

New species of frogs (Leptodactylidae: Eleutherodactylus) from the Amazonian lowlands of Ecuador

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NEW SPECIES OF FROGS (LEPTODACTYLIDAE:
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ELEUTHERODACTYLUS)
FROM THE AMAZONIAN LOWLANDS OF ECUADOR

AUG 12 1974

By

HARVARD UNIVERSITY
JOHN D. LYNCH¹

Herpetological exploration of tropical rainforest habitats at Lago Agrio and Santa Cecilia, Napo Province, Ecuador, has established the co-occurrence of sixteen species of the leptodactylid frog genus *Eleutherodactylus*. None of these species is known only from these two localities, and two do not occur at Santa Cecilia and another does not occur at Lago Agrio.

Ecological studies in progress and nearing completion require that the unnamed species be described. At the onset of field work in 1966, nine of the sixteen were already named (*E. acuminatus* Shreve, *E. altamazonicus* Barbour and Dunn, *E. conspicillatus* Günther, *E. diadematus* Jiménez de la Espada, *E. lacrimosus* Jiménez de la Espada, *E. nigrovittatus* Andersson, *E. ockendeni* Boulenger, *E. pseudoacuminatus* Shreve, and *E. sulcatus* Cope). Three species have been described since 1966 (*E. croceoinguinis*, *E. orphnolaimus*, and *E. variabilis*; Lynch, 1968a, 1970). Four species are currently unnamed. One is a species of the *E. fitzingeri* group and will be described elsewhere (Lynch, MS). The other three are species of the *E. unistrigatus* group (roughly equivalent to Group II of Cochran and Goin, 1970). The *E. unistrigatus* group is defined as follows: heads of "normal" width (head width 30-40% snout-vent length), skin of abdomen coarsely areolate, first finger shorter than second, all digits bearing discs on narrowly to broadly dilated pads,

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the fold of skin above the disc not markedly indented or notched distally, the tympanum frequently obscure or concealed beneath skin (rarely absent), and having narrow prevomerine odontophores that are oblique or slanted in some species to triangular in outline in others (rarely not visible; never arch-like and broad).

Synonymies also are recorded for three other names (*E. anderssoni* Lynch, *E. brevicrus* Andersson, and *E. festae* Peracca) of frogs reported from Amazonian Ecuador. These trivial names likewise apply to frogs of the *E. unistrigatus* group.

Acknowledgments.—Thanks are offered the members of the University of Kansas field parties (Martha L. Crump, William E. Duellman, Stephen R. Edwards, Thomas H. Fritts, Marsha C. Lynch, William B. Saul, John E. Simmons, Gerald R. Smith, and Linda Trueb) whose enthusiasm has measurably improved the numbers of specimens collected as well as the often detailed color notes, photographs, and ecologic data available for many of the specimens. Special thanks are given to Marsha Lynch, Bill Saul, and Gerry Smith for aid and companionship in the field.

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I am indebted to the following for loan of specimens or for provision of working space in their respective institutions: Werner C. A. Bokermann, the late Doris M. Cochran, Alice G. C. Grandison, Charles W. Myers, the late James A. Peters, Umberto Parenti, Dorothy Smith, Hobart M. Smith, Greta Vestergren, Charles F. Walker, Ernest E. Williams, and John W. Wright.

Abbreviations for collections used throughout the text are:

BMNH	British Museum (Natural History)
KU	Museum of Natural History, The University of Kansas
LACM	Los Angeles County Museum
MCZ	Museum of Comparative Zoology (Harvard University)
MIZ	Museo ed Istituto di Zoologia Sistemica della Università di Torino
NHRM	Naturhistoriska Riksmuseet, Stockholm
UIMNH	University of Illinois Museum of Natural History
USNM	National Museum of Natural History

***Eleutherodactylus martiae* new species**

Figure 1A

Holotype.—KU 152389, an adult female (22.2 mm in snout-vent length) of an amplexant pair (♂ KU 152390) collected at Santa Cecilia, Provincia Napo, Ecuador, 340 m, on 4 May 1973 by Martha L. Crump.

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Paratypes.—KU 123815-18, 126197-98, 149200-01, 149203-30, 152388, 152390-92, all from the type-locality, collected by various individuals between June 1968 and May 1973.

Diagnosis.—(1) skin of dorsum bearing low, flat warts (not uniformly shagreened), that of venter coarsely areolate; no dorsolateral folds; discoidal folds obscure; (2) tympanum concealed; (3) snout subacuminate in dorsal view, rounded in lateral profile, short (eye length greater than eye-nostril distance); (4) interorbital space flat; upper eyelid width equal to interorbital distance (IOD); (5) prevomerine odontophores usually concealed beneath tissue of palate, if visible, obliquely oriented posterior and medial to choanae; (6) males with subgular vocal sac and short vocal slits; (7) first finger shorter than second, all fingers bearing pads and discs, those on fingers 2-4 distinctly broader than digit below pad; (8) fingers bearing narrow, keel-like lateral fringes; (9) no ulnar tubercles present except antebrachial; (10) tarsus lacking tubercles or folds; heel bearing low, flattened tubercles (none conical); (11) inner metatarsal tubercle three times size of rounded outer metatarsal tubercle; supernumerary plantar tubercles low, obscure; (12) toes bearing narrow lateral fringes, not webbed; toes bearing pads and discs, pads of toes slightly larger than those of fingers; (13) color pattern polymorphic; dorsum brown with darker brown chevrons and with or without broad cream dorsolateral stripes; or, dorsum striped with brown. Venter gray to brown; concealed thigh and groin brown, not spotted with yellow or orange; (14) adults small, ♂♂ 13.2-16.8 mm, ♀♀ 18.3-23.0 mm in snout-vent length (SVL).

Few Group II *Eleutherodactylus* are so small as *E. martiae*. The equally small *E. carvalhoi* and *E. croceoinguinis* have yellow and orange spots respectively on the concealed surfaces of the groin and/or thighs. *Eleutherodactylus trachyblepharis* has visible tympana and like *E. carvalhoi* and *E. croceoinguinis* has prominent, although small, odontophores, whereas the odontophores are rarely visible in *E. martiae*. Male *E. altamazonicus* may be confused with female *E. martiae* unless sex and colors in life are known; bright red areas are found on the concealed surfaces of the limbs in *E. altamazonicus* (in *E. martiae* these areas are brown). The venter is darker in *E. altamazonicus* than in *E. martiae*, and *E. altamazonicus* has a slightly longer snout than does *E. martiae*. These five species have rounded snouts in lateral profile in contrast to the truncate snout of *E. pseudoacuminatus* (tympana visible) and the protruding snouts of *E. acuminatus* (tympana concealed) and *E. paululus* (tympana visible).

Description.—Head as wide as body, wider than long; head width 32.9-38.7 per cent SVL (\bar{x} =35.8, N =26); snout subacuminate to rounded (with pointed tip) in dorsal view, rounded or weakly pointed in lateral profile; snout short, eye-nostril distance

61.5-89.7 per cent eye length (\bar{x} =79.2, N =26); canthus rostralis moderately sharp, concave; loreal region concave, sloping to lips; lips not flared; nostrils weakly protuberant, directed laterally; inter-orbital space flat; no cranial crests, frontoparietals complete; upper eyelid width 83.8-123.1 per cent IOD (\bar{x} =98.8, N =25); upper eyelid bearing low flat warts but no enlarged tubercles; tympanum concealed; supratympanic fold thick, not prominent; choanae small, round, well within palatal shelf of maxillary arch; prevomerine odontophores usually concealed beneath tissue of palate—if visible, low, oblique, separated by a distance equal to 0.5-2.5 times choanal width; tongue longer than wide, notched posteriorly, posterior one-third to one-fourth not adherent to floor of mouth; males with sub-gular vocal sac and short vocal slits (at posterolateral corners of floor of mouth).

Skin of dorsum finely shagreened with low warts, lacking folds; lower flanks coarsely areolate; venter less coarsely areolate than flanks; warts about vent larger than those on rest of body; discoidal folds obscure; no ulnar tubercles except for antebrachial tubercle; palmar tubercle bifid, 1.5 times size of oval thenar tubercle; numerous close-set palmar supernumerary tubercles, none prominent; sub-articular tubercles round, simple, sub-conical; fingers bearing narrow lateral, keel-like fringes; all digits bearing pads and discs, those on thumbs not much broader than digit width below pad, other pads distinctly larger and broader than long; second finger slightly longer than first.

Tarsus lacking tubercles and folds; heel bearing low, flattened tubercles; two metatarsal tubercles, outer round, one-third size of non-compressed inner; plantar surface bearing low, indistinct supernumerary tubercles; subarticular tubercles round, simple, subconical, a little larger than those of fingers; toe pads and discs all large, slightly larger than those of fingers; hindlimbs short, shank of males 46.1-51.7 per cent SVL (\bar{x} =49.3, N =12), of females 43.3-49.0 per cent (\bar{x} =46.2, N =14); heel of adpressed leg reaches to posterior one-half of eye; heels of flexed legs barely overlap.

Color pattern polymorphic; ground color brown or gray; non-lineate morphs have darker brown chevrons, supra-inguinal bar, interorbital bar or triangle bordered anteriorly by a pale bar and a brown snout spot; canthal, supratympanic, and labial bars dark brown; supratympanic stripe continues onto anterior flank; posterior flank pale brown; venter pale brown to whitish with brown suffusion (darkest anteriorly); groin and anterior thigh pale brown; posterior surface of thighs uniform brown; anal triangle dark brown; limbs barred with dark brown, bars perpendicular to limb axis or weakly oblique, slightly wider than interspaces. The lineate pattern differs from the non-lineate pattern in having brown stripes of vary-

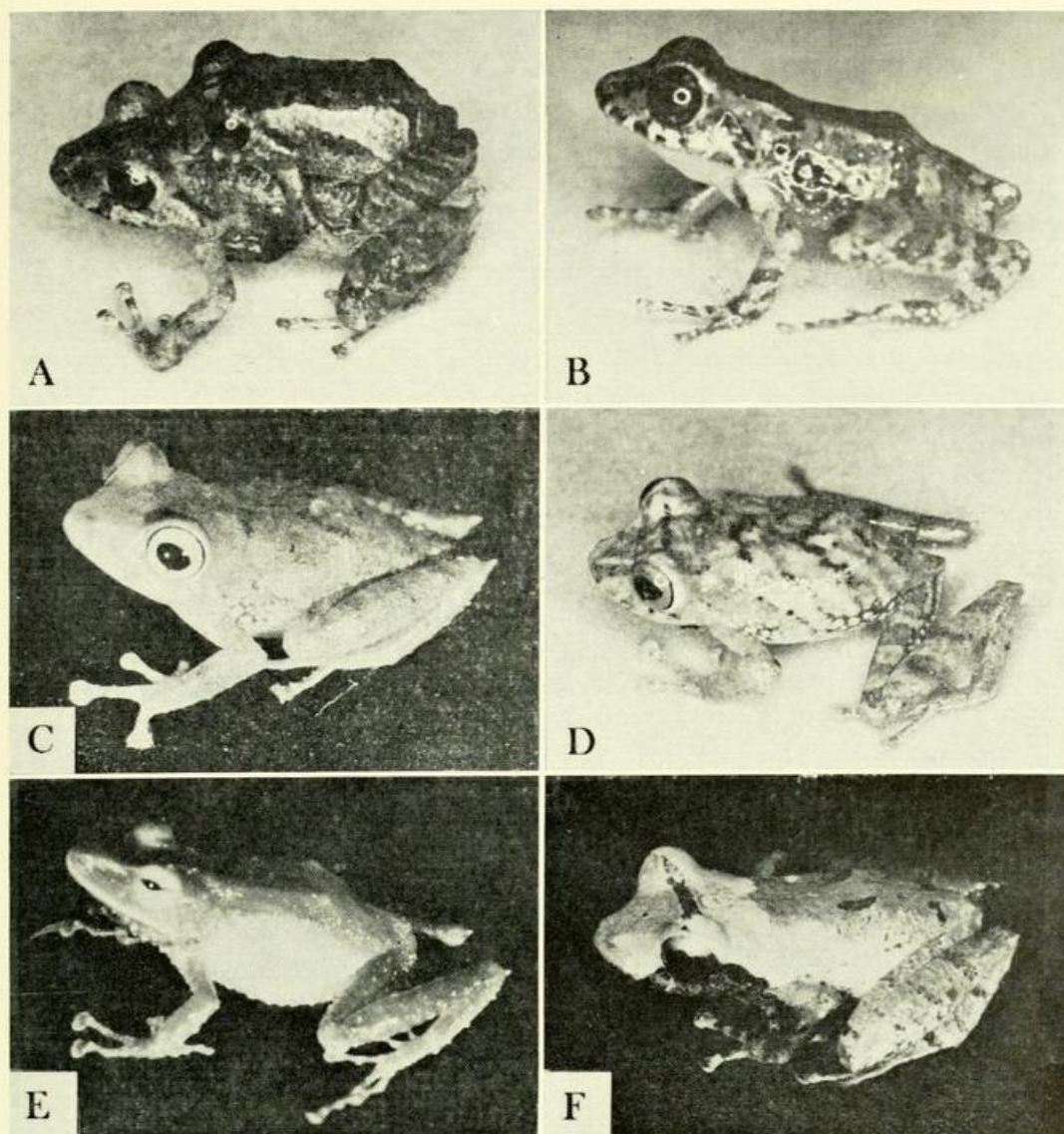


FIG. 1.—A, *Eleutherodactylus martiae*, KU 123815-16, ♀ 21.1 mm SVL; B, *E. paululus*, KU 126208, 15.4 mm SVL; C, *E. quaquaversus*, KU 123746, 22.5 mm SVL; D, *E. quaquaversus*, KU 143441, 21.8 mm SVL; E, *E. galdi*, KU 143416, 33.4 mm SVL; F, *E. ockendeni*, KU 126214, 20.7 mm SVL.

ing width from the tip of the snout to the vent; the more lateral brown stripes are darker than the more sagittal stripes.

In life *E. martiae* is brown above with darker brown markings and pale gray or pale brown below. The venter may bear white flecks. The concealed surfaces of the thighs are usually brown but may be pale tan. Lineate individuals are tan above with brown stripes. The iris is pale bronze with a median horizontal red-brown streak.

Measurements of the holotype in mm.—SVL 22.2, tibia 10.3, head width 7.8, upper eyelid width 2.3, IOD 2.4, eye length 2.7, eye-nostril 2.4. The oviducts of the holotype are convoluted, and ovarian eggs are yellow and large (2.0-2.5 mm in diameter).

Distribution.—Specimens are known from elevations of 300-1300

m on Amazonian slopes of the Andes of northern Ecuador as well as from the upper Río Pastaza drainage (Fig. 2).

Remarks.—Most specimens of *E. martiae* have been collected on low vegetation (1-2 m above ground) in forested situations at night. Claspings pairs have been taken in January, May, June, July, and August. A male (KU 123847) was collected calling at night on 20 July 1968. The call was described as a series of soft clicks (W. E. Duellman field notes).

Eleutherodactylus martiae is sympatric with *E. croceinguinis*, another dwarf eleutherodactyline frog (females to 23.0 mm SVL). Unlike *E. croceinguinis*, *E. martiae* exhibits pronounced pattern polymorphism. The lineate color pattern occurs in 22.2 per cent of the specimens examined. Frogs having a pattern of chevrons (non-lineate morph) comprise 77.8 per cent of the sample. Of the chevron-patterned frogs, 34 per cent have pale dorsolateral stripes superimposed on the pattern of chevrons. The roughly 3:1 proportion of chevron:lineate patterns may be a coincidence or may reflect a simple dominant gene for color pattern.

Etymology.—Named for Martha ("Marty") L. Crump whose quest for ecologic knowledge of Amazonian frogs has resulted in an outstanding collection of Amazonian eleutherodactyline.

***Eleutherodactylus paululus* new species**

Figure 1B

Holotype.—KU 126209, an adult female (19.4 mm SVL) of an amplexant pair, collected at Lago Agrio, Provincia Napo, Ecuador, 330 m, on 12 May 1969 by William E. Duellman.

Paratypes.—(3) KU 126205-06, 126208; collected at the type-locality in April and May 1969 by William E. Duellman and Thomas H. Fritts.

Diagnosis.—(1) skin of dorsum smooth with scattered, flattened warts, that of venter coarsely areolate; no dorsolateral folds; discoidal folds prominent; (2) tympanum visible, round, its length about one-third that of eye; (3) snout subacuminate in dorsal view (pointed at tip), protruding in lateral profile, short (eye length greater than eye-nostril); (4) interorbital space flat; upper eyelid width equal to IOD; (5) prevomerine odontophores elliptical in outline, posterior and median to choanae; (6) males with subgular vocal sac and short vocal slits; (7) first finger shorter than second, all fingers bearing pads and discs, those on fingers 2-4 largest; (8) fingers bearing narrow lateral fringes; (9) no ulnar tubercles aside from antebrachial; (10) tarsus and heel bearing small, low tubercles (none conical); (11) inner metatarsal tubercle four times size of rounded outer; supernumerary plantar tubercles numerous; (12) toes bearing narrow lateral fringes, no webbing; toes bearing pads and discs, smaller than those on outer fingers; (13) dorsum pale brown marked with darker browns; canthal and supratympanic

stripes present; concealed surfaces not pigmented; venter white; (14) adults small, ♂♂ 13.6-17.1 mm, adult ♀♀ 16.5-19.4 mm SVL.

The only other species of group II *Eleutherodactylus* having a protruding snout is *E. acuminatus*, which differs from *E. paululus* in having a concealed tympanum, shagreened dorsum, supratympanic stripe continuing onto flank as broadening stripe, and in being much larger (adult females 27-32 mm SVL). On the basis of size alone, *E. paululus* may be distinguished from all eleutherodactylines except for some of the Central American species of the *E. diastema* group; from these *E. paululus* differs in having narrower lateral fringes on the digits and less rounded digital pads.

Description.—Head slightly narrower than body, wider than long; head width 34.1-39.0 per cent SVL (\bar{x} =36.4, N =12); snout subacuminate with a pointed tip in dorsal view, protruding in lateral profile (Fig. 3), upper jaw extending considerably beyond lower; snout short (shorter in males than in females)—eye-nostril distance in males 67.4-76.9 per cent (\bar{x} =72.5, N =5) eye length, in females 86.7-94.7 per cent (\bar{x} =89.6, N =3) eye length; canthus rostralis moderately sharp (somewhat rounded, not angular), weakly concave; loreal region flat, sloping abruptly to lips; lips not flared; nostrils weakly protuberant, directed dorsolaterally; inter-orbital space flat, no cranial crests; upper eyelid width 80.5-105.6 per cent IOD (\bar{x} =95.6, N =7); upper eyelid bearing numerous small tubercles; temporal region nearly vertical; tympanum visible, round, its length 26.4-32.0 per cent eye length (\bar{x} =28.8, N =5) in males, 32.5-37.4 per cent eye length (\bar{x} =35.3, N =3) in females; tympanum separated from eye by distance equal to three-fourths tympanum diameter; supratympanic fold broad, concealing upper edge of tympanum; choanae large, round, not concealed by palatal shelf of maxillary arch; prevomerine odontophores visible, median and posterior to choanae, elliptical in outline, weakly slanted posteriorly, each odontophore about one-half size of a choana, bearing a clump of teeth; odontophores separated by a distance equaling one-half choanal diameter; tongue slightly longer than wide, not notched posteriorly, posterior one-fourth to one-third not adherent to floor of mouth; males with subgular vocal sac and short vocal slits posterolateral to tongue.

Skin of dorsum smooth with scattered tubercles or warts but lacking folds; lower flanks and venter coarsely areolate, that of flanks more so; discoidal folds prominent; large areolations occur on posterior thighs below the vent; anal opening not modified; no ulnar tubercles except for an antebrachial tubercle; palmar tubercle bifid, 1.5 times size of oval thenar tubercle; several low supernumerary palmar tubercles, all smaller than round, simple, non-conical sub-articular tubercles; fingers bearing narrow, keel-like lateral fringes;

all digits bearing pads and discs, all dilated but those of fingers 2-4 clearly larger than that on thumb; second finger longer than first.

Inner and outer edges of tarsus bearing small tubercles; heel bearing small, low tubercles (not conical); two metatarsal tubercles, inner twice as long as wide, non-compressed, four times size of rounded, subconical outer metatarsal tubercle; plantar surfaces bearing rows of supernumerary tubercles, all smaller than subarticular tubercles or outer metatarsal tubercle; subarticular tubercles round, simple, non-conical, smaller than those of fingers; toes bearing pads and discs, pads on toes 3-5 largest, but all smaller than pads of outer fingers; toes bearing narrow lateral fringes but no webbing; hindlimbs of moderate length, shank 47.1-54.4 per cent SVL ($\bar{x}=50.5$, $N=11$); heel of adpressed limb reaches to between middle and anterior edge of eye; heels of flexed legs narrowly overlap.

Ground color pale tan to pale brown; dorsum marmorated with brown but not forming a distinct pattern; what pattern is evident suggests scapular and sacral chevrons and an interorbital bar; canthal and supratympanic stripes brown, the latter broadening as a post-axial stripe on lower flanks; labial bars brown; most specimens have a Y-shaped mark at the tip of snout and indefinite spotting behind the sacral chevron; limbs barred, bars perpendicular to limb axis, as broad as pale tan or brown interspaces; top of thigh has a thin line of ground color interrupted by short brown bars; anal triangle pale brown; concealed surfaces of thigh and upper arm not pigmented; venter white with some brown suffusion extending from anterior lower flank, along anterior edge of upper arm, and anterior surface of thigh (especially toward knee).

In life, *E. paululus* is green above with dark brown markings. The canthal stripe is black. The concealed surfaces are not pigmented or have a faint green wash. The venter is green with small white spots. The iris is bronze with fine to coarse black reticulation.

Measurements of holotype in mm.—SVL 19.4, shank 9.6, head width 7.1, upper eyelid width 2.0, IOD 2.1, tympanum length 0.8, eye length 2.3, eye-nostril distance 2.2. The holotype is a gravid female with convoluted oviducts and large, yellow ovarian eggs.

Distribution.—Specimens are known from elevations of 300-570 m at the base of the Amazonian slopes of the Andes in northern and central Ecuador (Fig. 2).

Remarks.—Specimens have been taken by day on the forest floor and by night on low vegetation (1-1.5 m) in forested situations. Claspings pairs were found twice (29 March 1972 and 12 May 1969). No calls have been associated with *E. paululus*.

Eleutherodactylus paululus superficially resembles another green species, *E. acuminatus* but differs in being much smaller, having an exposed tympanum, having spotting on the dorsum and barring on

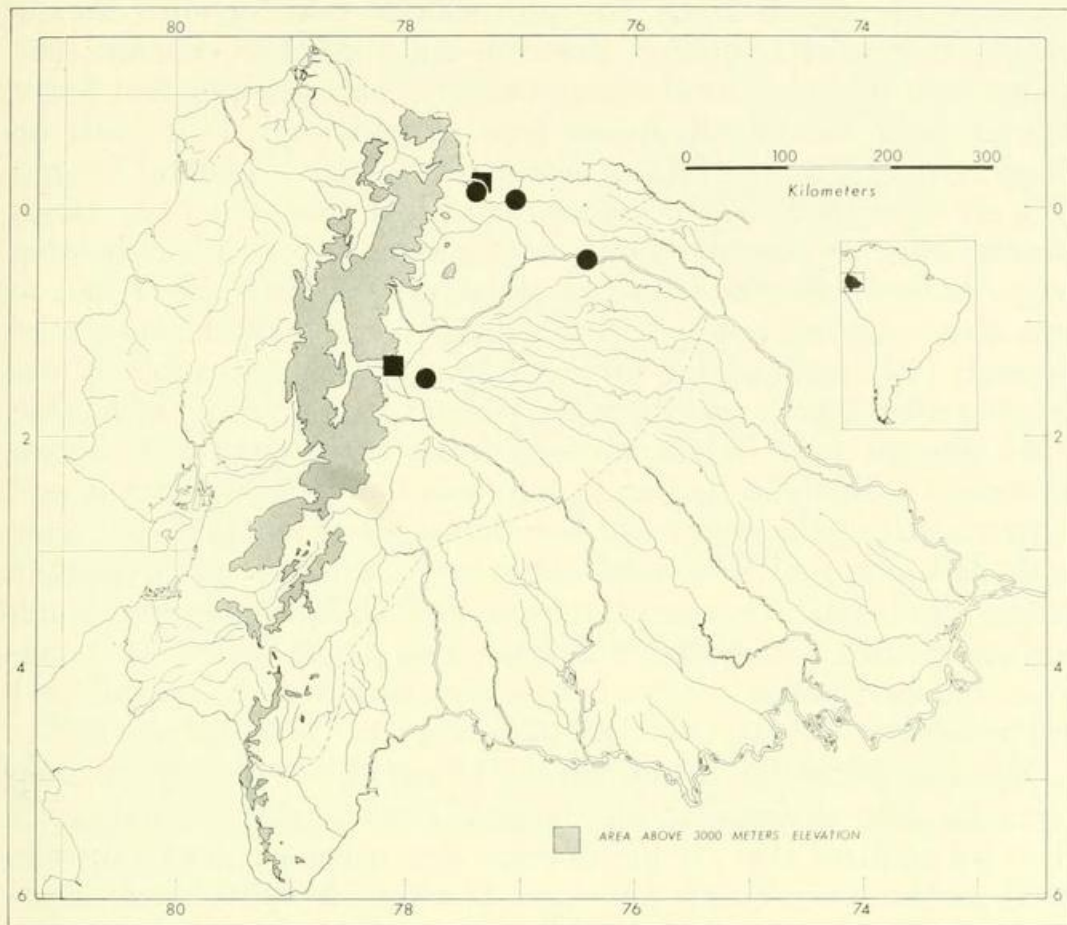


FIG. 2.—Distribution of *Eleutherodactylus martiae* (squares and circles) and *E. paululus* (circles only).

the limbs, and having smooth skin on the dorsum instead of a uniformly shagreened texture.

Etymology.—Latin, meaning least, in reference to the size of adult *E. paululus*, currently the smallest eleutherodactyline frog in the Amazonian basin.

Eleutherodactylus quaquaversus new species

Figure 1C,D

Holotype.—KU 123745, an adult female (26.1 mm SVL) from a series collected on the south slope of the Cordillera del Dué above the Río Coca, Provincia Napo, Ecuador, 1150 m, on 3 August 1968 by William E. Duellman and Stephen R. Edwards.

Paratypes.—(22) KU 123731-44, 123746-53; collected at the type-locality in August 1968 by Duellman and Edwards.

Diagnosis.—(1) skin of dorsum shagreened, that of venter coarsely areolate; upper eyelid bearing a conical tubercle; no dorso-lateral folds; discoidal folds prominent; (2) tympanum concealed or partially exposed; (3) snout subacuminate in dorsal view, rounded or feebly pointed in lateral profile; snout short (eye length greater than eye-nostril distance); (4) interorbital space flat; upper eyelid

width nearly equals IOD; (5) prevomerine odontophores usually visible, triangular in outline, posterior and medial to choanae; (6) males with subgular vocal sac and short vocal slits; (7) first finger shorter than second, all fingers bearing pads and discs, pads on fingers 3-4 largest; (8) fingers bearing inconspicuous lateral fringes; (9) no ulnar tubercles except antebrachial tubercle; (10) tarsus bearing obscure tubercles along inner and outer edges; heel bearing large, conical tubercle; (11) two metatarsal tubercles, inner four to five times size of outer; a few supernumerary plantar tubercles present; (12) toes bearing narrow lateral fringes, not webbed; toes bearing dilated pads and discs, toe pads as large as those of fingers; (13) dorsum pale brown to reddish-brown marked with brown chevrons, interorbital bar, and spots; some have cream dorsolateral stripes and/or pale interorbital bar; dorsal pattern variable but none with dark occipital W-shaped mark; no canthal or supratympanic stripes; limb bars, if present, narrow and oblique; posterior thigh surface reddish, reticulated with brown, or pigmentless (never uniform brown); venter white, frequently spotted with brown; (14) adults moderate-sized, ♂♂ 19.6-22.5 mm, ♀♀ 24.6-31.3 mm SVL.

Eleutherodactylus quaquaversus is readily distinguished from other *Eleutherodactylus* species because few have shagreened rather than tuberculate skin on the dorsum and a conical heel tubercle. Most northwestern South American *Eleutherodactylus* having conical heel tubercles also have large outer tarsal tubercles and tuberculate skin on the dorsum (*viz.*, *E. appendiculatus*, *E. calcaratus*, *E. crucifer*, *E. galdii*, and *E. rubicundus*). These also have a more pronounced heel tubercle than does *E. quaquaversus*. Two Colombian frogs without coarsely tuberculate skin but having heel tubercles comparable to those in *E. quaquaversus* are readily distinguished from *E. quaquaversus* in having an exposed tympanum, broad lateral fringes on the digits, and low flat warts on the dorsum (*E. erythroleurus*) or in having oblique prevomerine odontophores, prominent ulnar tubercles, and a truncate snout (*E. roseus*). *Eleutherodactylus quaquaversus* may be distinguished from *E. ockendeni* in having triangular prevomerine odontophores (Fig. 4) rather than oblique odontophores. Although the two species may be confused, the tympanum is more distinct in *ockendeni* than in *quaquaversus*; *ockendeni* rarely has a heel tubercle and when present, it is small, and *ockendeni* has scattered warts and/or ridges on the dorsum.

Description.—Head a little broader than body, wider than long; head width of males 36.0-41.7 per cent SVL (\bar{x} =37.8, N =15), of females 38.5-43.1 per cent SVL (\bar{x} =40.3, N =15); snout subacuminate in dorsal view, rounded in lateral profile (tip usually bearing a papilla-like point); upper jaw slightly overhanging lower; snout short, eye-nostril distance in males 70.6-85.7 per cent eye length

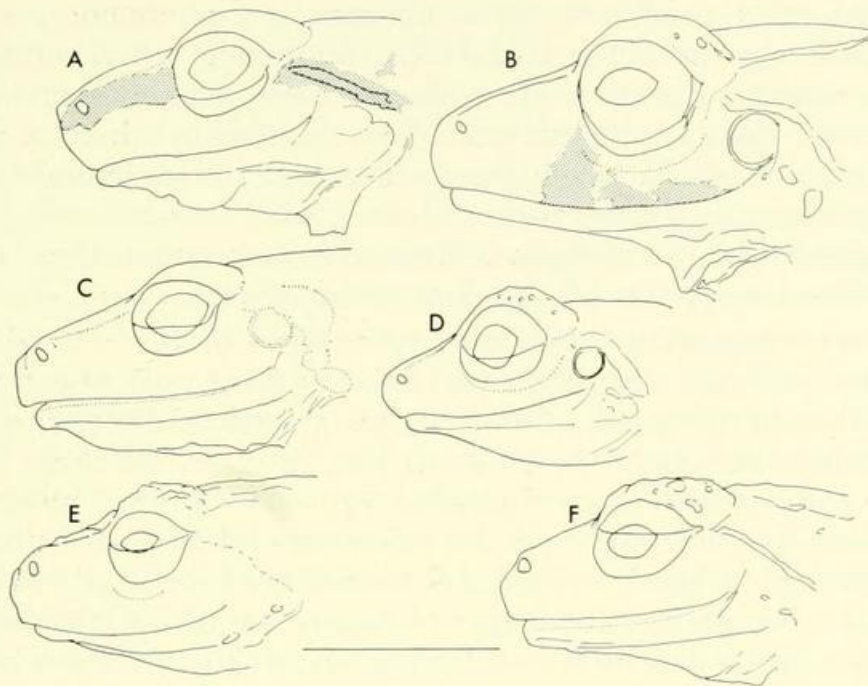


FIG. 3.—Profiles of heads of eastern Ecuadorian species of *Eleutherodactylus*. Labial markings stippled on only A and B. A, *E. acuminatus*, KU 123257; B, *E. ockendeni*, KU 104610; C, *E. pseudoacuminatus*, KU 126164; D, *E. paululus*, KU 126206; E, *E. croceoinguinis*, KU 119551; F, *E. martiae*, KU 123834. Line equals 5 mm.

(\bar{x} =77.0, N =15), of females 81.7-106.1 per cent eye length (\bar{x} =89.6, N =15); canthus rostralis sharp, straight or weakly concave; loreal region concave, sloping abruptly to lips; lips not flared; nostrils weakly protuberant, directed dorsolaterally; interorbital space flat; no cranial crests, no frontoparietal fontanelle; upper eyelid width 77.1-104.8 per cent IOD; (\bar{x} =93.7, N =28); supratympanic fold glandular, not distinct, obscuring upper and posterior portions of faintly visible tympanum; tympanum mostly concealed, upon drying, lower and anterior edges become visible; tympanic (temporal) region sloping (not vertical); choanae moderate-sized, round, well within borders of jaws, each as large as or smaller than a prevomerine odontophore; odontophores medial and posterior to choanae, triangular (rarely oval) in outline, bearing 4-5 teeth in a transverse row or clump on the posterior edge; odontophores separated by distance equal to width of an odontophore; tongue large, feebly notched posteriorly, posterior one-fourth to one-third not adherent to floor of mouth; males with subgular vocal sac and short vocal slits posterolateral to cornua of tongue.

Skin of dorsum finely shagreened with fine anastomosing ridges (no more prominent than minute granulations); no dorsolateral folds or occipital folds; upper eyelid bearing one or two small, conical tubercles along lateral edge; flanks, especially lower flanks, becoming coarsely areolate; coarse areolations continuing onto venter;

discoïdal folds prominent; anal opening not modified; no ulnar tubercles except for antebrachial tubercle; palmar tubercle bifid, not distinct from numerous small supernumerary palmar tubercles, but larger than elongate thenar tubercle; subarticular tubercles round, simple, somewhat flattened; fingers bearing narrow lateral fringes, all fingers bearing dilated pads and discs, smallest on thumb, largest on fingers 3-4; pads of digits 1-2 more or less round, those of 3-4 wider than long; second finger longer than first.

A large conical tubercle on upper edge of heel; no discrete tubercles on outer edge of tarsus; inner edge of tarsus bearing obscure tubercle just proximal to inner metatarsal tubercle; two metatarsal tubercles, inner 3-3.5 times as long as wide, 4-5 times size of round, subconical outer metatarsal tubercle; a few, moderately prominent supernumerary plantar tubercles (those most distinct are just proximal to basal subarticular tubercles of toes 3-4); subarticular tubercles smaller than those of fingers, subconical, round, simple; toes bearing narrow lateral fringes, not webbed; all toes bearing pads and discs, discs wider than long, largest (toes 3-5) as large as those of outer fingers; hindlimbs of moderate length, shank 46.0-57.0 per cent SVL ($\bar{x}=52.0$, $N=30$); heel of adpressed leg reaches to between eye and nostril; heels of flexed legs overlap.

Dorsum pinkish-brown to medium brown or brownish-red with brown chevrons and a thin interorbital bar; some individuals also have a pale interorbital bar; no canthal or supratympanic stripes; labial bars reduced to subocular spot (or bars); anal patch dark brown; limb bars thin and oblique in most individuals; in some individuals limb bars are broad and oblique but are not as broad as paler interspaces; thin area of ground color along top of thighs; concealed surfaces of thighs and groin not or weakly pigmented in individuals with brown ground color—those with reddish ground color have pale red pigmentation on the concealed surfaces; occasional individuals have brown areas extending laterally from the anal triangle onto the posterior surfaces of thighs and have pale

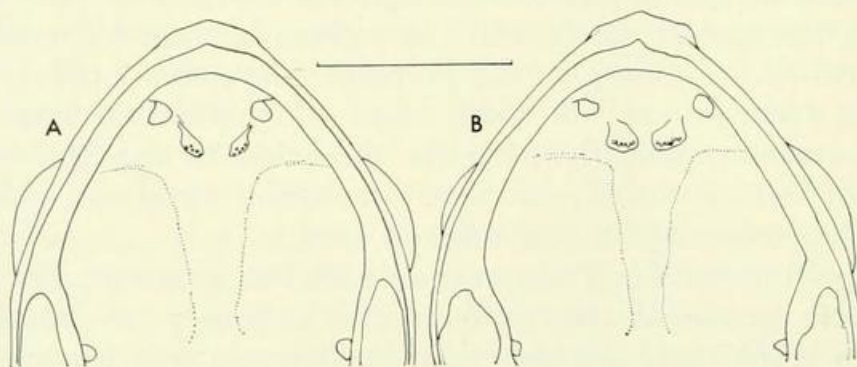


FIG. 4.—Outline drawings of palates of *Eleutherodactylus ockendeni*, KU 123261 A, and *E. quaquaversus*, KU 123725 B. Line equals 5 mm.

cream spots on the posterior thigh surface; flanks more pale than dorsum and usually spotted with brown; venter of adults and subadults cream and flecked to boldly spotted with brown—spotting most intense on chest; immature individuals have dark brown wash over the throat and anterior chest grading into yellow on belly.

Considerable variation occurs in color pattern. Occasional specimens from most localities (not the type-locality) have shiny-white spots along the upper lip and/or flank. A red supra-canthal stripe continuing posteriorly along the outer edge of the upper eyelid and down the back as a dorsolateral band occurs in less than 5 per cent of the specimens examined. Equally rare is a pattern in which the dorsal areas of the head and the back are dark brown (the dark area ends abruptly on the upper flank, side of the head, and canthus where it is replaced by pale reddish brown). A broad, pale interorbital bar precedes the thin dark interorbital bar in 10-18 per cent of the individuals from a given locality. The dorsal pattern of chevrons is broken up into vague flecking in about 15 per cent of the specimens. Between 0 and 10 per cent of the individuals from a given locality have no dorsal pattern. The majority of specimens have spotted venters but a few individuals with no spotting on the venter are found at every locality.

In life, *E. quaquaversus* is pale tan at night becoming pale brown, olive-tan, or dark brown by day. The markings are brown. In juveniles the venter is black anteriorly and yellow posteriorly (continuing onto legs). In adults the venter is white to cream-bronze with gray or brown spots. The lower flanks and groin are white to pale pink with black flecks or pink to purplish-red with white to yellow flecks. The posterior surfaces of the thighs are pale rose to purplish-red and may bear white spots. The pale interorbital bar (if present) is cream. The spots on the lips or flanks (if present) are white to pale yellow. The iris is silvery-gray to cream without a horizontal streak. The iris color of one individual (KU 123725) was red at night and by day had changed to pinkish-silver.

Measurements of holotype in mm.—SVL 26.1, shank 13.8, head width 10.4, upper eyelid width 2.7, IOD 2.9, eye length 3.3, eye-nostril distance 3.0. The holotype is a gravid female with convoluted oviducts and large (2.0-3.0 mm in diameter), yellow ovarian eggs.

Distribution.—Specimens are known from elevations of 300-1830 m on the Amazonian slopes of the Andes from northern Ecuador south to the Cordillera del Condor (Fig. 5). *Eleutherodactylus quaquaversus* is more common at localities between 700 and 1830 m than at lower elevations. No specimens of this species were taken at Lago Agrio (330 m) and only 18 have been found during the many man-months of field work at Santa Cecilia (340 m).

Remarks.—*Eleutherodactylus quaquaversus* is found in com-

paratively open forest (e.g., the often sparse forest along fast streams). Most specimens have been collected on low vegetation (1-2 m) at night. Calling males were collected 17 October 1971 at dusk on low herbs in a clearing in cloud forest. William E. Duellman described the call as "a single high note." Claspings pairs have been taken in August.

I consider *E. quaquaversus* to be a frog of intermediate elevations, replacing the lowland *E. ockendeni*. The two species are often confused once preserved, but are readily separable (see diagnosis). In spite of the similarity, I do not consider *E. ockendeni* to be an especially close relative of *E. quaquaversus*; the latter is probably more closely related to frogs occurring at higher elevations (viz., *E. bogotensis*, *E. erythroleurus*, and *E. unistrigatus*) in Colombia and Ecuador. *Eleutherodactylus ockendeni* is considered to be most closely related to *E. frater* of the Pacific lowlands and versant in Colombia, Ecuador, and Panamá.

Etymology.—Latin, *quaqua* (ablative feminine of *quisquis*) and *versus* (past participle of *vertere*) meaning turned in every direction; in reference to the variation in color pattern. The trivial name was suggested by William E. Duellman and Linda Trueb.

***Eleutherodactylus altamazonicus* Barbour and Dunn**

Barbour and Dunn's (1921) *E. altamazonicus* is a name seldom used in the literature on Amazonian frogs. In part this stems from lack of work on small frogs, especially eleutherodactylines, in the upper Amazon basin other than in Ecuador, but also because of the vague type-locality—"Upper Amazon; probably Nauta, Peru." When I began work on frogs from eastern Ecuador, I used *E. brevicrus* Andersson (more completely described and illustrated) as the name for a relatively abundant frog in collections from Limón Cocha and Santa Cecilia. The frog is brown or black above and below with obscure mottling on the dorsum and has bright red and brown or black areas in the groin and on the concealed limbs. The tympana are usually concealed, the snout rounded in lateral profile, the digits free of webbing, the digital pads are broad and large, and the prevomerine odontophores are oblique. The skin of the dorsum is tuberculate. I have examined the holotype of *E. altamazonicus* and compared it with extensive samples of this species in the collections of The University of Kansas Museum of Natural History. I have not seen the holotype of *E. brevicrus* but the holotype was so well described and illustrated by Andersson (1945) that I am convinced that both names represent the same species and accordingly, *Eleutherodactylus brevicrus* Andersson, 1945, is here placed in the synonymy of the older name, *Eleutherodactylus altamazonicus* Barbour and Dunn, 1921.

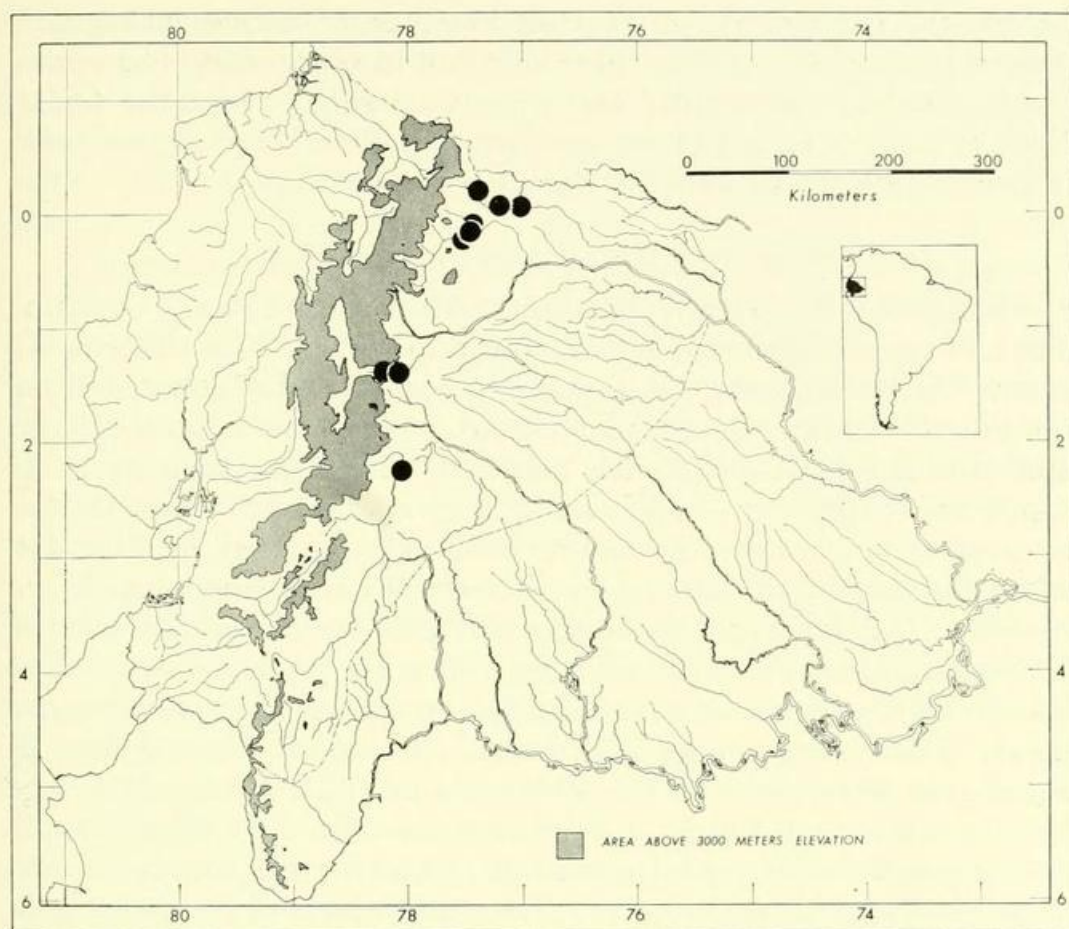


FIG. 5.—Distribution of *Eleutherodactylus quaquaversus*.

Eleutherodactylus galdi (Jiménez de la Espada)

This species does not occur at Lago Agrio or at Santa Cecilia but occurs at intermediate elevations on the Amazonian slopes of the Andes in Ecuador. In the course of searching for a possibly prior name for *E. martiae*, I examined the holotype of *Hylodes festae* Peracca. The holotype is a male with short vocal slits, prominent eyelid, ulnar, tarsal, and heel tubercles, tuberculate skin of the dorsum, large areolations on the venter, first finger shorter than the second, large digital pads with broad discs, having no webbing, having upturned edges of the frontoparietals (cranial crests), a small squamosal ridge (non-serrate), prominent tympanum, long snout, a cream venter with white spots, brown canthal and supratympanic stripes, interorbital bar, dorsal spotting, and narrow limb bars. There is a white stripe along the upper lip. Measurements of the holotype are as follows (in mm): SVL 21.4, shank 13.2, head width 8.0, tympanum length 0.8, eye length 2.7, eye-nostril distance 2.8.

All characteristics of *Hylodes festae* are identical with those of *Eleutherodactylus galdi* (see Lynch, 1969). The specimen is of intermediate size between the juvenile syntypes of *Hylodes margariti*-

fer and the presumably large adult holotype of *Pristimantis galdi*. Differences among the three are the result of ontogenetic change in development of the cranial and squamosal crests. *Hylodes festae* Peracca, 1904, is added to the synonymy of *Eleutherodactylus galdi* (Jiménez de la Espada), 1870 (see Lynch, 1969).

Eleutherodactylus ockendeni (Boulenger)

This species has been reported from Panamá and Perú (Gorham, 1966). Panamanian records probably apply to a close relative, *E. frater*. The specimens of *E. ockendeni* I examined originated from the Amazon basin (Ecuador and Perú). The species is relatively abundant at Santa Cecilia. The name *Eleutherodactylus anderssoni* Lynch was proposed (Lynch, 1968b) as a replacement name for *Syrrhophus calcaratus* Andersson, 1945 (preoccupied by *Hylodes calcaratus* Boulenger, 1908) and fortunately has not been used frequently. The holotype of *Syrrhophus calcaratus* and *Eleutherodactylus anderssoni* is virtually identical with the syntypes of *Hylodes ockendeni* in structural features, as well as the color pattern morph. Two pattern morphs occur in *E. ockendeni*. One of these is most easily recognized by the W-shaped occipital mark which frequently bears short ridges and enlarged warts. The other morph lacks a prominent occipital mark but frequently has isolated warts on the occipital region (Fig. 6). The morph lacking the prominent W-shaped marking and ridges is the morph represented by the type-specimens of *E. anderssoni* and *E. ockendeni*. In order to facilitate separation of *E. frater*, *E. ockendeni*, and *E. quaquaversus*, a diagnosis and description of *E. ockendeni* is presented below.

Diagnosis.—(1) skin of dorsum finely shagreened with or without W-shaped occipital ridges and dorsolateral folds, that of venter coarsely areolate; upper eyelid usually bearing small conical tubercles; discoidal folds prominent; (2) tympanum usually clearly visible, its length one-fourth to two-fifths eye length; (3) snout subacuminate in dorsal view, rounded or feebly pointed in lateral profile; snout short, eye length greater than eye-nostril distance; (4) interorbital space flat; upper eyelid width nearly as great as IOD; (5) prevomerine odontophores visible in larger specimens, slanted (oblique), concealed in smaller specimens; (6) males with subgular vocal sac and short vocal slits; (7) first finger shorter than second; all fingers bearing pads and discs, pads on fingers 3-4 largest; (8) fingers lacking lateral fringes or having narrow, obscure, keel-like fringes; (9) forearm bearing 2-5 minute ulnar tubercles; (10) tarsus lacking tubercles along inner edge, usually with a few small tubercles along outer edge; heel bearing rounded (non-conical) tubercle; (11) two metatarsal tubercles, inner elongate, 4-6 times size of round outer; few supernumerary plantar tubercles; (12) toes bearing narrow, keel-like lateral fringes, no webbing; toe pads dilated,

bearing discs, pads as large as those of outer fingers; (13) dorsum cream to brown with brown to black interorbital bar, subocular spot (Fig. 3), supratympanic stripe, dorsal chevrons, and lumbar bar; posterior surfaces of thighs uniform brown; venter white with or without brown suffusion; (14) adults moderate-sized, ♂♂ 18.1-21.3 mm, ♀♀ 24.8-28.2 mm SVL.

Eleutherodactylus ockendeni is most similar to *E. frater* found in lowland forests of the Pacific lowlands of Colombia and Ecuador (and probably in Panamá as well). *Eleutherodactylus frater* may be distinguished in having a shorter snout, more enlarged tubercles on the back, distinct inner tarsal tubercles, and in having slightly more prominent lateral fringes on the digits. Cochran and Goin (1970) suggested that the two species differ in widths of the upper eyelid, but I cannot verify the distinction.

Description.—Head as wide as body, slightly longer than wide; head width of males 35.2-39.2 per cent SVL (\bar{x} =37.1, N =13), of females 36.5-40.4 per cent SVL (\bar{x} =38.0, N =17); snout subacuminate in dorsal view (tip feebly pointed), rounded (or feebly pointed) in lateral profile; upper jaw overhanging lower; snout short, eye-nostril distance of males 75.4-96.5 per cent eye length (\bar{x} =85.9, N =12), of females 87.8-104.5 (\bar{x} =94.2, N =17); canthus rostralis rounded or obtuse (not sharp), concave; loreal region flat, sloping gradually to non-flared lips; nostrils weakly protuberant, directed dorsolaterally; interorbital space flat; no cranial crests, no frontoparietal fontanelle; upper eyelid width of males 88.0-119.0 per cent IOD (\bar{x} =98.8, N =12), of females 79.3-103.3 IOD (\bar{x} =92.4, N =17); temporal region sloping (not vertical); supratympanic fold thick, often with warts along dorsal edge, sometimes obscuring upper edge of tympanum; tympanum prominent, its length 27.3-40.3 per cent eye length (\bar{x} =34.2, N =29), size and shape not sexually dimorphic; tympanum separated from eye by distance equal to tympanum length; choanae moderate-sized, round, well within borders of jaws, each larger than a prevomerine odontophore; odontophores median and posterior to choanae, strongly slanted and teardrop-shaped (Fig. 5), bearing 0-6 teeth in an oblique row near posterior edge; odontophores separated medially by 1.5-2 times width of an odontophore; odontophores not visible in young or small individuals (usually obscure in adult males, prominent in adult females); tongue longer than wide, notched posteriorly, posterior one-fourth to two-fifths not adherent to floor of mouth; males with subgular vocal sac and short, lateral vocal slits.

Skin of dorsum very finely shagreened with anastomosing ridgelets and occasional scattered enlarged warts; skin of venter, but not lower flanks, coarsely areolate; skin about vent coarsely areolate; discoidal folds prominent; [in morph A (Fig. 6A), there are no enlarged warts on the body except for one or two small tubercles on the

upper eyelid and occasional warts of similar size along the lumbar bar; in morph B (Fig. 6B), there is a pair of prominent ridges with enlarged warts extending from the upper eyelid to the scapular region; these ridges are connected, forming a W-shaped series of warts and ridges; there is also a less prominent transverse band of warts above the groin; some individuals bear an obscure dorso-lateral row of tubercles extending from the eye to the groin;] two to five small, non-conical ulnar warts occur on forearm; palmar tubercle bifid, larger than elongate thenar tubercle; palm usually bearing some supernumerary tubercles, obscure to prominent, all smaller than subarticular tubercles; subarticular tubercles round, simple, somewhat flattened; fingers bear narrow, keel-like lateral fringes; all fingers bearing discs on pads, all pads wider than long, that on thumb scarcely wider than digit, those on digits 2-4 much wider (about equal to tympanum length); first finger shorter than second.

Heel usually bearing small, round, non-conical tubercle; outer edge of tarsus with or without small tubercles; inner edge of tarsus usually lacking tubercles, if any present, minute and near metatarsal tubercle; two metatarsal tubercles, outer round, subconical, one-fourth to one-sixth size of elongate (length 2.5-3 times width) inner; plantar surface bearing prominent supernumerary tubercles at base of toes 2-4, if others are present they are obscure; subarticular tubercles of toes as large as those of fingers, round, subconical, simple; toes bearing weak, keel-like lateral fringes, feebly webbed (webbing does not reach proximal edge of basal subarticular tubercles); all toes bearing pads and discs, wider than long, about same size as those of outer fingers; hindlimbs of moderate length, shank

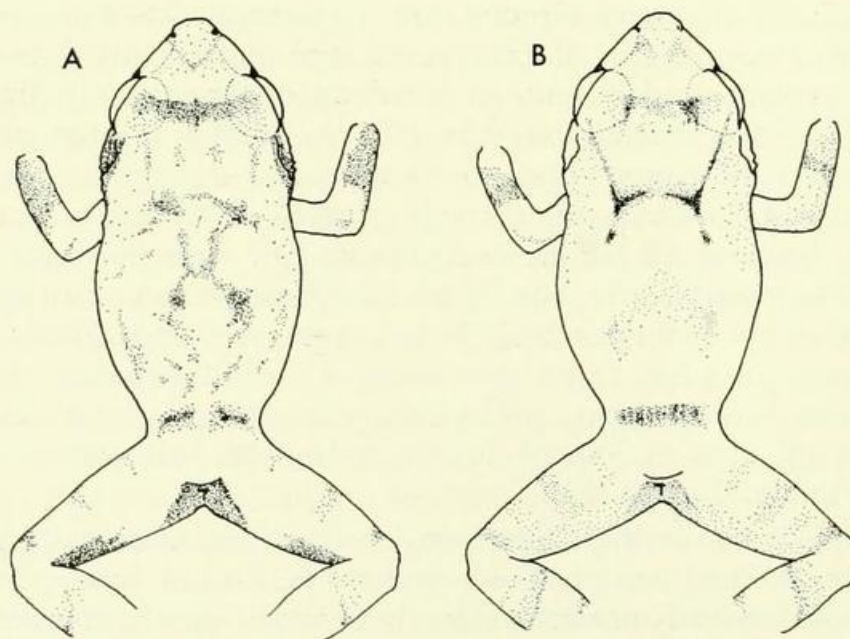


FIG. 6.—Pattern morphs of *Eleutherodactylus ockendeni*. A, based on KU 109118. B, Morph B, based on KU 126213.

of male 50.8-57.2 per cent SVL, (\bar{x} =54.1, N =13), of females 49.0-55.3 per cent (\bar{x} =53.1, N =17) SVL; heel of adpressed leg reaches to between nostril and tip of snout.

Color pattern (morph A): dorsum cream with brown markings (thin interorbital bar, subocular bars, supratympanic stripe, ill-defined scapular chevron or patch, sacral chevron, and lumbar bar); anal triangle dark brown; limbs cream with thin brown cross bars (oblique); concealed surfaces of thighs uniform brown; venter white; underside of knee bearing brown spot.

Color pattern (morph B): dorsum and limbs dark brown becoming pale brown on flanks; occipital W black; lumbar bar, subocular bars, supratympanic stripe, limb bars, and anal triangle dark brown to black; venter cream suffused with brown; posterior surfaces of thighs uniform brown. Some specimens of this morph have a pale (dusky cream) interorbital bar.

In the populations of this frog found along the Rio Aguarico in northern Napo Province, Ecuador, 7 per cent have the color pattern here termed morph A (Fig. 6A) and 93 per cent have the pattern called morph B. In these specimens, a pale interorbital bar occurs in only 5.6 per cent (of all specimens).

In life, *E. ockendeni* was colored as follows; (morph A)—“Dorsum reddish-brown with dark brown markings. Posterior thighs dull brown; iris metallic green with median red streak” (KU 109118-19; William E. Duellman field notes, 6 March 67). Morph B—“♀. Dorsum yellowish-tan with dark brown markings; groin and posterodorsal surface of thigh bright yellow; anterior and other posterior thigh surfaces, inner shank, and soles of feet black; ventral surface of thighs brown. ♂. Dorsum reddish tan with dark brown markings and pale gray blotches from eyelids to scapular region. No yellow in groin or on thigh; ventral limbs yellow tan.” In both, “. . . belly metallic cream with gray suffusion; throat gray. Iris metallic green above, dark red below” (KU 126213-14, amplexant pair; W. E. Duellman field notes, 14 May 69).

Distribution.—I have examined specimens from eastern Ecuador and Perú taken at elevations between 300 and 1200 m. In eastern Ecuador, *E. ockendeni* is more abundant at elevations below 700 m than at elevations higher than 700 m, where it is apparently replaced by *E. quaquaversus*.

Remarks.—The holotype of *Syrrhophus calcaratus* is an example of morph A, as are the three syntypes of *Hylodes ockendeni*. In the holotype of *calcaratus*, the prevomerine odontophores are concealed beneath the tissue of the palate and are oblique (as in the types of *ockendeni*). The heel tubercle is rounded rather than conical. There are no distinguishing features separating these two nominate forms except for size and the less distinct tympana in the type-series of *ockendeni*. For the present, I interpret the less distinct tympana

in frogs from southern Perú to be an artifact of small sample size, although this character possibly is subject to geographic variation.

SUMMARY

Three species of *Eleutherodactylus* belonging to the *E. unistri-gatus* group are named from Amazonian Ecuador. *Eleutherodac-tylus martiae* is a small species related to *E. carvalhoi* and *E. croceoinguinis* but differing in coloration and palatal dentition. *Eleutherodactylus paululus* is a very small green frog related to *E. acuminatus* but differing in size, color, and visibility of the tympana. *Eleutherodactylus quaquaversus* is a medium-sized species related to several high elevation Andean species but superficially similar to *E. frater* and *E. ockendeni* from the Chocoan lowlands and upper Amazonian lowlands, respectively.

Three names proposed for upper Amazonian *Eleutherodactylus* are assigned to the synonymies of three other species. *Eleuthero-dactylus anderssoni* Lynch (replacement name for *Syrrhophus cal-caratus* Andersson) is identical to *E. ockendeni* (Boulenger); *E. brevicrus* Andersson is identical to *E. altamazonicus* Barbour and Dunn; and *Hylodes festae* Peracca is identical to *E. galdi* (Jiménez de la Espada).

RESUMEN

Se nombran tres especies de *Eleutherodactylus* pertenecientes al grupo *unistrigatus* de la cuenca amazónica superior en Ecuador. *Eleutherodactylus martiae* es una especie pequeña emparentada con *E. carvalhoi* y *E. croceoinguinis*, pero difiere de ello en coloración y dientes palatinos. *Eleutherodactylus paululus* es una ranita verde muy pequeña emparentada con *E. acuminatus*, pero difiere en tamaño, color y el tímpano es visible. *Eleutherodactylus quaquaversus* es una especie de tamaño moderado emparentada con varias especies altoandinas, aunque con una semejanza superficial a *E. frater* y *E. ockendeni* de las tierras bajas del Chocó y cuenca amazónica superior, respectivamente.

Tres nombres propuestos para los *Eleutherodactylus* de la cuenca amazónica superior se relegan a los sinónimos de otras tres especies. *Eleutherodactylus anderssoni* Lynch (nombre reemplazo de *Syrrhophus calcaratus* Andersson) es lo mismo que *E. ockendeni* (Boulenger); *E. brevicrus* Anderson es lo mismo que *E. altama-zonicus* Barbour and Dunn; e *Hylodes festae* Peracca es lo mismo que *E. galdi* (Jiménez de la Espada).

SPECIMENS EXAMINED

Eleutherodactylus altamazonicus

ECUADOR: Morona-Santiago: Miazal, USNM-GOV 9654; Payamino, USNM-GOV 3897; Río Llushin, north of Arapicos, USNM-GOV 9639; Río Yuquipa,

Macas, USNM-GOV 9658. *Napo*: Lago Agrio, 330 m, KU 126111-31; Limón Cocha, 300 m, KU 104627, 106958, LACM 72217, 72164, 72174, UIMNH 54155, 63422; mouth of Río Guataracu, USNM-GOV 9630; Puerto Libre, Río Aguarico, 570 m, KU 123319-71; Puerto Ore, Río Aguarico, 420 m, KU 123372-73; Santa Cecilia, 340 m, KU 104445-60, 104585-88, 106962, 108979-81, 108982 (C&S skeleton), 110774-80, 111187, 123297-318, 123814, 126107-10, 146060-62, 148722-84, 152383-84. *Pastaza*: Montalvo, USNM-GOV 9665; Pucayacu, USNM-GOV 9648-49; 2½ km SE Puyo, 975 m, USNM-JAP 1943-49, 2160; Río Conambo near mouth of Río Romarizo, USNM-GOV 8281-82; Río Lipuno, trib of Río Villano, USNM-JAP 9160; Río Oglan, trib of Río Curaray, USNM-GOV 9652-53; mouth of Río Ollaguanga, trib of Río Conambo, USNM-JAP 8635, 8637; Río Pindo near village of Río Tigre, USNM-GOV 9638; Río Sandalias, trib of Río Puyo, USNM-GOV 7220; Río Villano, USNM-GOV 9645, 9661, USNM-JAP 3861; Veracruz, 1000 m, USNM-JAP 6106.

PERU: *Depto. Loreto*: Upper Amazon, probably near Nauta, MCZ 2028 (holotype).

Eleutherodactylus galdi

ECUADOR: *Morona-Santiago*: El Cruzado, 2195 m, USNM-JAP 7276; Miazal, USNM-GOV 8947; Pailas, 2195 m, USNM-JAP 6567-69; Río Piuntza, 1830 m, KU 146977-85; San José de Cuchipamba, MIZ An 513, ex 3776 (holotype of *Hylodes festae*). *Napo*: Loreto, USNM-GOV 8944-46, USNM-JAP 8828; Río Azuela, 1740 m, KU 143416. *Tungurahua*: El Topo, 1280 m, BM 1912.11.1.54-55 (RR 1947.2.16.78-79) (cotypes of *H. margaritifer*).

Eleutherodactylus martiae

ECUADOR: *Napo*: Bermejo No. 4 (Well site), Sierra Umbaqui, 740 m, KU 123819-20; Lago Agrio, 330 m, KU 126211, 126199-204; Limón Cocha, 300 m, KU 104622, 104624-26, 106961, UIMNH 54145, 93563; Puerto Libre, Río Aguarico, 570 m, KU 123776-77, 123785-91, 123793-99, 123801-03, 123805-07, 123821-48; Santa Cecilia, 340 m, KU 104603-08, 123770, 123773-74, 123812-13, 123815-18, 126197-99, 149200-01, 149203-30, 152388-92, UIMNH 93564. *Pastaza*: Abitagua, 1300 m, KU 120262; Canelos, 530 m, KU 120263, 120265.

Eleutherodactylus ockendeni

ECUADOR: *Napo Prov.*: Bermejo No. 4 (Well site), 15 km ENE Umbaqui, 740 m, KU 123269-77; Dureno, KU 104830; Lago Agrio, 330 m, KU 126102-06; Limón Cocha, 300 m, KU 104602, LACM 72181, 72192, 72209, 72212; Puerto Libre, Río Aguarico, 570 m, KU 123278-91, 123775, 123781-84, 123792, 123800, 123804; Puerto Ore, Río Aguarico, 420 m, KU 123292-96, 123808; Río Cosanga near Archidona, 800 m, NHRM 1921 (holotype of *Syrhophus calcaratus* and *Eleutherodactylus anderssoni*); Santa Cecilia, 340 m, KU 104610-13, 104618-19, 104621, 109115-31, 109135-36, 111182-85, 123261-68, 123768-69, 123771-72, 123850-51, 126213-14; south slope Cordillera del Dué above Río Coca, 1150 m, KU 123809-11. *Pastaza Prov.*: Canelos, 530 m, KU 120264, 120266; Chontoa, 780 m, KU 120267-68; Mera, 1140 m, 120261, 120269.

PERU: *Puno*: La Unión, Río Huacamayo, Carabaya, 610 m, BM 1907.5.7.19-21 (RR 1947.2.16.88-90) (syntypes of *Hylodes ockendeni*).

Eleutherodactylus paululus

ECUADOR: *Napo*: Lago Agrio, 330 m, KU 126205-06, 126208-09; Limón Cocha, 300 m, KU 108978, LACM 72219, UIMNH 93565; Puerto Libre, Río Aguarico, 570 m, KU 123849; Santa Cecilia, 340 m, KU 104609, 149238-41. *Pastaza*: Canelos, 530 m, KU 120250.

Eleutherodactylus quaquaversus

ECUADOR: *Morona-Santiago*: Río Piuntza, Cordillera del Condor, 1830 m, KU 146987-90. *Napo*: Bermejo No. 4 (Well site), 15 km ENE Umbaqui, 740 m, KU 123690-701; south slope Cordillera del Dué above Río Coca, 1150 m, KU 123731-53; Puerto Libre, Río Aguarico, 570 m, KU 123706-30, 123778-80; Río Azuela, 1740 m, KU 143448-54; Santa Cecilia, 340 m, KU 104593-96, 111181, 123702-05, 146161, 149197-99, 149232-37; 16½ km NNE Santa Rosa, 1700 m, KU 143441-47. *Pastaza*: Mera, 1140 m, KU 120165, 120169; 3 km S Puyo, 920 m, KU 127034; Río Alpayacu, 1100 m, KU 120166-68, 120170-72; Shell Mera, UIMNH 93562.

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