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SYSTEMATIC STATUS AND DISTRIBUTION OF SOME POORLY KNOWN FROGS OF THE GENUS *ELEUTHERODACTYLUS* FROM THE CHOCOAN LOWLANDS OF SOUTH AMERICA

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ABSTRACT: *Eleutherodactylus roseus* and *E. taeniatus*, previously known from holotypes, are reported from several localities and redescribed, as are *E. gaigeae* and *E. subsigillatus*. *Eleutherodactylus chalceus* (Peters) is the oldest name for the frog called *E. areolatus* (Boulenger). *Syrrhopus molinoi* Barbour is placed in the synonymy of *E. ridens* (Cope). *Eleutherodactylus caryophyllaceus*, *E. gaigeae*, *E. ridens*, and *E. subsigillatus* are reported for the first time from western Colombia.

Key words: Amphibia; Salientia; Leptodactylidae; *Eleutherodactylus*; Distribution; Systematic status; Colombia; South America

THE richest eleutherodactyline fauna of the Neotropics is apparently found in the Pacific lowlands of Colombia. Although no single site has yielded the 19 species known to inhabit the lowlands in the vicinity of the Ríos Anchicayá, Dagua, and San Juan, 13–15 species are present in several collections. The species include *Eleutherodactylus achatinus* (Boulenger), *E. anomalus* (Boulenger), *E. biporcatus* (Peters), *E. bufoniformis* (Boulenger), *E. caprifer* (Lynch), *E. chalceus* (Peters), *E. cruentus* (Peters), *E. diastema* (Cope), *E. fitzingeri* (Schmidt), *E. gaigeae* (Dunn), *E. gularis* (Boulenger), *E. latidiscus* (Boulenger), *E. longirostris* (Boulenger), *E. moro* Savage, *E. raniformis* (Boulenger), *E. ridens* (Cope), *E. roseus* (Boulenger), *E. taeniatus* (Boulenger), and at least one undescribed species ("Z" of Lynch, 1979). The species list will increase substantially when several undescribed taxa are reported.

Cochran and Goin (1970) listed only 33 species of *Eleutherodactylus* from Colombia and provided descriptions and illustrations for 9 of the 19 species found in the central Chocó (*E. achatinus* [as *E. brederi*], *E. anomalus*, *E. bufoniformis*, *E. diastema*, *E. gularis*, *E. latidiscus*, *E. longirostris*, *E. moro* [as *E. lehmanvalenciae*], and *E. raniformis*). *Eleutherodactylus caryophyllaceus*, *E. cruentus* (as *E. dubitus*), *E. fitzingeri* (as *E. ranoides*), and *E. ridens* were described by Taylor (1952); Taylor (1954) also described *E. biporcatus* (as *E. florulentus*). Lynch (1971) described *E. chalceus* (as *E. areolatus*) and *E. caprifer* (1977). Modern and/or detailed descriptions and illustrations are not available for five taxa known from western Colombia (*E. gaigeae*, *E. roseus*, *E. subsigillatus*, *E. taeniatus*, and the undescribed species—Z).

Lynch (1979) listed 24 species of *Eleutherodactylus* including two undescribed species of the *fitzingeri* group (listed as sp. A and sp. Z) for the trans-Andean lowland forests. The list includes six species not previously reported as occurring in Colombia (*E. achatinus*, *E. areolatus*, *E. caryophyllaceus* [see specimens examined for locality], *E. gaigeae*, *E. ridens*, and *E. subsigillatus*). *Eleutherodactylus achatinus* and the two undescribed species will be treated in a forthcoming review of the eight species of the *fitzingeri* group found in the chocoan lowlands (Lynch and Myers, in prep.). The present paper is concerned with certain poorly known species and is primarily devoted to (1) redescribing some species on the basis of larger samples, (2) clearing up nomenclatural problems that have plagued workers in the

area, and (3) delineating species distributions.

Materials and Methods

The specimens reported here are part of more than 6000 specimens examined from the trans-Andean lowlands in the past 10 years. Abbreviations for museum collections are as follows: AMNH (American Museum of Natural History), BM (British Museum [Natural History]), CAS-SU (Stanford University collection, now at California Academy of Sciences), FMNH (Field Museum of Natural History), ICN (Instituto Ciencias Naturales-Museo de Historia Natural, Universidad Nacional de Colombia), KU (University of Kansas Museum of Natural History), LACM (Natural History Museum of Los Angeles County), MCZ (Museum of Comparative Zoology), UIMNH (University of Illinois Museum of Natural History), UMMZ (University of Michigan Museum of Zoology), USNM (National Museum of Natural History), and WCAB (private collection of Werner C. A. Bokermann, São Paulo, Brasil). The format of descriptions follows that used previously (e.g., Lynch, 1974). Sizes of adults are reported as follows: range ($\bar{x} \pm 2$ SE, n).

Species Accounts

Accounts are arranged alphabetically within species groups. The frogs discussed here are members of the *fitzingeri* and *unistrigatus* groups as defined by Lynch (1976).

The *fitzingeri* Group

Eleutherodactylus gaigeae (Dunn)

This species is currently known from the lowlands of Costa Rica and western Panama (Dunn, 1931*a*; Taylor, 1952) but has not been reported from east of the Canal Zone. William Duellman and Charles Myers collected several specimens from eastern Panama and in the central Chocó. When Dunn (1931*a*) named the species he thought it a *Lithodytes*. Possibly for that reason but also because his descriptions were normally brief, the published descriptions of this species do not allow ready comparison with the descriptions of the many species recognized since the 1930s. *Eleutherodactylus gaigeae* is redescribed below based on eight adults from eastern Panama.

Description.—Head as wide as or broader than body, longer than wide; head width of males 35.8–37.9 ($\bar{x}$ = 36.9, n = 4) per cent SVL, of females 36.8–38.7 ($\bar{x}$ = 38.2, n = 4) per cent; snout acuminate in dorsal view, round in lateral profile; nostrils weakly protuberant, directed laterally; canthus rostralis sharp, straight or weakly sinuous; loreal region vertical, flat; lips not flared; E–N of males 90.0–95.6 ($\bar{x}$ = 92.3, n = 4) per cent eye length, of females 98.8–108.2 ($\bar{x}$ = 103.5, n = 4) per cent; interorbital space flat, no cranial crests; upper eyelid width of males 89.7–113.8 ($\bar{x}$ = 105.2, n = 4) per cent IOD, of females 86.8–102.7 ($\bar{x}$ = 94.5, n = 4) per cent; tympanum distinct, annulus partially concealed dorsally and posteriorly by supratympanic fold; tympanum round in males, scarcely separated from eye; tympanum higher than long in females, separated from eye in distance equal to ½ length of tympanum; tympanum length of males 52.5–65.1 ($\bar{x}$ = 58.9, n = 4) per cent eye length, of females 49.2–55.4 ($\bar{x}$ = 51.4, n = 4) per cent; postrictal tubercles round, not conical; choanae large, not concealed by palatal shelf of maxillary arch when roof of mouth is viewed from directly above (but well lateral); vomerine odontophores lying posterior to a line drawn through the centers of the choanae but partially between the choanae; odontophores elevated, oblique, bearing 5–7 teeth in an oblique row, separated on midline by a distance equal to a choanal width or to length of an odontophore (Fig. 1); tongue longer than wide, cordiform, its posterior border notched, posterior ½ to ⅗ not adherent to floor of mouth; males lacking vocal slits and vocal sac.

Skin of dorsal surfaces shagreened, that on face feebly shagreened; skin below and posterolateral to vent areolate; vent not extended in a sheath; no dorsolateral folds or enlarged tubercles on dorsal surfaces; skin of venter smooth (or feebly granular along lateral and posterior borders of ventral disk); discoidal folds prominent; arm slender; no ulnar tubercles; palmar tubercle bifid, much larger than oval thenar tubercle; several prominent supernumerary palmar tubercles (pungent), but smaller and less pungent than subconical basal subarticular tubercles; distal subarticular tubercles not conical, smaller than basal tubercles; fingers lacking lateral keels; first finger much longer than second; all fingers bearing terminal grooves, fingers III and IV have proximal definition to discs (Fig. 1); all fingers bearing narrow pads, pads on outer fingers truncate, about 0.6 times length of inner metatarsal tubercle

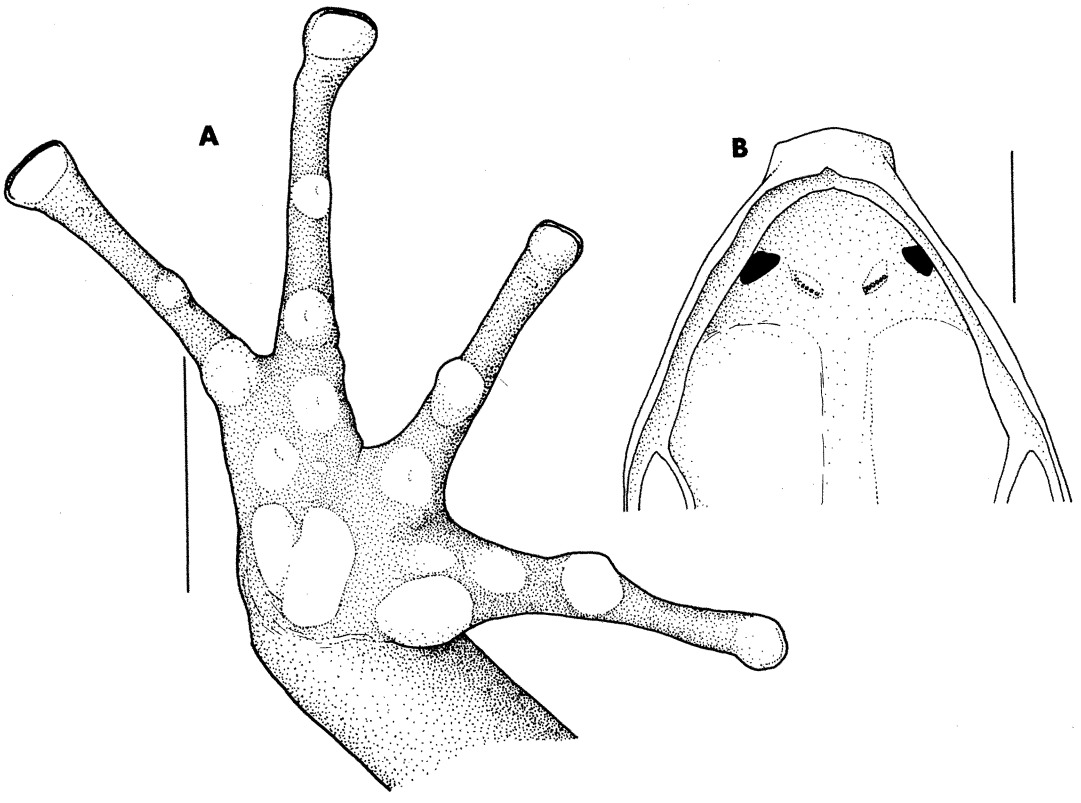

FIG. 1.—(A) Hand and (B) palate of *Eleutherodactylus gaigeae* (KU 114584). Lines equal 5 mm.

and twice width of digit below pad; pads on inner fingers narrower; males lacking nuptial asperities or swelling of thumb base.

Knee, heel, and tarsus lacking tubercles or folds; inner metatarsal tubercle elongate (length 3 times width), elevated; outer metatarsal tubercle slightly longer than wide, subconical, about ⅓ size of inner; plantar supernumerary tubercles present, one proximal to the basal subarticular tubercle of toe II, one below toe III, and a row of two to five below toe IV; supernumerary tubercles smaller than conical subarticular tubercles; toes long, slender, bearing feeble lateral keels, not webbed; toe tips feebly expanded (narrow pads) but bearing discs (terminal grooves and proximal limit to disc) that are as long as wide; shank 44.6–52.4 ($\bar{x}$ = 49.2, n = 8) per cent SVL.

In preservative, dark reddish-brown above, brown below; normally having narrow pale stripes extending from posterior corner of eye to about level of sacrum (stripe may be interrupted); these dorsolateral stripes sometimes evident along outer edge of upper eyelid but do not extend onto snout; similar pale spot or short blotch just anteriad to vent (above distal tip or coccyx); some individuals also have pale spots on face and upper flanks; occasionally, there are pale areas on posterior one-half of upper arm, top of thighs, upper shank, heel, and as a bracelet on the wrist (Fig. 2); venter normally uniformly brown but some individuals have faint loose reticulation of cream on venter.

Remarks.—Piatt (1934) placed *gaigeae* in *Eleutherodactylus* without comment on its relationships. Savage (1973) placed it in a monotypic species group without comment. Although superficially similar to *Lithodytes lineatus*, *E. gaigeae* is properly assigned to *Eleutherodactylus* because the sternum is not developed into a style (and there are no osseus pre- or postzonal elements) and because true discs (as opposed to pads) are present on the outer fingers and toes (and supported by T-shaped terminal phalanges). Lynch (1976) assigned it to the *fitzingeri* group on the basis of the frog having a long

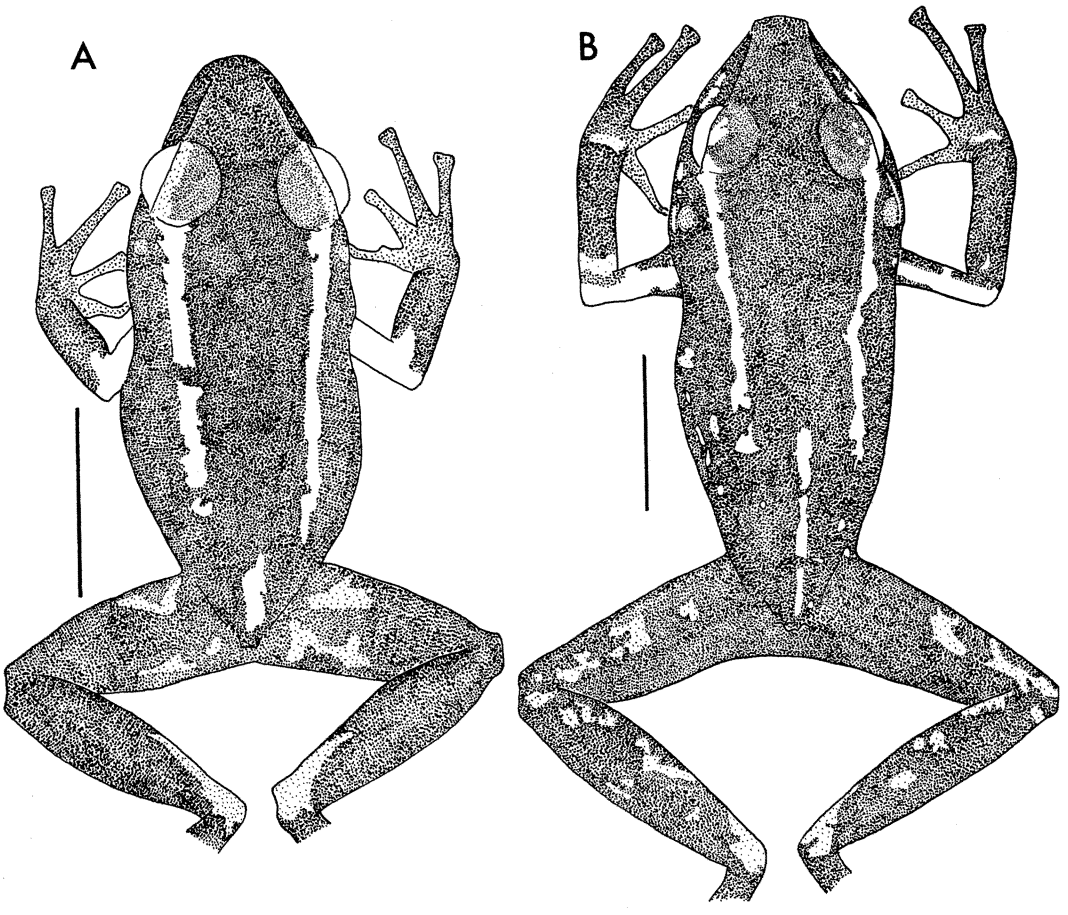

FIG. 2.—Color pattern extremes in *Eleutherodactylus gaigeae* (A) KU 76578, (B) KU 114585. Lines equal 10 mm.

thumb, smooth skin on the venter, and prominent tympana.

The *fitzingeri* group is comparatively large (ca. 40 species) and relatively well-studied (Lynch, 1975; Lynch and Hoogmoed, 1977; Savage, 1974, 1975). *Eleutherodactylus gaigeae* was anonymous in the group before revisionary studies of the group approached completion, but now *E. gaigeae* is anomalous within the group. No other species of the *fitzingeri* group has well-developed supernumerary tubercles. Most species of the group have vocal slits and non-spinous nuptial pads in males (the exceptions are some highland species in western Colombia and some members of what Savage [1975] termed the *rugulosus* group). Despite its dissimilarity to all other species of the *fitzingeri* group, *E. gaigeae* is retained in that group.

Dunn (1931*a*) indicated that the color pattern of *E. gaigeae* was similar to that of *Phyllobates* (compare Fig. 2 with illustrations in Savage [1968], Silverstone [1976], or Myers et al. [1978] for *Phyllobates aurotaenia*, *P. lugubris*, or *P. vittatus*). Comparable similarity of *Lithodytes lineatus* and *Dendrobates* (especially *D. femoralis*) led Nelson and Miller (1971) and Duellman (1978) to suggest the similarities are mimetic. Nelson and Miller (1971) considered the mimicry either Batesian or Mullerian whereas

Duellman suggested that *D. femoralis* was the model and *L. lineatus* the mimc. The distribution of *L. lineatus* (fide Lynch, 1979) is entirely encompassed by that of *D. femoralis* (fide Silverstone, 1976). The distributions of the comparably patterned *E. gaigeae* and *P. aurotaenia*, *P. lugubris*, and *P. vittatus* are less congruent suggesting a once wider distribution of the striped *Phyllobates* (as implied by Silverstone, 1976) if the similarities are mimetic.

Distribution.—Specimens are known from the lowlands of extreme southeastern Costa Rica through Panama and south to the drainage of the Río San Juan in Colombia. A single record is also available from the valley of the Río Cauca, Colombia (Fig. 3).

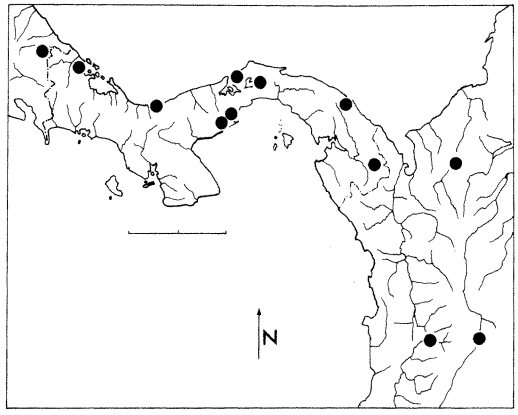

FIG. 3.—Distribution of *Eleutherodactylus gaigeae* in Colombia and lower Central America. Scale is 200 km.

The *unistrigatus* Group

Eleutherodactylus chalceus (Peters)

Phyllobates chalceus Peters, Monatsber. Dtsch. Akad. Wiss. Berlin, 1873:609 (1874).

Syrrhopus areolatus Boulenger, Proc. Zool. Soc. London, 1898:122 (1898). New synonymy.

Lynch (1968) placed both nominal species in *Eleutherodactylus*. Lutz and Kloss (1952) and Lynch (1968) confused *chalceus* with *E. lacrimosus* (Jiménez de la Espada) whereas *E. areolatus* was recognized in the Pacific lowlands of Ecuador (Lynch, 1971).

Peters' (1874) description of *Phyllobates chalceus*, when used in conjunction with Nieden's (1923) illustration, clearly associates the name with populations of frogs found in western Colombia and Ecuador. Peters' (1874) characterizations of the snout and canthal morphology, the texture of the skin of the dorsum, and the coloration are unlike any Amazonian or Amazonian-slope species but are identical to the conditions seen in what Lynch (1971) called *E. areolatus*. Neither Peters' (1874) description nor Nieden's (1923) illustration reveals one of the most distinctive character states of *E. chalceus*—the papillae at the tips of the digits (see illustrations in Lynch, 1971). In the absence of apparent differences, the two species are here treated as conspecific.

The three syntypes of *chalceus* are apparently lost (Ulrich Gruber, pers. com.). Peters (1874) reported the frog as coming from "Pastasasathal" whereas Nieden (1923) recorded it from "Pastassa-Tal (Colombia)." Lynch (1971) provided a redescription (as *E. areolatus*) and reported the species from four localities in western Ecuador. I have now seen more than 100 specimens from the Pacific lowlands of Colombia and Ecuador as far north as 6°N (Fig. 4).

Eleutherodactylus chalceus is found in primary forests as well as in somewhat less mesic and partially open habitats (banana, cacao, and orange groves) at elevations between 50–1540 m but is most abundant at elevations below 1000 m. The call is a loud 'click' and is made by the male while perched on leaves. Calling males elevate the body above the substrate. Lynch's (1971) earlier statement of body size is here emended to adult males 17.5–26.9 ($\bar{x}$ = 23.5 ± 0.9, n = 26) mm, adult females 27.7–31.2 ($\bar{x}$ = 29.7 ± 0.6, n = 13) mm SVL.

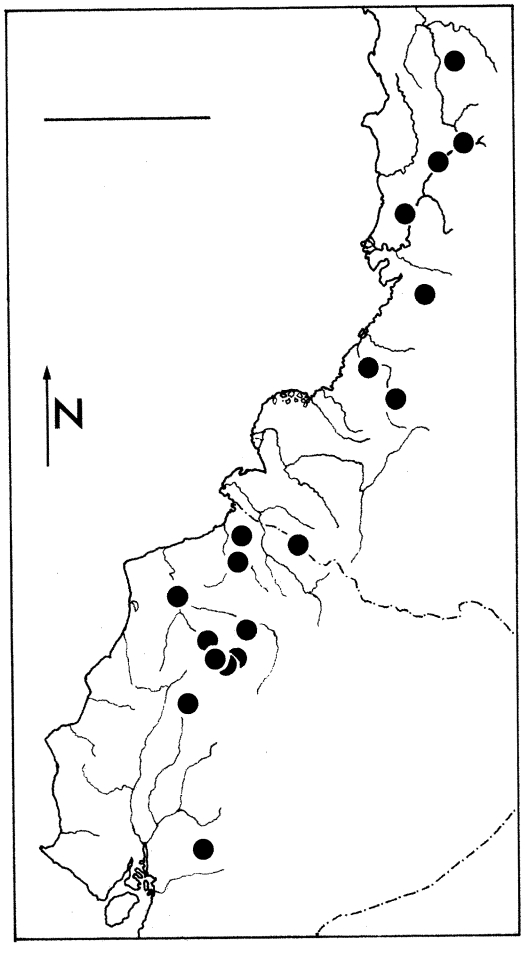

FIG. 4.—Distribution of *Eleutherodactylus chalceus* in western Colombia and Ecuador. Scale is 200 km.

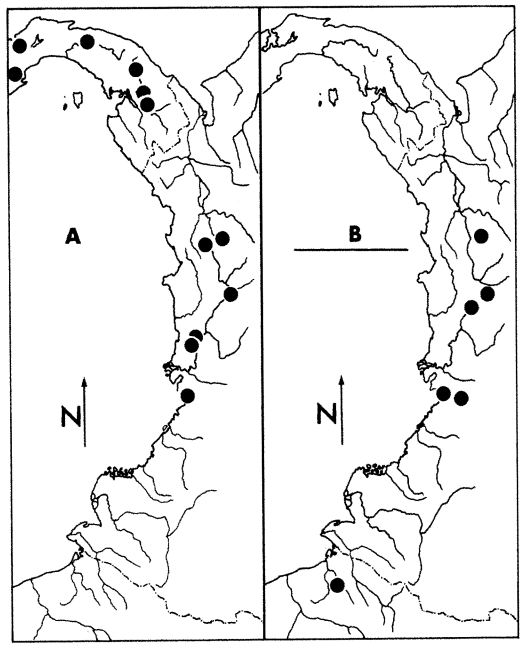

FIG. 5.—(A) Distribution of *Eleutherodactylus ridens* in eastern Panama and Colombia; (B) distribution of *E. roseus* in western Colombia and Ecuador. Scale is 200 km.

Eleutherodactylus ridens (Cope)

Phyllobates ridens Cope, Proc. Acad. Nat. Sci. Philadelphia, 18:131 (1866).
Syrrhopus molinoi Barbour, Proc. N. Engl. Zool. Club, 10:28 (1928). New synonymy.

Eleutherodactylus ridens is a small, apparently common, frog having remained inconspicuous in the literature. Taylor (1952) provided an excellent description and illustration based on material from Costa Rica. The species has apparently not been reported from Panama or Colombia under the name *E. ridens*. Barbour's (1928) *Syrrhopus molinoi* is based on a well-preserved female *E. ridens* (this observation was made earlier by J. M. Savage, whose identification is on record at the MCZ) from Barro Colorado Island. When studying a number of museum collections I frequently found female *E. taeniatus* mixed with adults of *E. ridens* and all identified as *E. ockendeni*. Some of these misidentifications may have entered the literature.

Eleutherodactylus ridens is found in Colombia as far south as 4°N (Fig. 5A) in Departamento Valle. There it might be confused with *E. roseus* (see following account).

Eleutherodactylus roseus (Boulenger)

Hylodes roseus Boulenger, Ann. Mag. Nat. Hist. (9) 2:429 (1918).

Holotype.—BM 1916.4.25.28/RR 1947. 2.16.94, collected at Andagoya, Depto. Chocó, Colombia, 21 November 1915 by H. G. F. Spurrell.

Inexplicably, Cochran and Goin (1970) did not mention *E. roseus* in their *Frogs of Colombia*. *Eleutherodactylus roseus* is redescribed below so that it can be recognized in the large fauna of western Colombia.

Diagnosis.—1) skin of dorsum smooth to finely shagreened without dorsolateral folds, that of venter coarsely areolate; 2) tympanum concealed beneath skin; 3) snout subacuminate in dorsal view, acutely rounded in lateral profile; canthus rostralis moderately sharp; 4) upper eyelid broader than IOD, bearing one elongate conical wart; no cranial crests; 5) vomerine odontophores oval in outline; 6) males lack vocal sac and slits, nuptial pads; testes of males black; 7) first finger shorter than second; pads large, discs broader than long; 8) fingers bearing lateral fringes, fringes weakly crenelate; 9) no ulnar tubercles; 10) heel and tarsus lacking tubercles except for faint inner tarsal tubercle; 11) two metatarsal tubercles, inner oval, 4–6 times size of outer; many supernumerary plantar tubercles; 12) toes bearing lateral fringes, not webbed; pads of toes same size as those of fingers; 13) brown above with darker brown markings (interorbital, labial, limb bars, canthal–supratympanic stripe, scapular W, spots on back), venter dirty cream with brown flecks; posterior flank and adjacent thigh colorless (red in life); posterior thigh cream peppered with brown and marbled with brown; 14) adults small, males 13.1–20.2 ($\bar{x}$ = 16.0 ± 1.2, n = 10) mm, females 24.7–27.9 mm ($\bar{x}$ = 26.2, n = 4) SVL.

Eleutherodactylus roseus is readily confused with the superficially similar *E. ridens*. Both have red areas on the flank and anterior thigh, concealed tympana, and tubercles on the upper eyelid. *Eleutherodactylus ridens* has a less well-developed color pattern, concealed or very slightly developed vomerine odontophores, vocal sac and slits in the male, white testes, is smaller (males 9.5–17.1 [$\bar{x}$ = 13.6 ± 0.6, n = 37] mm, females 17.3–23.3 [$\bar{x}$ = 20.2 ± 0.6, n = 27] mm SVL), has fewer warts on the head, and has a tiny tubercle on the heel. In color, habitus, having crenelate finger fringes, and the presence of eyelid tubercles, *E. roseus* resembles *E. calcaratus* (Boulenger) and *E. crucifer* (Boulenger) found at higher elevations on the Andean slopes of Colombia and Ecuador, respectively. Both of these species have visible tympana and enlarged tubercles on the forearm and tarsus.

Description.—Head wider than body, wider than long; head width 36.3–38.9 ($\bar{x}$ = 37.3, n = 5) per cent SVL in males, 34.4–42.1 ($\bar{x}$ = 40.1, n = 7) per cent in females; snout subacuminate in dorsal view, acutely rounded in lateral profile; snout short, E–N 77.1–88.4 ($\bar{x}$ = 82.6, n = 5) per cent eye length in males, 86.8–100.0 ($\bar{x}$ = 92.6, n = 5) per cent in females; nostrils protuberant, directed laterally; canthus rostralis moderately sharp, slightly concave; loreal region concave, sloping abruptly to lips; lips not flared; upper eyelid width 100.0–120.0 ($\bar{x}$ = 105.8, n = 5) per cent IOD in males, 109.4–134.8 ($\bar{x}$ = 117.9, n = 7) per cent in females; upper eyelid bearing several non-conical tubercles and one conical tubercle (height ≈ basal diameter); no cranial crests; tympanum concealed beneath skin; supratympanic fold thick; postrictal tubercles prominent, subconical; males lacking vocal sac and slits; tongue longer than wide, posterior border weakly notched, posterior $^2/_5$–$^1/_2$ not adherent to floor of mouth; choanae relatively large, round, not concealed by palatal shelf of maxillary arch when roof of mouth is viewed from directly above; vomerine odontophores median and posterior to choanae, oval in outline, separated medially by distance equal to width of one odontophore; each odontophore slightly larger than a choana, bearing nearly transverse row (slightly deflected near midline) of 4–5 teeth.

Skin of dorsum smooth or finely shagreened, some flattened warts on side of head and flanks; no dorsolateral folds; skin of lower flanks and venter coarsely areolate; discoidal folds prominent, well anteriad of groin; anal opening not extended; enlarged subconical tubercle lateral to anal opening; no ulnar tubercles except antebrachial; palmar tubercle bifid, larger than oval thenar tubercle; many supernumerary palmar tubercles, all small, pungent; subarticular tubercles round, subconical; fingers long, bearing prominent, feebly crenelate, lateral fringes; all fingers with discs (broader than long) on dilated pads; pads large, apically rounded, that on thumb smallest, those on fingers III–IV largest; first finger shorter than second; males lack nuptial pads.

Indistinct tubercle on inner margin of tarsus; no other tubercles on tarsus or heel (an indistinct small tubercle is on the heel of the holotype); inner meta-

tarsal tubercle pungent, oval (length three times width); outer metatarsal tubercle subconical, 1/4–1/6 size of inner (no outer metatarsal tubercle evident on the holotype); many supernumerary plantar tubercles, arranged in rows along metatarsal bones; subarticular tubercles subconical, smaller than those of fingers; toes fringed, fringe not crenelate, not webbed; toe pads like those of fingers, approximately same size; hind limbs short, shank 49.7–59.9 ($\bar{x}$ = 53.6, n = 5) percent SVL in males, 46.6–52.4 ($\bar{x}$ = 49.1, n = 5) per cent in females; heels of flexed hind limbs just overlap; heel of adpressed hind leg reaches to eye or between eye and nostril.

In preservative, brown above with darker brown markings (occipital W, interorbital bar, spots on snout and back, canthal and supratympanic stripes, labial bars, limb bars); occipital W and interorbital bar edged anteriorly with cream; anterior flanks densely marbled with brown; posterior to the dark pleural area the skin is not pigmented or has only sparse brown punctuations; pale area extends onto anterior face of thigh where it is limited by dark brown reticulation laterally; venter dirty cream with small brown spots (smaller than thumb pad); throat heavily dusted with brown punctations; limb bars approximately perpendicular, wider than interspaces; concealed shank and tarsus cream; underside of knee and heel heavily flecked with dark brown; posterior thigh cream, marbled with dark brown (uniform brown in small individuals); anal triangle obsolete.

In life, *E. roseus* is as follows: "Back light and dark shades of warm sepia brown marbled with green. Hidden surfaces of hind legs reddish pink" (H. G. F. Spurrell, 21 November 1915).

Measurements of holotype in mm.—SVL 24.7; shank 12.2; head width 10.2; head length 9.8; upper eyelid width 3.0; IOD 2.4; eye length 3.6; E–N 3.6. The holotype has extensively convoluted oviducts; the ovarian eggs are small to medium-sized (<1.5 mm in diameter).

Distribution.—The species occurs in primary forests in the central chocoan lowlands of Colombia south to northwestern Ecuador (Fig. 5B).

Eleutherodactylus subsigillatus (Boulenger)

Hylodes subsigillatus Boulenger, 1902, Ann. Mag. Nat. Hist. (7) 9:52 (1902).

Holotype.—BM 1901.8.3.14/RR 1947.2.17.1, adult female taken at Salidero (= Salinero), Esmeraldas Prov., Ecuador, 107 m, by Mr. Rosenberg.

Eleutherodactylus subsigillatus has not been reported since its description but is a relatively common frog in western Ecuador. In order that it may be identified by others, it is redescribed below.

Diagnosis.—1) skin of dorsum smooth or very finely shagreened, without dorsolateral folds, that of venter coarsely areolate; 2) tympanum distinct, its length 1/3–2/5 that of the eye; 3) snout round in dorsal view, truncate or protruding in lateral profile; canthus rostralis relatively sharp; 4) upper eyelid slightly narrower than IOD, not bearing pungent warts; no cranial crests; 5) vomering odontophores prominent, triangular in outline; 6) males with subgular vocal sac and slits, lacking nuptial pads on thumbs; 7) first finger shorter than second; fingers II–IV bearing large pads; discs broader than long; 8) fingers bearing lateral fringes; 9) ulnar tubercles not evident; 10) heel and tarsus lacking tubercles; 11) two metatarsal tubercles, inner pungent, oval, 6 times size of outer; supernumerary plantar tubercles not prominent; 12) toes bearing lateral fringes, not webbed; pads of toes smaller than those of fingers; 13) pale brown above with indistinct brown flecking, occasionally canthal and supratympanic stripes and limb bars evident; in adult females venter spotted with brown, concealed limb surfaces cream and marbled or spotted with brown; in males and young females venter cream or cream stippled with brown; flanks, groin, and concealed thighs pale brown; 14) adults small, males 19.3–28.5 ($\bar{x}$ = 24.4 ± 1.3, n = 17) mm, females 30.0–33.4 ($\bar{x}$ = 31.4 ± 0.9, n = 7) mm SVL.

Eleutherodactylus subsigillatus is most similar to the frog Ruthven (1915, 1922) erroneously called *E. cruentus*. That species, apparently undescribed (see Lynch, 1978), occurs at moderate elevations in northern Colombia and differs from *E. subsigillatus* in being smaller (males 20.6–25.1 [$\bar{x}$ = 23.2 ± 0.6, n = 18] mm, females 25.3–30.2 [$\bar{x}$ = 27.7 ± 1.3, n = 10] mm SVL), having larger digital pads, small warts on the upper eyelid and heel, and lacking spotting or marbling on the concealed limbs and/or venter. *Eleutherodactylus subsigillatus* also re-

sembles *E. phoxocephalus* Lynch from the Pacific slopes of Andean Ecuador, but differs in that *E. phoxocephalus* has a vertical keel on the snout and bold black and yellow marbling on the concealed surfaces of the thighs.

Description.—Head as wide as body, wider than long; head width in males 35.7–38.9 ($\bar{x}$ = 37.4, n = 5) per cent SVL, in females 38.2–41.7 ($\bar{x}$ = 39.9, n = 4); snout rounded (slightly acuminate) in dorsal view, truncate, angularly rounded, or protruding in lateral profile; snout short, E–N in males 87.1–96.0 ($\bar{x}$ = 90.6, n = 5) per cent eye length, in females 82.9–100.0 ($\bar{x}$ = 94.8, n = 4); nostrils weakly protuberant, directed laterally; canthus rostralis sharp in males, relatively sharp in females, weakly convex; loreal region weakly concave, sloping abruptly to lips; lips not flared anteriorly, slightly flared below tympana; interorbital space flat, no cranial crests; upper eyelid lacking tubercles, its width in males 84.6–100.0 ($\bar{x}$ = 90.7, n = 5) per cent IOD, in females 73.2–90.0 ($\bar{x}$ = 84.0, n = 4); tympanum distinct, round (males) to slightly higher than long (females), separated from eye by ⅔ its diameter; tympanum length in males 35.5–40.0 ($\bar{x}$ = 37.3, n = 5) per cent eye length, in females 34.5–39.0 ($\bar{x}$ = 37.8, n = 4); postrictal tubercles present, not conical; tongue as wide as long, posterior border notched, posterior ⅓ not adherent to floor of mouth; choanae relatively large, round, not concealed by palatal shelf of maxillary arch when viewed from directly above; vomerine odontophores median and posterior to choanae, oval to subtriangular in outline, elevated, bearing nearly transverse row of 5–7 teeth, separated medially by distance equal to odontophore width; each odontophore slightly larger than a choana; males with vocal slits and large subgular vocal sac.

Skin of dorsum smooth to finely shagreened, no dorsolateral folds; skin of throat and breast smooth, that of venter and underside of thighs coarsely areolate; discoidal folds prominent, well anteriad to groin; anal opening not extended; no enlarged warts near anus; flanks shagreened; no ulnar tubercles; palmar tubercle bifid, larger than oval thenar tubercle; 3–4 relatively large, pungent supernumerary palmar tubercles; subarticular tubercles larger than supernumerary tubercles, round, pungent; fingers bearing lateral fringes; all fingers bearing apically rounded pads, pads bearing discs (wider than long); pads of fingers III–IV larger than tympanum, of I–II smaller than tympanum; pads of III–IV more than twice as wide as digit; thumb shorter than second finger; male lacking nuptial pads.

Heel and tarsus lacking tubercles (or folds); inner metatarsal tubercle oval (length twice width), 6 times size of round outer metatarsal tubercle; supernumerary plantar tubercles present, pungent, smaller than subarticular tubercles (subconical, smaller than those of fingers); toes bearing lateral fringes, not webbed; toe pads like those of fingers but smaller; hind legs short, shank in males 45.2–53.4 ($\bar{x}$ = 49.0, n = 5) per cent SVL, in females 49.0–52.0 ($\bar{x}$ = 50.1, n = 4); heels of flexed hind limbs touch; heel of adpressed hind limb reaches to anterior edge of eye.

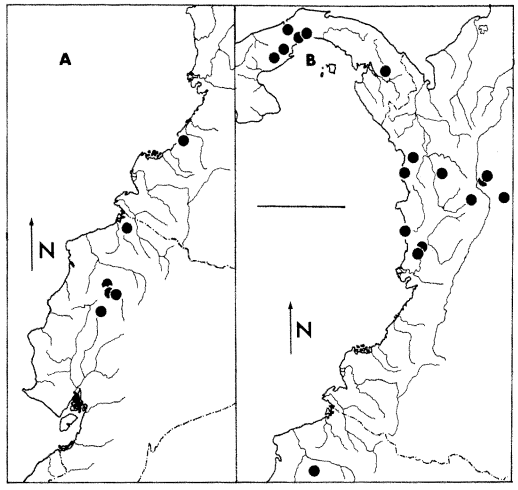

FIG. 6.—Distributions of (A) *Eleutherodactylus subsigillatus* and (B) *E. taeniatus* in chocoan South America and Panama. Scale is 200 km.

In preservative, pale to medium brown above with little indication of pattern; holotype heavily pigmented and has canthal and supratympanic stripes, labial and limb bars, interorbital bar, occipital W, and sacral chevron; in most individuals, scattered dark flecks give only vague hints of such markings; venter cream with sparse to intense brown spotting or reticulation; this pattern extends onto flanks and concealed limb surfaces; in the holotype, ventral surfaces of legs brown with cream spots; marbled pattern of venter, flanks, and concealed limbs evident only in adult females; vague suggestions of such pigmentation evident in males and young females.

In life, *E. subsigillatus* varies from pale green to light reddish brown; ventral surfaces white to pale yellow with brown flecks; in large females the brown blotches are extensive; concealed surfaces of limbs pale greenish-yellow in small specimens, blotched with black in large individuals; blue wash on flanks and concealed limb surfaces of large specimens; vocal sac pale green; iris yellow-bronze with a horizontal red streak and some black reticulation.

Distribution.—The species is found in the primary rainforest in southwestern Colombia and western Ecuador at elevations between 100–670 m (Fig. 6A).

Natural history.—In my field experi-

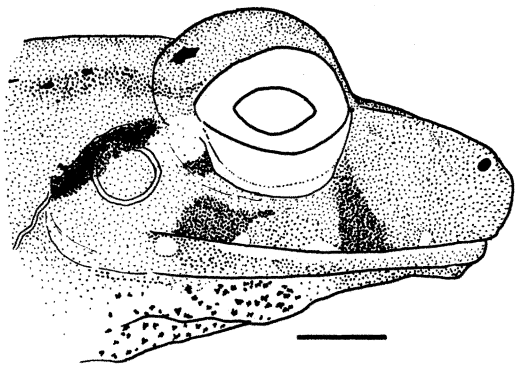

FIG. 7.—Side of head of *Eleutherodactylus taeniatus* (LACM 73214). Line equals 2 mm.

ence, *E. subsigillatus* is rare and/or elusive. An adult female was found in litter by day in a banana grove at the eastern edge of Santo Domingo de los Colorados, Ecuador. The only other specimen I found by day was in a bromeliad two meters above ground in an orange grove. At night (especially rainy nights), calling males were heard 2–5 m up in trees in orange groves and in remnants of primary forest. Some individuals were found on bushes but most were on twigs and leaves of trees or on bromeliads in trees. The call is a single sharp explosive "tweet."

On 8–9 May 1959, James A. Peters found *E. subsigillatus* in a chorus in the plaza in Santo Domingo de los Colorados. He noted the frogs were "sitting on low bushes and trees." The call was described as "a single, clear, bell-like note." Peters' series of 15 individuals consists of ten calling males, three juvenile females, and two gravid females. I have heard calling males in the vicinity of Santo Domingo de los Colorados in December, February, June, and August.

Eleutherodactylus taeniatus (Boulenger)

Hylodes taeniatus Boulenger, 1912, Ann. Mag. Nat. Hist. (8) 10:188 (1912).

Eleutherodactylus ockendeni (misapplication): Dunn, 1931*b*:411.

Eleutherodactylus frater (misapplication): Lynch, 1974:14.

Holotype.—BM 1909.10.30.41/RR 1947.2.16.99, adult female taken at Noanaoa (=Noanamá), Río San Juan, Depto. Chocó, Colombia by M. G. Palmer.

Eleutherodactylus taeniatus has been confused with *E. ockendeni* but the cis and trans-Andean populations are morphologically distinctive. The trans-Andean species is widespread and redescribed below.

Diagnosis.—1) skin of dorsum smooth to finely shagreened, no dorsolateral folds, that of venter coarsely areolate; 2) tympanum distinct, its length $^{1}/_{3}$–$^{2}/_{5}$ eye length; 3) snout subacuminate in dorsal view, rounded in lateral profile; canthus rostralis sharp; 4) upper eyelid slightly narrower than IOD, bearing small tubercles; no cranial crests; 5) vomerine odontophores small, oval in outline; 6) males with vocal slits and subgular vocal sac; non-spinous nuptial pad on thumb of males; 7) first finger shorter than second; pads on fingers II–IV at least twice as wide as digit; discs broad; 8) fingers bear narrow lateral fringes; 9) ulnar tubercles prominent, non-conical; 10) inner edge of tarsus bearing 2–3 tubercles; one tubercle on heel; 11) two metatarsal tubercles, inner elongate, 5 or more times size of outer; rows of supernumerary tubercles on sole; 12) toes with lateral fringes, no webbing; toe pads as large as those of outer fingers; 13) brown above with darker occipital W, sacral chevron; no canthal stripe (Fig. 7); anterior and posterior surfaces of thighs uniform brown; venter cream dusted with brown; 14) adults small, males 15.3–25.1 mm, females 24.6–32.4 mm SVL (largest frogs found in Panama). Panamanian males average 22.1 ± 1.3 mm SVL (n = 10), females average 31.9 mm SVL (n = 3); Colombian males average 17.8 ± 0.5 mm SVL (n = 20), females average 26.7 ± 0.6 mm SVL (n = 19).

Eleutherodactylus taeniatus is most similar to the cis-Andean *E. ockendeni* (Boulenger) and *E. quaquaversus* Lynch but differs from each in having 2–3 inner tarsal tubercles. Additionally, *E. qua-*

quaversus has a calcar on the heel and a spotted venter.

Description.—Head as broad as or slightly broader than body, nearly as long as wide; head width in males 35.8–38.5 ($\bar{x}$ = 36.8) per cent SVL, in females 38.3–40.0 ($\bar{x}$ = 39.1) per cent; snout subacuminate in dorsal view, rounded (or somewhat truncate) in lateral profile; snout short, E–N in males 81.2–92.0 ($\bar{x}$ = 86.7) per cent eye length, in females 88.5–100.0 ($\bar{x}$ = 95.6) per cent; nostrils protuberant, directed dorsolaterally; canthus rostralis distinct, concave; loreal region weakly concave, sloping gradually to lips; lips slightly flared; interorbital space flat (no cranial crests), upper eyelids bear small tubercles; upper eyelid width 79.4–111.1 ($\bar{x}$ = 95.0) per cent IOD; supratympanic fold distinct, obscuring upper edge of tympanic annulus, extending to just above arm insertion; tympanum distinct, slightly higher than long, its length 31.6–41.6 ($\bar{x}$ = 35.3) per cent eye length, separated from eye by distance equal to tympanum length; postrictal tubercles distinct, subconical; pad on second finger as wide as tympanum, of fingers III and IV larger than tympanum; choanae round, relatively large, not concealed by palatal shelf of maxillary arch; vomerine odontophores small, median and posterior to choanae, oval in outline (broader than long), elevated, bearing 4–6 teeth, separated on midline by distance equal to twice width of an odontophore; tongue longer than wide, its posterior border notched, posterior 2/5 not adherent to floor of mouth; long vocal slits lateral to tongue in male; vocal sac subgular.

Skin smooth anteriorly, becoming shagreened posteriorly, bearing many fine ridgelets, and on upper eyelid, flanks, and lower back, small tubercles; throat smooth, venter coarsely areolate; no dorsolateral folds; discoidal fold well anteriad to groin; no anal sheath; ulnar tubercles prominent, usually 4; palmar tubercle bifid, median lobe largest but smaller than elongate thenar tubercle; supernumerary palmar tubercles pungent, smaller than round, subconical subarticular tubercles; fingers bearing narrow lateral fringes; each finger bearing dilated pad and disc (broader than long); pad smallest on thumb, those on II–IV at least twice width of digit below pad; first finger shorter than second; males bearing granular, white, non-spinous nuptial pad on top of thumb.

Usually one round tubercle on heel; outer edge of tarsus usually devoid of small tubercles; one large and 1–2 small tubercles on inner edge of tarsus; inner metatarsal tubercles 3 times as long as wide, outer 1/5 (or less) size of inner, subconical, longer than wide; supernumerary plantar tubercles numerous, arranged in rows, the largest nearly as large as basal subarticular tubercles on toes IV and V; subarticular tubercles subconical, round; toes bearing prominent lateral fringes, not webbed; toe pads as large as those of outer fingers, discs broader than long, apically round; heels of flexed hind legs overlap; heel of adpressed hind leg reaches anterior edge of eye; shank of males 55.0–59.5 ($\bar{x}$ = 57.4) per cent SVL, of females 52.0–57.1 ($\bar{x}$ = 54.3) per cent.

In preservative, brown above with black flecks and spots defining an occipital W; sacral chevron, suprainguinal bar, and sometimes interorbital bar, brown; area between occipital W and sacral chevron may be dark tan; snout anterior to interorbital bar may be tan; supratympanic stripe dark brown as are two labial bars below eye; loreal region lacking markings; limb bars narrow, oblique on shank; anal triangle dark brown, cream line sometimes evident above vent; anterior and posterior surfaces of thighs, ventral surface of shank uniform brown; groin and flanks cream with brown stippling; venter cream with brown stippling; throat more heavily stippled.

Variation.—The most obvious variants of *E. taeniatus* are color pattern variants (Fig. 8). The normal pattern (Fig. 8A) is exhibited in most specimens (at least 90%). The striped morph (Fig. 8B,D) has dorsolateral stripes punctated with black (remnants of the occipital W) and two pairs of paravertebral stripes, the most lateral of which encroach on the eyelids; in this morph, a feeble canthal stripe is evident. The remaining variants are variations on the normal pattern (Fig. 8C) with narrow to broad pale median stripes. When a broad stripe occurs, black pigment is redistributed along the stripe. Redistribution does not occur if the stripe is narrow.

Remarks.—Lynch (1974) applied the name *E. frater* (Werner) to *E. taeniatus*. *Eleutherodactylus frater* is a smaller species found at moderate elevations on the Amazonian slopes of the Cordillera Oriental of Colombia. Dunn (1931*b*) applied the name *E. ockendeni* to Panamanian specimens and his identification was followed by virtually all herpetologists working in central Panama in the ensuing years.

Distribution.—*E. taeniatus* ranges from central Panama east through the Darién to the Río Nechi in Departamento Antioquia and south through the chocoan lowlands into northwestern Ecuador (Fig. 6B).

Specimens Examined

Eleutherodactylus caryophyllaceus (1).—COLOMBIA. Depto. Antioquia: Río Arquía, Finca west of Finca Chibiquí (LACM 47141).

Eleutherodactylus chalceus (123).—COLOMBIA. Depto. Antioquia: Río Arquía, Puerto Palacios (LACM 47166–67). Depto. Caldas: Santa Cecilia, 800 m (KU 138721). Depto. Cauca: Quebrada Guanguí, 0.5 km above Río Patria, 100–200 m (AMNH 86355, 88944, 88968); Río Michenque, El Tambo,

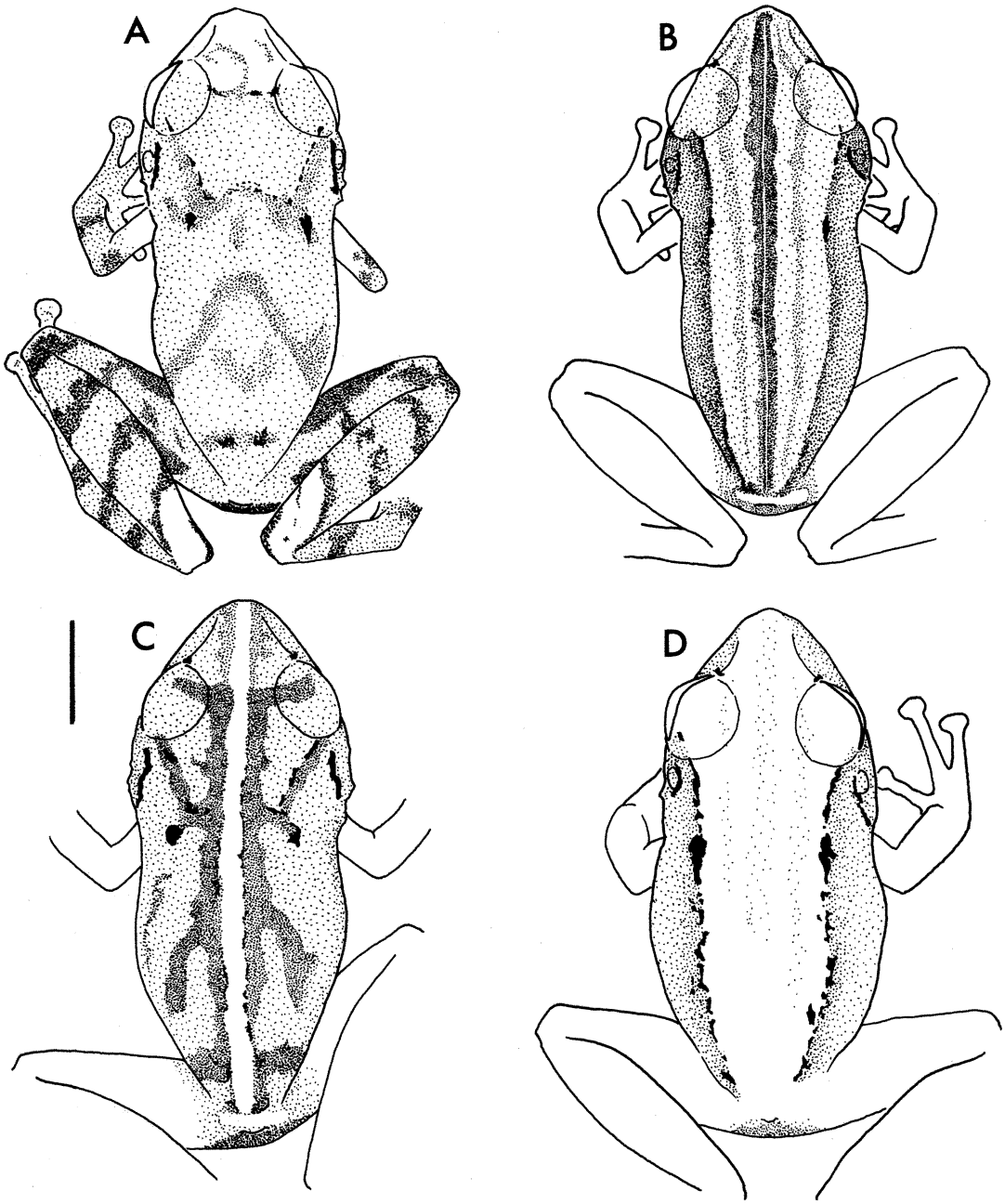

FIG. 8.—Pattern variation in *Eleutherodactylus taeniatus*: (A) LACM 73214; (B) striped morph, based on BM 1947.2.16.99 (holotype) and LACM 73207; (C) LACM 73208; (D) LACM 73212. Scale is 5 mm.

800 m (KU 138720). Depto. Chocó: Andagoya (USNM 152760); 2 km above Playa de Oro, upper Río San Juan, 210 m (AMNH 87016–19, 87022–23); Quebrada Docordó, ± 10 km above junction with Río San Juan, 120 m (AMNH 87015); Quebrada Bochoramá, Loma de Encarnación (LACM 47089–90). Depto. Valle: Anchicayá, 87 km W Cali, 500–600 m (KU 152149–51); Río Anchicayá, 300 m (KU 167900–02). ECUADOR. No other locality (WCAB 35709–10). Prov. Carchi: Maldanado, 1410 m (KU

JDL 8591). Prov. Esmeraldas: 10 ½ km N Quinindé, 130 m (KU 141774–75); Río San Miquel, ca. 1 km up from Río Cayapas (MCZ 92972–76, 93016); San Javier de Cachabí (BM 98.4.28.110/RR 1947. 2.15.38—cotype of *S. areolatus*); San Miquel (MCZ 92977–80); 38 km NW Santo Domingo de los Colorados, 305 m (USNM 204730–32). Prov. Guayas: Puente del Chimbo (BM 98.4.28.111/RR 1947.2.15.39—cotype of *S. areolatus*). Prov. Pichincha: Centro Cientifico, Río Palenque, 220 m (MCZ 88415–16, 89948–53, 91890, 92836); 3.5 km NE Mindo, 1540 m (KU 165143–49); 5 km NW Nanegal Chico, rd to Nanegal (USNM 204721); Río Baba, 4 km E, 10 km S Santo Domingo de los Colorados, 400 m (KU 141773); Río Baba, 5 km E, 19 km S Santo Domingo de los Colorados (UIMNH 77409); Río Faisanes, 13.5 km above La Palma, hwy 28, 1380 m (MCZ 94471–73, 94813, 95628); hwy 28, 14.4 km above La Palma, 1380 m (MCZ 91887–89); Santo Domingo de los Colorados, hotel Zaracay and vic., 600 m (KU 117487–91, 118129, 119474–501, 120252, MCZ 88413–14, WCAB 44396–400); 6 km E Santo Domingo de los Colorados, km 121 (USNM 204724–28); 5 km W Santo Domingo de los Colorados (USNM 204722–23); 18 km W Santo Domingo de los Colorados, km 19, rd to Chone (USNM 204729).

Eleutherodactylus gaigeae (30).—COLOMBIA. Depto. Caldas: Samana, Río Hondo (FMNH 69732). Depto. Chocó: vic. Playa del Oro, Río San Juan, 200 m (AMNH 87061, ICN 4947–48, 4950); upper Río San Juan, vic. jct Río Llorandó (KU 108572). Depto. Córdoba: Serranía de San Jeronimo, ca. 5 km E Tierra Alta (LACM 114491). COSTA RICA. Prov. Limón: Talmanca Valley (MCZ 9901, 9904). PANAMA. Prov. Bocas del Toro: ca. 4.8 km W Almirante, 50–100 m (KU 108567). Prov. Canal Zone: Fort Randolph (MCZ 10011—holotype). Prov. Coclé: El Valle, 550–560 m (KU 76581, 108568). Prov. Colón: ca. 4 km SE Puerto Pilon, 190–240 m (KU 114584–85). Prov. Darién: Laguna, 820 m (KU 76578–79); Tacarcuna, 550 m (KU 76580). Prov. Panamá: Cerro La Campana (MCZ 82073), S slope, 740 m (KU 108569); near town of Altos de Pacora, 750–800 m (KU 108570–72). Prov. San Blas: Camp Summit, 300–400 m (KU 114586–90). Prov. Veraguas: mouth of Río Concepción, 1 m (KU 106297–98, 114591).

Eleutherodactylus ridens (101).—COLOMBIA. Depto. Antioquia: Río Arquía, Belen (LACM 46924), Finca Chibiquí (LACM 47027–28), Finca Los Llanos (LACM 47013–15, 47019–20, 47029–31), Puerto Palacios (LACM 46882, 46996–97, 47000–09), above Puerto Palacios (LACM 47010); Río Atrato, Arquía (LACM 46990–95). Depto. Caldas: N Santa Cecilia (LACM 50549–50). Depto. Chocó: Camposanto (LACM 50577); 2 km S Dipurdú de Guacimo, Río San Juan, 100–120 m (AMNH 87076–77); Playa de Oro (LACM 47033–34); 2 km above Playa del Oro, 210 m (AMNH 87081–85); Quebrada Docordó, 10 km above Río San Juan, 100 m (AMNH 87079–80); Quebrada Vicordó, 5 km above Noanamá, 80–110 m (AMNH 87078); shore Río Buey (LACM 50578). Depto. Valle: Río Raposa biological station (LACM 50563). PANAMA. Depto. Canal Zone: Barro Colorado Island (MCZ 13051—holotype of *Syrrhopus molinoi*, UMMZ 69315, 69316[2], 69317[2], 69318[4], 69319[4], 69499–502, 69504–08, 69510, 69511[2], 68512, 68516, 98423, 131086[2]). Prov. Coclé: Cerro Campana (UMMZ 131087). Prov. Darién: Canclones (UMMZ 125032, 125548); mouth of Río Mortí (UMMZ 125030); mouth of Río Subcutí (UMMZ 125547); bet. Río Ucurgantí and Río Metetí (UMMZ 137864). Prov. Panamá: Cerro Campana, Posado San Antonio (UMMZ 131811), 1.6 km NW Posado San Antonio (UMMZ 131816[4], 137820, 137823, 137825, 137828), 4.8 km NW Posado San Antonio (UMMZ 137831–32); bet. Río Silugantí and Río Canitas (UMMZ 131084); Río Siluganti at PanAm hwy (UMMZ 131083[2], 131085, 137732).

Eleutherodactylus roseus (34).—COLOMBIA. Depto. Antioquia: Río Arquía, Belen (LACM 46925, 47035), Finca Chibiquí (LACM 47163), Finca Los Llanos (LACM 46917–23, 47011, 47016–18, 47021–26, 47160), Pto. Palacios (LACM 46998–99). Depto. Chocó: Andagoya (BM 1916.4.25.28/RR 1947. 2.16.94—holotype); 2 km above Playa del Oro, 210 m (AMNH 87106–07, 87113). Depto. Valle: coast S of Buenaventura (KU 154532); Río Anchicayá, 300 m (KU 168553–56); Río Raposa biological station, (LACM 50567). ECUADOR. Prov. Esmeraldas: Río San Miguel, ca. 1 km above Río Cayapas (MCZ 92937–38).

Eleutherodactylus subsigillatus (33).—COLOMBIA. Depto. Cauca: Quebrada Quanquí, Río Saija drainage, 100 m (AMNH 86359). ECUADOR. Prov. Esmeraldas: Hda. Equinox, 38 km NW Santo Domingo de los Colorados, 305 m (USNM JAP 1839); Salidero (= Salinero), 107 m (BM 1901.8.3.14/RR 1947.2.17.1—holotype). Prov. Pichincha: Estación Biología, Río Palenque, 220 m (KU 165587, MCZ 90140–42, 94459); Santo Domingo de los Colorados, town square, 670 m (USNM JAP 3964, 4112–22, 4143, 4167–68); E edge Santo Domingo de los Colorados, 620–660 m (KU 117572, 117776–77, 177839–41); 2 km E, 1 km S Santo Domingo de los Colorados, 600 m (KU 177842–44); Hda. Espinosa, 9 km W Santo Domingo de los Colorados, rd to Chone (CAS-SU 10508, 10516).

Eleutherodactylus taeniatus (113).—COLOMBIA. Depto. Antioquia: Andes (AMNH 14091, 14095); El Clara creek, 6 miles from Angelopolis (AMNH 39897, 39963); Envigado (AMNH 39797); 7 miles from Medellin on mountain slope (AMNH 38766–70); Río Arquía, Belen (LACM 46883), Finca Chibiquí (LACM 46884); Sonsón (AMNH 33401, 38772–76, 38778, 39327, 39329–38, 39340–43). Depto. Chocó: Alto de Buey, N slope, 420–1070 m (LACM 47231–32, 47229); Camino de Yupe, 350–400 m (LACM 73206–08), 420–625 m (LACM 73209, 73211–12, 73214–24), 420–700 m (LACM 73225); Noananoa (= Noanamá), Río San Juan (BM 1909.10.30.41/RR 1947.2.16.99—holotype); Pizarro (FMNH 44074); Quebrada Docordó, 10 km above

Río San Juan, 120 m (AMNH 87120–21); Quebrada Vicordó, 5 km above Noanamá, 80–110 m (AMNH 87111–12, 87116–19); hills near upper Río Napipí (LACM 46885–93); upper Río Opogodó above Río Merendó (LACM 46894–95); Serranía de Baudo, ridges paralleling Río Yupe (LACM 46896–902). ECUADOR. Prov. Esmeraldas: sector de Lagartera, region de Río Caoni (UIMNH 53396, 53398, 53422–23, 53426, 53431). PANAMA. Prov. Canal Zone: Barro Colorado Island (MCZ 24223, UMMZ 69503, 69509, 69510[2], 101794, 137759, 137761, 137763, 137767–68); Corozal (UMMZ 98422); US Forest Reserve, Galliard Rd, Summit (MCZ 21831). Prov. Coclé: El Valle, Río Anton, ca 650 m (AMNH 87319–20). Prov. Darién: Canclones (UMMZ 125031, 137871); mouth of Río Canclon (UMMZ 125033); 2 miles from mouth of Río Canclon (UMMZ 125034). Prov. Panamá: Cerro Campana (UMMZ 131087 [IJ 2516]); 0.5 km SW Campana, 150 m (AMNH 87318); Río Tocuman (MCZ 10020).

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SOCIAL BEHAVIOR AND COMMUNICATION OF A DENDROBATID FROG (*COLOSTETHUS TRINITATIS*)

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ABSTRACT: The social behavior and communication of *Colostethus trinitatis* were studied for 1.5 months at Simla, in the Northern Range of Trinidad. Females were territorial and defended sites with visual displays and aggressive behavior against all intruders. Most females remained at the same sites throughout the study. Males were more mobile and seldom remained in one place for more than a few days. Males turned black when calling and were aggressive only toward other black males. Non-calling males were light brown. Males gave an advertisement call and at least two courtship calls, but lacked agonistic encounter calls. Males carried tadpoles from terrestrial oviposition sites to water. The behavior of *C. trinitatis* appears to be similar to that of *C. collaris* and *C. palmatus*, but differs substantially from that of the Panamanian *C. inguinalis*.

Key words: Amphibia; Salientia; Dendrobatidae; *Colostethus*; Behavior; Communication; Aggression; Vocalizations; Trinidad

NEOTROPICAL frogs in the family Dendrobatidae exhibit complex social behavior and are excellent subjects for comparative studies (Wells, 1977*a*, *b*, 1978, 1980*a*). I report the results of a 1.5 month study of courtship, aggressive behavior, and vocal communication in *Colostethus trinitatis*, a small (♂♂ 19–22 mm; ♀♀ 22–26 mm) diurnal frog from Trinidad, West Indies. I then compare the behavior of this species with that of other *Colostethus* living in similar habitats, especially the Panamanian species *C. inguinalis*.

Colostethus trinitatis lives near permanent and intermittent streams in the mountain ranges of Trinidad and northern Venezuela (Kenny, 1969). Although population densities are highest in rocky areas near water, the frogs often move 50 m or more from water in wet weather. Both males and females seem to prefer large boulders, but also forage for insects in leaf litter or on logs. Eggs are laid in rock crevices or under dead leaves. Males carry tadpoles on their backs to water (Kenny, 1969; Van Meeuwen, 1977; pers. observations).

Previous studies of a population in Venezuela indicated that females defend individual territories for at least two months (Test, 1954; Sexton, 1960). Males also were aggressive toward one another, but it was not clear if they defended ter-