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Leptodactylid Frogs of the Genus <u>Eleutherodactylus</u> from the Andes of Southern Ecuador

By John D. Lynch

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The University of Kansas Museum of Natural History

Miscellaneous Publication No. 66 ——— February 28, 1979 ———

Leptodactylid Frogs of the Genus *Eleutherodactylus* From the Andes of Southern Ecuador

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The University of Kansas Lawrence 1979

UNIVERSITY OF KANSAS PUBLICATIONS, MUSEUM OF NATURAL HISTORY

Editor: E. O. Wiley

Miscellaneous Publication No. 66 pp. 1-62; 23 figures; 4 tables Published February 28, 1979

Museum of Natural History The University of Kansas Lawrence, Kansas 66045 U.S.A.

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Printed by University of Kansas Printing Service Lawrence, Kansas

CONTENTS

INTRODUCTION	1
Acknowledgments	2
Key To Eleutherodactyline Frogs of Southern Andean Ecuador	4
ACCOUNTS OF SPECIES	
Eleutherodactylus atratus new species	5
Eleutherodactylus balionotus new species	7
Eleutherodactylus baryecuus new species	10
Eleutherodactylus bromeliaceus new species	12
Eleutherodactylus cajamarcensis Barbour and Noble	14
Eleutherodactylus colodactylus new species	15
Eleutherodactylus cryophilius new species	19
Eleutherodactylus cryptomelas new species	21
Eleutherodactylus lymani Barbour and Noble	23
Eleutherodactylus orestes new species	24
Eleutherodactylus percultus new species	26
Eleutherodactylus phoxocephalus new species	
Eleutherodactylus proserpens new species	
Eleutherodactylus pycnodermis new species	35
Eleutherodactylus riveti (Despax)	37
Eleutherodactylus ruidus new species	40
Eleutherodactylus spinosus new species	43
Eleutherodactylus versicolor new species	45
Eleutherodactylus vidua new species	49
Eleutherodactylus w-nigrum (Boettger)	51
DISCUSSION	51
Relationships of the southern fauna	51
Ecological segregation	52
Correlates with species densities and diversities	53
Comparisons with distributions of other Andean genera	56
SUMMARY	
RESUMEN	58
LITERATURE CITED	58
APPENDIX: SPECIMENS EXAMINED	60

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INTRODUCTION

The genus Eleutherodactylus is a prominent component in most faunas from northwestern South America. The genus is well represented in the faunas of the lowlands as well as the high Andean páramo and pajonal (of Acosta-Solís, 1968) habitats. Such habitats generally occur at elevations above 3000 m. The Andes of northern Ecuador have considerable contiguous areas at elevations above 3000 m, whereas in southern Ecuador (south of the Nudo de Azuay) areas above the 3000 m contour are discontinuous (Fig. 1). This patchiness of high montane territory continues into northern Perú, where south of the Huancabamba pass the Andes again have vast areas of contiguous high altitude habitats which grade into the *puna* in southern Perú and Bolivia. The genus *Eleutherodactylus* is found in the high montane localities in Ecuador and extreme northern Perú, but south of Huancabamba, suitable habitat is meager or other frogs occupy the habitats occupied by *Eleutherodactylus* at more northern localities.

The eleutherodactyline fauna of northern Andean Ecuador is now relatively well known (at least taxonomically). In contrast, that of the Andes of southern Ecuador is poorly known.



FIG. 1.—Map of Ecuador illustrating the distribution of *Eleutherodactylus phoxocephalus* (circles). The area in southern Ecuador enclosed by the box is shown in greater detail in Figure 2.

Lynch (1969a) reported *E. cajamarcensis* Barbour and Noble from the mountain ranges to the north and east of the Loja *hoya* and *E. lymani* Barbour and Noble from the Loja *hoya*. *Phrynopus flavomaculatus* (Parker) is found at high altitudes on the mountain ranges to the north and east of the Loja *hoya* and is distributed along the Cordillera Oriental to east of Cuenca (Lynch, 1975). The type-locality of *Eleutherodactylus w-nigrum* (Boettger) is on the interior slopes of the Cordillera Occidental just west of Cuenca.

In June 1968 I visited a mountain range approximately 15 km E of Cuidad Loja, Ecuador (Abra de Zamora), the type-locality for Phrynopus flavomaculatus. Five species of eleutherodactyline frogs were collected on the crest and the western slopes in 1968. William E. Duellman collected there in 1971 and 1975 and obtained five other species. In 1968, 1970, and 1971, several collectors made collections of eleutherodactyline frogs in *páramos* and *pajonales* at many localities in the Andes south of Cuenca. In addition to these collections, those made by the late James A. Peters were made available for study; Peters' collections were made along two transects crossing the Cordillera Oriental to the northeast and east of Cuenca.

Within the area I term southern Andean Ecuador (Fig. 2), 21 species of eleutherodactyline frogs are found. These include one species of Phrynopus (P. flavomaculatus) and 20 species of Eleutherodactylus. Two of the Eleutherodactylus belong to the predominantly lowland fitzingeri group: 1) E. lymani, found in the interandean valleys from the Río Jubones south to the vallevs of the Río Catamayo and Río Zarumilla (draining to the Pacific) as well as in the valleys of the Río Huancabamba and Río Mayo or Chinchipe (draining to the Amazon), and 2) E. w-nigrum, which was found at one *pajonal* (the type-locality); E. w-nigrum also occurs on both the Amazonian and the Pacific slopes peripheral to the high Andean regions.

The other 18 species belong to what I called the *unistrigatus* group (Lynch, 1976a). All are termed "southern" even though one ranges considerably northward as a Pacific versant frog (Fig. 1). Only two of the 18 southern species of the unistrigatus group have been named. Lynch (1969a) redescribed E. cajamarcensis on the basis of specimens from the Loja *houa* and also reported specimens from north-central Andean Ecuador. At present I do not consider the frogs reported from Provincia Tungurahua by Lynch to be conspecific with the frog found in southern Ecuador. The status of those northern specimens will be discussed in a paper treating E. unistrigatus. A species commonly found on the mountains surrounding the Cuenca hoya is E. riveti (Despax). This name had not been previously associated with any specific Andean population.

In the species accounts the following abbreviations are used: SVL (snoutvent length), E-N (eye-nostril distance), and IOD (interorbital distance). Adult females include only those females having extensively convuluted oviducts and/or large, yellow, ovarian eggs.

Acknowledgments

Field work in Ecuador was supported by grants from the Watkins Fund of the Museum of Natural History, The University of Kansas, the Penrose Fund of the American Philosophical Society, and by the University of Nebraska Research Council. Robert W. Henderson accompanied me during the summer of 1968. William E. Duellman, Thomas H. Fritts, Richard Montanucci, and Linda Trueb have contributed substantially by making collections and recording notes on habitat and colors in life at the expense of their own field-oriented studies on other groups.

The late James A. Peters made his collections and those of Gustavo Orces-



Fig. 2.—Map of southern Ecuador showing localities at which *Eleutherodactylus* discussed in the text were collected. Land masses above 3000 m are hatched; dotted line traces the 2000 m contour.

V. available for study. Material and/or provision of working space were made available by Werner C. A. Bokermann, William E. Duellman, Alice G. C. Grandison, Jean Guibé, W. Ronald Heyer, Ronald A. Nussbaum, Douglas Rossman, Richard Thomas, Charles F. Walker, Ernest E. Williams, and George R. Zug. I am especially grateful to Alice Grandison, Jean Guibé, Konrad Klemmer, and Ernest Williams for loan of type-specimens or photographs of type specimens. Jaime Péfaur kindly provided the Spanish summary.

Lastly, to those in agreement with Barbour's (1921:25) dictum, my apologies.

Abbreviations for collections used throughout the text are:

AMNH	American Museum of
	Natural History

- BMNH British Museum (Natural History)
- KU University of Kansas Museum of Natural History
- LSUMZ Louisiana State University Museum of Zoology

MCZ Museum of Comparative

Zoology, Harvard University

- MHNP Muséum National d'Histoire Naturelle (Paris)
- UMMZ University of Michigan Museum of Zoology
- USNM National Museum of Natural History (Washington)
- WCAB Private collection of Werner Bokermann (São Paulo)

KEY TO ELEUTHERODACTYLINE FROGS OF SOUTHERN ANDEAN ECUADOR

- 2. Digits lacking discs _______ ______ Phrynopus flavomaculatus All digits bearing discs on pads ____3
- 3. Inner tarsal fold present ______ Eleutherodactylus lymani No inner tarsal fold ______ Eleutherodactylus w-nigrum

- 6. Groin not patterned _______ Eleutherodactylus vidua Groin black with white spots ______ Eleutherodactylus orestes
- 7. Tympana absent ______8 Tympana clearly visible or concealed ______10
- 8. Small frogs (< 22 mm SVL) without vomerine odontophores; digits short and thick _________ Eleutherodactylus colodactylus

- Prominent conical tubercles on eyelids and heels ______ 11 No tubercles on eyelid and heel, or if tubercles present, their length ≤ basal width (not elongate) _____ 13
- 11. Skin of dorsum tuberculate; males lacking vocal slits and sac; venter usually reticulated with brown __12 Skin of dorsum smooth with longitudinal ridges; males with vocal sac and slits; venter white, occasionally with brown spots (not reticulate) ______ *Eleutherodactylus atratus*

- 13. Outer edge of tarsus bearing row of conical tubercles 14
 Outer edge of tarsus lacking conical tubercles 18

- 17. Groin, posterior thigh, and concealed shank black _______ *Eleutherodactylus cryptomelas*

Concealed surfaces of hind limb dull gray _____ Eleutherodactylus balionotus

- Fingers bearing prominent lateral fringes Eleutherodactylus riveti Fingers lacking lateral fringes or having narrow, keel-like lateral fringes 19
- 19. Skin of body areolate, digits short Eleutherodactylus proserpens Skin of dorsum finely shagreened 20

ACCOUNTS OF SPECIES

In the following accounts I attempt to make comparable statements in the diagnoses and descriptions. The diagnoses consist of a series of 14 numbered statements (or set of statements) and follow the format used in several other papers on Ecuadorian species of Eleutherodactylus (Lynch, 1968a, 1969a, 1970a, b, 1971, 1972a, 1974a, b, and 1976b). The sequence was used (but without numbers) in Lynch (1968b, 1969b) and Lynch and Schwartz (1972). Following the numbered statements is a paragraph distinguishing the taxon from those species it most nearly resembles (in my opinion). Measurements and proportions are given for each sex when the means differ significantly (p \leq 0.05); otherwise these data are combined.

Complete accounts are provided for each of sixteen species. The accounts for *E. cajamarcensis*, *E. lymani*, and *E.* *w*-nigrum include only updating information [for more detail on these species see Lynch (1969a) and Cochran and Goin (1970)].

Eleutherodactylus atratus new species Fig. 3A

Holotype.—USNM 199675, an adult female, obtained at Suro Rancho, Provincia Morona-Santiago, Ecuador, 2683 m, by James A. Peters on 23 August 1962.

Paratypes.—USNM 199679-82, topotypes; between Sapote and Suro Rancho, 2604-22 m, USNM 199683-89.

Diagnosis.—(1) skin of dorsum bearing low ridges, venter arcolate; (2) tympanum round, $\frac{1}{4}$ - $\frac{2}{3}$ diameter of eyc; (3) snout subacuminate in dorsal view, short, E-N less than length of eye; (4) interorbital space broader than upper eyelid; cranial crests low; (3) vomerine odontophores oval, oblique; (6) males

with subgular vocal sac and vocal slits; (7) first finger shorter than second; all digits bearing broad discs on dilated pads; (8) fingers lacking lateral fringes; (9) ulnar tubercles indistinct; (10) heel and outer edges of tarsus bearing conical tubercles: short inner tarsal fold present; (11) two metatarsal tubercles, outer round, ½ size of non-compressed, elongate inner; numerous supernumerary plantar tubercles; (12) toes bearing narrow lateral fringes, all bearing discs and pads as large as those of fingers; (13) tan above with brown stripes; flanks, concealed surfaces of thigh, shank, and tarsus densely spotted with black; venter creamy-yellow, sometimes bearing small brown spots; (14) adults small, ô ô 17.4-24.0 mm, 9 9 24.9-29.2 mm SVL.

Eleutherodactylus atratus is a member of the *unistrigatus* group and might be confused with only *E. cryptomelas*. It is smaller than *E. cryptomelas*, has vocal sac and slits, is less tuberculate, and colored differently. They are similar in having heel, tarsal, and eyclid tubercles, and in having black areas on the concealed surfaces of the hind leg.

Description.—Head narrower than to as wide as body, wider than long; head width 34.6-38.6 percent SVL ($\bar{x} =$ 36.8, N = 29; snout subacuminate in dorsal view, rounded in lateral profile, short, E-N 64.7-96.4 percent eye length in males ($\bar{x} = 82.6$, N = 18), 78.9-96.7 percent in females ($\bar{x} = 88.2, N = 10$); nostrils weakly protuberant, directed dorsolaterally; canthus rostralis sharp, straight; loreal region weakly concave, sloping abruptly to lips; lips not flared; interorbital space broad, edges of fron-(low upturned toparietals cranial crests); upper evelid bearing 1-2 conical warts; width of upper eyelid 64.3-91.7 percent IOD in males ($\bar{x} = 74.1$, N = 18), 59.4-78.1 in females ($\bar{x} = 67.4$, N = 10; supratympanic fold present, concealing upper edge of tympanum; tympanum distinct, round, directed posterolaterally, separated from eye by twothirds its diameter, its length 23.5-44.4 percent eye length ($\bar{x} = 33.9$, N = 28); no enlarged postrictal tubercles; choanae small, round, not concealed by palatal



FIG. 3.—(A) Eleutherodactylus atratus, KU 165236; (B) E. balionotus, KU 142136; (C) E. cajamarcensis, KU 120007; (D) E. colodactylus, KU 165219.

shelf of maxillary arch; vomerine odontophores prominent, median and posterior to choanae, oval in outline, slanted, bearing 4-5 teeth in a slanted row, separated by distance equal to one-half odontophore width, each 3-5 times size of a choana; tongue as long as wide, posterior % not adherent to floor of mouth, posterior border not notched; males with vocal slits and subgular vocal sac.

Skin of dorsum bearing numerous low ridges; on lower back, ridges break up forming rows of small warts; flanks smooth; venter and posteroventral surfaces of thighs coarsely areolate; discoidal folds prominent; anal opening not extended in sheath; upper limb surfaces coarsely shagreened; ulnar tubercles present, small and indistinct; palmar tubercle bifid, larger than oval thenar tubercle; supernumerary palmar tubercles round, pungent, smaller than round, non-conical subarticular tubercles: fingers lacking lateral fringes, keeled laterally; all fingers bearing discs (broader than long) on dilated pads; pad of thumb small, round; those on outer fingers broad, rounded apically, slightly larger than ear; thumb shorter than second finger.

Knee lacking tubercles; heel bearing small, conical tubercle; outer edge of tarsus bearing indistinct, subconical tubercles; inner edge of tarsus bearing indistinct fold; inner metatarsal tubercle twice as long as wide, not compressed, 2½-3 times size of round outer metatarsal tubercle; numerous plantar supernumerary tubercles; subarticular tubercles round, non-conical; toes bearing narrow lateral fringes; outer edge of sole bearing keel; all toes bearing discs (broader than long) on dilated pads; pads of toes as large as those of outer fingers; heels overlapping when legs flexed at right angles to sagittal plane; heel of adpressed hind limb reaching to eye; shank 44.5-52.9 percent SVL ($\bar{x} = 48.8$, N = 29).

In preservative, tan to pale brown above with pale brown stripes; flanks and limbs gray-brown; canthal and supratympanic stripes pale brown; no labial bars; limbs not or only faintly barred, if present, bars oblique; flanks, axillae, groin, anterior thigh, posterior thigh, concealed shank, and concealed tarsus spotted with black; spotting on thighs and shank sometimes so dense as to appear solid black with cream spots or lines; extent of black increases ontogenetically; venter creamy-yellow with or without small brown spots.

In life, *E. atratus* is yellowish brown above with pale brown stripes; flanks more yellowish than dorsum; groin, concealed thigh and shank surfaces deep black with shiny white spots; venter cream.

Measurements of holotype in mm.— SVL 27.3, shank 13.7, head width 10.0, head length 9.6, width of upper eyelid 2.0, IOD 3.2, tympanum 1.2, length of eye 3.2, E-N 2.7. The holotype is a gravid female.

Etymology.—Latin, meaning dressed in black, in reference to the black areas on the concealed surfaces.

Natural history.—James Peters and his associates collected calling males at night on bushes and by day caught individuals of both sexes beneath rocks and logs along the trail between Gualaceo and General Plaza. The species was found only on the more southerly of the two transects made by Peters and his associates across the Páramos de Matanga. All specimens were found on the Amazonian slopes. William E. Duellman found 4 individuals in terrestrial bromeliads on the Abra de Zamora.

Distribution.—Eleutherodactylus atratus occurs at elevations of 2195-2850 m on the Amazonian slopes of the eastern Andean Cordillera in southern Ecuador.

Eleutherodactylus balionotus new species Fig. 3B

Holotype.—KU 142136, an adult female from 13.5 km E Loja, at the crest of the cordillera (Abra de Zamora) between Provincia Loja and Provincia Zamora-Chinchipe, Ecuador, 2800 m, obtained 22 July 1971 by William E. Duellman.

Paratypes.—KU 142135, 142137-44, collected syntopically with the holotype.

Diagnosis.-(1) skin of dorsum tuberculate, that of venter areolate; no dorsolateral folds; (2) tympanum visible, round to slightly higher than long. its length two-fifths to three-fifths that of eve: (3) snout subacuminate in dorsal view, rounded in lateral profile; E-N slightly greater than eye length; (4) interorbital space flat, no cranial crests; upper eyelid width subequal to IOD; (5) vomerine teeth and odontophores present, round; (6) male with vocal slits and subgular vocal sac; (7) first finger shorter than second, all digits bearing discs on dilated pads, dilation ratios I: 1.4, II: 1.6, III: 1.6, IV: 1.6; (8) fingers bearing lateral fringes; (9) ulnar tubercles present, obscure; (10) inner tarsal surface bearing indefinite tubercles, outer surface bearing a row of tubercles; heel bearing non-conical, but distinct, tubercles; (11) two metatarsal tubercles, outer round, conical, one-fourth to one-half size of oval, non-compressed inner; numerous indefinite supernumerary plantar tubercles; (12) toes bearing lateral fringes, not webbed; toes bearing discs on pads, pads as large as those on outer fingers; (13) dorsum gray with small black spots on center of back; venter pale gray without markings; no markings in groin or on concealed thighs; (14) adults small, males 21.8-22.2. females 27.1-29.1 mm SVL.

Eleutherodactylus balionotus is most easily recognized by its distinctive color pattern. This species is most similar to *E. riveti* (Despax) from which it differs in width of the digital pads (pads slightly wider in *riveti*), snout length (slightly shorter in *riveti*), width of upper eyelid (narrower in *riveti*), and skin texture (warts on dorsal surfaces flatter in *riveti*, more tuberculate in *balionotus*).

Description.—Head as wide as body, wider than long; head width 37.5-40.8 percent SVL ($\bar{x} = 39.5$, N = 10); snout subacuminate in dorsal view, rounded in

lateral profile, tip pointed; canthus rostralis moderately sharp, concave; loreal region concave, sloping abruptly to lips; lips not flared; snout of moderate length (length of eye slightly less than E-N distance); nostrils directed dorsolaterallv. weakly protuberant; interorbital space flat, no cranial crests; frontoparietals complete (no fontanelle); nasals in contact; eyes large, eyelid width 88.2-110.4 percent IOD ($\bar{x} = 103.2, N = 10$); tympanum distinct, round or slightly higher than long, its length 39.6-55.9 percent length of eye ($\bar{x} = 47.8$, N = 10); tympanum separated from eve by distance equal to tympanic diameter; supratympanic fold present, thick, concealing upper edge of tympanum, warty; tongue slightly longer than wide, not notched posteriorly, posterior onethird not adherent to floor of mouth: choanae and vomerine odontophores small and equal in size; choanae widely separated, completely visible when roof of mouth is viewed from directly above; vomerine odontophores situated well posterior and median to choanae, separated by twice width of one odontophore: each odontophore rounded, elevated, bearing a clump of 4-6 teeth; males with vocal slits and a subgular vocal sac.

Skin on top of head shagreened, that on eyelids bearing a few large warts (as large as those on back), that on face smooth; skin of body and limbs covered with various-size warts (not flattened); no dorsolateral folds; some females having a thin sagittal fold; skin of venter coarsely areolate, discoidal folds prominent; skin of throat weakly areolate.

Forearm areolate but some enlarged tubercles present along ulnar edge (in an indefinite row); two palmar tubercles, median larger, both smaller than oval thenar tubercle; numerous supernumerary palmar tubercles, not extending onto digits; subarticular tubercles prominent, round, subconical, simple; fingers bearing discs on pads; pad on thumb round, those on other fingers wider than long, not emarginate; dilation ratios I: 1.2-1.7 ($\bar{x} = 1.4$), II: 1.4-1.8 ($\bar{x} = 1.6$), III: 1.4-1.8 ($\bar{x} = 1.6$), IV: 1.4-1.8 ($\bar{x} = 1.6$); fingers bearing lateral fringes (Fig. 4); first finger shorter than second.

Hind limbs short, shank 44.8-52.7 pereent SVL ($\bar{x} = 47.0$, N = 10); heel bearing three or four rounded tubercles (not conical); tarsus bearing a row of similar tubercles along its outer edge and a less definite row along its inner edge; two metatarsal tubercles, both longer than wide, inner two to four times size of outer; numerous, indefinite plantar supernumerary tubercles; subarticular tubercles round, somewhat flattened, simple, smaller than those of fingers; toes bearing lateral fringes but no basal webbing; all toes bearing discs on pads which are wider than long.

In preservative, the dorsal surfaces are gray, flecked and spotted with black. The flecking is most intense on the back but usually some flecking is found on the limbs. The venter is dull grayishwhite with oceasional brown or black spots. The tympanum is brown. Canthal and supratympanic stripes are brown to black and the lips are not barred. The posterior surfaces of the thighs are pale rusty-brown with or without indefinite faint brown marbling. The limbs are not barred.

In life, *E. balionotus* was described as follows: "When collected dark brown; dorsum later changed to pinkish or grayish tan with black flecks; venter dirty white with or without black flecks; iris bronze with median horizontal red streak." (William E. Duellman field notes, 22 July 1971).

Measurements of holotype in mm.— SVL 28.4, shank 12.8, head width 11.5, head length 10.7, upper eyelid width 3.1, IOD 2.8, tympanum length 1.7, eye length 3.3, eye-nostril 3.6. The holotype has heavily convoluted oviducts and large yellow ovarian eggs.



FIG. 4.—(A) Eleutherodactylus balionotus, KU 142136; (B) E. riveti, KU 131172. Lines equal 5 mm.

Etymology.—Greek, meaning speckled back, in reference to the predominant color pattern.

Natural history.—E. balionotus is known only from the type-series which was collected by day from terrestrial bromeliads in the subparamo habitats atop the windswept ridge east of Ciudad Loja. The type-series consists of two males, one immature female (KU 142143), and seven gravid females with strongly convoluted oviducts and large yellow eggs.

Remarks.—The lateral fringes on the digits, large inner metatarsal tubercle, and large nasal bones (in median contact) suggest that E. balionotus is allied to the squat-bodied species found in central and northern Andean Ecuador (E. orcesi, E. riveti, E. thymelensis, and E. unistrigatus). Eleutherodactylus ruidus differs markedly in lacking the middle ear and vocal apparatus; in proportions, skin texture, and most features of the hand and foot it resembles E. balionotus and E. riveti. Eleutherodactylus balionotus is most like E. riveti; more fieldwork on the isolated and semi-isolated mountain ridges of southern Andean Ecuador (Cordilleras de Chilla and Condorcillo) is needed to establish whether E. balionotus is a distinct species from E. riveti or a geographic variant.

Eleutherodactylus baryecuus new species Fig. 5

Holotype.—USNM 199714, an adult female, obtained at Suro Rancho, Provincia Morona-Santiago, Ecuador, 2683 m, by James A. Peters on 24 August 1962.

Paratypes.—All Provincia Morona-Santiago: USNM 199715, Cerro Negro, 2927 m; USNM 199717-22, between San Juan Bosco and El Cruzado, 2226 m; USNM 199723-24, El Cruzado, 2195 m; USNM 199725, San Juan Bosco, 2195 m; USNM 199726-28, Sapote, 2470 m; USNM 199729, San Vicente, 2805-2835 m; USNM 199730, 3 km W San Vicente, 2988 m; USNM 199716, between Sevilla de Oro and Méndez (probably between the crest and Pailas).

Diagnosis.—(1) skin of dorsum smooth with scattered, low warts, venter finely areolate; (2) tympanum absent; (3) snout round in dorsal view, truncate in lateral profile, short; (4) interorbital space as wide as upper eyelid in males, broader in females; low cranial crests present; (5) vomerine odontophores elevated, triangular in outline; (6) males lacking vocal sac and slits; (7) first finger shorter than second; all digits bearing broad discs on dilated pads; distal subarticular tubercles grooved; (8) fingers lacking lateral fringes; (9) ulnar tubercles indistinct except antebrachial; (10) non-conical tubercles on heel, none on tarsus; (11) two metatarsal tubercles, inner oval, non-compressed, 1.5-2 times size of subconical outer; no supernumerary plantar tubercles; (12) toes bearing lateral fringes, broad discs on dilated pads; toe pads as large as those of fingers; (13) brown



FIG. 5.—Eleutherodactylus baryecuus, USNM 199727; line equals 10 mm.

above with darker brown spots, limb bars narrow, oblique; venter cream reticulated with brown; (14) adults moderate-size, males 27.2-30.4 mm, females 38.2-43.5 mm SVL.

Eleutherodactylus baryecuus is a member of the unistrigatus group most similar to E. surdus (Boulenger) from the Pacific slopes of Andean Ecuador. Both lack ears, have relatively smooth skin of the dorsum, moderate-sized digital pads, and low cranial crests. The two frogs are identical in size (6 & surdus have a mean SVL of 28.0 ± 1.9 mm and 16 $\,$ ° have a mean SVL of 40.5 \pm 1.3 mm). Eleutherodactulus surdus does not have so rounded a snout as does E. baryecuus in dorsal view [compare Fig. 5 with Boulenger's (1882) illustration of surdus], has larger eyes (and hence a lower upper evelid width/IOD ratio, see Lynch, 1970a: 140), and longer legs than E. baryecuus; E. surdus also has poorly developed, but evident, dorsolateral folds.

Description.-Head narrower than body, wider than long; head width 35.1-40.8 percent SVL ($\bar{x} = 36.9, N = 13$); snout rounded in dorsal view, angularly rounded to truncate in lateral profile, short; E-N 64.7-77.4 percent eye length in males ($\bar{x} = 70.0, N = 5$), 67.3-90.0 percent in females ($\bar{x} = 78.5$, N = 8); nostrils not protuberant, directed dorsolaterally: canthus rostralis moderately sharp, weakly concave; loreal region concave, sloping gradually to lips, lips not flared; upper eyelid width 92.8-113.0 percent IOD in males ($\bar{x} = 104.6$, N = 5), 70.0-97.1 percent in females ($\bar{x} =$ 86.7, N = 8; edges of frontoparietals upturned forming low cranial crests; upper eyelid bearing flattened tubercles; supratympanic fold thick; tympanic annulus, cavum tympanicum absent; postrictal tubercles prominent; choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, elevated, triangular in outline, each 3-4 times as wide as a choana, separated by a choanal width, bearing a transverse row of 4-6 teeth along posterior edge; tongue as broad as long, posterior % not adherent to floor of mouth, posterior border not notched; males lacking vocal sac and slits.

Skin of dorsum smooth but bearing low flat warts, those on eyelids and behind eye pungent; no dorsolateral folds evident in adult females, males have weakly evident glandular dorsolateral folds; anal opening extended onto back of thighs by sheath; venter finely areolate: discoidal folds obscure: 1-2 ulnar tubercles evident on distal quarter of forearm; palmar tubercle bifid, much larger than oval thenar tubercle; supernumerary palmar tubercles small, round: subarticular tubercles larger than supernumeraries, round to slightly broader than long; distal subarticular tubercles on fingers III and IV grooved (in some males, nearly bifid); fingers lacking lateral fringes; all fingers bearing discs (broader than long) on apically rounded, dilated pads; pads on thumb smallest; males with swollen, non-spinous nuptial pad on thumb; thumb shorter than second finger.

Heel bearing non-conical tubercles; no tubercles on knee or tarsus; inner metatarsal tubercle twice as long as wide, non-compressed; outer metatarsal tubercle ½-% size of inner, low, subconical, round; no supernumerary plantar tubercles; basal subarticular tubercles longer than wide, distal subarticular tubercles round on toes I, II, V, grooved on III and IV; toes bearing narrow lateral fringes but not webbed; all toes bearing discs on dilated pads; toe pads as large as those of outer fingers: when legs are flexed at right angles to body. heels just overlap; heel of adpressed hind limb reaches area just posterior to eye; shank 43.4-48.9 percent SVL ($\bar{x} =$ 45.8, N = 13).

In preservative, brown above with darker brown markings (*viz.*, canthalsupratympanic stripes, labial bars, interorbital bar, spots on back sometimes coalescing forming scapular W, sacral chevron); flanks tinged with yellow and spotted with dark brown; anal triangle faint; brown bar across thigh coaleseing on posterior thigh forming brown background which may be spotted with yellow; shank bars, if complete, oblique, narrower than interspaces; venter cream, spotted and retieulated with brown; spotting on venter most prominent in large females; males and small females have cream venters with faint, if any, spotting.

In life, *E. baryecuus* is olive to brown above with black markings. The venter is gray with dull yellow spots. The throat is dull yellow with some gray reticulation. Between the bands on the thigh and to a lesser extent on the posterior flanks the ground color is stippled with yellow. In some individuals a yellow wash is seen adjacent to the black markings.

Measurements of holotype in mm.— SVL 40.2; tibia 19.5; head width 14.1; head length 12.3; upper eyelid width 3.1; IOD 3.5; eye length 4.1; E-N 3.2. The holotype is an adult female with heavily convoluted oviducts and large yellow ovarian eggs.

E t y m o l o g y.—Greek, baryecoos, meaning hard of hearing; in reference to the loss of the middle ear in this frog.

Natural history.—Most of the specimens were found beneath logs and rocks; James Peters found one clasping pair (USNM 199718-19). The eight adult females contain large ovarian eggs, and the five adult males have swollen thumbs and large testes. These observations as well as the capture of an amplectant pair suggest the species was ready to breed when collected in August 1962.

Remarks.—I once (Lynch, 1970a) included E. chloronotus, E. devillei (Boulenger), and E. surdus (Boulenger) in the surdus group within what I then referred to as the unistrigatus complex. With the recognition of the unistrigatus group as a species group (Lynch, 1976a), I now view my earlier surdus group as an Artenkreis but am no longer convinced that E. chloronotus is

a member. I do include, as vicariants, E. baruecuus, E. devillei, and E. surdus. The differences between the three are adequate to insist on species level recognition for each and in spite of the retention of a complete middle ear in E. *devillei* and the loss of the ear in E. baruecuus and E. surdus. I do not view the latter two as more closely related to one another than either is to *E. devillei*. The three species are separated by formidable barriers (the valley of the Río Pastaza and the interandean valley and páramos of the Cordillera Oecidental). All three species occur in forested habitats near tree-line. At present I am aware of no members of this Artenkreis among the faunas of Colombia or Perú.

Distribution.—Known only from the eastern face of the Cordillera de Oriental east of Cuenca at elevations of 2195-2988 m.

Eleutherodactylus bromeliaceus new species Fig. 6

Holotype.—USNM 199731, an adult female, obtained in bromeliads between Sapote and Suro Rancho, Provincia Morona-Santiago, Ecuador, 2622 m, by Manuel Olalla on 24 August 1962.

Paratypes.—USNM 199732-34, Pailas, 2195 m; USNM 199735, Mirador, 1982 m; USNM 199736-37, Plan de Milagro, 1707 m; USNM 199738-39, El Cruzado, 2195 m; USNM 199740, ½ km E Sapote, 2393 m; USNM 199742, mountain above Sapote to south, 2500 m; USNM 199741, 1 km E Sapote, 2332 m; all in Provincia Morona-Santiago, Ecuador.

Diagnosis.—(1) skin of dorsum smooth (eyelid bearing tubercles), that of venter coarsely areolate; no dorsolateral folds; (2) tympanum visible, round, its length $\frac{1}{4}$ - $\frac{1}{8}$ that of eye; (3) snout subacuminate in dorsal view (tip pointed), pointed in lateral profile; (4) interorbital space broad, no cranial crests; (5) vomerine odontophores oblique, prominent; (6) males with vocal slits and external subgular vocal sac;

(7) first finger shorter than second; all digits bearing broad dises on dilated pads: numerous supernumerary palmar tubercles; (8) fingers bearing lateral fringes; (9) ulnar tubercles absent; (10) heel and outer edge of tarsus bearing low tubercles; inner tarsal tubercle present; (11) two metatarsal tubereles, inner oval, three times size of outer; numerous supernumerary plantar tubercles; (12) toes bearing lateral fringes; pads and discs of toes slightly smaller than those of fingers; (13) tan above becoming brown on flanks; dorsum fleeked or blotched with brown; venter cream (flecked with brown in adult females); limb bars transverse, narrower than interspaces; concealed thigh brown with diffuse yellow spots; (14) adults small, males 16.7-23.2 mm, females 22.9-28.1 mm SVL.

Eleutherodactylus bromeliaceus is most similar to E. lacrimosus (Jiménez de la Espada) and perhaps E. chalceus (Peters). The latter purportedly lacks vomerine odontophores; E. lacrimosus has a more rounded snout (see illustration in Lynch and Schwartz, 1972) and is a smaller frog lacking supernumerary palmar and plantar tubercles, lateral fringes on the digits, and tubercles on the eyelid and tarsus.

Description.—Head as broad as body, wider than long; head width 34.4-

39.8 percent SVL ($\bar{x} = 37.1$, N = 12); snout subacuminate in dorsal view, tip pointed, pointed in lateral profile (acutely rounded); snout relatively long, E-N 75.0-97.0 percent eve length ($\bar{x} = 84.4$, N = 12; nostrils weakly protuberant, directed anterodorsolaterally; canthus rostralis obtuse; loreal region weakly concave, sloping rapidly to lips; lips not flared; interorbital space broad, flat, no cranial crests; upper eyelid width 66.7-95.6 percent IOD ($\bar{x} = 80.3$, N = 12); upper evelid bearing 2-3 non-conical tubercles; temporal region sloping (tympanum directed dorsolaterally); supratympanic fold thin, distinct, concealing upper edge of tympanic annulus; tympanum prominent, round, its length 28.6-42.3 percent eye length ($\bar{x} = 38.0$, N = 12), separated from eye by ³/₂ tympanic length; postrictal tubercles not prominent; choanae moderate-sized, oval, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, oblique, each ½ size of a choana, bearing a clump of 4-5 teeth, separated by 1½ choanal widths; tongue much longer than wide, posterior ¼ not adherent to floor of mouth, posterior edge not notched; males with vocal slits and large external subgular vocal sac.

Skin of dorsum (except eyelid) smooth, no dorsolateral folds, that of



FIG. 6.-Eleutherodactylus bromeliaceus, USNM 199731; line equals 5 mm.

flanks areolate, that of venter coarsely areolate; discoidal folds prominent; no anal sheath; limbs finely areolate; ulnar tubercles not evident; palmar tubercle bifid, twice as large as oval thenar tubercle; many supernumerary palmar tubercles; subarticular tubercles round, non-conical, elevated; fingers bearing prominent fringes, discs (broader than long), and dilated pads; pad on thumb smallest, those on fingers III and IV as large as tympanum; first finger shorter than second.

Knee and heel bearing small warts; tarsus bearing row of non-conical tubercles along outer edge, single tubercle along inner edge; inner metatarsal tubercle twice as long as wide, non-compressed; outer metatarsal tubercle elongate, non-conical, ¹/₃ size of inner; many supernumerary plantar tubercles; subarticular tubercles round, non-conical; toes bearing lateral fringes; toes bearing broad discs on dilated pads (slightly smaller than those of outer fingers); heels of flexed legs overlap, heel of adpressed hind limb reaches eve; shank 47.4-52.6 percent SVL ($\bar{x} = 50.0$, N = 12).

In preservative, males are pale cream-tan with few brown spots on the head, back, and lower limbs; adult females are tan above becoming brown on the flanks, dorsum bearing brown chevron, interorbital bar, suprainguinal spots, and marbling; no canthal stripe; labial bars, supratympanic stripe brown; venter cream in males, cream heavily flecked with brown in females; posterior surface of thigh brown with diffuse cream spots.

In life, *E. bromeliaceus* is pale green to olive above with brown to black markings. The venter is pale bronzeyellow and the throat dull yellow. The iris is brown flecked with gold or bronze. One adult female (USNM 199740) had a dull orange ground color; the dark markings resulted in a large orange blotch on the center of the back.

Measurements of the holotype in mm.—SVL 27.2; tibia 13.5; head width 9.9; head length 9.3; upper eyelid width

2.1; IOD 3.1; tympanum length 1.3; eye length 3.1; E-N 3.0. The holotype is an adult female with extensively convoluted oviducts and large yellow ovarian eggs.

Etymology.—Latin, meaning living in bromeliads; most of the specimens secured by Peters and his associates were collected in bromeliads on trees.

Natural history.—Some specimens were collected at night on leaves of elephant ear plants but most specimens were collected during the day in the axils of bromeliads taken from trees. Two specimens were collected by day in the axils of elephant ear plants. Many of the males have distended vocal sacs suggesting that they may have been calling. All five adult females contain large ovarian eggs.

Remarks.—In addition to the lowland *E. lacrimosus* ranging from Colombia and Ecuador east to Belém in Brasil and *E. bromeliaceus* from the Amazonian versant of the Cordillera de Matanga in southern Ecuador, I am aware of two allied species in Ecuador (one of the Amazonian Andean versant of northern Ecuador and another in the valley of the Río Pastaza). The species in the Pastaza valley is possibly *E. chalceus* (Peters). Another allied apparently undescribed species is found in the Andean foothills in Bolivia.

Distribution.—The Amazonian versant of the Cordillera de Matanga, in Provincia Morona-Santiago, Ecuador, at elevations of 1707-2622 m.

Eleutherodactylus cajamarcensis Barbour and Noble Fig. 3C

Lynch (1969a) presented a redescription of this species based largely on series collected between Loja and Saraguro, Ecuador; he also identified some specimens from central Andean Ecuador as possibly conspecific. At that time I anticipated that the specimens from Provincia Tungurahua would prove to be a distinct subspecies and that *E. cajamarcensis* would be collected in the intervening 200 km of interandean Ecuador. The Gustavo Orces-V and James A. Peters collections at the National Museum of Natural History and the continued field work of William E. Duellman and his associates at the University of Kansas yielded more specimens of each population but none from the intervening area. The northern populations represent a related but distinct species of frog having closer relationships with a complex of species including *E. lehmanni* (Boettger) and *E. unistrigatus* (Günther).

Eleutherodactylus cajamarcensis remains known from the Loja basin and transandean Perú at elevations between 1870 and 3000 m. The additional specimens examined do not appreciably enlarge the known distribution given by Lynch (1969a).

Eleutherodactylus colodactylus new species Fig. 3D

Holotype.—KU 142151, an adult female from 13.5 km E Loja, at the crest (Abra de Zamora) on the frontier between Loja and Zamora-Chinchipe provinces, Ecuador, 2800 m, obtained on 22 July 1971 by William E. Duellman.

Paratunes.—KU 142152-59 topotypes; KU 142160-61, 14 km E Loja, Provincia Zamora-Chinchipe, 2770 ii; KU 142162-64, 15 km E Loja, Provincia Zamora-Chinchipe, 2710 m.

Diagnosis.—(1) skin of dorsum and venter areolate; (2) tympanic annulus, cavum tympanicum, and columella absent; (3) snout rounded or obtuse in dorsal view, rounded or truncate in lateral profile; E-N greater than eyc length; (4) interorbital space flat, no cranial crests; upper eyelid width onehalf to three-fourths IOD; (5) vomerine teeth and odontophores present, concealed beneath tissue of palate; (6) male lacking vocal sac and slits; (7) first finger shorter than second, all digits short; distal subarticular tubercles tend to be bifid; all digits bearing discs on pads: dilation ratios I: 1.1, II: 1.2, III: 1.4, IV: 1.4; (8) fingers bearing broad lateral fringes (reducing dilation ratio values); (9) no ulnar tubercles; (10) no tarsal tubercles; prominent tubercle on heel (rounded); (11) two metatarsal tubercles, outer rounded, one-fifth to onefourth size of oval (length twice width) inner; plantar surface areolate, numerous supernumerary tubercles continue onto toes; (12) toes bearing prominent lateral fringes, basal webbing, discs and pads; toe pads as large as those of fingers; (13) dorsum brown (rarely gray) with pale dorsolateral stripes or pale interorbital bar; dark brown canthal and postocular stripes present; limbs not barred; venter cream with varying intensity of brown peppering; (14) adults minute, & & 14.0-20.7, 9 9 16.5-25.8 mm SVL.

Eleutherodactylus colodactulus is readily distinguished from all other eleutherodactyline frogs except E. anotis, E. baryecuus, E. pugnax, E. ruidus, and E. surdus by virtue of having discs on digital pads (and T-shaped terminal phalanges) and lacking the tympanic annulus, cavum tympanicum, and columella. Eleutherodactylus colodactylus has short, stubby fingers (Fig. 7) and toes and does not have readily visible vomerine odontophores in contrast to E. anotis, E. baryecuus, E. pugnax, E. ruidus, and E. surdus all of which are considerably larger frogs (adult females measure—*E. anotis* $\circ \circ$ 39.0-47.0 mm; E. pugnax, $1 \neq 30.8$ mm; E. surdus $\circ \circ 35.5-43.8 \text{ mm}$). Eleutherodactylus colodactylus is included in Cochran and Coin's (1970) group II but has no close relatives among the described species of that group.

Description.—Head as broad as body; head as broad as long; head width 33.1-40.2 percent SVL ($\bar{x} = 36.0$, N = 14); snout obtuse in dorsal view, rounded or truncate in lateral profile; canthus rostralis rounded; loreal region flat, sloping gradually to lip; lips not flared; nostrils weakly protuberant, directed dorsolaterally; snout short, E-N slightly greater than eye length; eyes small; width of upper eyelid 56.3-71.8 percent IOD ($\bar{x} = 63.3$, N = 14); interorbital region flat, no cranial crests; no frontoparietal fontanelle; tympanum absent; tongue large, round, not notched posteriorly, posterior two-fifths free; choanae moderate-sized, round, completely visible when roof of mouth is viewed from directly above, separated by a distance equal to four times width of a choana; no vomerine dentigerous processes, vomerine teeth present (2-4) in a clump beneath skin of palate; male lacking vocal sac and vocal slits.

Skin of body finely areolate; no dorsolateral folds or discoidal folds; upper eyelid bearing one or two small but prominent tubercles; skin of posterior surfaces of thigh and concealed shank smooth; areolation less pronounced on dorsal surfaces; shank 42.0-47.8 percent SVL ($\bar{x} = 44.1$, N = 14); areolation on forearm not enlarged to form ulnar tubercles; two palmar tubercles, median largest, larger than oval thenar tubercle, outer palmar tubercle not always distinguishable from supernumerary thenar tubercles; palmar surface areolate; supernumerary tubercles present on ventral surfaces of digits; subarticular tubercles broader than long, non-conical, tending to bifurcate distally; digits short, broad, flat; edges of digits coalesce proximally to form thick, basal web (Fig. 7); all digits bear pads, pads broader than long; dilation ratios I: 0.9-1.2 $(\bar{x} = 1.1)$, II: 1.1-1.3 $(\bar{x} = 1.2)$, III: 1.3-1.5 ($\bar{x} = 1.4$), IV: 1.3-1.6 ($\bar{x} =$ 1.4); first finger shorter than second.



FIG. 7.—Hands of *Eleutherodactylus* having narrow digital pads. (A) *E. colodactylus*, KU 142154; (B) *E. orestes*, KU 141998; (C) *E. vidua*, KU 120089; line equals 5 mm.

Heel bearing moderate-sized conical tubercle; inner and outer edges of tarsus lacking tubercles or folds; two metatarsal tubercles, not compressed, non-conical, inner larger than outer, inner one and one-half to two times as long as wide, four to five times as large as rounded outer metatarsal tubercle; plantar surface areolate, supernumerary tubercles continue onto toes; subarticular tubercles bifid or wider than long and tending to be bifid; toes short, broad, and flat, lateral edges coalescing to form basal web; all toes bear pads, pads wider than long.

In preservative, the ground color is usually brown (pale to reddish brown) although some individuals have a grav ground color. The venter is speckled with brown and thus appears dark; individuals with pale dorsal coloration appear dirty cream ventrally. The limbs are not barred and the posterior surface of the thigh is uniform brown. All individuals have a dark brown canthal stripe and postocular stripe. Five individuals have silvery or cream flecking in a line above the canthal stripe, across the upper eyclid, and to above the groin as a dorsolateral stripe. In five specimens, the dorsum is flecked with silver or white; the flecks are edged in brown.

In life, *E. colodactylus* was described as "dorsum greenish tan; venter pale yellow; iris reddish bronze" (William E. Duellman field notes 21 July 1971); "dorsum varying from brown to red to tan with or without orange or tan dorsolateral stripes; venter gray; iris reddish-bronze" (W. E. Duellman field notes 22 July 1971).

Measurements of the holotype in

mm.—SVL 20.7, shank 8.7, head width 7.9, eyelid width 1.8, interorbital distance 2.8. The holotype is an adult female with convoluted oviducts and yellow ovarian eggs (2.0-2.3 mm in diameter).

Etymology.—Greek, *kolos* + *dakty-los*, meaning stunted tocs, in reference to the stubby fingers and toes.

Natural history.-All specimens for which data are available were collected in bromeliads by day. Those from the Abra de Zamora and those from Depto. Piurá (Perú) were collected in terrestrial bromeliads (see Duellman, 1974, for a habitat photograph). James A. Peters and his associates collected many (most ?) in arboreal bromeliads at lower elevations (2200-2550 m). The northern-most samples (eastern slopes of Cerro El Picacho, Páramos de Matanga) were taken at lower elevations than the more southern samples and contain smaller frogs (Table 1). There appears to be a cline in size among males; females from the three areas and altitudes do not differ significantly in size.

Remarks.—The specimens from the vicinity of the type-locality exhibit only two pattern morphs (dorsolateral stripes vs a pattern lacking such stripes). Five of 14 specimens have dorsolateral stripes (35.7 percent). Three morphs are evident among the specimens from El Picacho. The dorsolateral stripe morph occurs in 4 of 27 specimens (14.8 percent). An equally abundant morph has a brown hour-glass on the dorsum. The most common morph is gray or brown with or without brown spots and/or cream flecks and may exhibit darker flanks than the center of the back; this

	5	
Altitude	Males	Females
2200-2550 m	$15.9 \pm 0.9 \; (19)^1$	20.4 ± 1.4 (18)
	$11.5 - 20.7^{\circ}$	16.5 - 25.8
2850 m	17.0 ± 0.6 (8)	20.6 ± 0.3 (6)
	15.6 - 18.2	20.1 - 21.2
2745-3100 m	18.3 ± 0.4 (19)	21.5 ± 0.9 (9)
	16.8 - 19.6	19.1 - 23.2
	Altitude 2200-2550 m 2850 m 2745-3100 m	

TABLE 1. Size of Eleutherodactylus colodactylus.

 1 mean \pm 2 standard errors (N)

² Range

morph accounts for 70.4 percent of the specimens and is not more abundant in the El Picacho population than in the populations from the type-locality (64.3 percent). Specimens from Depto. Piurá, Peru, exhibit continuous variation in color pattern from having a few dark flecks to having a well-defined hourglass pattern.

The absence of the middle ear is rare among Eleutherodactylus—I am aware of only five other earless species -E. anotis Walker and Test (Venezuela), E. baryecuus Lynch, E. pugnax Lynch, E. ruidus Lynch, and E. surdus (Boulenger) (all Ecuadorian); all are members of the *unistrigatus* group as currently defined (Lynch 1976a). In these five species, unlike E. colodactylus, the fingers and toes are comparatively long and slender and the vomerine odontophores are prominent structures on the palate. The bifid (or near bifid) distal subarticular tubercles of colodactylus are unlike the "normal" subarticular tubercles found in the other five earless species. Bifid distal subarticular tubercles occur in E. areolatus, a small species found on the Pacific lowlands in Colombia and Ecuador, but the similarity is not convincing evidence of relationship (E. areolatus is a close relative of E. gularis, a member of the diastema group).

In dorsal view, the skull of E. colo*dactylus* is not especially noteworthy; the nasals are comparatively large but not in median contact and are separated from the frontoparietals (Fig. 8). The sphenethmoid is large and extends well anteriad beneath the nasals. The frontoparietals are complete and appear to be fused to the prootics. In ventral view, the vomers are small but not greatly reduced in size. The palatines are short (compare with Fig. 11). The median rami of the pterygoids are short and are widely separated from the parasphenoid alae. The alae of the parasphenoid are weakly deflected posteriorly. An unusual condition is the greatly elongate anterior ramus of the parasphenoid, extending anteriorly to a point anterior to the palatines and between the dentigerous rami of the vomers. This condition is similar to that seen in some of the species of the Phrynopus flavomaculatus group (Lynch, 1975) but E. colodactylus differs markedly in having very short palatines (as well as in digital morphology). The skull of E. colodactylus exhibits the character-states of the Alpha group of Eleutherodactylus.

Distribution.—E. colodactylus is known from the high Amazonian slopes of the Andes in southern Ecuador between 2200 and 2850 m and from the



FIG. 8.—Dorsal (A) and ventral (B) views of skull of Eleutherodactylus colodactylus, KU 142155.

crest and Pacific versant of the Cordillera between Chanchaque and Huancabamba, Depto. Piurá, Perú, at elevations of 2745-3100 m.

Eleutherodactylus cryophilius new species Fig. 9A

Holotype.—USNM 199993, an adult male, obtained 6 km W San Vicente, Provincia Morona-Santiago, Ecuador, 3110 m, on 27 August 1962 by Robert Mullen, Manuel Olalla, James A. Peters, and Peter Spoecker.

Paratypes.—USNM 200391-93, topotypes; USNM 200390, crest between Sevilla de Oro and Méndez, Provincia Morona-Santiago, 3384 m; KU 120091, Laguna de Zurucuchu, Provincia Azuay, 3200 m; AMNH 13970. Bestión on southwestern slopes Cerro Bestión, 3079 m; all from Ecuador.

Diagnosis. -(1) skin of dorsum bearing flattened warts; dorsolateral folds present, indistinct; skin of venter coarsely areolate; (2) tympanum concealed beneath skin; (3) snout subacuminate in dorsal view, pointed in lateral profile; (4) interorbital space broader than upper eyelid; cranial crests prominent; (5) vomerine odontophores triangular in outline, prominent; (6) males lacking vocal sac and slits; (7) first finger shorter than second; all digits bearing discs on narrowly dilated pads; (8) fingers bearing indefinite lateral fringes; (9) no ulnar tubercles; (10) heel and tarsus lacking tubercles; (11) two metatarsal tubercles, outer ½ size of oval, noncompressed inner; supernumerary plantar tubercles indistinct; (12) toes keeled laterally, no lateral fringes; toes bearing discs on narrow pads; (13) brown with darker brown reticulation above; venter pale brown; concealed limb surfaces brown, sometimes with cream spots; upper lip bears cream stripe; (14) adults relatively large, & & 28.9-36.8 mm, 9 9 43.1-49.8 mm SVL.

Eleutherodactylus cryophilius is most similar to *E. buckleyi* (Boulenger) and

E. curtipes (Boulenger); it differs from buckleyi in not having visible tympana and having a dark venter instead of a white to cream venter with brown reticulation. Eleutherodactulus cryophilius resembles E. curtipes in having the tympana concealed but differs in that the tympanic annulus is reduced in size compared to that of E. curtipes. Eleutherodactulus curtipes has lateral fringes on the toes whereas E. cryophilius does not. Although there is considerable geographic variation in size and ventral pigmentation in E. curtipes, no population reaches the body size of E. cryophilius. The largest E. curtipes I have seen include a male 32.5 mm (USNM JAP 5883, 10 km W Baños, Provincia Tungurahua) and a female 42.9 mm (KU 130867, Volcán Pichincha, Provincia Pichincha). The populations (with range, mean and ± 2 standard errors) from which these extremes are drawn have the following sizes-Volcán Pichincha: 12 & δ , range 21.6-30.6 mm SVL ($\bar{x} =$ 26.3 mm \pm 1.6 mm), 8 \circ \circ , range 35.3-42.9 mm SVL ($\bar{x} = 40.4$ mm ± 1.5 mm); 7-10 km W Baños: 26 & & 20.6-32.5 mm SVL ($\bar{x} = 26.6 \text{ mm} \pm 1.0$ mm), 15 \circ \circ , range 32.4-41.8 mm SVL $(\bar{x} = 37.4 \text{ mm} \pm 1.4 \text{ mm})$. Eleutherodactulus buckleyi is about the same size as E. cryophilius [E. buckleyi-31 & & 24.5-38.7 mm SVL ($\bar{x} = 33.1 \text{ mm} \pm 1.7$ mm); 10 $\circ \circ$ 37.1-48.8 mm SVL ($\bar{x} =$ $45.3 \text{ mm} \pm 2.4 \text{ mm}$)].

Description.—Head narrower than body, wider than long, its width 34.6-37.5 percent SVL ($\bar{x} = 33.6$, N = 9); snout subacuminate in dorsal view. pointed in lateral profile; snout short, E-N 68.2-87.2 percent eye length ($\bar{x} =$ 80.0, N = 9; nostrils not or weakly protuberant, directed laterally; canthus rostralis sharp, straight; loreal region weakly concave, sloping abruptly to lips; lips not flared; interorbital space deeply furrowed, furrow extends onto snout (edges of nasals higher than midline; edges of frontoparietals upturned); upper eyelid width 72.5-95.4 percent IOD ($\bar{x} = 81.6$, N = 6; upper eyelid lacking tubercles:



FIG. 9.—(A) Eleutherodactylus cryophilius, KU 120097; (B) E. cryptomelas, KU 120096; (C) E. lymani, KU 119503; (D) E. orestes, KU 120094.

temporal region swollen, tympanic region vertical; supratympanic fold prominent; tympanic annulus small, reduced in size, concealed beneath skin; choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores large, median and posterior to choanae, triangular in outline, bearing a transverse row of 4-5 teeth along posterior margin, each 4-5 times width of a choana, separated by distance equal choanal width; tongue longer than wide, posterior ½ not adherent to floor of mouth, posterior edge feebly notched; males lacking vocal sac and slits.

Skin of dorsum and flanks bearing low, flat warts; indefinite dorsolateral folds present; skin of venter coarsely areolate; discoidal folds indistinct; anal opening not extended in sheath; no ulnar tubercles or fold; palmar tubercle bifid, larger than oval thenar tubercle; supernumerary palmar tubercles present, non-conical, slightly smaller than subarticular tubercles which are round, elevated, simple; fingers bearing indefinite lateral fringes; all fingers bearing discs (broader than long) on pads; pad of thumb not wider than digit below pad, those on fingers II-IV slightly wider than digit below pad; first finger shorter than second; base of thumb swollen in males.

Knee, heel, and tarsus lacking tubereles; inner metatarsal tubercle 2½ times as long as wide, not compressed, twice as large as round, non-elevated outer metatarsal tubercle; supernumerary plantar tubercles obscure, low, flattened, s m aller than subarticular tubercles which are round to slightly longer than wide, non-conical, elevated, simple; toes not bearing lateral fringes (edges of toes weakly keeled); all toes bearing discs (wider than long) on pads; pads slightly broader than width of digit below pad; heels of flexed legs touch; heel of adpressed hind limb reaches eye; hind legs short, shank 42.4-50.3 percent SVL $(\bar{x} = 46.8, N = 9)$.

Brown with darker brown reticulation on dorsun, limbs, and flanks; venter paler than dorsum; groin, concealed limb surfaces brown with or without cream spots; canthal and supratympanic stripes indefinite; upper lip bears cream stripe.

In life, *E. cryophilius* is medium brown with a network of darker brown on the body and limbs; some yellow flecking on flanks; posterior surface of thigh and venter rose-brown, latter flecked with cream. The iris is golden yellow flecked with brown.

Measurements of holotype in mm.— SVL 36.8; tibia 17.3; head width 13.2; head length 11.7; upper eyelid width 2.9; IOD 4.0; eye length 4.4; E-N 3.0. The holotype is an adult male with swollen thumbs and large white testes.

Etymology.—Greek, *kryos*, cold and *philios*, loving; in reference to a habitat preference for the general climate where the species is found.

Natural history.—E. cryophilius was found beneath rocks and logs in subpáramo and páramo habitats on the mountain ranges surrounding the Cuenca hoya. All five adult females are mature and contain large ovarian eggs. The five males have swollen thumbs and large testes.

Remarks.—All available evidence points to E. cryophilius as the southern vicariant of the E. curtipes Artenkreis. The known distribution of E. cryophilius is small compared to those of E. buckleyi and E. curtipes but I am confident E. cryophilius does not range further south. I likewise doubt that E. cryophilius and E. curtipes will prove to be sympatric. The distribution of E. curtipes is totally within Ecuador from the Colombian border south along both Cordilleras to the Palmira desert at the southern end of the Riobamba *houa*. Eleutherodactylus buckleyi is found from northern Ecuador to Cauca and Valle departamentos of Colombia. The vocal apparatus progressively declines and the ear is progressively reduced as one proceeds southward through the series of three species: *E. buckleyi* (vocal slits present, vocal sac subgular; tympanum visible externally)—*E. curtipes* (vocal sac and slits absent; tympanum concealed, annulus large)—*E. cryophilius* (vocal sac and slits absent; tympanum concealed, annulus large)—*E. cryophilius* (vocal sac and slits absent; tympanum concealed, annulus reduced in size).

Distribution.—Known from subpáramo and páramo habitats east and west of Cuenca at elevations of 2835-3384 m.

Eleutherodactylus cryptomelas new species Fig. 9B

Holotype.—KU 141992, an immature female, taken 15 km E Loja, Provincia Zamora-Chinchipe, Ecuador, 2710 m, May 1971 by William E. Duellman.

Paratypes.—KU 141993, taken syntopically with holotype; KU 120095-96, 8-9 km N San Lucas, Provincia Loja, Ecuador, 3000 m; USNM 198480-82, Sapote, Provincia Morona-Santiago, Ecuador, 2470 m; USNM 198483, 2 km W Sapote, Provincia Morona-Santiago, Ecuador, 2560 m.

Diagnosis. (1) dorsum shagreened and bearing conical warts and ridges, skin of venter areolate; no dorsolateral folds; (2) tympanum visible, round, one-third to two-fifths eye length; (3) snout subacuminate in dorsal view, tip pointed, rounded in lateral profile; (4) no cranial crests, interorbital space flat. as wide as or slightly wider than upper evelid; (5) vomerine teeth and odontophores present, odontophores round to oval; (6) males lacking vocal sac and slits; (7) first finger shorter than second; all digits bearing discs on dilated pads: mean dilation ratios I: 1.3; II: 2.1; III: 2.6; IV: 2.5; (8) fingers bearing weakly defined lateral fringes; (9) ulnar tubercles prominent; no enlarged tubercle on elbow; (10) inner edge of tarsus bearing indistinct tubercle, outer edge of tarsus bearing a series of conical tubercles continuing onto heel; (11) two metatarsal tubercles, outer conical, onesixth to one-fourth size of oval inner; numerous supernumerary plantar tubercles; (12) toes fringed, no basal webbing; digits bearing discs on pads, toe pads smaller than those of fingers; (13) dorsum gray to brown sparsely marked with brown; limb bars oblique; venter white to cream reticulated with brown; anterior and posterior thigh surfaces, posterior lower flank, and concealed shank dark black (in life and in preservative); (14) adults of moderate size. 4 males 28.2-30.2 mm, one adult female 38.6 mm SVL.

Eleutherodactulus cryptomelas is a long-legged species with broad digital pads and unlike the other high Andean Eleutherodactylus (short limbs, stocky habitus, comparatively narrow digital pads). The black areas on the concealed thigh and groin together with the tuberculate skin texture (with evelid tubercles, ulnar tubercles, and heel and outer tarsal tubercles) recall the conditions seen in *E. crucifer* (Boulenger) from intermediate elevations on the Pacific slopes of Ecuador. Eleutherodactulus crucifer is green in life with red eyes and upon preservation, loses the black areas in the groin and on the concealed thigh surfaces. The evelid tubercles and the heel and tarsal tubercles of E. crucifer are considerably more prominent than are those of E. cryptomelas.

Description.-Head as wide as or slightly wider than body, head as long as or slightly longer than wide in males, slightly wider than long in females; head width 36.6-41.9 percent SVL ($\bar{x} = 39.9$, N = 8; snout subacuminate in dorsal view, tip tends to be pointed, rounded in lateral profile; canthus rostralis rounded but distinct, slightly concave; loreal region concave, sloping gradually to lips; lips not flared; nostrils near tip of snout, not protuberant, directed dorsolaterally; snout of moderate length, eye length equal to or slightly greater than E-N distance; upper eyelid width 85.7-

112.9 percent IOD ($\bar{x} = 99.2, N = 8$); interorbital space flat, frontoparietal bones complete (no fontanelle), not forming lateral crests (although crests may occur in larger individuals); tympanum prominent, round, its length 30.0-39.1 percent eve length ($\bar{x} = 34.8$, N = 8) (slightly larger in males than in females); upper edge of tympanum partially concealed by thick supratympanic fold; tongue round, weakly notched posteriorly, posterior one-third to twofifths not adherent to floor of mouth; choanae moderate-sized, round, completely visible when palate is viewed from directly above; vomerine teeth and odontophores present, round to oval in outline, each about twice the size of a choana, lying medial and posterior to choanae, separated medially by a distance equal to choanal width, each bearing 3-5 teeth in a transverse row across posterior edge of process; males lacking vocal sac and vocal slits.

Skin of dorsum finely tuberculate and bearing tuberculate ridges beginning at posterolateral corners of upper evelids and converging medially onto scapular region; upper eyelids tuberculate, no tubercle greatly enlarged; flanks weakly tuberculate; throat and venter coarsely areolate, skin on undersurfaces of thighs areolate, that on undersurfaces of forearms, shanks, and tarsi smooth; no dorsolateral folds; discoidal folds prominent, disc ending posteriorly well anterior of groin; forearm bearing prominent ulnar tubercles, that on elbow not greatly elongate; two palmar tubercles, median largest; thenar tubercle oval, larger than either palmar tubercle; thenar surface bearing numerous, low supernumerary tubercles; subarticular tubercles large, round, flattened, simple; fingers bearing ill-defined lateral fringes; digits bearing discs on large pads, pads on thumb smallest; dilation ratios I: 1.2-1.4 ($\bar{x} = 1.3$), II: 1.9-2.2 ($\bar{x} = 2.1$), III: 2.4-3.0 ($\bar{x} = 2.6$), IV. 2.2-2.7 ($\bar{x} = 2.5$); pad on thumb nearly round, those on other fingers broader than long; first finger shorter than second.

Hind limbs of moderate length. shank 49.2-55.4 percent SVL ($\bar{x} = 52.7$, N = 8; inner edge of tarsus bearing a short tubercle-like fold just proximal to inner metatarsal tubercle; outer edge of tarsus bearing a series of enlarged spinelike tubercles beginning on the heel and extending distally to base of fifth toe; inner metatarsal tubercle large, not compressed, twice as long as wide, four to six times size of conical outer metatarsal tubercle; plantar surface bearing numerous weakly-defined supernumerary tubercles; toes bearing lateral fringes and basal webbing (web not extending bevond proximal edge of basal subarticular tubercles except between toes IV and V; subarticular tubercles like those of fingers but smaller; digits bearing dises on rounded pads, pads smaller than those of fingers; heel of adpressed limb reaches to between eye and nostril.

In preservative, E. cryptomelas is grav to reddish-brown above with brown markings (interorbital bar, scapular W, sacral chevron, limb bars). Canthal stripes are absent and labial bars and supratympanic stripes are obscure. The limb bars are oblique and slightly narrower than the interspaces. The venter is off-white or cream with slight to prominent brown reticulation. The dorsal color extends onto the upper flanks where it is abruptly replaced by cream. The posterior lower flanks, anterior and posterior surfaces of the thighs, concealed surfaces of the shank, and axilla are deep black. The black areas in the groin are not continuous across the venter.

In life, *E. cryptomelas* was as follows: "Dorsum tan, reticulated with brown markings; cream lines on upper flank; flanks cream reticulated and spotted with black; black patch in groin; limbs colored as dorsum; posterior surfaces of thighs black; hidden shank cream bronze reticulated with black; venter bronze-cream with less definite black reticulations; iris coppery with broad reddish-copper median stripe." (J. D. Lynch field notes, 16 VI 1968). Measurements of holotype in mm.— SVL 28.5, shank 15.8, head width 11.3, head length 10.5, upper eyelid width 3.2, IOD 3.2, tympanum length 1.2, eye length 3.5, E-N distance 3.5. The holotype is an immature female with straight oviducts and small white ovarian eggs.

Etymology.—Greek, in reference to the black areas on the concealed limb surfaces and in the groin and axilla.

Natural history.—The only specimens of this species available were found beneath rocks or in terrestrial bromeliads in páramo and subpáramo habitats. Four females (19.7-29.1 mm SVL) are immature and show no beginnings of oviducial convolutions or enlargement of eggs. The males lack vocal slits but are mature (enlarged testes, swollen thumbs); hence the species is probably mute. One adult female (JDL 10396) was found by day under a rock ledge beside a stream in a pasture (7 January 1978) 7 km N San Lucas, Provincia Loja, Ecuador, 2840 m.

Remarks .- Too few specimens are available to warrent preparation of a skeleton, thus restricting the number of characteristics with which to compare E. cryptomelas with other species. The appearance of the frog suggests to me that this species is not closely allied to the other high Andean species but is a member of one of the complexes of species found primarily on the Andean slopes. The black areas in the groin and on the concealed thigh surfaces, large digital pads, and row of tubercles along the outer edge of the tarsus serve to distinguish this species from all other congeners.

Distribution.—Known only from elevations between 2470 and 3100 m on the eastern Andean cordillera of southern Ecuador.

Eleutherodactylus lymani Barbour and Noble Fig. 9C

Descriptions of this species are available in Barbour and Noble (1920) and Parker (1932), the latter under the name

E. carrioni (Lynch, 1969a). Several more specimens of *E. lymani* have become available establishing the occurrence of the species in the semi-arid valley of the Río Catamayo in Provincia Loja, Ecuador, as well as in the semi-arid valley of the Río Jubones in Azuay Province, Ecuador. The altitudinal range is 690-2500 m.

Eleutherodactylus orestes new species Fig. 9D

Holotype.—KU 141998, an adult female, obtained 11 km NE Urdaneta, Provincia Loja, Ecuador, 2970 m, 24 July 1971 by William E. Duellman and Bruce MacBryde.

Paratypes.—KU 141999-142003, collected syntopically with the holotype.

Diagnosis.—(1) skin of dorsum finely tuberculate, that of venter areolate; no dorsolateral folds: (2) tympanum obscure, round, its length one-third to one-half that of eye; (3) snout rounded to subacuminate in dorsal view, rounded in lateral profile; E-N less than eye length; (4) interorbital space flat, no cranial crests; upper eyelid width threefourths IOD; (5) vomerine teeth and odontophores visible, odontophores flattened, oval; (6) males with vocal slits and median, subgular vocal sac; (7) first finger shorter than second, all digits bearing discs on moderately dilated pads; dilation ratios I: 1.2, II: 1.3, III: 1.6, IV: 1.5; (8) fingers lacking lateral fringes; (9) ulnar tubercles obscure; (10) inner and outer tarsal tubercles present, outer tarsal tubercles prominent; tubercles on heel small, non-conical; (11) two metatarsal tubercles, outer round, conical, one-half to three-fourths size of non-compressed, slightly longer than wide inner metatarsal tubercle; plantar surface areolate; (12) toes not fringed, basal web present, all bearing discs on pads as large as those of outer fingers; (13) dorsum gray to brown with darker interorbital bar and dorsal chevrons; flanks darker than dorsum; venter gray to pale, brown spotted with brown: groin, anterior and posterior surfaces of thigh, concealed shank black enclosing large white spots; (14) adults small, one & 19.8, \heartsuit \heartsuit 18.1-27.2 mm SVL.

The small size, color pattern, and comparatively narrow digital pads of *E. orestes* prevent its confusion with any of the other named species of *Eleutherodactylus*. It is probably most closely allied to a sympatrant, *E. vidua* sp. nov., from which it differs in having a visible, although obscure, tympanic disk, larger digital pads (see Fig. 7B), and the bold black and white areas in the groin and on the concealed limb surfaces.

Description.—Head narrower than body, slightly wider than long; head width 33.9-37.7 percent SVL ($\bar{x} = 35.4$, N = 12; snout obtuse to subacuminate in dorsal view, rounded in lateral profile; canthus rostralis moderately sharp, weakly concave; loreal region weakly concave, sloping abruptly to lips; lips not flared; nostrils weakly protuberant, directed dorsolaterally, near tip of snout; snout short, E-N much less than eye length; upper eyelid width 68.0-84.2 percent IOD ($\bar{x} = 76.8, N = 11$); interorbital space flat, no cranial crests; frontoparietal bones in median contact, no fontanelle; tympanum present, visible externally although obscure in some specimens, its horizontal diameter 33.3-49.6 percent eye length ($\bar{x} = 41.4$, N = 11); tongue longer than wide, posterior one-fourth to one-third not adherent to floor of mouth, not notched posteriorly; choanae small, situated near edge of palate, partially concealed by palatal shelf of maxillae when roof of mouth is viewed from directly above; vomerine odontophores present, median and posterior to choanae, each process approximately twice the size of a choana, and bearing 4-6 teeth in a patch; odontophores low and flattened; males with median subgular vocal sac and short vocal slits.

Skin of dorsal surfaces finely tuberculate, that of venter areolate; discoidal folds present, poorly defined, ending anterior to groin; vertebral ridge pres-

24

ent; no dorsolateral or paravertebral folds present, except as rows of pustules; skin around anus not modified; ulnar tubercles poorly defined; two palmar tubercles, inner much larger than outer (Fig. 7), inner larger than oval thenar tubercle; palm usually bearing numerous supernumerary tubercles, all low, flat; subarticular tubercles of fingers moderate-sized, round, non-conical, simple: fingers not bearing lateral fringes; digit tips dilated into pads broader than long, bearing discs on ventral surfaces; pads of inner fingers smaller than those of outer fingers; dilation ratios I: 1.1-1.2 $(\bar{x} = 1.2), \text{ II: } 1.0\text{-}1.4 \ (\bar{x} = 1.3), \text{ III: }$ 1.5-1.7 ($\bar{x} = 1.6$), IV: 1.4-1.6 ($\bar{x} = 1.5$); first finger shorter than second.

Hind limbs short, shank 38.3-49.8 percent SVL ($\bar{x} = 42.7$, N = 16); tarsus bearing ill-defined tubercles on inner and outer edges, those on outer edge better defined than inner tarsal tubercle: several small, non-conical tubercles on heel; two metatarsal tubercles, inner larger, one and one-half to two times size of outer (Fig. 10); inner metatarsal tuberele slightly longer than wide, not compressed, outer longer than wide, conical; plantar surface areolate, none of the supernumerary tubercles especially prominent; subarticular tubercles round, not conical, simple; toes not bearing lateral fringes but basally webbed; fifth toe fused to fourth for nearly one-third its (fifth) length (Fig. 10); tips of toes bearing discs on pads, all pads equally large, slightly broader than long.

In preservative, the dorsal surfaces vary from gray to dark brown with darker markings. The dorsal markings include an indefinite interorbital bar and chevrons on the back. The lower flanks are darker than the dorsum and suffused with dark brown marbling. The limbs are barred. The face is gray to dark brown with markings (labial bars, canthal stripe) visible in the more pale individuals but not in the more darkly pigmented individuals. The venter varies from dusky gray to pale brown usually marbled and spotted with brown.



FIG. 10.—(A) Foot of Eleutherodactylus orestes, KU 141995; (B) foot of E. phoxocephalus, KU 142063; line equals 5 mm.

The throat tends to be paler than the spots on the venter. The groin, anterior thigh, posterior thigh, concealed shank, and concealed tarsus are dark brown to black with large white spots. This pattern is also evident in the axillae of a few individuals.

In life, *E. orestes* is brown (rarely black) above with brown markings. The venter is gray with cream and/or dark brown to black spots. The posterior surface of the thigh and groin are black bearing ivory white, bluish-white, or pale pink spots. The iris is gray-bronze with a brown median horizontal streak.

Measurements of the holotype in mm.—SVL 23.7, tibia 9.4, head width 8.4, head length 7.8, upper eyelid width 2.4, IOD 2.8, tympanum length 0.75, eye length 2.9. The holotype is a gravid female with heavily convoluted oviducts and large, yellow, ovarian eggs.

Etymology.—Greek, *Orestes*, a mountaineer.

Natural history.—Adult females collected in May, June, and July have large eggs but no egg masses have been found. The frogs have been taken from terrestrial bromeliads but most individuals were found beneath stones, in dirt banks, or in mulch in *subpáramo* habitats. A single male has been collected—it has vocal slits but was not observed or heard calling. No amplectant pairs have been found.

Remarks.—The skull of E. orestes differs from those of most Andean Eleutherodactulus in that the nasals are perceptibly separated (Fig. 11). The sympatric E. vidua has a similar arrangement of the nasal bones. The frontoparietals appear to be fused to the prootics and have a narrow, anterior fontanelle. The sphenethmoid is relatively large and extends anteriorly about onehalf way beneath the comparatively small nasals. In ventral view, the vomers are relatively small and separated medially. The palatines are moderately long (compare with those of E. colodactylus). The anterior ramus of the parasphenoid is neither greatly shortened nor elongate. The parasphenoid alae are oriented at right angles to the anterior ramus and in tenuous contact with the median rami of the pterygoids. The zygomatic ramus of the squamosal is greatly shortened (Fig. 12), recalling the condition usually seen in West Indian species of *Eleutherodactylus*.

The comparatively narrow digital pads and the color pattern in the groin caused me initially to suspect that this species was Paludicola simonsii (=Phrynopus simonsii) named by Boulenger (1900) from Cajamarca, Perú. Certain discrepancies in the description of simonsii prompted reservations which were borne out following examination of the cotypes of that species. However, the large sphenethmoid and separated nasal bones are features usually associated with frogs of the genus *Phrynopus* (although not of the group to which simonsii belongs). The skulls of E. orestes and E. vidua do resemble those of the Phrynopus wettsteini group but the digital structure (external and internal) of these narrow-toed *Eleutherodac*tylus precludes assignment of these species to Phrynopus.

Distribution.—Eleutherodactylus orestes occurs at elevations between 2720 and 3120 m on the eastern Andean cordillera from the Cuenca hoya to the Loja hoya in southern Ecuador.

Eleutherodactylus percultus new species Fig. 13A

Holotype.—KU 166058, an adult male, obtained at the Abra de Zamora, Provincia Zamora-Chinchipe, Ecuador, 2850 m, on 8 March 1975 by Dana K. Duellman.

Paratype.—KU 166057, an adult female topotype, obtained on 7 March 1975.

Diagnosis.—(1) skin of dorsum shagreened anteriorly, covered with large flat warts posteriorly, that of venter areolate; no dorsolateral folds; (2) tympanum prominent, its length %-½ eye length; (3) snout subacuminate in dorsal view, tip pointed, acutely rounded in lateral profile, long; (4) upper eyelid narrower than IOD; low cranial crests; (5) vomerine odontophores prominent, triangular in outline; (6) males lacking vocal sac and slits; (7) first finger shorter than second; all fingers bearing broad discs on dilated pads; (8) fingers bearing lateral fringes; (9) ulnar tubercles non-conical; (10) heel tubercles subconical; outer edge of tarsus and foot bearing large conical tubercles; ventral surface of tarsus bearing non-conical warts; (11) two metatarsal tubercles, inner oval, non-compressed, 4 times size of outer; numerous supernumerary plantar tubercles; (12) toes bearing lateral fringes and broad discs on dilated pads; toe pads as large as those of fingers; (13) brown with gray and dark brown flecking and marbling; venter cream; flanks spotted with brown; upper lip bearing broad cream stripe from tip of snout to tympanum; in life, upper lip red; (14) adults moderate-sized, one a 29.8 mm, one 9 38.2 mm SVL.

On the basis of its coloration *E. percultus* is readily distinguished from all other *Eleutherodactylus*. Several spe-



FIG. 11.—Skulls of Andean Eleutherodactylus. (A-C) lateral, dorsal, and ventral views of E. nicefori, KU 150724; (D-E) dorsal and ventral views of E. orestes, KU 151052; (F-G) dorsal and ventral views of E. vidua, KU 120093; line equals 5 mm.





FIG. 12.—(A) Right squamosal of *Eleutherodactylus unistrigatus* (JDL S-263) and posterolateral corners of skulls of (B) *E. orestes*, KU 151052, and (C) *E. vidua*, KU 120093.



FIG. 13.—(A) Eleutherodactylus percultus, KU 166058; (B) E. phoxocephalus, KU 131408; (C) E. versicolor, KU 119858; (D) E. vidua, KU 120089.

cies have color variations including a pale lip stripe (*E. achatinus*, *E. fitzingeri*, *E. lanthanites*, *E. pygmaeus*, *E. rhodopis*) but in all of these the stripe is whitish or bronze-yellow in life and the labial pigmentation is all that distinguishes the morph from other individuals of the species. *Eleutherodactylus percultus* resembles *E. balionotus* in tuberculation of the tarsus, size of the digital pads, and proportions but is nearly twice as large, males lack vocal sac and slits, and the skin on the anterior one-half of the body is shagreened rather than tuberculate.

Description.—Head as broad as body, broader than long; snout rounded with pointed tip to subacuminate in dorsal view, acutely rounded in lateral profile: snout long; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis rounded but evident: loreal region flat, sloping gradually to lips; lips weakly flared; interorbital space broader than upper eyelid; edges of frontoparietals upturned slightly; upper eyelid bearing small, non-conical tubercles: temporal region sloping: supratympanic fold thick, concealing upper edge of tympanum: tympanum distinct, round, separated from eve by 1½ times its diameter: postrictal tubercles prominent, non-conical: choanae moderate-sized to small. round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, elevated, triangular in outline, each 1-4 times size of a choana, separated by distance nearly equal odontophore width, each bearing 4-5 teeth in transverse row across posterior border; tongue slightly longer than broad, posterior % not adherent to floor of mouth, posterior edge notched; male lacking vocal sac and slits.

Skin of dorsum shagreened anteriorly, covered with large flat warts posteriorly; that of flanks and limbs like that of lower back; no dorsolateral folds; skin of venter coarsely areolate; discoidal folds not prominent; ulnar tubercles nonconical; palmar tubercle bifid, as large as oval thenar tubercle; supernumerary palmar tubercles indistinct; subarticular tubercles round, non-conical, simple; fingers bearing lateral fringes; all fingers bearing discs (broader than long) on pads; pads rounded apically; dilation rations: I: 1.5-1.8; II: 1.8-2.7; III: 2.1-2.7; IV: 1.8-2.4; first finger shorter than second; thumb swollen in male.

Knee and heel tuberculate; tubercles on heel subconical; outer edge of tarsus and sole bearing large conical tubercles; inner edge of tarsus bearing row of low warts; ventral surface of tarsus bearing non-conical warts; inner metatarsal tubercle twice as long as wide, non-compressed, four times size of elongate, nonconical outer; plantar supernumerary tubercles numerous, obscure; subarticular tubercles round, low, simple; toes bearing lateral fringes coalescing at base of toes forming basal web (enclosing proximal one-half of proximal subarticular tubercle on toes I-IV); all toes bearing discs (broader than long) on dilated pads; pads of toes as large as those of fingers; hind limbs long; heels of flexed hind limbs overlap; heel of adpressed hind limb reaches between eye and nostril.

Brown above flecked with gray and darker brown; limb bars not evident; upper lip bearing cream stripe from tip of snout to tympanum; flanks spotted brown; venter cream with or without brown spots; undersides of limbs mottled brown; posterior surface of thigh brown with indefinite cream reticulation or flecking; anal triangle indistinct.

In life, *E. percultus* was "Dull olivebrown becoming reddish brown posteriorly and on limbs. Flanks bluish gray mottled with black. Upper lip bright orange. Throat creamy white with orange flecks. Belly bluish gray. Iris black with greenish gold flecks" (W. E. Duellman field notes, 7 March 1975).

Measurements in mm (holotype, paratype).—SVL 29.8, 38.2; tibia 15.5, 21.2; head width 12.1, 15.0; head length 11.0, 13.2; upper eyelid width 3.4, 3.2; IOD 3.9, 4.3; tympanum length 1.5, 2.0; eye length 3.5, 4.4; E-N 3.4, 4.3. The holotype is an adult male with swollen thumb and large, non-pigmented, granular testes. The venter bears few spots.

Etymology.—Latin, meaning highly adorned, in reference to the orange lip stripes.

Natural history.—The holotype was found in a terrestrial bromeliad during the day. The paratype, a gravid female, was found on a branch of a bush at night.

Eleutherodactylus phoxocephalus new species Fig. 13B

Holotype.—KU 142075, an adult male, obtained at Pilaló, Provincia Cotopaxi, Ecuador, 2340 m, on 7 July 1971 by William E. Duellman and Linda Trueb.

Paratypes.—KU 142076-103, collected with the holotype.

Diagnosis.-(1) skin of dorsum shagreened, that of venter areolate; no dorsolateral folds; (2) tympanum visible, round, its length one-third to one-half that of eye; (3) snout round in dorsal view except for pointed tip (a vertical keel), pointed in lateral profile; E-N slightly greater than eye length; (4) interorbital space flat, no cranial crests, upper evelid width narrower than IOD; (5) vomerine teeth and odontophores present, odontophores slanted and teardrop-shaped; (6) males with vocal slits and subgular vocal sac; (7) first finger shorter than second; all digits bearing discs on dilated pads, dilation ratios: I: 1.6, II: 2.1, III: 2.3, IV: 2.2; (8) fingers bearing indistinct lateral fringes; (9) ulnar tubercles inconspicuous or absent: (10) tarsal surfaces lacking tubercles or folds (occasional individuals have indistinct outer tarsal tubercles); (11) two metatarsal tubercles, outer conical, round, one-sixth to one-fourth size of oval inner; plantar surfaces areolate; (12) toes bearing lateral fringes and basal webbing; all toes bearing discs on pads, pads on outer toes larger than those on inner toes, toe pads smaller than those of fingers; (13) dorsum gray to brown, brown most evident posteriorly; little or no dorsal color pattern evident; groin, lower flanks, axilla, concealed surfaces of hind legs bearing white field bordered by and reticulated with dark brown or black; venter dirty cream, usually without brown flecking; (14) adults small to moderate-sized, males 22.3-29.9 mm, females 29.6-38.4 mm SVL.

Eleutherodactylus phoxocephalus is unlikely to be confused with other species of Eleutherodactylus because it has a vertical keel at the tip of the snout; E. phoxocephalus is superficially similar to a frog called E. cruentus by Ruthven (1922) and Cochran and Goin (1970). That frog lacks a keel on the snout (it has a pointed snout), has slightly longer legs and a slightly broader head than *E. phoxocephalus*, and has a shorter snout (E-N three-fourths to four-fifths eye length compared to the nearly equal E-N and eye length of *E. phoxocephalus*).

Description.—Head narrower than body, wider than long; head width 33.4-38.0 percent SVL ($\bar{x} = 36.1, N = 40$) (females have slightly broader heads than do males); outline of head semicircular in dorsal view except for vertical keel at tip of snout, in lateral profile snout pointed, tip extending beyond edge of lower jaw; canthus rostralis obtuse or rounded, concave; loreal region flat, sloping gradually to non-flared lips; nostrils weakly protuberant, directed dorsolaterally; snout of moderate length, E-N 78.4-100.0 percent eye length in males $(\bar{x} = 93.7, N = 20)$, 94.7-113.3 percent in females (\bar{x} = 102.6, N = 20; upper eyelid width 72.5-106.7 percent IOD ($\bar{x} = 92.5$, N = 40); interorbital space flat, no cranial crests; frontoparietals complete, no fontanelle; supratympanic fold not prominent, but concealing upper edge of tympanum; tympanum round, distinct, oblique in orientation (directed dorsolaterally and somewhat posteriorly), separated from eye by distance equal to one-half tympanic diameter; tympanum of male smaller than that of female, tympanum length 32.4-54.5 percent eye length in males ($\bar{x} = 40.3$, N = 20), 38.5-54.7 percent in females ($\bar{x} = 46.1$, N = 20; tongue longer than wide, posterior one-half to two-fifths not adherent to floor of mouth, notched posteriorly; choanae small, round, completely visible when palate is viewed from directly above; vomerine odontophores lie median and posterior to choanae, each is larger than a choana, separated medially by distance less than width of a choana, bearing 1-7 teeth; odontophores strongly slanted (oblique) and not greatly elevated above palatal surface; males have short vocal slits and a large external. subgular vocal sac.

30
Skin of dorsum finely shagreened without folds or large warts except for thin sagittal ridge in larger females; flanks and skin posterior to ear areolate; skin of venter coarsely areolate, that of throat shagreened; concealed surfaces of limbs smooth except about vent; discoidal folds prominent.

Most specimens lack ulnar tubercles or folds other than the antebrachial tubercle: palmar tubercle bifid, larger than oval thenar tubercle; palm bearing scattered supernumerary tubercles; subarticular tubercles simple, round, non-conical: fingers bear weak, keel-like lateral fringes; all digits bearing discs on dilated pads, pad of thumb slightly wider than long, those on other fingers distinctly wider than long; dilation ratios I: 1.5-1.8 $(\bar{x} = 1.6)$, II: 1.7-2.5 $(\bar{x} = 2.1)$, III: 1.9-2.6 ($\bar{x} = 2.3$), IV: 1.9-2.6 ($\bar{x} =$ 2.2); first finger shorter than second; outer edge of hand bearing a cutaneous fold.

Hind limbs of moderate length, shank 41.7-52.8 percent SVL ($\bar{x} = 47.5$, N = 40) (shank of males slightly longer than those of females); limbs lacking tubercles except for faint inner tarsal tubercle in most individuals and a trace of outer tarsal tubercles in some individuals; inner metatarsal tubercle twice as long as wide, not compressed, four to six times as large as rounded, weakly elevated outer metatarsal tubercle (Fig. 10); toes bearing lateral fringes and a brief basal web (web not reaching base of basal subarticular tubercles except that between toes IV and V); plantar surface bearing numerous supernumerary tubercles; subarticular tubercles like those of fingers but smaller; toes bearing discs on dilated pads, pads of toes wider than long, about same size as those of fingers.

In preservative, *E. phoxocephalus* is gray-brown above with the lower back more brown than gray. The body usually lacks any trace of a color pattern. The posterior surfaces of the thighs are white with black edging and black reticulations on the white field. A similar pattern is evident in the groin and on the anterior surface of the thighs. The venter is dirty cream with indefinite brown flecking (weak reticulation). The throat and breast lack reticulation and are vellowish-cream. A few adults do exhibit diffuse color patterns. Some individuals have brown and black flecking forming a loose pattern of chevrons, circles, and lines on the back. A frequent pattern consists of a dirty-brown spot on the snout and another above the sacrum. No individual has distinct limb bars although a few have faint transverse bars on the shanks. An individual from the slopes of Volcán El Corazon (KU 109137) has a canthal stripe and a series of short black interrupted stripes on the dorsum (similar to the color pattern exhibited by E. ornatissimus).

In life, E. phoxocephalus was described as follows: "Iris pale bronze with fine black reticulations and a brown horizontal streak; ground color highly variable-pale greenish-brown, pale yellow, rusty brown, and light to dark brown, mottled and finely reticulated with brown to black (black toward center of back); axilla, groin, posterior thigh and concealed shank yellow, reticulated with dark brown (reticulations on flash colors developed ontogenetically); venter cream, faintly washed with green, finely reticulated with brown; throat of female dusky, of male pale yellow, individuals having pale dorsal spots have enamel-cream or cream spots edged in black" (J. D. Lynch field notes, 3 July 1970).

Measurements of holotype in mm.— SVL 27.9, shank 13.6, head length 10.6, head width 10.4, upper eyelid width 2.9, IOD 3.5, tympanum length 1.3, eye length 3.2, E-N 3.2. The holotype is an adult male with vocal slits and a vocal sac. The testes are small and granular.

Etymology.—Greek, in reference to the keel at the tip of the snout which gives the frog a "pointed head" appearance.

Natural history.—In subpáramo habitats south of the type-locality, *E. phoxocephalus* has been found beneath rocks as well as in terrestrial bromeliads. At the type-locality, this species was the most abundant eleutherodactyline frog encountered in early July but nearly every specimen found was taken from bromeliads. The bulk of the bromeliads checked were the large terrestrial plants where other animals (*Gastrotheca* and *Proctoporus* as well as two other *Eleutherodactylus*) were found, but *E. phoxocephalus* was also taken in bromeliads in trees up to 3 meters above the ground.

Sporadic calling at night from the large terrestrial bromeliads was heard in early July 1970, and late June 1977, but could not be identified to a particular frog. In January 1978, male E. phoxocephalus were actively calling at night and during afternoon rains. The call is a single sharp whistle. Males were calling on bushes and trees up to 5 m above the ground. Gravid females were taken in number during June and July. Individuals placed together frequently engaged in axillary amplexus, and one amplectant pair was found in a bromeliad (June 1970). The smallest gravid female collected is 29.6 mm SVL—the largest juvenile female (small ovarian eggs, nonconvoluted oviducts) is 30.1 mm SVL. The smallest "adult" male (with vocal slits) found is 22.3 mm SVL. A subadult male (no vocal slits) is 21.0 mm SVL.

Remarks.—The southern samples of E. phoxocephalus (Azuay, Cañar, Loja, and Zamora-Chinchipe provinces) were taken in subpáramo habitats at elevations between 2060 and 2960 m. The northern samples (Cotopaxi and Pichincha provinces) were taken in cloud forest habitats at elevations between 2030 and 2580 m. In spite of the striking ecologic differences among localities, the frogs all seem to be conspecific. Collections made at the appropriate elevations in Provincia Bolivar failed to yield specimens of this species, but the absence may have been due to the locally arid environments around Guaranda. I was unable to collect at what seemed to be ideal habitat between Guaranda and Balzapamba (elevation of 2000-2200 m).

In attempting to discover if this species had been previously named, I encountered specimens of a similar species from Colombia identified as E. cruentus. The frog Ruthven (1922) reported from Colombia under this name is not cruentus of Peters. That frog was named E. dubitus by Taylor (1952) from Costa Rica and E. marshae by Lynch (1964) from Panamá (as pointed out by Savage, 1965) and is similar to, but not identical with, E. latidiscus (Boulenger) of the Pacific lowlands of Colombia and Ecuador. The Colombian frog confused with cruentus by Ruthven and Cochran and Goin (1970) apparently is unnamed.

Distribution.—Intermediate elevations (2030-2960 m) on the Pacific slopes of the Ecuadorian Andes from Volcán El Corazon to the Loja *hoya*; *E. phoxocephalus* enters the interandean *hoja* south of Cuenca and occurs along the northern and eastern edges of the Loja *hoja*.

Eleutherodactylus proserpens new species Fig. 14

Holotype.—USNM 198484, an adult female obtained between Sapote and Suro Rancho, Provincia Morona-Santiago, Ecuador, 2622 m, by M. Olalla on 24 August 1962.

Paratypes.—USNM 198486-91, ½ km W Sapote, 2546 m; USNM 198492-95, 198502, bet. Sapote and Suro Rancho, 2622 m; USNM 198496-98, mountain above Sapote to south, 2500 m; USNM 198499-501, 1 km E Sapote, 2332 m; all Provincia Morona-Santiago, Ecuador.

Diagnosis.—(1) skin of body areolate, no dorsolateral or discoidal folds; anal opening extended by skin sheath onto posterior surface of thighs; (2) tympanum prominent, round, its length ½-½ that of eye; (3) snout subacuminate in dorsal view, round to pointed in lateral profile, tip bearing papilla; (4) interorbital space flat, broader than upper eyelid width; (5) vomerine odontophores low, oval; (6) males lacking vocal sac and slits; (7) first finger shorter



FIG. 14.—(A-B) head of *Eleutherodactylus proserpens*, USNM 198499; (C) hand of *E. proserpens*, USNM 198494; lines equal 1 mm.

than second; all digits short, stocky, bearing discs on broad, non-emarginate pads; distal subarticular tubercles of III and IV bifid; (8) fingers bearing ridgelike lateral fringes; (9) no ulnar tubercles or folds; (10) knee, heel, and tarsus lacking tubercles; (11) two metatarsal tubercles, inner twice size of outer; plantar surface areolate; (12) toes bearing ridge-like lateral fringes; toes short, stocky, bearing discs on broad pads; (13) color pattern polymorphic, most common morph is: dorsum tan to brown with darker brown limb bars, interorbital bar, X-shaped mark on back, postocular bar; venter pale brown; posterior thigh cream to brown; other frogs have pale dorsolateral stripes; (14) adults small, males 15.2-21.0 mm, females 20.2-23.5 mm SVL.

Eleutherodactylus proserpens is similar to E. celator Lynch and E. colodactylus Lynch in size, having rounded canthi, short limbs, and areolate skin. It resembles *E. colodactylus* in having stubby digits. Some of these features may be adaptations to living in bromeliads (where all known examples of all three species have been found). *Eleutherodactylus proserpens* differs from *E. celator* and *E. colodactylus* in having an anal sheath and differs from *E. colodactylus* in having fully developed ears and prominent vomerine odontophores. *Eleutherodactylus proserpens* differs from *E. celator* in having a prominent papilla on the snout.

Description.—Head as wide as body (not as wide as body in gravid females), wider than long; head width 31.8-40.6 percent SVL ($\bar{x} = 34.1$, N = 15); snout acuminate in dorsal view, tip pointed, round or weakly pointed in lateral profile; snout long, E-N 87.8-122.2 percent eye length ($\bar{x} = 105.5$, N = 15); canthus rostralis rounded, straight; nostrils not protuberant, directed dorsolaterally; loreal region weakly concave, sloping

gradually to lips; lips not flared; interorbital space flat, no cranial crests; upper evelid width 54.2-78.3 percent IOD $(\bar{x} = 63.0, N = 13)$ (eves small); supratympanic fold thick, concealing upper edge of tympanum; tympanum distinct, round, separated from eve by 11/2-2 times tympanic diameter, its length 30.3-50.0 percent eye length ($\bar{x} = 38.2$, N = 15); one to several non-conical tubercles on upper eyelid; tongue moderate-sized, 1½ times as long as wide, posterior edge not notched, posterior % not adherent to floor of mouth; choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores round, low, posterior and median to choanae, separated by 1/2-1/2 width of a choana or odontophore, each bearing clump of 2-4 teeth; males lacking vocal sac and slits.

Skin of body areolate (smooth skin in axillae, groin, behind knee, concealed shank and tarsi); no dorsolateral folds; anal opening enclosed in sheath extending vent onto posterior surfaces of thighs; no discoidal folds; ulnar tubercles not distinct from areolations of skin except for antebrachial tubercle; two palmar tubercles, inner largest, slightly larger than oval thenar tubercle; numerous supernumerary palmar tubercles; basal subarticular tubercles broader than long, non-conical; distal subarticular tubercles of fingers III-IV bifid; fingers bearing ridge-like lateral fringes; all fingers bearing discs on dilated pads; discs slightly broader than long; all digits short; first finger shorter than second.

No prominent tubercles on knee or heel (each does have one larger areolation but this wart is not conical or elongated); tarsus lacking distinct tubercles or folds; outer metatarsal tubercle round, non-conical, %-% size of elongate, non-compressed inner metatarsal tubercle; numerous supernumerary plantar tubercles, some as large as subarticular tubercles; subarticular tubercles round, non-conical, simple; toes bearing ridgelike lateral fringes and basal webbing (coalesced lateral fringes); toes bearing discs on round pads; discs as broad as long; all toes short; shank short, shank of males 41.0-47.2 percent SVL ($\bar{x} = 43.3$, N = 11), of females 37.8-46.4 percent ($\bar{x} = 40.7$, N = 7).

In preservative, tan to brown or reddish-brown above with brown interorbital bar, X-shaped mark on back, postocular bar, and limb bars; or with same ground color—and cream dorsolateral stripes edged medially with dark brown; all have gray to brown venter. Eleven individuals have the first pattern listed above; two others have a single blotch extending from the eyes to the sacrum (dorsal pattern similar to that of *Hyla leucophyllata*); five have pale dorsolateral stripes enclosing a dark dorsum; and two have dark dorsolateral stripes enclosing a pale dorsum.

In life, \vec{E} . proserpens was described as "dorsum orange with gray markings, venter gray; dorsum rusty brown with darker brown markings, venter pale yellow with minute brown flecks; and dorsum tan, venter light tan" (John E. Simmons field notes, 4-7 January 1972).

Measurements of holotype in mm.— SVL 22.5; tibia 8.5; head width 7.3; upper eyelid width 1.6; IOD 2.5; tympanum length 0.9; eye length 2.0; E-N 2.2. The holotype is a gravid female with convoluted oviducts and large ovarian eggs (2.5-2.7 mm diameter).

Etymology.—Latin, one who creeps, in reference to the short limbs and presumed non-hopping gait of this small frog.

Natural history.—All of the specimens secured by Peters and his associates were collected in bromeliads. All males over 15 mm SVL have large granular testes (lacking brown or black peritoneal linings) and swollen thumbs. Peters' field notes are not precise but apparently *E. proserpens* and *E. colodactylus* were collected in the same bromeliads. Both species are of similar size and coloration and could be easily confused in life. The specimens collected by John Simmons on the Cordillera del Condor were found on low vegetation at night. Gravid females were found in January and August.

Remarks.—At present, E. proserpens seems to be related to E. colodactylus, and I know of no other species sufficiently similar to these two to be considered close relatives. Eleutherodactylus proserpens is larger than E. colodactylus (adult females of former $\bar{x} = 22.0$, of latter $\bar{x} = 20.5$) and the size difference is significant (p < 0.05); the size differential ($\phi = 1.07$) is much lower than that suggested by Hutchinson and Mac-Arthur (1959) as adequate to prevent competition.

Distribution.—Known at elevations between 1707-2622 m on the Amazonian slopes of the castern Andean Cordillera in southern Ecuador and from the adjacent Cordillera del Condor.

Eleutherodactylus pycnodermis new species Fig. 15

Holotype.—USNM 199754, adult female taken at San Vicente, Provincia Morona-Santiago, Ecuador, 2805-2835 m, by James A. Peters on 26 August 1962.

Paratypes.—(Provincia Azuay) USNM 199851-53, 3 km E Sevilla de Oro, 2713 m; USNM 199854, 5 km ESE Sevilla de Oro, 2957 m; USNM 199855-59, crest at Azuav-Morona-Santiago border, ca. 8 km SE Sevilla de Oro, 3354 m; USNM 199758-59, 199860-65, crest at Azuay-Morona-Santiago border, ca. 8 km SE Sevilla de Oro, 3384 m; (Provincia Morona-Santiago) USNM 199755-57, between Cerro Negro and Pailas, 2652 m; USNM 199815-50, San Vicente, 2805-35 m; USNM 199813-14, San Vicente, 2851 m; USNM 199794-812, 3 km W San Vicente, 2988 m; USNM 199787-93, 6 km W San Vicente, 3100 m; USNM 199760-66, Suro Rancho, 2683 m; USNM 199767-86, 0.5 km W Suro Rancho, 2744 m.

Diagnosis.—(1) skin of dorsum thick and glandular, surface texture coarsely shagreened; no dorsolateral folds; skin of venter coarsely areolate;



FIG. 15.—Eleutherodactylus pycnodermis, USNM 199801; line equals 10 mm.

(2) tympanum prominent, its length $\frac{1}{4}$ - $\frac{1}{2}$ eye length; (3) snout subacuminate in dorsal view, truncate in lateral profile; (4) interorbital space broader than upper eyelid; low cranial crests present; (5) vomerine odontophores prominent, oblique in males, triangular in outline in females; (6) males with vocal slits and subgular, external vocal sac; (7) first finger shorter than second; fingers bearing discs on broad pads; (8) fingers bearing narrow lateral fringes; (9) no ulnar tubercles except antebrachial; (10) no tubercles on heel or tarsus; (11) two metatarsal tubercles, inner oval, 4 times size of outer; few plantar supernumerary tubercles; (12) toes bearing lateral fringes; pads on toes dilated, smaller than those of outer fingers; (13) brown without limb bars; large black blotches on flanks, concealed surfaces of thigh, shank, and tarsus; venter creamy, frequently spotted with brown; (14) adults moderate-sized, males 18.0-32.3 mm, females 32.5-44.4 mm SVL

Two features set *E. pycnodermis* apart from the other nearly 400 species of the genus—none has the thick glandular skin covering the dorsal surfaces of the body and limbs and no other species has the very distinctive color pattern of this frog. Like most other highland

Ecuadorian species of *Eleutherodactylus*, *E. pycnodermis* has short legs and some evidence of cranial crests.

Description.-Head narrower than body, wider than long; head width 34.6-41.1 percent SVL ($\bar{x} = 37.5$, N = 35); snout subacuminate in dorsal view, truncate in lateral profile; snout short, E-N 65.8-82.1 percent eye length in males $(\bar{x} = 72.8, N = 16), 73.3-95.1$ percent in females ($\bar{x} = 82.8$, N = 18); nostrils not protuberant. directed dorsolaterally; canthus rostralis sharp, straight; loreal region weakly concave, sloping abruptly to lips; lips not flared; interorbital space flat, edges of frontoparietals weakly upturned forming low cranial crests; upper eyelid width 67.4-111.1 percent IOD $(\bar{x} = 89.2, N = 25)$; no tubercles on eyelid; temporal region vertical; supratympanic fold present, concealing upper edge of tympanum; tympanum prominent, round, its length 22.6-48.7 percent eve length in males ($\bar{x} = 35.4$, N = 16), 32.5-50.0 percent eye length in females $(\bar{x} = 40.2, N = 18)$, separated from eye by tympanic width; choanae moderate sized, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, each 1½-2 times size of a choana. oblique in smaller individuals (males and young females), triangular in outline in large females, elevated, bearing a transverse row of 3-7 teeth along posterior edge; tongue longer than wide, posterior % not adherent to floor of mouth, its posterior border not notched; males with vocal slits, large external vocal sac.

Skin of dorsum and limbs coarsely shagreened, very thick and glandular; no dorsolateral folds; skin of flanks smooth, that of venter coarsely areolate; discoidal folds prominent; no anal sheath; antebrachial tubercle prominent, no other ulnar tubercles; palmar tubercle bifd, larger than oval thenar tubercle; supernumerary palmar tubercles present, indistinct; subarticular tubercles round, elevated, non-conical; fingers bearing weak lateral fringes; all fingers bearing broad discs on dilated, apically rounded pads; pads on fingers II-IV larger than tympanum; first finger shorter than second.

No distinct tubercles on knee, heel, or tarsus; inner metatarsal tubercle elevated, non-compressed, its length $1\frac{1}{2}$ times its width, 4 times size of low, rounded outer metatarsal tubercle; supernumerary plantar tubercles obscure, small; subarticular tubercles round, low; toes bearing narrow lateral fringes; toes bearing broad discs on dilated pads; pads of toes smaller than those on outer fingers; when legs are flexed at right angles to body, heels overlap; heel of adpressed hind limb reaches to tympanum; shank 39.4-49.2 percent SVL ($\bar{x} = 43.5$, N = 35).

In preservative dark brown without limb bars, dorsal spotting, labial bars, or canthal and supratympanic stripes; large black blotch behind eve extending onto anterior flank, smaller blotch on upper arm, large blotch on posterior flank extending to above insertion of hind leg with a lateral ramus extending along anterodorsal surface of thigh to knee, another on posterior surface of thigh from vent to knee, another along concealed surface of shank, and one or two on dorsal surface of tarsus and foot: black blotches edged above by cream; no anal triangle; inner digits creamyyellow; venter dull cream or yellowish cream lightly to heavily spotted with brown; ventral to the black areas in the axilla, groin, and posterior thigh, the skin is pale yellow.

Unfortunately colors in life were not recorded by the collectors nor were colored photographs taken of this abundant species.

Measurements of holotype in mm.— SVL 37.3; tibia 16.6; head width 13.6; upper eyelid width 3.6; IOD 4.3; tympanum length 1.6; eye length 4.0; E-N 3.2.

Etymology.—Greek, *pyknos* and *derma*, meaning thick skin, in reference to the distinctive thick glandular skin of this species.

Natural history.—Eleutherodactylus pycnodermis was collected in páramo as well as in meadows within the upper reaches of montane forests 700 meters lower on the Andean slopes. All specimens having specific field notes were collected by day beneath rocks and logs. Many males have wrinkled, distended vocal sacs and one adult female (USNM 199841) had ovulated. None of the adult females is spent. The smallest adult female is 32.5 mm SVL. Several young females (weakly convoluted oviducts, small ovarian eggs) are larger than the smallest adults. Twelve young females are 28.1-35.7 mm SVL [$\bar{x} = 32.1$ $\pm 1.5 \ (\pm 2 \text{SE})$].

Remarks.—Eleutherodactylus pycnodermis is a member of the unistrigatus group (Lynch, 1976a) but its peculiarly thick skin is quite different from all other species of the genus. The frog seems best viewed as a large member of the assemblage including *E. balionotus* Lynch, *E. coeruleus* (Andersson), *E. orcesi* Lynch, *E. riveti* (Despax), *E. thymelensis* Lynch, and *E. unistrigatus* (Günther); I do not now consider it closely related to any of these.

Distribution.—Known only from the Cordillera de Matanga east of Cuenca at elevations of 2652-3384 m.

Eleutherodactylus riveti (Despax) Fig. 16

- Hylodes riveti Despax, 1911:92 [Holotype.— MHNP 1902-357, an adult female from "Equateur"].
- Eleutherodactylus riveti—Barbour and Noble, 1920:404.
- [Eleutherodactylus curtipes (part)]—Lynch, 1969:266.

Eleutherodactylus w-nigrum (misapplication) —Lynch, 1972:144.



FIG. 16.—*Eleutherodactylus riveti*. (A) KU 119814; (B) KU 119813; (C) KU 120028; (D) KU 120026.

Diagnosis.—(1) skin of dorsum bearing flattened warts, that of venter areolate: dorsolateral folds coarselv faintly evident; (2) tympanum prominent, round, its length one-third to twothirds that of eve; (3) snout subacuminate in dorsal view, rounded in lateral profile; snout short, E-N less than to equal eye length; (4) interorbital space broad, flat, no cranial crests; upper eyelid width three-fourths IOD; (5) vomerine odontophores round; (6) males with vocal slits and subgular vocal sac; (7) first finger shorter than second, all digits bearing discs on apically dilated pads; dilation ratios I: 1.3, II: 1.6, III: 1.7, IV: 1.7; (8) fingers bearing prominent lateral fringes; (9) ulnar tubercles present, but ill-defined; (10) tarsus tuberculate, but distinct tubercles not apparent; (11) two metatarsal tubercles, outer conical, one-fifth to one-fourth size of oval (length twice width) inner metatarsal tubercle; few supernumerary plantar tubercles, at base of toes; (12) toes bearing lateral fringes; only basal webbing present between toes IV and V; all toes bearing discs on pads, pads as large as those of fingers; (13) dorsum brown with or without dark brown and/or black markings: venter cream, usually with brown reticulations: individuals from most localities have prominent canthal and supratympanic stripes, broad limb bars and dorsal chevrons and spots or a dorsal pattern of brown and black stripes; the stripes or portions of dorsal chevrons on the upper flanks are black; in populations having little dorsal markings, the upper flanks are spotted with black (Fig. 16); concealed thigh and groin dull brown; (14) adults small, males 20.6-26.8 mm, females 25.6-32.7 mm SVL.

Eleutherodactylus riveti is considered to be most closely allied to *E. bali*onotus. Both are readily distinguished from *E. curtipes* in having larger digital pads, prominent tympana, and in lacking cranial crests. *Eleutherodactylus ri*veti has very short limbs (equally short as those of *E. thymelensis* of northern Andean Ecuador). These two species have even shorter limbs than *E. curtipes*, a slightly larger species with cranial crests which is sympatric with *E. thymelensis*. *Eleutherodactylus balionotus* has longer limbs although they are still appropriately described as short. *E. riveti* has weakly developed dorsolateral folds and thereby resembles *E. curtipes* (prominent dorsolateral folds).

Description.—Head narrower than body, wider than long; head width 35.5-39.0 percent SVL ($\bar{x} = 37.1$, N = 32); snout subacuminate in dorsal view. rounded in lateral profile; canthus rostralis sharp, straight; loreal region weakly concave, sloping abruptly to lips; lips not flared; snout of moderate length, eve length equal to or slightly greater than E-N; interorbital space flat, no cranial crests: frontoparietals complete, no fontanelle; upper evelid width 69.1-93.3 percent IOD ($\bar{x} = 77.0, N = 31$); tympanum prominent, round, its horizontal diameter 35.5-69.8 percent eve length ($\bar{x} = 44.6$, N = 32), its upper edge concealed by thick supratympanic fold; tongue large, longer than wide, posterior one-third not adherent to floor of mouth, weakly notched posteriorly; choanae small, round, completely visible when roof of mouth is viewed from directly above or partially concealed by edge of jaw; vomerine odontophores round, situated between and well posterior to choanae, nearly in median contact, bearing teeth arranged in a transverse row; each odontophore about twice size of a choana; male with vocal slits and subgular vocal sac.

Skin of dorsum appears smooth but bears low, flattened warts, that of flanks, venter and posterior surfaces of thighs areolate, warts flat; discoidal folds prominent; dorsolateral and postocular folds faintly evident in many specimens; upper eyelid not tuberculate.

Ulnar tubercles present but not prominent; two palmar tubercles, median largest, larger than oval thenar tubercle; thenar surface bearing a few low, flattened supernumerary tubercles; subarticular tubereles round, flattened, moderate-sized, simple; fingers bearing thin lateral fringes; all fingers bearing discs on dilated pads, pads on outer two fingers larger than those on inner two fingers; pad on first finger round, those on other fingers wider than long; dilation ratios I: 1.1-1.6 ($\bar{x} = 1.3$), II: 1.2-2.0 ($\bar{x} = 1.6$), III: 1.5-2.0 ($\bar{x} = 1.7$), IV: 1.4-1.9 ($\bar{x} = 1.7$); first finger shorter than second.

Hind limbs short, heel of adpressed limb reaches to shoulder, vicinity of tympanum, or in very young specimens, to posterior edge of eye; shank 37.2-45.9 percent SVL ($\bar{x} = 41.6$, N = 32); skin of heel and tarsus tuberculate, none on heel enlarged; ill-defined row of outer tarsal tubercles present, one or two tubercles on inner edge of tarsus; inner metatarsal tubercle oval, not compressed, twice as long as wide, four to five times as large as conical outer metatarsal tubercle; plantar surface bearing two to four supernumerary tubercles at bases of toes II, III, IV, and V; subarticular tubercles of toes like those of fingers; toes bearing lateral fringes; basal web between toes IV and V; toes bearing discs on pads, pads wider than long, about as large as those of outer fingers.

In preservative, E. riveti from those populations with a distinct color pattern (Fig. 16A, B) is brown to rusty-brown (rarely gray) with dark brown and/or black spots or stripes. The flanks are cream reticulated with brown or black. The canthal and supratympanic stripes are dark brown. The labial bars are obscure and the lips are not striped with The limbs are barred with eream. brown, the bars are wider than the interspaces and edged with gray-brown lines. The dorsal markings may also be edged with gray-brown or cream. The venter is cream reticulated with dark brown or black. The concealed thigh, shanks, and groin are colorless and speekled with cream. Specimens from "pattern-less" populations (Paramos de Matanga) have a bronze or brown ground color. The venter is cream and may or may not be reticulated with brown. The upper flanks may bear spots (Fig. 16, C, D) but the limbs, center of the back, and face lack markings.

In life, E. riveti (patterned populations) is 'colored as follows: "Dorsum pale to medium brown, some yellowbrown with dark brown or black stripes; some rust above, all with some brown markings; shout tan in some individuals; some individuals with a green wash on markings; limb bars brown; flanks tan to light brown with brown to black bars and spots; vocal sac of male pale vellow; venter pearl white to pale rose with brown reticulations; posterior surfaces of thighs pale maroon brown to rust reticulated with cream; iris pale copper-tan above, brown below with black reticulations" (J. D. Lynch field notes, 19 June 1968). The "patternless" populations are gray, gray-brown, reddish, or orange in life with black spots on the upper flanks; the lower flanks are colored as the dorsum but a paler hue; venter off-white to cream, sometimes flecked with black; posterior surface of thigh same color as dorsum, sometimes more cream with faint thin brown reticulation. The iris of living specimens appears as above or may be "pale blue green, heavily reticulated with black; with a dull reddish-brown horizontal streak" (I. D. Lynch field notes, 18 June 1968) or "gray with a faint green cast and a brown to reddish brown horizontal streak; some black flecking" (J. D. Lynch field notes, 26 July 1970).

Measurements of holotype in mm.— SVL 32.5, shank 13.0, head width 12.5, head length 11.6, upper eyelid width 3.2, IOD 3.6, tympanum length 1.5, eye length 3.7. The holotype is a gravid female (large yellow ovarian eggs and strongly convoluted oviducts).

Natural history.—At the four localitics where I collected E. riveti (Laguna de Zurucuchu, S km NW Biblian, 10 km S Cumbe, and Páramos de Raranga, SE of Cuchil) only two other species of Eleutherodactylus were found (E. cryophilius at Laguna de Zurucuchu and E. orestes south of Cuchil, Páramos de Raranga), although E. phoxocephalus was found at slightly lower elevations on the slopes of the Cuenca hoja. No direct evidence of reproductive activity has been found in spite of the great abundance of these frogs beneath rocks and in dirt banks. Gravid females have been collected whenever the species was found.

E. riveti inhabits subpáramo and páramo habitats between 2620 and 3420 m in the Andes of Ecuador south of Cuenca. The frogs were equally abundant in the predominantly grassy páramos and in the shrubby subpáramos. These are the same type of ecologic situations in which to the north one encounters E. curtipes.

Remarks.—I have twice misapplied names to this frog. In redescribing E. cajamarcensis (Lynch, 1969a), I indicated that E. riveti was the same as E. curtipes. This action was based on a translation of Despax's (1911) description, the illustrations he provided, and the discovery of some E. curtipes labeled as *E*, *riveti* in the collections amassed by the late James A. Peters. In 1968 I collected at Laguna de Zurucuchu in an attempt to collect topotypes of Hylodes w-nigrum. I assumed the frogs collected there to be *w*-nigrum and under that assumption applied that name to this species (Lynch, 1972a). The specimens from Zurucuchu did not fit the description and following study of photographs of the holotype of H. w-nigrum generously provided by Dr. Konrad Klemmer I realized that I had again misapplied a name to this population. Eleutherodactylus w-nigrum, as correctly pointed out by Cochran and Goin (1970) is a species of the *fitzingeri* group, previously called E. buergeri.

Eleutherodactylus riveti lacks a pronounced frontoparietal fontanelle, has moderately large nasals in tenuous median contact, and has a comparatively large part of the sphenethmoid exposed dorsally, characteristics also seen in E. curtipes and E. unistrigatus (Fig. 17). The frontoparietals appear to be fused to the prootics. The vomers are moderate-sized and are in contact with the elongate palatines. The anterior ramus of the parasphenoid does not reach the vomers or palatines and the parasphenoid alae are slightly deflected posteriorly but in contact with the median rami of the pterygoids.

Distribution.—Both Andean cordilleras and the connecting *nudos* at elevations of 2620-3420 m surrounding the Cuenca *hoja* in southern Ecuador.

Eleutherodactylus ruidus new species Fig. 18

Holotype.—AMNH 17590, adult female obtained at Molleturo, Provincia Azuay, Ecuador, 2317 m, on 5-19 June 1922 by G. H. Tate.

Paratypes.—AMNH 17588-89, 17591-96, 17598-601, 17603, topoparatypes.

Diagnosis.—(1) skin of dorsum warty, that of venter coarsely areolate; no discoidal folds; (2) tympanum, cavum tympanicum, and plectrum absent; (3) snout round in dorsal view (tip feebly pointed), angularly round in lateral profile, short; (4) interorbital space as wide as upper eyelid; no cranial crests; (5) vomerine odontophores triangular in outline; (6) males lacking vocal sac and slits; (7) first finger shorter than second; digits bearing broad discs on dilated pads; (8) fingers bearing lateral fringes; (9) ulnar tubercles absent; (10) heel bearing non-conical tubercles, none on outer edge of tarsus; inner tarsal fold present; (11) two metatarsal tubercles, inner oval, twice size of round outer; supernumerary plantar tubercles only at bases of toes II-IV; (12) toes bearing lateral fringes; toe pads smaller than those of outer fingers; (13) brown above with darker scapular chevron, interorbital bar, postocular stripe, and labial bars; venter dusky cream with diffuse spotting on throat; groin, anterior and posterior thigh surfaces, concealed shank brown; (14) adults moderate-sized, males 25.8-31.1 mm, females 37.1-39.8 mm SVL.

In its most obvious characteristics, *E. ruidus* is similar to two members of the surdus Artenkreis, E. baryecuus Lynch and E. surdus (Boulenger). Both differ from E. ruidus in having cranial crests, smooth skin on the dorsum, longer



FIG. 17.—Skulls of Andean Eleutherodactylus. (A) E. unistrigatus, KU 111137; (B-C) E. curtipes, KU 109057; lines equal 5 mm.



FIG. 18.-Eleutherodactylus ruidus, AMNH 17590; line equals 5 mm.

legs, and in color patterns. Too few data are available to assert that *E. ruidus* is a member of the *surdus Artenkreis*. In body proportions and other shape characteristics, *E. ruidus* resembles *E. balionotus* Lynch and *E. riveti* (Despax); it differs from them in lacking the middle ear and vocal apparatus. The three are likewise similar in the features of the hands and feet, skin texture, proportions, and lack of cranial crests.

Description.—Head wider than body, wider than long; head width of males 30.2-33.8 percent SVL ($\bar{x} = 32.8$, N = 7), of females 34.5-35.9 percent $(\bar{x} = 35.2, N = 7)$; snout round in dorsal view (tip feebly pointed), angularly round in profile; E-N 64.7-88.9 percent eve length in males $(\bar{x} = 73.4, \bar{N} = 7)$, 71.1-87.8 percent in females ($\bar{x} = 80.0$, N = 7; nostrils not or weakly protuberant, directed dorsolaterally; canthus rostralis rounded: loreal region concave, sloping to non-flared lips; upper eyelid 80.8-124.1 percent IOD ($\bar{x} = 94.9$, N = 13); interorbital space flat (no cranial crests); upper eyelid warty (not bearing enlarged tubercles); supratympanic fold prominent, extending from corner of eye to base of arm; no tympanum, cavum tympanicum, or plectrum; two large postrictal tubercles; choanae small, not concealed by palatal shelf of maxillary arch, round; vomerine odontophores elevated, triangular in outline, median and posterior to choanae, separated by a choanal width, each slightly larger than a choana, bearing 1-6 teeth in a transverse row; males have fewer vomerine teeth (1-3 per odontophore) than do females (2-6 per odontophore); number of vomerine teeth positively correlated (r = 0.778, N - 2 = 13, p < 0.01) with body size; tongue slightly longer than wide, rounded posteriorly, posterior onefourth not adherent to floor of mouth: no vocal sac or slits in male.

Skin of dorsal surfaces (including upper eyelid) warty, W-shaped ridge on occiput; some larger warts on flanks; no dorsolateral folds; venter coarsely areolate, throat smooth; discoidal folds relatively prominent; skin of thigh (ventral surface) coarsely areolate; pair of large warts ventrolateral to vent; anus opens at posterior level of thighs (in a short sheath); ulnar tubercles indistinct; palmar tubercle bifid, twice size of oval thenar tubercle; supernumerary palmar tubercles elongate; subarticular tubercles round, non-conical; digits bearing relatively prominent lateral fringes (most evident on inner margins of fingers); all digits bearing broad (wider than long) discs on pads; pad of thumb round, those of fingers II-IV broadly dilated, all rounded apically, none bearing ungual notch; thumb shorter than second finger.

One or two small round tubercles on heel, none on outer edge of tarsus; inner edge of tarsus bearing fold along distal one-half; inner metatarsal tubercle not compressed, its length twice its width, two times size of round, non-conical outer metatarsal tubercle; plantar surface bearing small supernumerary tubercles at bases of toes II-IV; subarticular tubercles round except for most basal tubercle on toes IV and V (those smaller than others, longer than wide); toes bearing prominent lateral fringes (including outer edges of inner and outer toes); toes basally webbed only in that fringes coalesce basally; toes bearing discs (broader than long) on dilated pads (1.5 times width of digit); toe pads smaller than those of fingers; when legs are flexed at right angles to sagittal plane, heels touch; heel of adpressed hind limb reaches to posterior corner of eye; shank 42.1-46.5 percent SVL in males ($\bar{x} = 44.5$, N = 7), 42.4-49.3 percent in females ($\bar{x} = 47.3, N = 7$).

In preservative brown with darker brown sacral chevron, interorbital bar, and dark stripes lateral to occipital W (latter is high-lighted with cream); prominent brown postocular (supratympanic) stripe; 2-4 brown labial bars; canthal stripe not evident; flanks suffused with brown, becoming more pale (dusky cream) ventrally; limbs gray-brown with indistinct brown bars, if evident they are relatively broad (about equal to interspaces) and transversely oriented; in some specimens (especially AMNH 17592) oblique barring of the flanks is evident. Venter dirty cream with some diffuse brown spotting on throat; edge of lip more densely brown giving impression of incomplete barring; under magnification all ventral surfaces are peppered with brown. Anterior and posterior thigh surfaces and ventral surface of shank rich brown; no anal triangle.

Measurements of holotype in mm.— SVL 38.4; tibia 16.3; head width 13.4; head length 11.4; upper eyelid width 3.6; IOD 2.9; eye length 4.5; E-N 3.2. The holotype is a gravid female with large, yellow ovarian eggs and extensively convoluted oviducts.

Etymology.—Latin, meaning rough, in reference to the skin texture.

Natural history.—G. H. Tate found these frogs beneath stones in pastureland and scrubby growth; he noted the area had "very little forest." Two small females are not mature. AMNH 17602 is a juvenile female (21.1 mm SVL); AMNH 17597 (29.0 mm SVL) has moderate oviducal convolution and small eggs. *Remarks.*—The absence of auditory and vocal apparati in *E. ruidus* suggest it is related to the *E. surdus Artenkreis* but I think the available data support an argument of relationship with *E. balionotus* and *E. riveti*. The three are dichopatrically distributed in the Andes of southern Ecuador. The three may represent the southern vicariants of the more northern *E. orcesi* and *E. thymelensis*.

Distribution.—Known only from the type-locality on the Pacific slopes of the Cordillera Occidental (2317 m).

Eleutherodactylus spinosus new species Fig. 19

Holotype.—USNM 199891, an adult female obtained at Sapote, Provincia Morona-Santiago, Ecuador, 2470 m, by Peter Spoecker on 23 August 1962.

Paratypes.—(all Provincia Morona-Santiago, Ecuador) USNM 199916, between Cerro Negro and Pailas, 2652 m; USNM 199917, between Cerro Negro and Pailas, 2439-2561 m; USNM 199945-66, El Cruzado, 2195 m; USNM 199967-71, Loma de Puerco, 2226 m; USNM 199918-35, Pailas, 2195 m; USNM 199936-44, San Juan Bosco, 2195 m; USNM 199972, San Vicente, 2835 m; USNM 199892-915, Sapote, 2470 m.



FIG. 19.-Eleutherodactylus spinosus, USNM 199950, line equals 10 mm.

44

Diagnosis, ---(1) skin of dorsum finely tuberculate, that of venter coarsely areolate: no dorsolateral folds; (2) tympanum prominent, its length %-¼ that of eve in males, ¹/₅⁻¹/₅ in females; (3) snout subacuminate in dorsal view, truncate in lateral profile, short; (4) interorbital space broader than upper evelid; low cranial crests present; upper evelid bearing 2-3 elongate tubercles; (5) vomerine odontophores oval to triangular in outline; (6) males lacking vocal sac and slits; (7) first finger shorter than second; digits bearing broad discs on dilated pads; (8) fingers bearing narrow lateral fringes; (9) ulnar tubercles subconical: (10) heel and outer edge of tarsus bearing subconical tubercles; (11) two metatarsal tubercles, inner oval, 5-6 times size of round outer; many supernumerary plantar tubercles; (12) toes bearing lateral fringes; toe pads as large as those of fingers; (13) brown above with indefinite darker blotching; flanks paler with brown bars; groin and concealed surface of hind leg black enclosing white spots; venter dull cream with heavy brown reticulation; some specimens have pale cream lines (reticulation) on flanks; (14) adults moderate-sized, males 16.1-25.0 mm, females 28.3-34.5 mm SVL.

Eleutherodactylus spinosus is probably most closely allied to *E. nigrogris*eus (Andersson). The two are readily distinguished in that *E. nigrogriseus* is smaller ($\delta \delta$ 19.3-26.0 mm, $\Im \Im$ 28.5-29.4 mm SVL), does not have prominent tubercles along the outer edge of the tarsus, has shagreened skin with scattered tubercles on the dorsum (not finely tuberculate), lacks enlarged tubercles on the eyelids, and has yellow spots (in life) on the posterior surface of the thighs.

Description.—Head narrower than body, broader than long; head width of males 37.2-41.5 percent SVL ($\bar{x} = 38.6$, N = 19), of females 36.7-41.6 percent (\bar{x} = 39.7, N = 21); snout subacuminate to subovoid in dorsal view, nearly truncate in lateral profile; snout short, E-N of males 66.7-86.2 percent eye length $(\bar{x} = 75.8, N = 19)$, of females 77.8-97.1 percent ($\bar{x} = 86.4$, N = 21); nostrils weakly protuberant, directed dorsolaterally; canthus rostralis moderately sharp, concave: loreal region concave, sloping to lips; lips not flared in most specimens, weakly flared in large adult females: interorbital space nearly flat. frontoparietals weakly upturned, low cranial crests most evident in large females; upper evelid width 87.0-129.4 percent IOD in males ($\bar{x} = 104.6$, N = 17), 81.2-103.1 percent in females ($\bar{x} =$ 94.8, N = 20; upper eyelid tuberculate, bearing 2-3 long, conical tubercles; temporal region sloping; supratympanic fold heavy, concealing upper edge of tympanum; tympanum prominent, round to higher than long, its length in males 17.2-27.6 percent eve length ($\bar{x} = 22.8$, N = 19), in females 20.5-37.2 percent $(\bar{x} = 28.3, N = 21)$; separated from eve by 1½ times its length; choanae moderate-sized, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, oval to triangular in outline, bearing 4-5 teeth in a transverse row on posterior edge of odontophore; odontophores 2-3 times size of a choana, narrowly separated (about one choanal width); tongue longer than wide, posterior % not adherent to floor of mouth, posterior edge not notched; males lacking vocal sac and slits.

Skin of dorsum finely tuberculate, that of head and anterior back least so, heavy ridge from eye across scapular region; no dorsolateral folds; skin of venter coarsely areolate, discoidal folds prominent; no anal sheath; ulnar tubercles prominent, subconical; palmar tubercle bifid, larger than oval thenar tubercle; many supernumerary palmar tubercles, all smaller and less prominent than round, elevated, non-conical subarticular tubercles; fingers bearing narrow lateral fringes; fingers bearing discs (broader than long) on dilated, apically rounded pads; pad on thumb smallest, those on fingers II-IV as large as tympanum; thumb shorter than second finger.

Heel and outer edge of tarsus bearing large subconical tubercles; inner tarsal fold along distal 1/2-1/4 of tarsus; inner metatarsal tubercle oval, twice as long as wide, non-compressed, 5-6 times size of round outer metatarsal tubercle; many supernumerary plantar tubercles, all smaller than non-conical subarticular tubercles: subarticular tubercles of toes smaller than those of fingers, slightly longer than wide: toes bearing lateral fringes; pads and discs of toes as large as those of outer fingers; heels of flexed hind legs touch; heel of adpressed hind limb reaches to eve; shank of males 50.2-54.8 percent SVL ($\bar{x} = 52.4$, N = 19), of females 47.8-55.4 percent ($\bar{x} = 51.3$, N = 21).

In preservative light to dark brown with black labial bars. In dark individuals no dorsal pattern is evident; in more pale individuals, the dorsum is marbled (Fig. 19); the limb bars are narrow and oblique, and slanted bars are evident on the flanks. Innermost digits cream. Flanks and concealed surfaces of limbs are black with cream spots (especially evident in axillae, groin, concealed thigh, and shank). Posterior thigh bears small cream flecks in males and small females, large cream spots in larger females. The venter is dull creamy-vellow heavily spotted and reticulated with brown; the throat is generally darker than the venter. Twenty-six of the 98 specimens examined have pale cream reticulation on the flanks (Fig. 19).

In life, *E. spinosus* is pale to dark brown with brown chevrons on back, scapular W, and limb bars. The venter is dull cream heavily reticulated with brown, to black with a gray reticulation. The posterior thigh, concealed shank, anterior thigh, groin, and axilla are black enclosing white spots. The flanks are dark brown reticulated with dull yellow.

Measurements of holotype in mm.— SVL 34.3; tibia 17.2; head width 12.6; upper eyelid width 3.3; IOD 3.3; tympanum length 1.2; eye length 4.2; E-N 3.6. The holotype is a gravid female with extensively convoluted oviducts and large, yellow ovarian eggs. This individual lacks the pale reticulation on the upper flanks.

Etymology.—Latin, in reference to the tuberculate skin of the dorsum.

Natural history.—Peters and his associates found specimens beneath rocks along trails and on elephant ear plants at night. The largest non-gravid females are 26.2-28.5 mm SVL; these females do not have extensively convoluted oviducts or large eggs. The largest juvenile female (straight oviducts, small eggs) is USNM 199946 (25.7 mm SVL).

Remarks.—Eleutherodactulus spinosus is currently known only from the eastern slopes of the Cordillera de Matanga (where it is evidently most abundant between 2200 and 2500 m) and on the adjacent Cordillera del Condor. Lynch (1969b) recorded E. nigrogriseus from the eastern slopes of the Andes in Napo, Pastaza, and Tungurahua provinces at elevations of 1150-1800 m. Peters and his associates collected 16 specimens of E. nigrogriseus sympatrically with E. spinosus. Their specimens were taken at elevations between 2195 and 2835 m; most were found at night on vegetation in the montane forests.

Eleutherodactylus cryptomelas appears related to *E. nigrogriseus* and *E. spinosus*. Although fewer data are available for *E. cryptomelas*, this species appears to occur at slightly higher elevations than does either of the other species and is more southern in its distribution.

Distribution.—Known from the Amazonian slopes of the Cordillera de Matanga at elevations of 1707-2835 m.

Eleutherodactylus versicolor new species Fig. 13C

Holotype.—KU 119858, an adult male obtained "15 km E Loja, 2800 m" (= 13.5 km E. Loja, 2800 m), a locality just cast of the crest on the mountain range dividing Loja and Zamora-Chinchipe provinces, Ecuador, on 10 June 1968 by Robert W. Henderson and J. D. Lynch.

Paratypes.—KU 119859-71 and 119911-44, topotypes collected on 10 June and 13 June 1968 by R. W. Henderson and J. D. Lynch.

Diagnosis.—(1) skin of dorsum shagreened and finely tuberculate, that of venter areolate; no dorsolateral folds; (2) tympanum visible, round, its length two-fifths to one-half that of eve; (3) snout subacuminate in dorsal view, rounded in lateral profile; E-N greater than or equal to eye length; (4) interorbital space flat, no cranial crests; upper eyelid width less than IOD; (5) vomerine teeth and odontophores present, odontophores teardrop-shaped and oblique; (6) males lacking vocal slits and vocal sac; (7) first finger shorter than second; all fingers bearing discs on dilated pads; dilation ratios I: 1.5, II: 1.9, III: 2.1, IV: 2.0; (8) fingers with very poorly-developed lateral fringes or none; (9) ulnar tubercles present, not prominent; (10) inner edge of tarsus bearing a short ridge-like tubercle, outer edge bearing a row of small conical tubercles; no heel tubercles; (11) two conical metatarsal tubercles, outer round, one-fourth to one-third size of oval inner; supernumerary plantar tubercles numerous, conical; (12) toes not fringed, no basal webbing; all digits bearing discs on dilated pads, pads not as large as those of fingers; (13) ground color usually brown on dorsal surfaces blotched with brown (chevrons, interorbital bar, canthal and supratympanic stripes); flanks barred or spotted; limbs barred; venter cream reticulated with brown; posterior surface of thighs brown with cream flecks; (14) adults small, males 19.3-25.2 mm, females 22.7-29.8 mm SVL.

Aside from coloration, *E. versicolor* is similar to *E. cajamarcensis* and *E. unistrigatus*. *E. versicolor* differs from both of these species in lacking a vocal sac and slits. Both *E. cajamarcensis* and *E. versicolor* differ from *E. unistrigatus* in having flattened warts on the upper eyelids and distinct supernumerary plantar tubercles. In life, the three are readily distinguished—*E. versicolor* has a green ground color and lacks red areas in the groin and on the concealed thighs, *E. cajamarcensis* is usually brown and has red areas on the concealed thigh and in the groin, and *E. unistrigatus* is tan, cream, or rarely brown above and cream below and lacks bright colors on the concealed thigh surfaces and groin.

Description.-Head as wide as or slightly wider than body, as wide as or slightly wider than long; head width 35.0-40.6 percent SVL ($\bar{x} = 37.9$, N = 33); snout subacuminate in dorsal view, rounded in lateral profile; canthus rostralis sharp, straight or slightly concave; loreal region concave, sloping to lip; lips not flared; nostrils weakly protuberant, near tip of snout, directed dorsolaterally; snout of moderate length, eye length equal to or slightly greater than E-N; upper eyelid width 75.8-113.7 percent IOD ($\bar{x} = 90.3$, N = 33), eyelid slightly wider in males than in females; interorbital space flat, no cranial crests; no frontoparietal fontanelle; tympanum visible, prominent, round, its upper and posterior edges partially concealed by thick, glandular supratympanic fold; tympanum 38.9-50.2 percent eye length in males ($\bar{x} = 43.8$, $\bar{N} = 16$), 40.4-55.0 percent in females ($\bar{x} = 46.2, N = 17$); tongue thick, longer than wide, posterior one-third not adherent to floor of mouth, weakly notched posteriorly; choanae small, round, well within border of jaws when palate is viewed from directly above; vomerine odontophores slanted, median and posterior to choanae, separated medially by distance about equal to twice width of an odontophore; each odontophore bearing 2-4 teeth in a clump at posterior end of process; males lacking vocal sac and slits.

Skin or dorsum shagreened and finely tuberculate; no dorsolateral folds; skin on upper eyelids more coarsely tuberculate than that on rest of dorsum; skin on flanks and upper surfaces of limbs shagreened and finely tuberculate, that on venter coarsely areolate; skin below vent and on underside of thighs areolate, that on undersides of forelimbs and shank smooth; discoidal folds prominent.

Forearm bearing small ulnar tubereles; two palmar tubercles, partially fused, median largest and equal in size to oval thenar tubercle; few supernumerary thenar tubercles; subarticular tubercles prominent, round, not conical, simple; fingers lacking lateral fringes or having only keel-like lateral fringes; digits bearing discs on dilated pads, pads wider than long, not emarginate; dilation ratios I: 1.2-1.8 ($\bar{x} = 1.5$), II: 1.7-2.3 ($\bar{x} = 1.9$), III: 1.8-2.4 ($\bar{x} = 2.1$), IV: 1.7-2.4 ($\bar{x} = 2.0$); first finger shorter than second (Fig. 20).

Hind limbs moderately long, shank 48.4-58.4 percent SVL ($\bar{x} = 55.0$, N = 33); heel weakly tuberculate, none enlarged; outer edge of tarsus bearing series of small tubereles which continue along outer edge of foot to base of toe V; inner edge of tarsus bearing a short ridge-like tuberele: inner metatarsal tuberele oval, about one and one-half times as long as wide, not compressed, three to four times as large as rounded, conical, outer metatarsal tubercle; plantar surface bearing numerous conical supernumerary tubercles: subarticular tubereles of toes like those of fingers but slightly smaller; toes lacking lateral fringes or having only indistinct ridges along the edge of toes; toes not webbed except between toes IV and V; toes bearing dises on dilated pads, pads broader than long, slightly smaller than those of fingers.

In preservative, *E. versicolor* has a ground color of tan, gray, or, more often, shades of brown. The ground color of the body lightens on the flanks and thighs. The dorsum is blotched with brown to nearly black and the blotches are usually outlined with cream. The dark markings on the face consist of a distinct canthal stripe, which continues behind eye as a supratympanic stripe, and labial bars. The tympanum is paler

than the rest of the head and is cream with a bronze wash. The dorsal blotches continue onto the flanks as slanted bars. The flank bars are broken up into rows of spots in some individuals. A dark interorbital bar is present in all but the striped individuals (see below) and is bordered anteriorly by a pale interorbital bar or patch of cream to brown. The forelimbs are strongly barred with dark brown usually edged with cream or tan. The hind limbs are barred like the forelimbs except that the ground eolor on the thigh is more pale than that on the shank or tarsus. Most individuals have two bars on the thigh and two on the shank as well as one on the knee. The dark bars are about as wide as or slightly wider than the pale interspaces. An anal triangle is present but is not as dark as the limb bars. The anterior and posterior thigh surfaces and to a lesser extent, the top of the thighs, are mottled brown with cream flecking. Many individuals (24.4%) have one to 55 distinct enamel-like white spots on the flanks (the spots are outlined in black). The venter is cream to pale brown with a dense brown or black retirulation. The dark flecking on the venter is sometimes accentuated on the throat-these individuals have dark bars on the margin of the lower jaws.

The variegated pattern (Fig. 13C) is found in 93% of the specimens. Seven percent have a striped pattern. The striped individuals differ in pattern from the variegated individuals only in the pattern on the back and flanks. Most striped individuals have dark flanks delimited dorsally by a sharp edge to the almost black flank. Between the dark dorsolateral areas are dark stripes or rows of spots. These individuals lack interorbital bars. One-half of the striped individuals have white spots on the flanks (2-6 spots per individual).

In life, *E. versicolor* is green (or rarely tan or brown) with brown, reddish brown, or black markings bordered with cream. A few individuals have a reddish-orange patch on the center of the back and a reddish-orange interorbital bar. The concealed surfaces of the limbs and flanks are brown to black with reddish-pink flecks. The venter is cream to pale reddish-pink with black or brown reticulations. The iris is bronze-white with a reddish-brown horizontal streak and faint black reticulations. The enamel-like white spots of preserved individuals were dull white in life.

Measurements of holotype in mm.— SVL 22.2, shank 12.4, head width 8.7, head length 8.5, upper eyelid 2.3, IOD 2.7, tympanum length 1.4, eye length 3.4.

Etymology.—Greek, meaning variegated, in reference to the dominant color pattern.

Natural history.—No egg clutches were found but females with large eggs were collected at the same time equally large females with only small, white, ovarian eggs were found. The specimens I collected between 10 and 16 June 1968 were found beneath stones and logs in sparsely wooded pasture or in cloud forest habitats at elevations between 2750 and 3100 m. Based on limited observations, it appears that *E. versicolor* occurs at higher elevations than does *E. cajamarcensis*.

Remarks.—Eleutherodactylus versi*color* is considered a close relative of *E*. cajamarcensis and E. unistrigatus. The similarities between the three species are extensive, and they differ in color pattern, skin texture, size of digital pads (Fig. 20), and proportions. The skulls of the three species are not appreciably different-all have moderate-sized nasal bones in median contact but separated from the frontoparietals, no frontoparietal fontanelle, no cranial crests, the frontoparietals fused to the prootics, moderate-sized vomers that are not in median contact, long anterior rami of the parasphenoid (reaching palatines and vomers), and median rami of the pterygoids in contact with the parasphenoid alae.



FIG. 20.—Hands of (A) Eleutherodactylus unistrigatus, KU 120019, and (B) E. versicolor, KU 119919; line equals 5 mm.

Distribution.—Intermediate elevations (2750-3100 m) in the Andes of southern Ecuador.

Eleutherodactylus vidua new species Fig. 13D

Holotype.—KU 120082, adult female obtained 15 km E Cuidad Loja, Provincia Zamora-Chinchipe, Ecuador, 2800 m, on 10 June 1968 by John D. Lynch.

Paratypes.—KU 120083-88, 120090-91, topotypes; KU 141994, 15 km E Loja, Provincia Zamora-Chinchipe, Ecuador, 2710 m; KU 120089, 13-14 km E Loja, Provincia Loja, Ecuador, 2850 m; KU 120092, 8-9 km N San Lucas, Provincia Loja, Ecuador, 3000-3100 m.

Diagnosis.-(1) skin of dorsum finely shagreened with ill-defined dorsolateral folds, that of venter areolate; (2) tympanum concealed beneath skin; (3) snout broadly rounded (obtuse) in dorsal view, rounded in lateral profile, short; (4) interorbital space flat (no cranial ridges), wider than upper evelid width; (5) vomerine teeth and dentigerous processes present; (6) males unknown; (7) first finger shorter than second, digits bearing narrow pads, dilation ratios 1.26-1.31 for outer fingers; (8) fingers lacking lateral fringes; (9) no ulnar tubercles or fold; (10) tarsus bearing ill-defined tubercle along inner edge, series of obscure tubercles along outer edge; no heel tubercles; (11) two metatarsal tubercles, inner slightly larger than outer; plantar surface bearing numerous supernumerary tubercles; (12) toes lacking lateral fringes and basal webbing; (13) no bright spots in axilla. groin, concealed limb surfaces, or on venter: venter cream with brown flecking; dorsum tan to brown, mottled with darker brown or bearing cream dorsolateral stripes; (14) females 18.0-23.1 mm SVL.

Eleutherodactylus vidua is most similar to four other narrow-disced Andean Eleutherodactylus—E. ginesi, E. myersi, E. nicefori, and E. trepidotus—E. vidua differs from all of these in having the tympanum concealed and differs from *E. myersi* and *E. trepidotus* in lacking spots in the groin and on the venter. Vomerine teeth are not visible in *E. myersi* or *E. trepidotus*, but are visible in the other three species. *E. ginesi* lacks dorsolateral folds and is uniform black. *Eleutherodactylus nicefori* is a somewhat larger frog but like *E. vidua* is darker above and cream, flecked or reticulated with brown, below.

Description.—Head narrower than body, slightly wider than long; head width 36.2-39.9 percent SVL ($\bar{x} = 38.7$, N = 8; snout obtuse in dorsal view, rounded and slightly sloping in lateral profile; snout short, eye length greater than E-N; canthus rostralis sharp, weakly concave; loreal region concave, sloping abruptly to non-flared lips; nostrils weakly protuberant, directed laterally, near tip of snout; upper eyelid width 65.6-81.4 percent IOD ($\bar{x} = 73.5$, N = 8); interorbital space flat, no cranial crests present; frontoparietal bones in median contact for their entire lengths, no fontanelle; tympanum present, concealed beneath skin; tongue large, round, fleshy, not notched posteriorly, posterior one-third free; choanae small, round, completely visible when roof of mouth is viewed from directly above: dentigerous processes of vomerine bones present, round in outline, as large as or slightly larger than a choana, situated between and posterior to choanae, each bearing 2-4 teeth in a transverse row.

Skin of dorsum finely shagreened with poorly defined dorsolateral folds and flattened warts on flanks: small scattered tubercles are present on the dorsum and evelids; skin of throat and venter areolate, discoidal folds prominent; ventral surfaces of limbs smooth except on ventral face of thighs; forearm lacking ulnar tubercles; two palmar tubercles, inner largest, larger than oval thenar tubercle; palm bearing indefinite supernumerary tubercles; subarticular tubercles of fingers large, round, flattened, simple; fingers not bearing lateral fringes; digit tips bearing discs, weakly dilated, pads on outer two fingers slightly larger than those of inner fingers (Fig. 7C) and broader than long; dilation ratios I: 1.0 ($\bar{x} = 1.0$), II: 1.0-1.2 ($\bar{x} = 1.1$), III: 1.2-1.6 ($\bar{x} = 1.4$), IV: 1.2-1.4 ($\bar{x} = 1.3$); first finger shorter than second.

Hind limbs short, shank 37.8-46.4 percent SVL ($\bar{x} = 42.3$, N = 8); inner edge of tarsus bearing short, ill-defined tubercle separated from inner metatarsal tubercle; outer edge of tarsus bearing a series of weakly defined tubercles: no tubercles on heel: two metatarsal tubercles, inner about twice as long as wide, not compressed, one and one-half to two times size of rounded outer metatarsal tubercle: plantar surfaces bearing numerous poorly defined supernumerary tubercles; subarticular tubercles of toes smaller than those of fingers, round, flattened, simple; toes lacking lateral fringes and basal webbing; basal one-third of fifth toe fused to fourth toe; tips of digits weakly expanded, pads slightly broader than long, bearing discs.

In preservative, the dorsum and limbs are gray to dark brown with a reddish cast. Seven of the twelve individuals have prominent dorsolateral stripes. Of the five non-striped individuals, two are reddish-brown with very faint darker brown markings except on the limbs where brown bars are distinct. The other three non-striped individuals have extensive dark brown or blackish marbling on the dorsum and flanks; the ground color in these specimens is brown or gray-brown. In the seven striped individuals, the cream or white stripe begins at the tip of the snout and runs posteriorly along the canthus, on the outer edge of the upper eyelid, and down the body terminating above the thighs. The light stripe is edged by wider brown to black stripes (Fig. 13D). The center of the back is not spotted with dark brown or black. Two of the striped individuals are gray-the other five are brown to rust-brown. The limbs are barred with brown.

All individuals have a dark brown to black anal patch edged laterally with cream or white stripes. The posterior surface of the thigh is dull brown with loosely-defined cream spots. The venter is cream with minute brown flecking. The throat differs from the rest of the venter in having more dense flecking (especially anteriorly). The lips are barred and a prominent dark brown or black canthal and supratympanic stripe is present; this stripe is usually outlined with cream.

In life, *E. vidua* is tan to brown with brown markings. If dorsolateral stripes are present, they are cream. The tan individuals have a faint green wash. The venter is cream, dusky gray, or light brown. The posterior surfaces of the thighs are flesh colored to pale rose. The iris is gray with a horizontal brown streak and fine black reticulations. William E. Duellman described the iris as "pale green above, reddish bronze below" (KU 141994, notes 21 July 1971).

Measurements of the holotype in mm.—SVL 21.8, shank 9.0, head width 8.7, head length 7.9, upper eyelid 2.1, IOD 2.6, eye length 2.4. The holotype is an adult female with heavily convoluted oviducts and large (1.8-2.4 mm in diameter), yellow, ovarian eggs. Its color pattern is of the striped morph.

Etymology.—Latin, a widow, used as a noun in apposition. The choice of this name reflects my belief that this species is all-female, a notion requiring careful checking.

Natural history.—All but one individual (KU 120092) were collected beneath rocks or vegetation on the Cordillera de Zamora, east of Loja, at elevations between 2710 and 2800 m. When uncovered these small frogs would walk towards the nearest cover or crouch none was seen to hop. No direct evidence of reproduction was discovered but one adult female (KU 120092) contained only small ovarian eggs whereas the other nine adult females contained large ovarian eggs and were presumably ready to deposit the eggs.

A total of fifteen specimens has been obtained and each is a female. This

small sample is not adequate to assert that the species is all-female in view of two other cases of frogs of this genus in which males are rare. E. orestes exhibits a similar preponderance of females (one male: sixteen females) and E. trepidotus presents an even more pronounced bias (2 males: 81 females). In each of these cases the bias is clearly towards females and coupled with another case of apparent all-female species (Phrynopus peraccai), also from Andean Ecuador, stand in marked contrast to the other twenty to thirty species of high Andean Ecuadorian eleutherodactylines exhibiting nearly one to one sex ratios.

Remarks.—Eleutherodactulus vidua has the least digital dilation of any Andean Eleutherodactylus. The width of the digital pads of this species are comparable with the bulbous digital pads seen in several species of the disc-less Andean genus Phrynopus. The skull of E. vidua (Fig. 11F-G) closely resembles that of E. orestes. The nasals are moderate-sized and separated, lying on a large sphenethmoid that extends anteriorly nearly to the tip of the nasal bones. The frontoparietals are complete (no fontanelle) and are fused to the prootics. The zygomatic ramus of the squamosal is short (Fig. 12C). The vomers are moderate-sized and separated. The palatines are more normal in extent than those of E. orestes and E. colodactylus. The anterior ramus of the parasphenoid is comparatively elongate, approaching the condition seen in *E. colodactylus* (Fig. 8) and that seen in several *Phrynopus* species (Lynch, 1975). The parasphenoid alae are oriented at right angles to the anterior ramus and are narrowly separated from the median rami of the pterygoids.

Distribution.—Eleutherodactylus vidua is known from the mountain crests east and north of Loja, Ecuador, at elevations of 2710 to 3100 m.

Eleutherodactylus w-nigrum (Boettger)

The southern extent of the distribution of E. *w*-nigrum is in southern Ecuador. The species is widely distributed at moderate and intermediate elevations on both Amazonian and Pacific versants in Ecuador and Colombia and also invades the valleys of the Río Cauca and Río Magdalena in Colombia.

The collections by Peters and his associates on the Amazonian versant of the Cordillera Oriental east of Cuenca establish an altitudinal range of 1890 to 2604 m for *E. w-nigrum*, but in northern Ecuador it occurs at elevations between 1200 and 3000 m. This species will be treated in detail in a review of the species of the genus found on the Amazonian slopes of the Andes in Ecuador (in prep., Lynch and Duellman).

DISCUSSION

Relationships of the southern fauna. —The genus Eleutherodactylus ceases to be a component of the high Andean frog fauna south of the area here termed "southern Andean Ecuador." The twenty species living within this area belong to two of the species groups recognized by Lynch (1976a). Two are members of the fitzingeri group (E. lymani and E. w-nigrum) and are closely related within that group. The other eighteen are referable to the unistrigatus group. The intragroup relationships of the group are poorly known, in part because the group is so large (more than 100 species now recognized). As now understood, the relationships of the 18 species in the *unistrigatus* group found in southern Andean Ecuador are as follows:

1. E. cajamarcensis and E. versicolor are southern vicariants of northern species (E. coeruleus, E. lehmanni, and E. unistrigatus) found in southern Colombia and northern Ecuador.

2. E. balionotus, E. riveti, and E. ruidus form a vicariant series and are possibly the southern elements of a northern series (E. orcesi and E. thy-

melensis, northern Ecuador) which may be upland replacements of the unistrigatus series. E. percultus and E. pycnodermis are very tentatively associated with the balionotus-riveti-ruidus series.

3. E. baryecuus is the southern element of an Artenkreis also containing E. devillei (Amazonian slope, northern Ecuador) and E. surdus (Pacific slope, northern Ecuador).

4. E. cryophilius is the southern element of the curtipes Artenkreis (buckleyi and curtipes) distributed on the Central Cordillera of Colombia south through northern Ecuador.

5. E. cryptomelas and E. spinosus appear related to one another and to an Amazonian versant species, E. nigrogriseus, which ranges northward through Ecuador; E. atratus may be allied to this assemblage.

6. *E. phoxocephalus* is apparently the southern member of a series of poorly known Pacific versant frogs in Colombia and Ecuador.

7. E. bromeliaceus is an upland relative of E. lacrimosus which is found in Amazonian Brasil, Colombia, Ecuador, and Perú.

8. *E. colodactylus* may be related to *E. proserpens* and *E. celator*; the latter occurs on the Pacific versant in northerm Ecuador.

9. E. orestes and E. vidua seem closely related and moderately well-separated from other species of the group. Their resemblance to E. ginesi (Venezuela), E. myersi and E. nicefori (Colombia), and E. trepidotus (northern Ecuador) may be a reflection of relationship.

Ecological segregation.—As a whole, the southern Andean fauna has affinities with northern Andean species although a northern connection is tenuous for the balionotus-riveti series and the orestesvidua series. Only one species of the unistrigatus group, E. bromeliaceus, has obvious Amazonian affinities. Eleutherodactylus lymani is related to a wide-spread Andean slopes species (E. w-nigrum) ranging through Colombia and Ecuador; as a whole, the fitzingeri group is a lowland (< 1000 m) group, but endemic, moderate elevation species are also present on the Cordillera Occidental and Sierra Nevada de Santa Marta in Colombia, the Talamanca Range in lower Central America, and the Sierra Madre del Sur in nuclear Central America.

The twenty species may be assigned to ecogeographic units as follows:

Pacific slope (cloud forest, 2000-3000 m): *E. phoxocephalus* and *E. ruidus*.

Intercordilleran belt (relatively xeric, < 2600 m): *E. cajamarcensis* and *E. lymani.*

 $Páramo \ (> 3000 \text{ m, cool, moist}): E.$ cryophilius and E. riveti.

Subparamo (Amazonian slopes, 2800-3000 m): E. balionotus, E. orestes, E. percultus, E. pycnodermis, E. versicolor, and E. vidua.

Amazonian slope (cloud forest, 1800-2800 m): E. atratus, E. baryecuus, E. bromeliaceus, E. colodactylus, E. cryptomelas, E. proserpens, E. spinosus, and E. w-nigrum.

The ecogeographic contingencies readily support the conclusion of a more diverse Amazonian slope fauna. The relative depauperity of the Pacific slopes is probably a reflection of the aridity imposed by the proximity of the cold Humboldt current and partly a function of the pronounced absence of high altitude habitat on the western face of the Andes in southern Ecuador.

With the exception of E. bromeliaceus cited above, all of the southern Andean species appear related to northern species found on the higher slopes and in the intercordilleran belt (cloud forests, subparamos or pajonales, and páramos). The distributional and phylogenetic data are suggestive of dispersal or vicariance within altitudinal zones rather than between them and are therefore consistent with Janzen's (1967) general hypothesis, and concordant with the conclusions of Peters (1973) for Atelopus, that the most pronounced barriers are those of altitude (and the associated climates).

Correlates with species densities and diversities .- Some of the greater richness of species among eleutherodactylines of southern Andean Ecuador compared to that of northern Andean Ecuador is real. If an equal-sized area of pajonales and páramos in northern Andean Ecuador is compared to one in southern Andean Ecuador, the latter clearly has more species (6-8 species compared to 2-3); however, the pajonales and páramos of northern Ecuador are relatively contiguous whereas, in southern Ecuador, these habitats are patchy. Thus, part of the greater richness is a function of a continental islands or archepelagar paradigm (topographic relief of Simpson, 1964). Additionally, the Andes in southern Ecuador are less high than are those in northern Ecuador allowing slope species to occur on the subpáramo patches on the relatively low (ca. 2800 m) crests and peaks in southern Ecuador (viz., Abra de Zamora in Provincia Loja). Lastly, the pajonales and paramos of northern Andean Ecuador were subjected to extensive Pleistocene vulcanism (Sauer, 1957); such perturbation would tend to reduce species diversity by rendering the habitat more uniform. North of the "faunal break" (between Guamote and Cañar) noted by Lynch (1971, 1972a, b), one finds two wide-spread species, E. curtipes and E. unistrigatus, and ten other species of restricted distributions over an area some 8-10 times the size of southern Andean Ecuador.

Species diversity computations require abundance/species data. I have used data extracted from my own fieldwork in southern Ecuador to approximate relative abundances even though collecting was seldom random. Fieldwork in 1968 and 1970 was designed to reveal what species were found in southern Ecuador and because most species were undescribed, selectivity in collection was minimized. Biases of preferred microhabitat (of the animals and of the collectors) and of collecting schedules vs activity cycles of the organisms are inescapable. However, to await an ecologist venturing into this area before anyone discusses relative abundance or species diversities is unrealistic; anecdotal data have some applicability. In computing species density values, I employed MacArthur's (1972) formula $D_s = 1 / \sum_{i=1}^{s} p_i^2$. The simplicity of computations and MacArthur's assertion that the formula is more appropriate in community studies were the only reasons this formula was used instead of the more frequently used Shannon-Weaver index.

Species densities for 50 Andean localities in Ecuador show that northern. and thus more often, higher elevation. sites exhibit lower densities than do the southern sites (Table 2). One could argue that there is a latitudinal (1°N to $3^{\circ}S$) effect but the altitudinal effect seems to explain the variation because lower elevation sites in northern Ecuador (on the Andean versants) have high species densities (e.g., Tandapi, Provincia Pichincha, 1450 m, 8 species; Pilaló, Provincia Cotopaxi, 2500 m, 7 species). Species density is negatively correlated with altitude (r = -0.560, N - 2 = 48. p < 0.01).

Species diversity is also negatively correlated with altitude (r = -0.524). N - 2 = 48, p < 0.01) as one might expect in light of the highly significant correlation between species density and altitude. I do not have D_s values for any lowland sites but two Pacific slope localities have D_s values comparable to those for the *subparamo* and cloud forest localities in southern Andean Ecuador (Tandapi, $D_s = 2.6$; Pilaló, $D_s =$ 4.6). The low species densities and diversities at high Andean sites are not consistent with the area-diversity curves advanced by Simpson (1974) for Andean floras or by Vuilleumeir (1970) for Andean birds.

Lynch (1976b) suggested that resource partitioning by the eight species of *Eleutherodactylus* found at a Pacific slope cloud forest locality (Tandapi) in central Ecuador might be mediated by

Locality	Altitude (m)	S1	N ²	$D_s{}^3$
Carchi: Tulcán	3000	1	25	1.00
Volcán Chiles	3500	3	24	2.27
Páramo del Angél	3700	2	61	1.34
10-13 km SSE Tulcán	3020	3	37	2.59
Atal	2700	1	89	1.00
Imbabura: 1 km N Otavalo	2560	2	13	1.16
Urcusíqui	3300	2	25	1.68
8 km NW Otavalo	3100	1	8	1.00
4 km W San Pablo	3050	1	44	1.00
Nudo de Mojanda	3400	3	9	2.79
Nudo de Mojanda	3440	1	25	1.00
Nudo de Mojanda	3680	1	73	1.00
Pichincha: ½ km N Cayambe	2820	1	47	1.00
Quito	2860	1	103	1.00
Volcán Pichincha	3700	1	37	1.00
6-7 km W Chillogallo	3000	3	29	1.78
Napo: E slope, Paso de Guamaní	3650	2	94	1.07
Laguna de Papallacta	3350	4	163	1.39
Cotopaxi: Nudo de Tiopullo	3490	2	80	1.02
Mulaló	3000	1	25	1.00
Páramo de Milín	3900	1	34	1.00
Páramo del Apagua	3800	1	25	1.00
Tungurahua: 10 km SW Mocha	3700	2	29	1.31
3 km SSW San Miguelito	2620	1	95	1.00
10 km W Cotaló	3300	2	41	1.40
Chimborazo: 12 km SW Sta. Rosa	3400	1	25	1.00
18-20 km SW Sta. Rosa	3650	1	22	1.00
Urbina	3610	2	46	1.14
10 km W San Juan	3400	1	60	1.00
12 km SW Cajabamba	3800	1	24	1.00
Bolivar: crest E of Guaranda	3700	2	53	1.04
SW slope Nevado Chimborazo	3800	2	21	1.32
[Faunal h	oreak noted by Lynd	ch (1971, 1972	a, b)]	
Cañar: 8 km NW Biblian	3420	ĺ	64	1.00
Azuay: Laguna de Zurucuchu	3200	2	47	1.04
Páramo de Matanga	3400	1	51	1.00
8 km SSE Sevilla de Oro	3350	4	23	2.08
Cerro Negro	2930	3	7	1.81
6 km W San Vicente	3110	3	31	2.28
3 km W San Vicente	2990	3	23	1.19
San Vicente	2835	8	78	2.44
3 km E Sevilla de Oro	2700	3	16	1.91
Suro Rancho	2700	4	59	2.32
bet. Sapote and Suro Rancho	2615	6	20	4.00
Sapote	2470	8	121	5.73
El Cruzado	2220	9	52	3.91
Pailas	2200	6	73	3.02
San Juan Bosco	2200	5	41	2.66
Plan de Milagro	1700	3	8	2.46
Loja: 10 km S Saraguro	3120	5	26	2.41
Abra de Zamora	2800	10	296	2.27

TABLE 2. Eleutherodactyline frog faunules (Eleutherodactylus and Phrynopus).

 1 S = number of species

 2 N = number of individuals 3 D_s = 1/ Σ p², MacArthur's (1972) diversity formula

sexual dimorphism and narrower niches because interspecies ø values were low $(\bar{x} = 1.14)$ compared to Hutchinson and MacArthur's (1959) value of $\phi = 1.28$. Phi is a measure of the size difference necessary to avoid competition (size of larger/size of smaller) (Hutchinson and MacArthur, 1959). Crump (1974) noted marked sexual dimorphism and a "regular" increase in sizes among the Eleutherodactulus species found at an upper Amazonian rainforest site (Santa Cecilia, Provincia Napo, Ecuador). Using her data sets and augmenting them with my own, I find an even lower range of ø values for the Amazonian lowland fauna than that at Tandapi (Table 3).

When the southern Andean fauna is

broken into the four most obvious ecogeographic units, the more species-rich units on the Amazonian slope have \emptyset values equally as low as that for the Amazon lowland fauna whereas those for the *páramo* and the interandean-west slope faunules are more comparable to those of the Pacific lowlands and Tandapi. In all seven faunules, the degree of sexual dimorphism is identical (Table 3; sizes for the species found in southern Ecuador are provided in Table 4).

In part, these low \emptyset values are likely a function of pooling ecologic contingencies within localities (Lynch, 1976b, noted higher $\bar{x} \ \emptyset$ for contingencies than for the entire faunule). However, the propriety of comparing $\bar{x} \ \emptyset$ values among

TABLE 3. Sexual dimorphism and ø values for seven Ecuadorian Eleutherodactylus faunules.

Faunule	S	Dimorphism	ø
Tandapi	8	$1.20-1.78(7); 1.38 \pm 0.15^{1}$	$1.01 - 1.36(13); 1.14 \pm 0.06$
Loja-W slope ²	4	1.29 - 1.86(4); 1.45	1.06 - 1.55(6); 1.20
Páramo ²	3	1.25 - 1.51(3); 1.38	1.04 - 1.33(4); 1.21
Ceja andina ²	14	$1.12 - 1.72(12); 1.39 \pm 0.09$	$1.01 - 1.29(22); 1.08 \pm 0.03$
Bosque humédo ²	10	$1.18 - 1.72(8); 1.39 \pm 0.14$	$1.00-1.45(14); 1.09 \pm 0.04$
Santa Cecilia	17	$1.19 - 1.65(15); 1.39 \pm 0.07$	$1.00-1.17(27); 1.06 \pm 0.02$
Pacific lowlands	12	$1.21-1.81(10); 1.49 \pm 0.12$	$1.00-1.66(20); 1.14 \pm 0.07$

¹ range (N); $\mathbf{\bar{x}} \pm 2SE$

² size data for species of these faunules are given in Table 4

TABLE 4. SVL of Eleutherodactylus in southern Andean Ecuador.

Species	8 8	Q Q
E. atratus	$21.7 \pm 1.7(19)^{1}$	$27.4 \pm 1.3(10)$
E. balionotus	22.0(2)	$28.1 \pm 0.6(7)$
E. baryecuus	29.0(5)	$40.8 \pm 1.3(8)$
E. bromeliaceus	$20.8 \pm 0.9(14)$	26.5(5)
E. cajamarcensis	$22.4 \pm 0.7(15)$	$29.8 \pm 1.0(17)$
E. colodactylus	$17.1 \pm 0.5(46)$	$20.8 \pm 0.8(33)$
E. cryophilius	33.3(5)	45.1(5)
E. cryptomelas	29.2(4)	
E. galdi	$21.0 \pm 1.7(8)$	$31.7 \pm 1.6(9)$
E. lymani	$31.7 \pm 2.4(19)$	$58.9 \pm 4.7(6)$
E. nigrogriseus	$23.2 \pm 0.9(15)$	
E. orestes	19.8(1)	$22.1 \pm 1.4(13)$
E. percultus	29.8(1)	38.2(1)
E. phoxocephalus	$27.2 \pm 0.7(29)$	$35.1 \pm 1.1(22)$
E. proserpens	$18.6 \pm 1.0(11)$	22.0(4)
E. pycnodermis	$25.1 \pm 1.4(30)$	$38.0 \pm 1.1(40)$
E. riveti	$24.1 \pm 0.6(35)$	$30.1 \pm 0.8(30)$
E. ruidus	$28.9 \pm 1.4(7)$	$37.9 \pm 0.7(7)$
E. spinosus	$20.1 \pm 0.6(34)$	$31.8 \pm 0.6(29)$
E. versicolor	$23.0 \pm 0.8(16)$	$28.4 \pm 0.7(15)$
E. vidua		$21.5 \pm 0.8(8)$
E. w-nigrum ²	$34.5 \pm 1.0(43)$	$59.2 \pm 2.6(9)$
$1 = \pm 9 \text{ SE(N)}$		

 $\frac{1}{\mathbf{x}} \pm 2$ SE(N)

² based on samples from the Amazonian slope in Provincia Morona-Santiago, Ecuador

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several faunules is questionable in that the several faunules differ in the relative proportions of species of the fitzingeri and the unistrigatus groups. If ø and the size of the larger of the two species are compared (Fig. 21), the two are significantly correlated (r = 0.70, N - 2= 49, p < 0.01). This sample consists of 51 pair of species (using only females). The correlation of ϕ values and size where only members of the *fitzingeri* group are involved is also highly significant (r = 0.83, N - 2 = 10, p < 0.01) whereas that where only members of the unistrigatus group are involved is not significant (r = 0.40, N - 2 = 37, p > 0.01, < 0.05). The correlation for unistrigatus group species is significant at $p \leq 0.05$. Thus one might expect higher \bar{x} ø values in faunules having greater proportions of fitzingeri group species. However, using only seven faunules that is not true (Fig. 22); the correlation between $\bar{x} \neq and$ the percent *fitzingeri* group species is non-significant (r =0.141, N - 2 = 5, p > 0.05). There is a highly significant negative correlation between $\bar{x} \notin$ and species density (Fig. 23) (r = -0.928, N - 2 = 5, p < 0.01). This is not a function of altitude (the correlation of $\bar{x} \neq w$ with altitude is not significant, r = 0.415, p > 0.05). Our knowledge of Andean eleutherodactylines is too fragmentary to decide if the approach to unity of ϕ values means smaller niches or increased niche overlap (the alternatives mentioned by Pianka, 1966) but the habitat segregation by the species in a Pacific slope cloud forest (Lynch, 1976b) suggests that the frogs have smaller niches.

Comparisons with distributions of other Andean genera.—The high Andean frog fauna in northern Ecuador consists of Atelopus ignescens, Eleutherodactylus curtipes and E. unistrigatus, Gastrotheca riobambae, and Telmatobius niger. Atelopus ignescens ranges south to at least the Abra de Zamora without a geographic replacement. Gastrotheca riobambae and T. niger range south into the Cuenca hoya (both to the



Fig. 21.—Magnitude of size difference (Ø) as a function of body size in *Eleutherodactylus*.
(▲) Ø values where one (or both) species is a member of the *fitzingeri* group; (●) Ø values for pairs of the *unistrigatus* group.



FIG. 22.—Magnitude of average ø in seven Eleutherodactylus faunules as a function of proportion of the faunule made up of members of fitzingeri group.



FIG. 23.—Magnitude of average ø in seven Eleutherodactylus faunules as a function of species density (S).

Nudo de Portete in Azuay Prov.). South of the Nudo de Portete, G. riobambae is replaced by three allopatric species, G. loyana, G. monticola, and G. psychrophilia (Duellman, 1974), and T. niger by two allopatric species, T. vellardi and an undescribed species (Trueb, pers. Eleutherodactylus comm.). curtipes ranges south to the Desierto de Palmira and is replaced on the *páramos* ringing the Cuenca hoya by E. cryophilius. Eleutherodactylus unistrigatus ranges south to the headwaters of the Río Chambo: south of the Nudo de Azuav it is replaced by E. riveti (on the ranges surrounding the Cuenca hoya), E. cajamarcensis and E. versicolor (on the Cordilleras Chilla, Sabanilla, and Zamora), E. ruidus (on the Cordillera de Molleturo), E. pycnodermis (on the Cordillera de Condorcillo), and E. balionotus and E. percultus (on the Cordillera de Zamora). In southern Andean Ecuador, frogs of the genus Colostethus are prominent and in the Loja hoya one encounters Bufo spinulosus.

High altitude iguanids of the genus Stenocercus exhibit a distributional pattern congruent with that of Eleutherodactylus (Fritts, 1974). Stenocercus guentheri ranges over northern Andean Ecuador, S. festae and S. simonsi occur in the Cuenca and Saraguro hoya, S. humeralis and S. ornatus occur on the north and west edges of the Loja hoya, and S. carrioni and S. rhodomelas range over the xeric Pacific slopes (Fritts, 1974). A less congruent pattern is seen in the teiid genus Pholidobolus where species' range limits correspond with the Cordillera de Igualata and the Pastaza Valley and, to a lesser extent, the Nudo de Azuay, where P. prefrontalis leaves interandean habitats and inhabits the Pacific slopes (Montanucci, 1973).

In some respects, the species of Ate-

lopus, Eleutherodactulus, Gastrotheca, and *Telmatobius* are exposed to the same general selective regimes and ecogeographic barriers, and one might anticipate concordant variation among the four genera. On the other hand, Eleutherodactulus differs from the others in exhibiting direct development; intuitively, they seem more sensitive to environmental variation. However, Scott (1976) implied that *Eleutherodactulus*, freed as they are of the uncertainty of water. might be more uniformly populated (than frogs having a tadpole stage) encouraging freer gene flow (and less fragmentation of populations). The parapatric (rather than dichopatric) distributions of most Artenkreisen of Eleutherodactulus suggests that gene flow is inhibited by ecogeographic barriers.

The high densities of Eleutherodactylus and the putative non-patchiness of their microhabitat (at least in the lowlands, Hever and Breven, 1973) suggest that a parapatric speciation model functions because these frogs exhibit a very low vagility. The lack of parapatric speciation among the frogs now grouped as A. ignescens may be a result of searching patterns by the female of an amplectant pair for a suitable ovoposition site (Peters, 1973). Similarly, the apparent lack of speciation by G. riobambae may result from the admixture of local populations coming from vocal attraction by calling males and/or dumping of larvae in suitable Andean ponds by the female. The restrictions on reproductive sites for Atelopus and Gastrotheca presumably override the impact of slight ecogeographic barriers whereas Eleutherodactulus are more sensitive to those barriers because they may deposit their eggs where they are living rather than needing to move to ovoposition sites.

SUMMARY

The frog fauna of the Andes of southern Ecuador consists of no fewer than 21 species of eleutherodactylines belonging to the genera *Eleutherodac*- tylus and Phrynopus. A single species of Phrynopus and twenty species of Eleutherodactylus occur in the Andes south of the Nudo de Azuay and north of the Huancabamba depression in northern Perú. Of the eighteen representatives of the *unistrigatus* group of *Eleutherodactylus* found in the region, sixteen are named as new species.

With a single exception, the affinities of the 20 species of *Eleutherodactylus* are with high altitude and moderate altitude species found in northern Ecuador and southern Colombia. *Eleutherodactylus bromeliaceus* is most similar to a species of the Amazon basin, *E. lacrimosus*.

The greater diversity of eleutherodactylines in the Andes of southern Ecuador as compared to northern Ecuador may be a function of 1) the Pleistocene vulcanism of northern Andean Ecuador, 2) habitat contiguity in north-

La fauna anfibia de los Andes del sur del Ecuador está representada al menos por 21 especies de eleutherodactilinos pertenecientes a los géneros *Eleutherodactylus* y *Phrynopus*. Entre el Nudo de Azuay, por el norte, y la Depresión de Huancabamba (norte del Perú), por el sur, se encuentra una sola especie de *Phrynopus* y 20 de *Eleutherodactylus*. Dieciseis especies del grupo *unistrigatus* de *Eleutherodactylus* que se encuentran en esta región son descritas como nuevas.

Con una excepción, todas éstas especies de *Eleutherodactylus* muestran afinidad con especies de moderada y de pronunciada elevación del norte del Ecuador y del sur de Colombia. Sólo hay una excepción, *Eleutherodactylus bromeliaceus*, la cual es más similar a una especie de la cuenca amazónica, *E. lacrimosus*.

La mayor diversidad de eleutherodactilinos en los Andes Sud-ecuatorianos, comparada con aquella del norte ern Andean Ecuador, or 3) the invasion of *subparamo* habitats in southern Ecuador by species found on the Andean slopes at more northern latitudes.

In general, the Andean species of *Eleutherodactylus* are parapatrically distributed, and the distribution areas of the southern species are smaller than those of the largely sympatric representatives of the genera *Atelopus*, *Gastrotheca*, and *Telmatobius*. These observations suggest that *Eleutherodactylus* are less vagile and more sensitive to ecogeographic barriers than are the frogs of the genera *Atelopus*, *Gastrotheca*, and *Telmatobius*, all of which are larger than most *Eleutherodactylus* and have restrictions on oviposition sites (all have aquatic tadpoles).

RESÚMEN

ecuatoriano, puede ser función de: 1) Vulcanismo pleistocénico de los Andes del norte del Ecuador, 2) continuidad ecológico-ambiental en la región norte de los Andes ecuatorianos, ó 3) la invasión de los ambientes subpáramicos en el sur del Ecuador por especies que se encuentran en las laderas andinas en latitudes más nortinas.

En general, las especies andinas de Eleutherodactulus se encuentran distriduidas parapatricamente; las áreas de distribución de las especies sureñas son más pequeñas que aquellas de los géneros Atelopus, Gastrotheca, y Telmatobius que son ampliamente simpátricos. Estas observaciones sugieren que los Eleutherodactylus son menos vagiles y más sensitivos a las barreras ecogeográficas que los sapos de los géneros Atelopus, Gastrotheca, y Telmatobius, los cuales en general son de mayor tamaño y que además tienen restricciones en cuanto a los sitios de oviposición por tener renacuajos acuáticos.

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APPENDIX: SPECIMENS EXAMINED

Eleutherodactylus atratus (43 spec.)

ECUADOR: Morona-Santiago: El Cruzado, 2195 m, USNM 199690-99; San Vicente, 2835 m, USNM 199712; Sapote, 2470 m, USNM 199701-10, 199713 (cleared and stained skeleton); 2 km W Sapote, 2561 m, USNM 199711; between Sapote and Suro Rancho, 2604-2622 m, USNM 199683-89; Suro Rancho, 2683 m, USNM 199675-82; ½ km W Suro Rancho, 2744 m, USNM 199700. Zamora-Chinchipe: Abra de Zamora, 2850 m, KU 165236-38.

Eleutherodactylus balionotus (10 spec.)

ECUADOR: Loja: 13.5 km E Loja, Abra de Zamora, 2800 m, KU 142135-44.

Eleutherodactylus baryecuus (17 spec.)

ECUADOR: Morona-Santiago: Cerro Negro, 2927 m, USNM 199715; El Cruzado, 2195 m, USNM 199723-24; San Juan Bosco, 2195 m, USNM 199725; between San Juan Bosco and El Cruzado, 2226 m, USNM 199717-22; San Vicente, 2805-2835 m, USNM 199729; 3 km W San Vicente, 2988 m, USNM 199730; Sapote, 2470 m, USNM 199726-28; between Sevilla de Oro and Méndez (probably between the crest and Pailas), USNM 199716; Suro Rancho, 2683 m, USNM 199714.

Eleutherodactylus bromeliaceus (20 spec.)

ECUADOR: Morona-Santiago: El Cruzado, 2195 m, USNM 199738-39; Mirador, 1982 m, USNM 199735; Pailas, 2195 m, USNM 199732-34, 199743-45; Plan de Milagro, 1707 m, USNM 199736-37, 199746-47; ½ km E Sapote, 2393 m, USNM 199740, 199748-49; 1 km E Sapote, 2332 m, USNM 199741; mountain above Sapote (to the south), 2500 m, USNM 199742, 199750; between Sapote and Suro Rancho, 2622 m, USNM 199731.

Eleutherodactylus cajamarcensis (137 spec.)

ECUADOR: Loja: 5 km NE Cariamanga, 1870 m, KU 141896-909; 12 km NE Catacocha, 2060 m, KU 141890-95; 9 km E Loja, 2660 m, KU 119949-50; 12½ km S Loja, 2250 m, KU 165190-92; 6 km N San Lucas, 2760-2900 m, KU 120007-15, 165193-99; 7-8 km N San Lucas, 2940-3000 m, KU 119951-120005, 120006(5), 120022-24 (cleared and stained skeletons); 13 km E Veracruz, 2250 m, KU 141860-89.

PERU: Cajamarca: pre-Inca ruins near Huambos, MCZ 5407. Piurá: summit of Cordillera between Chanchaque and Huancabamba, 3100 m, KU 135495, 135502.

Eleutherodactylus colodactylus (113 spec.)

ECUADOR: Aznay: 8 km ESE Sevilla de Oro (on Azuay-Morona-Santiago frontier), 3140 m, USNM 198458. Morona-Santiago: El Cruzado, 2195 m, USNM 198436; Pailas, 2195 m, USNM 198431-33, 198459; San Juan Bosco, 2195 m, USNM 198434-35, 198460-61; immediate environments of San Vicente, 2790-2820 m, USNM 198465-79; 1 km W San Vicente, 2851 m, USNM 198462-64; 1 km E Sapote, 2332 m. USNM 198457; mountain above Sapote to the south, 2500 m, USNM 198456; 1/2 km W Sapote, 2546 m, USNM 198437-55. Zamora-Chinchipe: Abra de Zamora, 2800 m, KU 142151-59 (142155 cleared and stained skeleton), 165219-21; 14 km E Loja, 2770 m, KU 142160-61; 15 km E Loja, 2710 m, KU 142162-64.

PERU: *Piurá*: 33 km SW Huancabamba, 2745-3050 m, LSUMZ 32368-414.

Eleutherodactylus cryophilius (10 spec.)

ECUADOR: Azuay: Bestión (southwest-

ern slopes Cerro Bestión), 3080 m, AMNH 13970; Laguna de Zurucuchu, 3200 m, KU 120091; between Sevilla de Oro and Azuay-Morona-Santiago frontier, 3354 m, USNM 199994. *Morona-Santiago:* on crest between Azuay and Morona-Santiago provinces (approximately 8 km ESE Sevilla de Oro), 3384 m, USNM 200390; San Vicente, 2835 m, USNM 199995-96; 6 km W San Vicente, 3110 m, USNM 199993, 200391-93.

Eleutherodactylus cryptomelas (8 spec.)

ECUADOR: Loja: 8-9 km N San Lucas, 3000-3100 m, KU 120095-96. Morona-Santiago: Sapote, 2470 m, USNM 198480-82; 2 km W Sapote, 2560 m, USNM 198483. Zamora-Chinchipe: 15 km E Loja, 2710 m, KU 141992-93.

Eleutherodactylus lymani (77 spec.)

ECUADOR: Azuay: 4 km SW Catavina, 1600 m, USNM JAP 3541; Río Minas, 20 km W Santa Isabel, 1250 m, USNM JAP 3625; 55.4 km E Pasáje, ca. 1000 m, KU 152009. El Oro: El Chiral, 1630 m, AMNH 13961, 13964; Cordillera de Chilla, Llanos de Guavos, AMNH 13738; Guainche, AMNH 16256; Piñas, AMNH 16257; Portovelo, 610 m, AMNH 16334, 16339, 16341-44. Loja: Loja, 2150 m, BM(NH) 1931.2.12.1-3/RR 1947.2.15.99-101, KU 119502; 8 km NE Loja, 2300-2500 m, USNM GOV 8734-35, 8737, 9533-39, 9541, WCAB 39912-13; 2 km E Loja, 2210 m, KU 119504-12; 3 km E Loja, 2100 m, USNM JAP 2455; 7 km E Loja, 2500 m, KU 119503; 10 km W Loja City, 3000 m, USNM 98931; 7.6 km S Loja, 2210 m, KU 141962-64; 9 km S Loja, 2230 m, KU 165539-40, 165231 (lot of eggs); 12.2 km S Loja, Río Malacatos valley, road to Vilcabamba, 2275 m, KU 141292; 17 km NE Macará, 1240 m, KU 141965; Pta. Santa Ana, 1100 m, AMNH 13734, 13966, 13973; Río Puyango, AMNH 16211-15, 16224.

PERU: *Cajamarca*: Bellavista, MCZ 5423, 5426-27, 5429, 5431, UMMZ 55774(3); Palamba, MCZ 5436; Perico, MCZ 5408, 5410, 5412, 5415, 5418-21, 5422.

Eleutherodactylus orestes (20 spec.)

ECUADOR: Azuay: 2.1 km S Cutchil, 2720 m, KU 141468; 3.1 km S Cutchil, 2730 m, KU 141467; 5 km ESE Sevilla de Oro, 2957 m, USNM JAP 6580-81. Loja: Saraguro, 2570 m, KU 141995; 9.5 km S Saraguro, 3120 m, KU 141469-72, 151052 (cleared and stained skeleton); 10 km S Saraguro, 3100 m, KU 141996-97; 11 km NE Urdaneta, 2970 m, KU 141998-2003. Zamora-Chinchipe: Abra de Zamora, 2850 m, KU 120094, 165550.

Eleutherodactylus percultus (2 spec.)

ECUADOR: Zamora-Chinchipe: Abra de Zamora, 2850 m, KU 166057-58.

Eleutherodactylus phoxocephalus (193 spec.)

ECUADOR: Azuay: 10 km SW Victoria del Portete, Parque Nacional Portete de Tarqui, 2700 m, KU 131281-82. Cañar: 18.4 km NW El Tambo, 2960 m, KU 142118-30. Cotopaxi: Pilaló, 2320 m, KU 142075-103, USNM JAP 3208-11, 3213-14, 3329-36; Pilaló, 2460 m, KU 131404-78, 131485-88, 131698; Pilaló, 2580 m, KU 131480-84, 131699-716. Loja: Saraguro, 2500 m, KU 135460-62; 3.3 km NNE Saraguro, 2400 m, KU 142117; 2 km S Saraguro, 2680 m, KU 142114-16; Río Zamora, 6.5 km N Loja, 2060 m, KU 142113. Pichincha: 4 km W Chiriboga, 2120 m, KU 142072-74; Finca Santa Lucia, 7.7 km E Chiriboga, 2120 m, KU 142063-71; Los Alpes, 2500 m, KU 140876-77; San Ignacio, 10 km E Tandapi, 2030 m. KU 109137. Zamora-Chinchine: 15 km E Loja, 2710 m, KU 142104-12.

Eleutherodactylus proserpens (27 spec.)

ECUADOR: Morona-Santiago: El Cruzado, 2195 m, USNM 199751; Plan de Milagro, 1707 m, USNM 198485, 198504; 1 km S Plan de Milagro, 1707 m, USNM 198503; Río Piuntza, Cordillera del Condor, 1830 m, KU 147044-46; ½ km E Sapote, 2393 m, USNM 199752; 1 km E Sapote, 2332 m, USNM 198499-501, 199753; mountain above Sapote (to the south), 2500 m, USNM 198496-98; ½ km W Sapote, 2546 m, USNM 198486-91; between Sapote and Suro Rancho, 2622 m, USNM 198484, 198492-95, 198502.

Eleutherodactylus pycnodermis (137 spec.)

ECUADOR: Azuay: 3 km E Sevilla de Oro, 2713 m, USNM 199851-53; 5 km ESE Sevilla de Óro, 2957 m, USNM 199854, 199867; between Sevilla de Oro and Cerro Negro, 3110 m, USNM 199868; crest at Azuay-Morona-Santiago frontier, ca. 8 km SE Sevilla de Oro, 3354 m, USNM 199855-59, 199866; crest at Azuay-Morona-Santiago frontier, ca. 8 km SE Sevilla de Oro, 3384 m, USNM 199758-59, 199860-65. Morona-Santiago: between Cerro Negro and Pailas, 2652 m, USNM 199755-57, 199869-71; San Vicente, 2805-35 m, USNM 199754, 199815-50, 199884, 199888-90; San Vicente, 2851 m, USNM 199813-14, 199885-87; 3 km W San Vicente, 2988 m, USNM 199794-812, 199882-83; 6 km W San Vicente, 3100 m, USNM 199787-93, 199880-81; Suro Rancho, 2683 m, USNM 199760-66;

½ km W Suro Rancho, 2744 m, USNM 199767-86, 199872-79.

Eleutherodactylus riveti (318 spec.)

ECUADOR: "Equateur" MHNP 1902-357. Azuau: Cerro Negro (E of Sevilla de Oro), 2927 m, USNM JAP 6545, 6695-98; Cuenca, USNM 146277; 9 km S Cumbe, 3300 m, KU 131077-79; 10 km S Cumbe, 3350 m, KU 131080-145; 21.6 km S Cumbe, 3310 m, KU 141988-91; 28.6 km S Cumbe, 3190 m, KU 141986-87; 2.1 km S Cutchil, 2720 m, KU 141438-42; 3.1 km S Cutchil, 2730 m, KU 141433-34; 3.5 km S Cutchil, 2785 m, KU 141424-29; 9.6 km S Cutchil, 2935 m, KU 141430-32; 11.5 km S Cutchil, 2820 m, KU 141435-37; Laguna de Zurucuchu, 3200 m, KU 119812-56, 119857 (cleared and stained skeleton); 3 km E Sevilla de Oro, 2713 m, USNM JAP 6445-49; 5 km ESE Sevilla de Oro, 2957 m, USNM JAP 6582-87; 8 km ESE Sevilla de Oro, 3140 m, USNM JAP 6704; crest of Azuay-Morona-Santiago frontier, ca. 8 km SE Sevilla de Oro, 3354 m, USNM JAP 6482, 6484; crest at Azuay-Morona-Santiago frontier, ca. 8 km SE Sevilla de Oro, 3384 m, USNM JAP 6566-67. Canar: 1/2 km N Biblian, 2620 m, KU 141418; 8 km (by road) NW Biblian, 3100 m, KU 141419-23; 8 km NW (airline) Biblian, 3420 m, KU 131146-209; 15 km SSE Cañar, road to Azoques, UMMZ 132917; 20 km NE Gun, 2927 m, USNM JAP 6395, 6686, 6407, 6410, 6700. Morona-Santiago: Páramo de Raranga, 12 km S (airline) Cutchil, 3400 m, KU 120025-70; 8 km S (airline) Cutchil, 3040 m, KU 120071-79, 120080-81 (cleared and stained skeletons), 120303; 3 km W San Vicente, 2988 m, USNM JAP 7732; 6 km W San Vicente, 3110 m, USNM JAP 7878-79, 7881-96.

Eleutherodactylus ruidus (16 spec.)

ECUADOR: Azuay: Molleturo, 2317 m, AMNH 17588-603.

Eleutherodactylus spinosus (100 spec.)

ECUADOR: Morona-Santiago: between Cerro Negro and Pailas, 2652 m, USNM 199916; between Cerro Negro and Pailas, 2439-2561 m, USNM 199917; El Cruzado, 2195 m, USNM 199945-66; Loma de Puerco, 2226 m, USNM 199967-71; Pailas, 2195 m, USNM 199918-35, 199973-77; 1 km S Plan de Milagro, 1707 m, USNM 199978; Rio Piúntza, Cordillera del Condor, 1830 m, KU 147039; San Juan Bosco, 2195 m, USNM 199936-44, 199979-82; San Vicente, 2835 m, USNM 199972, 199988-89; Sapote, 2470 m, USNM 199891-915, 199986-87; between Sapote and Suro Rancho, 2604-2622 m, USNM 199983-95.

Eleutherodactylus versicolor (177 spec.)

ECUADOR: Loja: 13.2 km E Loja, 2770 m, KU 141443-45; 8-9 km N San Lucas, 3000-3100 m, KU 119945. Zamora-Chinchipe: Abra de Zamora, 2800 m, KU 119948 (cleared and stained skeleton), 119872-910, 141446-48, 142011-12, 165593-645; 14 km E Loja, 2775 m, KU 119946-47 (cleared and stained skeletons), 119858-71, 119911-44, 141449-60, 141465-66, 142004; 15 km E Loja, 2685-2710 m, KU 141461, 142005-09; 15.4 km E Loja, 2645 m, KU 141462-63; 16.6 km E Loja, 2560 m, KU 141464; 18 km E Loja, 2510 m, KU 142010.

Eleutherodactylus vidua (18 spec.)

ECUADOR: Azuay: 32 km S Cumbe, 3180 m, KU (WED 47603). Loja: 8-9 km N San Lucas, 3000-3100 m, KU 120092. Zamora-Chinchipe: Abra de Zamora, 2800 m, KU 120082-91, 120093 (cleared and stained skeleton), 141994, 165648-51.







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