	1.0	—	—
	c	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	—	—	—	—	—
	d	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
IDH	a	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
	b	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	—	—	—	—	—
	c	—	—	—	—	—	—	—	—	—	1.0	1.0	1.0	—	1.0
LDH-1	a	—	—	—	—	—	—	1.0	—	—	—	—	—	—	—
	b	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
	c	—	—	—	—	—	—	—	—	—	1.0	—	1.0	—	—
	d	—	0.03	—	—	—	—	—	—	—	—	—	—	—	—
	e	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
	f	—	—	—	—	—	—	—	—	—	—	1.0	—	—	—
	g	1.0	0.97	1.0	1.0	1.0	1.0	—	1.0	1.0	—	—	—	—	—
LDH-2	a	—	—	—	—	1.0	1.0	—	—	—	—	—	—	—	—
	b	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
	c	—	—	—	—	—	—	—	—	—	—	1.0	—	—	—
	d	—	—	—	1.0	—	—	—	—	—	—	—	—	—	—
	e	—	—	—	—	—	—	—	—	—	—	—	1.0	—	—
	f	1.0	1.0	1.0	—	—	—	1.0	—	—	1.0	—	—	—	1.0
	g	—	—	—	—	—	—	—	1.0	1.0	—	—	—	—	—
MDH-1	a	—	—	—	—	—	1.0	1.0	1.0	1.0	0.76	1.0	1.0	—	—
	b	—	—	—	—	1.0	—	—	—	—	—	—	—	—	—
	c	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—
	d	—	0.92	1.0	1.0	—	—	—	—	—	—	—	—	—	—
	e	—	—	—	—	—	—	—	—	—	0.24	—	—	—	—
	f	—	0.08	—	—	—	—	—	—	—	—	—	—	—	—
	g	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
	h	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
MDH-2	a	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
	b	—	—	—	—	1.0	1.0	1.0	—	—	1.0	1.0	1.0	—	—
	c	1.0	1.0	1.0	1.0	—	—	—	—	—	—	—	—	—	—
	d	—	—	—	—	—	—	—	1.0	1.0	—	—	—	—	—
	e	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
MPI	a	1.0	0.82	0.83	—	—	—	—	—	—	—	—	—	—	—
	b	—	—	—	—	—	—	—	—	—	—	—	—	0.50	—
	c	—	—	—	—	—	—	—	—	—	—	—	—	0.50	—
	d	—	—	—	—	0.75	—	—	—	—	—	—	—	—	—
	e	—	—	—	—	0.25	—	—	—	—	—	—	—	—	—
	f	—	—	—	—	—	—	—	—	—	0.17	—	—	—	—
	g	—	—	—	—	—	—	—	—	—	0.13	—	—	—	—
	h	—	—	—	—	—	—	—	1.0	—	—	—	—	—	—
	i	—	—	—	—	—	—	—	—	—	0.04	—	—	—	—
	j	—	—	—	—	—	—	—	—	0.07	—	—	—	—	—
	k	—	—	—	—	—	—	1.0	—	—	—	—	—	—	—
	l	—	—	—	1.0	—	—	—	—	—	—	—	—	—	—
	m	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
	n	—	—	—	—	—	—	—	—	—	0.65	1.0	1.0	—	—
	o	—	—	—	—	—	1.0	—	—	—	—	—	—	—	—
	p	—	0.18	0.17	—	—	—	—	—	—	—	—	—	—	—

APPENDIX II
Continued.

Locus	Allele	*G. espeletia*	*G. riobambae*	*G. cavia*	*G. ruizi*	*G. orophylax*	*G. plumbea*	*G. psychrophila*	*G. monticola*	*G. litonedis*	*G. pseustes*	*G. marsupiata*	*G. griswoldi*	*G. weinlandii*	*G. testudinea*
	q	—	—	—	—	—	—	—	—	0.93	—	—	—	—	—
	r	—	—	—	—	—	—	—	—	—	0.01	—	—	—	—
α-MAN	a	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
	b	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
	c	—	—	—	—	—	—	—	—	1.0	—	—	—	—	—
	d	1.0	0.97	1.0	1.0	—	—	1.0	1.0	—	0.97	—	—	—	—
	e	—	—	—	—	1.0	1.0	—	—	—	—	—	—	—	—
	f	—	0.03	—	—	—	—	—	—	—	—	—	—	—	—
	g	—	—	—	—	—	—	—	—	—	0.03	1.0	—	—	—
	h	—	—	—	—	—	—	—	—	—	—	—	1.0	—	—
6-PGD	a	—	—	—	—	—	0.60	—	—	—	—	—	—	—	—
	b	1.0	1.0	1.0	1.0	—	—	—	—	—	—	—	—	1.0	1.0
	c	—	—	—	—	1.0	0.40	1.0	—	1.0	—	—	—	—	—
	d	—	—	—	—	—	—	—	—	—	0.98	1.0	1.0	—	—
	e	—	—	—	—	—	—	—	1.0	—	—	—	—	—	—
	f	—	—	—	—	—	—	—	—	—	0.02	—	—	—	—
PGM	a	—	0.03	—	—	—	—	—	—	—	—	—	—	1.0	1.0
	b	—	—	—	—	—	—	—	—	—	0.38	—	1.0	—	—
	c	—	—	—	—	—	—	—	—	—	—	1.0	—	—	—
	d	1.0	0.89	1.0	0.62	—	—	—	—	—	—	—	—	—	—
	e	—	—	—	—	1.0	—	—	—	—	—	—	—	—	—
	f	—	—	—	—	—	—	1.0	—	—	—	—	—	—	—
	g	—	—	—	—	—	—	—	—	—	0.62	—	—	—	—
	h	—	0.08	—	—	—	—	—	—	—	—	—	—	—	—
	i	—	—	—	—	—	—	—	1.0	1.0	—	—	—	—	—
	j	—	—	—	—	—	1.0	—	—	—	—	—	—	—	—
	k	—	—	—	0.38	—	—	—	—	—	—	—	—	—	—
SDH	a	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
	b	—	—	—	—	—	—	—	—	—	0.01	—	—	—	—
	c	1.0	1.0	1.0	1.0	1.0	1.0	—	1.0	1.0	—	—	—	—	—
	d	—	—	—	—	—	—	1.0	—	—	0.99	1.0	1.0	—	—
	e	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
SOD-1	a	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	—	1.0	1.0	1.0	—	—
	b	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
	c	—	—	—	—	—	—	—	—	1.0	—	—	—	—	—
	d	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
SOD-2	a	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
	b	—	—	—	—	—	—	—	—	—	—	—	1.0	—	—
	c	—	—	—	—	—	—	—	—	—	0.04	—	—	0.50	—
	d	—	—	—	—	—	—	0.75	1.0	—	—	—	—	—	—
	e	—	—	—	—	—	—	—	—	—	—	—	—	0.50	—
	f	—	—	—	—	—	0.60	—	—	—	—	—	—	—	—
	g	—	—	—	—	—	—	—	—	1.0	—	—	—	—	—
	h	—	—	—	—	—	—	—	—	—	—	1.0	—	—	—
	i	1.0	1.0	1.0	1.0	1.0	0.40	0.25	—	—	0.96	—	—	—	—
TPI	a	1.0	1.0	1.0	1.0	1.0	1.0	1.0	—	1.0	1.0	1.0	1.0	—	1.0
	b	—	—	—	—	—	—	—	1.0	—	—	—	—	—	—
	c	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
XDH	a	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
	b	—	—	—	—	—	—	—	—	—	0.78	1.0	1.0	—	—
	c	—	—	—	—	—	—	—	—	—	0.22	—	—	—	1.0
	d	—	—	—	1.0	—	—	—	—	—	—	—	—	—	—
	e	—	—	—	—	1.0	1.0	0.62	1.0	0.29	—	—	—	—	—
	f	1.0	1.0	1.0	—	—	—	0.38	—	0.71	—	—	—	—	—

APPENDIX III

Allelic symplesiomorphies (1–13) and synapomorphies (14–189) of *Gastrotheca*. Numbers correspond to those in Fig. 11. Hypothesized transitions are shown for synapomorphies (e.g., ACP-2^{c-b} indicates a change from plesiomorphic allele c to apomorphic allele b at locus ACP-2). Undetermined plesiomorphic alleles are indicated by x.

1. ACP-2^{c}; 2. ACP-3^{c}; 3. G-6-PD^{c}; 4. β-GUR^{c}; 5. GOT-1^{b}; 6. α-GPD^{a}; 7. IDH^{c}; 8. LDH-2^{f}; 9. 6-PGD^{b}; 10. PGM^{a}; 11. SOD-2^{c}; 12. TPI^{a}; 13. XDH^{c}; 14. ACP-1^{x-c}; 15. ADA^{x-g}; 16. CAT^{x-h}; 17. GOT-2^{x-a}; 18. ACP-2^{c-e}; 19. ADH^{x-a}; 20. FUM^{x-d}; 21. GPI^{x-c}; 22. GOT-1^{b-a}; 23. G-3-PD^{x-c}; 24. G-3-PD^{x-g}; 25. HDH^{x-d}; 26. IDH^{c-a}; 27. LDH-1^{x-b}; 28. LDH-2^{f-b}; 29. MDH-1^{x-g}; 30. MDH-2^{x-e}; 31. MPI^{x-b}; 32. MPI^{x-c}; 33. α-MAN^{x-a}; 34. SDH^{x-e}; 35. SOD-1^{x-d}; 36. SOD-2^{c-e}; 37. TPI^{a-c}; 38. XDH^{c-a}; 39. ADH^{x-g}; 40. FUM^{x-c}; 41. GPI^{x-a}; 42. G-3-PD^{x-b}; 43. α-GPD^{a-b}; 44. HDH^{x-a}; 45. LDH-1^{x-e}; 46. MDH-1^{x-h}; 47. MDH-2^{x-a}; 48. MPI^{x-m}; 49. α-MAN^{x-b}; 50. SDH^{x-a}; 51. SOD-1^{x-b}; 52. SOD-2^{c-a}; 53. CAT^{x-e}; 54. FUM^{x-b}; 55. GOT-2^{x-g}; 56. G-3-Pd^{x-e}; 57. MDH-1^{x-a}; 58. MDH-2^{x-b}; 59. α-MAN^{x-d}; 60. SOD-1^{x-a}; 61. SOD-2^{c-i}; 62. ACP-1^{x-e}; 63. ADH^{x-d}; 64. GPI^{x-f} (see 128); 65. β-GUR^{c-b}; 66. HDH^{x-b}; 67. LDH-1^{x-c}; 68. MPI^{x-n}; 69. 6-PGD^{b-d}; 70. PGM^{a-b}; 71. SDH^{x-d} (see 134); 72. XDH^{c-b}; 73. ADA^{x-j}; 74. CAT^{e-b}; 75. GOT-2^{g-f} (see 85); 76. LDH-2^{f-e}; 77. α-MAN^{d-h}; 78. SOD-2^{i-b}; 79. ADA^{x-d}; 80. α-MAN^{d-g}; 81. ACP-2^{c-d}; 82. CAT^{c-a}; 83. G-6-PD^{c-d}; 84. GOT-1^{b-d}; 85. GOT-2^{g-f} (see 75); 86. LDH-1^{c-f}; 87. LDH-2^{f-c}; 88. PGM^{b-c}; 89. SOD-2^{i-h}; 90. ACP-1^{e-d}; 91. ADA^{d-b}; 92. ADA^{d-h}; 93. ADH^{d-e}; 94. GPI^{f-e}; 95. GOT-2^{g-b}; 96. GOT-2^{g-d}; 97. G-3-PD^{e-f} (see 130); 98. α-GPD^{a-d}; 99. MDH-1^{a-e}; 100. MPI^{n-f}; 101. MPI^{n-g}; 102. MPI^{n-i}; 103. MPI^{n-r}; 104. 6-PGD^{d-f}; 105. PGM^{b-g}; 106. SDH^{d-b}; 107. ACP-1^{x-b}; 108. ACP-2^{c-b}; 109. ACP-3^{c-b}; 110. ADA^{x-e}; 111. ADH^{x-b}; 112. GPI^{x-d}; 113. α-GPD^{a-c}; 114. HDH^{x-c}; 115. IDH^{c-b}; 116. LDH-1^{x-g}; 117. SDH^{x-c}; 118. XDH^{c-f}; 119. FUM^{b-a}; 120. 6-PGD^{b-c}; 121. XDH^{f-e}; 122. ADH^{b-h}; 123. GOT-2^{g-e}; 124. SOD-2^{i-d}; 125. ADA^{e-a}; 126. ADA^{e-c}; 127. GPI^{d-b}; 128. GPI^{d-f} (see 64); 129. β-GUR^{c-a}; 130. G-3-PD^{e-f} (see 97); 131. LDH-1^{g-a}; 132. MPI^{x-k}; 133. PGM^{a-f}; 134. SDH^{c-d} (see 71); 135. ACP-2^{b-a}; 136. G-3-PD^{e-a}; 137. LHD-2^{f-g}; 138. MDH-2^{b-d}; 139. PGM^{a-i}; 140. CAT^{e-f}; 141. GPI^{d-g}; 142. MPI^{x-h}; 143. 6-PGD^{c-e}; 144. TPI^{a-b}; 145. ACP-3^{b-a}; 146. ADA^{e-i}; 147. GOT-1^{b-c}; 148. MPI^{x-j}; 149. MPI^{x-q}; 150. α-MAN^{d-c}; 151. SOD-1^{a-c}; 152. SOD-2^{d-g}; 153. CAT^{c-e}; 154. GOT-2^{g-c}; 155. LDH-2^{f-a}; 156. α-MAN^{d-e}; 157. MDH-1^{a-b}; 158. MPI^{x-d}; 159. MPI^{x-e}; 160. PGM^{a-e}; 161. G-6-PD^{c-a}; 162. MPI^{x-o}; 163. 6-PGD^{c-a}; 164. PGM^{a-j}; 165. SOD-2^{i-f}; 166. G-6-PD^{c-b}; 167. MDH-1^{a-d}; 168. MDH-2^{b-c}; 169. PGM^{a-d}; 170. ADH^{b-c}; 171. CAT^{e-g}; 172. GOT-1^{b-f}; 173. G-3-PD^{e-d}; 174. LDH-2^{f-d}; 175. MPI^{x-l}; 176. PGM^{d-k}; 177. XDH^{f-d}; 178. MPI^{x-s}; 179. CAT^{e-d}; 180. GOT-1^{b-e}; 181. MDH-1^{d-c}; 182. ACP-1^{b-a}; 183. ADA^{e-f}; 184. ADH^{b-f}; 185. LDH-1^{g-d}; 186. MDH-1^{d-f}; 187. α-MAN^{d-f}; 188. MPI^{a-p}; 189. PGM^{d-b}.

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IDENTIFYING SPECIES IN THE CHILEAN FROGS BY PRINCIPAL COMPONENTS ANALYSIS

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ABSTRACT: Principal components analysis (PCA) is applied for the first time to the identification of frogs of the genus *Eupsophus*. *Eupsophus vittatus* and *E. calcaratus* are clearly distinguishable, but a second PCA was required on the *E. roseus-E. migueli* subsample. The associated plot did distinguish these latter species.

Key words: Amphibia; Salientia; Leptodactylidae; *Eupsophus*; Principal components analysis; Chile

THE general habitat of the frog genus *Eupsophus* is the temperate forest in southern Chile (Formas, 1979). The species content of this genus has been recently discussed by Lynch (1978) and Formas (1978, 1980).

Principal components analysis (PCA) is a statistical multivariate technique for reducing data dimensionality. When reduced dimensionality has been attained, scatter plots can show groupings of the observations. When groups have been distinguished previously, the validity of this prior classification can be assessed.

Within this framework, I took the existence of *E. vittatus*, *E. roseus*, *E. mi-*