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THE IDENTITIES OF THE COLOMBIAN FROGS CONFUSED WITH *ELEUTHERODACTYLUS LATIDISCUS* (BOULENGER) (AMPHIBIA: ANURA: LEPTODACTYLIDAE)

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ABSTRACT *Eleutherodactylus latidiscus* (Boulenger) is a lowland species found in western Ecuador and southwestern Colombia; the species is replaced geographically (to the north) by *E. cruentus* (W. Peters). *Eleutherodactylus latidiscus* is assigned to the *E. cruentus* species group. The records attributed to *E. latidiscus* in Andean Colombia apply to other species (mostly *E. supernatis* Lynch and *E. permixtus* sp. nov.). *Eleutherodactylus tamsitti* Cochran and Goin is not a geographic race of *E. latidiscus* and is redescribed. *Eleutherodactylus permixtus*, *E. supernatis*, and *E. tamsitti* are not each other's nearest relatives but are assigned to the *E. devillei* species group. At moderate and intermediate elevations on the western flanks of the Cordillera Occidental of Colombia and Ecuador, one finds a series of long-legged species (*E. crenunguis* Lynch, *E. ocellatus* Lynch and Burrowes, *E. labiosus* sp. nov., and *E. orpacobates* sp. nov.) allied to *E. rubicundus* (Jiménez de la Espada), a species found on the cis-Andean slopes of Ecuador. The Central American representative of this group is *E. cerasinus* (Cope). This series of six species is termed the *E. cerasinus* species group.

Key words: Andes; *Eleutherodactylus cerasinus* group; *E. cruentus* group; *E. devillei* group; *Eleutherodactylus latidiscus*; Taxonomy.

RESUMEN *Eleutherodactylus latidiscus* (Boulenger), una especie de tierras bajas, se encuentra en Ecuador occidental y Colombia suroccidental. Esta especie es remplazada geográficamente (al norte) por *E. cruentus* (W. Peters). *Eleutherodactylus latidiscus* es una especie del grupo *cruentus*. Los registros de *E. latidiscus* de los Andes de Colombia pertenecen a otras especies (principalmente a *E. permixtus* esp. nov. y *E. supernatis* Lynch). *Eleutherodactylus tamsitti* Cochran y Goin no es una raza geográfica de *E. latidiscus* y aquí se redescrive. *Eleutherodactylus permixtus*, *E. supernatis*, y *E. tamsitti* pertenecen al grupo *devillei*. En los bosques nublados de los flancos occidentales de la Cordillera Occidental de Colombia y Ecuador, se encuentran una serie de especies con piernas largas (*E. crenunguis* Lynch, *E. ocellatus* Lynch y Burrowes, *E. labiosus* esp. nov., y *E. orpacobates* esp. nov.) que tienen parentescos con *E. rubicundus* (Jiménez de la Espada), una especie de las faldas amazónicas de los Andes del Ecuador. El representante centroamericano de este grupo es *E. cerasinus* (Cope). Esta serie de seis especies componen el grupo *cerasinus*.

Palabras claves: Andes; Grupo de *Eleutherodactylus cerasinus*; Grupo de *E. cruentus*; Grupo de *E. devillei*; *Eleutherodactylus latidiscus*; Taxonomía.

Aside from some debate concerning the identification of certain frog species in Costa Rica and Panama (Dunn, 1933; Taylor, 1952), the first application of the name *Eleutherodactylus latidiscus* (Boulenger) in any modern sense was by Cochran and Goin (1970), who reported specimens from Colombia, Ecuador (type locality only), and Panama (using Dunn's, 1933, early identifications). Within Colombia, Cochran and Goin reported material from the cordilleras Central and Occidental (primarily high altitudes), the middle Magdalena valley, and the southern extreme of the Cordillera Oriental. The last record was described by them as a new subspecies, *Eleutherodactylus latidiscus tamsitti*.

Very large digital disks were noted in *Eleutherodactylus cruentus* and *E. latidiscus* by Boulenger (1898), Dunn (1931; 1933), and Taylor (1952). Other large-disked forms from Guatemala and Mexico had been treated as the *Eleutherodactylus alfredi* Group earlier (Smith, 1939; Smith and Taylor, 1948). This condition represents one extreme in the near continuum of disk sizes found within the genus *Eleutherodactylus* (Lynch, 1976a; 1978). While most *Eleutherodactylus* species have relatively narrower digital disks (disk width about twice that of digit below disk), the large-disked species have disks approximately 3.0–3.5 times the width of the digit below the disk (Fig. 1). Species with relatively narrower digital disks have narrow disks or lack fleshy lateral fringes on the digits.

Eleutherodactylus latidiscus was named by Boulenger (1898) on the basis of two large (49.7–53.4 mm snout-vent length [SVL]) adult females from the coastal lowlands of extreme northwestern Ecuador. Dunn (1933) used the name for *E. cruentus* in Panama. (Only 2 yr earlier, Dunn [1931] applied the name *E. ventrimarmoratus* to *E. cruentus*.) However, the

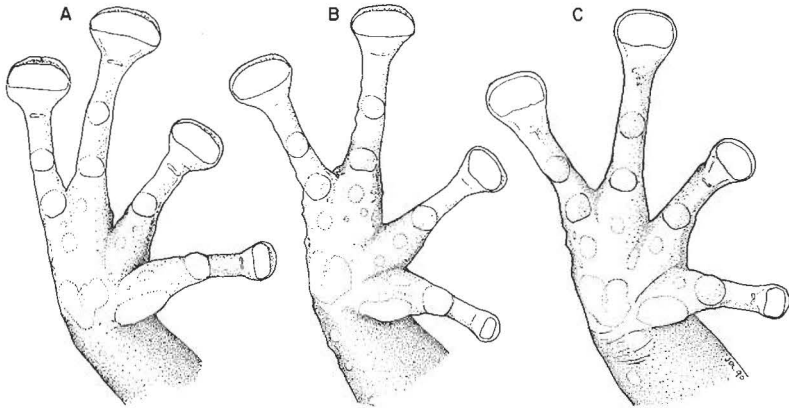


Fig. 1. Hands of *Eleutherodactylus*. A. *E. latidiscus*, ICNMHN 13340. B. *E. tamsitti*, ICNMHN 22949. C. *E. permixtus*, ICNMHN 22629.

broadest misapplication of the name was made by Cochran and Goin (1970), who used the name for several species in Colombia (Lynch, 1980). Although not every specimen they reported has been located, they apparently examined only a syntype of *E. latidiscus*. Lynch (1976a) elevated their new subspecies, *E. latidiscus tamsitti*, to species status without providing evidence in support of the taxonomic change. He wanted to emphasize that there was no evidence that *E. tamsitti* was the same species that had been named by Boulenger from the lowland Pacific forests.

As mentioned by Lynch (1980), there are serious problems with Cochran and Goin's accounts for certain species. They reported the same individual (AMNH 38831) three times as three different species (*E. cruentus*, *E. latidiscus*, and *E. vertebralis*). Seventeen other specimens were reported as both *E. latidiscus* and *E. vertebralis*. Most of their material belongs to one of the subpáramo species they confused with *E. vertebralis*; in turn, that species was confused with *E. supernatis* by Lynch (1980) and is described below. Beginning about 1979, Lynch consistently applied the name *E. latidiscus* to still a very different frog. As a result, the name *E. latidiscus* was used by Lynch and his coworkers (Lynch, 1979; Lynch and Duellman, 1980; Lynch and Miyata, 1980) for the species described below as *E. labiosus*. Because Lynch associated Boulenger's *latidiscus* with that undescribed species, he applied the name *E. cruentus* (W. Peters) to what we here call *E. latidiscus*. Savage (1981) disputed some of Lynch's distributional claims for *E. cruentus*, but that species does range into northwestern Colombia (but not as far south as Ecuador). In describing *E. loustes*, Lynch (1979) suggested that it was allied to *E. latidiscus* as well. That suggestion derived from undue attention to the shape of the head as seen in large females.

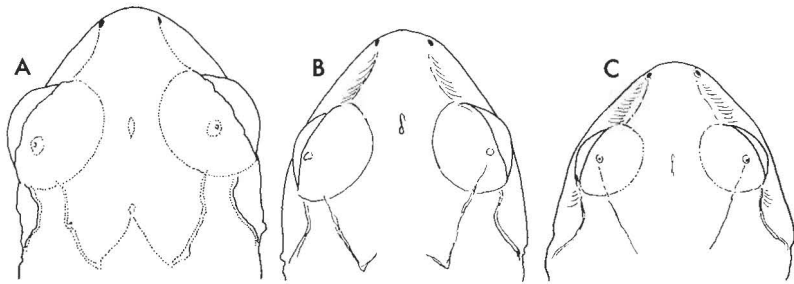


Fig. 2. Dorsal views of heads of *Eleutherodactylus latidiscus*. A. ICNMHN 13336, male, 24.7 mm SVL. B. ICNMHN 13335, juvenile female, 26.9 mm SVL. C. ICNMHN 13340, adult female, 47.9 mm SVL.

When one of us (JDL) first began to study the Ecuadorian frogs of the genus *Eleutherodactylus*, he was struck by the peculiar head shape of Boulenger's (1898) illustration of *Hylodes latidiscus*. Cochran and Goin (1970) emphasized the large head with flared lips in their touched-up illustration of one of the syntypes. Following study of the syntypes in 1972, Lynch searched for more recently collected specimens having the same peculiar morphology without realizing that the peculiar head shape was a sexually dimorphic trait (Fig. 2). The confusion persisted in part because he found relatively few sexually mature females and they were scattered through collections. It was not until 1984 that sufficient material was found to re-evaluate and reject the notions that Lynch had harbored for 20 yr. Among those now-rejected notions is the belated discovery that the frog he called *E. cruentus* from western Ecuador was *E. latidiscus* (Boulenger).

Although several frog species have been associated with the name *Eleutherodactylus latidiscus*, apparently the only references that actually apply to the species are those dealing explicitly with the syntypes or the use of the name in faunal lists. (They were listed because the name was given for a frog in the Pacific lowlands; the reference implied is to Boulenger's original description and the type-specimens). The frogs that Lynch and Miyata (1980) called *E. latidiscus* from western Ecuador are not of that taxon. They emphasized two features evident in the syntypes (the fine granulation [shagreen] of the skin of the dorsum and the peculiar head shape [flared lips on proportionately large heads]). This combination of characteristics is most evident in females (whose lips are more flared than those of the males) and occurs in several species that resemble one another in being large, relatively slender frogs with relatively large digital pads (Fig. 1).

MATERIALS AND METHODS

Measurements follow Lynch and Duellman (1980). The following measurements are identified by abbreviations: SVL (snout-vent length), HW (head width), HL (head length, measured so as to estimate snout-occiput distance), IOD (interorbital distance), E-N (eye to nostril distance). Specimens were measured to the nearest 0.1 mm with dial calipers. Means are reported ± 1 standard error of the mean. Crania were prepared either as double-stained preparations (following Dingerkus and Uhler, 1977) or by picking away musculature and fascia, followed by washing 0.5–3 min in warm dilute (25%) Clorox solution, and washing in cold water for 12 h.

In the following accounts, the term tympanum refers to the structure evident on the side of the head of the frog. When the skin covering the tympanic annulus is not adpressed against the annulus, no tympanum is apparent externally (= tympanum concealed). In several *Eleutherodactylus*, the annulus is only partially visible (Lynch and Duellman, 1980). In the following accounts, the term odontophore is used to identify the projection bearing teeth that lies near (or at) the posterior extent of the dentigerous process of the vomer. In each case, these usages are consistent with the uses of such terms for more than a century in descriptions of frogs and to change terminology would lead to ambiguity.

Specimens are identified by catalogue number and an abbreviation for the collection (following Leviton et al., 1985). Place names are arranged by country, department (or province), and municipio; in some cases, veredas (subdivisions of a municipio) are given. The specimens examined are listed in the appendix.

SYSTEMATIC ACCOUNTS

Between the confusion generated by Cochran and Goin (1970) and by Lynch and his coworkers (Lynch, 1979; Lynch and Duellman, 1980; Lynch and Miyata, 1980) over the name *E. latidiscus* (Boulenger), a variety of frog species has been associated in the literature. The sequence of systematic accounts presented below is intended to order these taxa in such a way that some of the historical conflation can be sorted out. Three units are buried in this confusion and those units have geographic and phylogenetic components: (1) taxa from the Pacific lowlands, (2) Andean taxa (subpáramo and high cloud forests), and (3) taxa from intermediate elevations of the western slopes of the Andes of Ecuador and the Cordillera Occidental of Colombia.

THE IDENTITY OF *ELEUTHERODACTYLUS LATIDISCUS*

Boulenger (1898) named *Eleutherodactylus latidiscus* on the basis of two adult females from Cachabe, Provincia Esmeraldas, Ecuador. Dunn (1933) applied the name to what is now called *E. cruentus* (Savage, 1981) and Breder's (1946) use of the name is probably at Dunn's suggestion. Taylor (1952), reacting to Dunn's (1931; 1933) suggestions, pointed out that *E. latidiscus* and *E. ventrimarmoratus* were distinct from the Central American species that have large digital pads, but erred in reporting that these species (*E. latidiscus* and *E. ventrimarmoratus*) have smooth skin on the venter. Cochran and Goin's (1970) account of *E. latidiscus* [*latidiscus*] is useful in that they provided a detailed description and illustration [albeit improved with pencil tracings] of one of the syntypes. However, because the species exhibits considerable sexual dimorphism (as does the closely allied *E. cruentus*), a redescription of the species is desirable.

Eleutherodactylus latidiscus (Boulenger)

Figure 3

Hylodes latidiscus Boulenger, 1898:121.

Both syntypes of *Hylodes latidiscus* (BMNH 98.4.28.108–09, re-registered as 1947.2.15.66–67) are adult females from "Cachabe ... Prov. Esmeraldas" (= Cachabí, 16 km SE Concepción, 200 m; Peters, 1955:339). Cochran and Goin (1970:416–417, Pl. 55) described BMNH 1947.2.15.67, whereas Boulenger (1898) used the other syntype as the basis for his description and illustration.

Diagnosis.—(1) Skin of dorsum tuberculate in males, shagreen with scattered tubercles in females, that of venter areolate; dorsolateral folds absent; (2) tympanum distinct, round, its length 22–43% eye length; (3) snout subacuminate to rounded in dorsal view, angularly rounded in lateral view; lips flared in larger females; canthus rostralis concave in males, less distinct in females; (4) interorbital space narrower than upper eyelid; cranial crests absent; subconical tubercle on upper eyelid; (5) vomerine odontophores elevated, triangular in outline; (6) males lacking vocal slits; males with glandular nuptial pad on thumb; (7) first finger slightly shorter than second; Digits II–IV bearing broad disks; (8) fingers bearing lateral fringes; (9) ulnar tubercles absent; (10) small tubercle on heel, thick tuberclelike fold on distal tarsus; (11) two metatarsal tubercles; inner oval, four times size of rounded outer; supernumerary plantar tubercles indistinct; (12) toes bearing lateral fringes, no webbing; toe disks broad, slightly smaller than those of fingers; (13) dorsal pattern polymorphic, usually with pale lines along outer edge of W-shaped occipital mark; venter white with some brown stippling; groin bearing pale area (no spots); posterior surfaces of thighs brown with small cream spots; (14) adults moderate sized, males

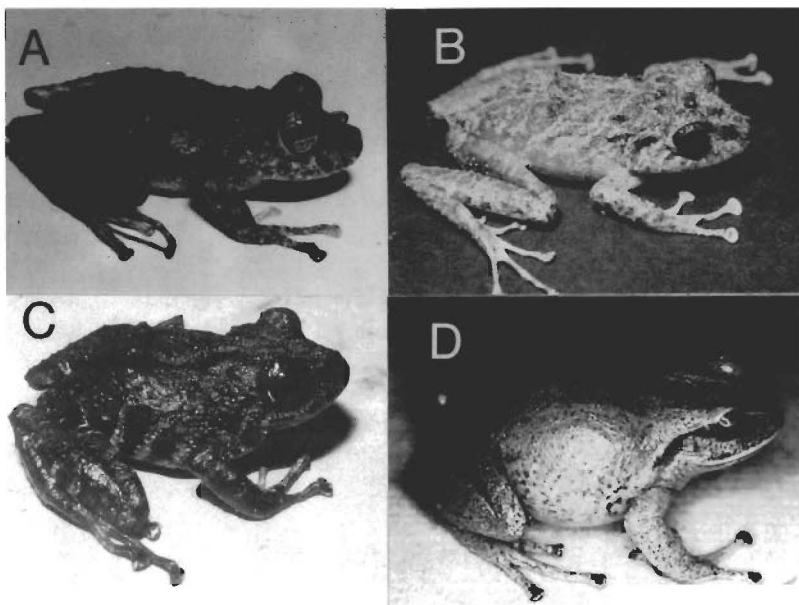


Fig. 3. A. *Eleutherodactylus hybotragus*, ICNMHN 13337, female, 36.5 mm SVL. B. *E. latidiscus*, ICNMHN 13340, female, 49.0 mm SVL. C. *E. tamsitti*, ICNMHN (JDL 17736), female, 50.5 mm SVL. D. *E. supernatis*, ICNMHN 8069, female, 42.6 mm SVL.

21.9–25.9 ($\bar{x} = 23.8 \pm 0.3$, $n = 16$) mm SVL, females 35.2–53.4 ($\bar{x} = 42.3 \pm 1.3$, $n = 14$) mm SVL.

Eleutherodactylus latidiscus is most like *E. cruentus*, but the two differ in that males of *E. cruentus* have pale spots edged with dark pigment in the groin and have concealed tympana. The tympanum is less prominent in female *E. cruentus* and is smaller than in *E. latidiscus*. The heel tubercle, tubercles along the outer edge of the tarsus, and ulnar tubercles are more prominent and larger in *E. cruentus* than in *E. latidiscus*. The dark pigment on the posterior surfaces of the thigh is darker with better definition of pale spots (if present) in *E. cruentus*.

Description.—(See Table 1 for proportions.) Head wider than body (except in gravid females), longer than wide; snout shape variable sexually and by size (Fig. 2)—Males: snout subacuminate in lateral view, angularly rounded (= nearly truncate) in lateral view; nostrils protuberant, directed dorsolaterally; canthus rostralis prominent, concave; loreal region concave, sloping abruptly to lips; lips not flared. Females, snout subacuminate to rounded in dorsal view, angularly rounded in lateral view; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis less distinct, straight to sinuous; loreal region concave, sloping gradually to flared lips.

Table 1. Proportions (as percents) of three species of *Eleutherodactylus*. First line gives range of values; second line gives mean \pm 1 SE.

Species	Sex	<i>n</i>	Tib/SVL	HW/SVL	Eyelid/IOD	Tymp/Eye	E-N/Eye
<i>E. latidiscus</i>	♂♂	16	46.8–54.7	35.4–40.2	96.0–145.8	22.0–42.9	66.7–106.4
			52.5 ± 0.6	37.6 ± 0.3	115.3 ± 3.9	35.1 ± 1.4	85.2 ± 2.5
	♀♀	22	44.7–55.8	36.9–43.3	81.1–117.8	26.7–38.3	91.7–113.3
<i>E. tamsitti</i>	♂♂	15	51.2 ± 0.7	40.3 ± 0.3	99.0 ± 2.2	33.1 ± 0.8	101.7 ± 1.4
			50.9–59.4	38.1–41.9	109.7–142.4	18.4–25.5	76.0–89.4
	♀♀	10	55.5 ± 0.6	39.7 ± 0.2	128.1 ± 2.8	20.4 ± 0.5	81.2 ± 1.1
			51.9–58.5	40.1–41.5	84.2–125.6	17.0–26.2	82.5–96.9
			55.3 ± 0.6	40.8 ± 0.2	111.0 ± 3.8	20.0 ± 0.9	89.8 ± 1.4
<i>E. permixtus</i>							
Departamentos Caldas and Tolima:	♂♂	28	47.0–53.6	37.4–41.0	66.7–100.0	25.0–41.4	79.5–106.4
			50.3 ± 0.3	38.9 ± 0.2	84.9 ± 1.6	33.5 ± 0.8	93.6 ± 1.2
Departamento Tolima:	♀♀	20	44.9–55.2	37.8–41.0	63.6–102.7	28.3–50.0	83.3–119.4
			51.4 ± 0.5	39.5 ± 0.2	78.7 ± 2.1	38.2 ± 1.1	103.4 ± 2.3
Departamento Caldas:	♀♀	20	43.3–53.7	37.5–42.8	65.8–105.0	28.8–45.0	89.8–120.0
			50.6 ± 0.5	39.8 ± 0.3	82.0 ± 2.5	38.0 ± 1.1	104.9 ± 2.5
Departamento Antioquia:	♂♂	17	43.4–50.0	37.8–40.8	67.7–114.8	29.4–44.1	85.7–106.4
			47.4 ± 0.5	39.1 ± 0.2	91.3 ± 3.2	37.0 ± 1.0	92.9 ± 1.7
	♀♀	25	42.6–54.9	36.1–41.6	59.6–111.1	39.1–54.4	90.7–125.0
			47.9 ± 0.6	39.3 ± 0.3	79.4 ± 2.2	45.1 ± 0.8	108.4 ± 1.8

Subconical tubercle on upper eyelid; IOD narrower than upper eyelid; in females, shallow interorbital furrow beginning at level of nasals, but edges of frontoparietals not upturned; supratympanic fold distinct, obscuring upper edge of tympanum. Tympanum shape variable—Males: tympanum round, separated from eye by distance equal tympanum length. Females: tympanum higher than long, separated from eye by distance twice tympanum length. Postrictal tubercles subconical, not prominent; choanae large, oval, longer than wide, not concealed by palatal shelf of maxillary arch when roof of mouth is viewed from directly above; vomerine odontophores median and posterior to choanae, triangular in largest individuals, but slanted and oval in smaller specimens, separated medially by distance equal to half width of odontophore, bearing from four or five teeth (males) to eight to eleven teeth (females) in transverse rows; tongue longer than wide, ovoid, posterior edge with shallow notch, posterior two fifths not adherent to floor of mouth; vocal slits absent in males.

Skin of dorsum tuberculate in males, largest tubercles on snout, between eyes, on folds of occipital W; in females, skin more shagreen with scattered tubercles (those of head nearly always present); dorsolateral folds absent; anal sheath absent; flanks smoother than dorsum (but nevertheless textured); venter areolate, but areolations shallow; discoidal fold prominent, well anteriad to groin; skin on undersides of limbs smooth, nearly smooth on upper surfaces of limbs.

Forearm lacking obvious ulnar tubercles; palmar tubercle bifid, much larger than oval thenar tubercle; numerous supernumerary palmar tubercles; subarticular tubercles round, not elevated; fingers bearing narrow lateral fringes (most obvious in larger females); disks of Fingers II–IV large, rounded at tips; those of III–IV 2.5–3 times width of digit below disk, of II about twice width of digit; disk of thumb about 1.5 times width of digit below disk; glandular nuptial pad atop thumb of males; first finger slightly shorter than second (tip of I reaching midway up disk of II when equally adpressed).

Small subconical tubercle on heel; even smaller tubercles evident along outer edge of tarsus; thick foldlike tubercle on inner edge of tarsus (distal sixth of tarsus); inner metatarsal tubercle three times as long as wide, outer metatarsal tubercle low, round, one-fourth size of inner; low supernumerary plantar tubercles; toes bearing lateral fringes, lacking webbing; subarticular tubercles round to slightly longer than wide; toes bearing large disks (only slightly smaller than those of fingers); fifth toe much longer than third when each is adpressed against fourth; tip of fifth toe reaches to distal edge of distal subarticular tubercle of Toe IV, whereas tip of third toe reaches just beyond distal border of penultimate subarticular tubercle of Toe IV; heels touching when flexed hind legs held at right angles to sagittal plane.

Color in preservative: Dorsal pattern often poorly developed, consisting of interorbital bar, pale lateral borders of brown occipital W, sacral chevron, supra-inguinal spots; flanks barred with oblique brown bars, palest towards groin; canthal-supratympanic stripe and labial bars present (no pale labial stripe); limb bars distinct, slightly oblique on shank, about as wide as interspaces; posterior surfaces of thighs brown with small cream spots; venter mostly white or cream with some brown stippling on throat (occasional individuals with dense stippling); undersides of limbs spotted with brown. In a common pattern variant, pale dorsolateral bands extending from tip of snout, along outer edge of eyelid, posteriorly to level of sacrum.

Color in life: Dorsum yellow with brown flecks and markings to brown with darker brown markings; occipital ridges pale green to cream; dorsolateral bands (if present) dull yellow, becoming orange-yellow posteriorly;

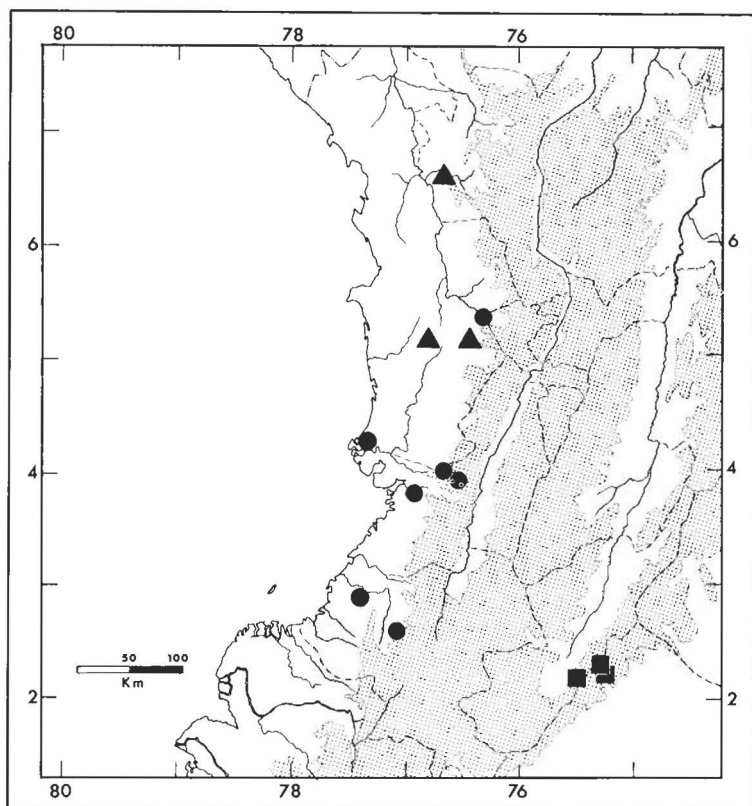


Fig. 4. Map of locality records in Colombia for *Eleutherodactylus cruentus* (▲), *E. latidiscus* (●), and *E. tamsitti* (■).

venter dirty yellow, pale gray, or white, usually mottled with gray or brown; lemon-yellow blotch in groin; posterior surfaces of thighs uniform brown, brown with yellow spots, blotched with brown, or black with yellow spots; iris pale to bright copper above, gray below, with reddish-brown horizontal streak, and flecked or reticulated with brown or black (JDL field notes, May 1983).

Cranium.—Although *Eleutherodactylus latidiscus* is judged too rare at present to allow preparation of skeletons, its cranium probably is similar to that of *E. cruentus*, which we suspect is its sister species. In *E. cruentus* (Fig. 5A–C), the nasals are narrowly separated and the frontoparietals cover the frontoparietal fontanelle except at its anterior edge. The frontoparietals are equally broad through the length of the orbit and are not fused to the preotics. No cranial crests are evident, even in large females. The alary processes of the premaxillae are directed dorsally. The palatal shelf of the premaxilla is broad and deeply dissected. The vomers are relatively narrow (i.e., not contacting one another). The cultriform process of the parasphenoid is relatively short (not reaching level of planum antorbitale) and does not taper to a point anteriorly; the parasphenoid alae are perpendicular to the cultriform process. The posterior end of the maxilla and quadratojugal are not deepened in lateral aspect. The zygomatic and otic rami of the squamosal are approximately equal in length and the otic plate is narrow. The most lateral portion of the crista parotica is cartilaginous.

Distribution.—*Eleutherodactylus latidiscus* is uncommon in collections; it occurs in lowland forests below 800 m in northwestern Ecuador and southwestern Colombia (Fig. 4). Too few specimens are available to argue convincingly that *E. latidiscus* is parapatric to *E. cruentus*, but the available data support that view. *Eleutherodactylus cruentus* is found in northwestern Colombia and probably is distributed across eastern Panama as well (*contra* Savage, 1981). Although no synapomorphy is known, *E. cruentus* and *E. latidiscus* seem to be each other's nearest relatives.

Eleutherodactylus latidiscus may vary geographically in size. Colombian females (Cauca, Valle del Cauca) between 40.2 and 47.9 mm SVL are gravid, but those 35.0–37.6 mm SVL are juveniles or young (some oviducal convolutions). Ecuadorian females (KU, MCZ) 35.2–38.6 mm SVL are gravid (but the largest gravid females, 49.7–53.4 mm SVL, come from the Ecuadorian coast). Too few males are available to verify that the size trends follow for males as well as females.

Remarks.—Although *Eleutherodactylus latidiscus* is a primary focus of this paper, its relationships are not obvious at present. It seems clear that it is allied closely with *E. cruentus*, but we are reluctant to suggest which other species are near relatives of this pair until better collections are available for the Pacific versant of the Cordillera Occidental and from the

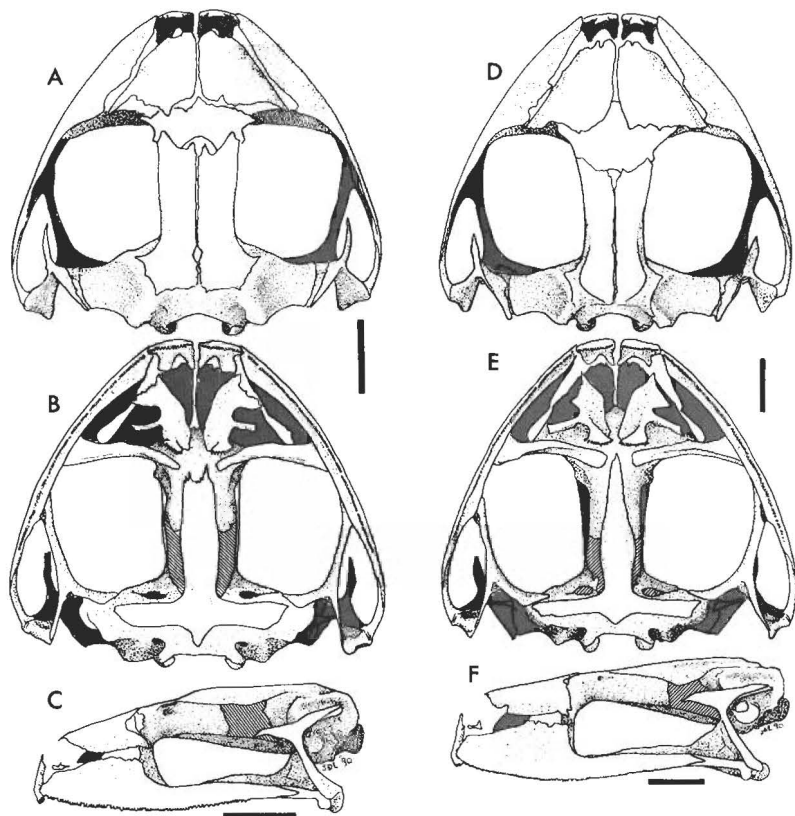


Fig. 5. Crania of (A–C) *Eleutherodactylus cruentus* (KU 103297, female, 35.9 mm SVL) and (D–F) *E. tamsitti* (ICNMHN 23638, female, 48.9 mm SVL). Scales = 3 mm.

Cordillera Central, or until more taxa have been surveyed osteologically. Herein, we place this pair of species in an undiagnosed species group taking the oldest name (*Eleutherodactylus cruentus* Group). Although Savage (1981) discussed *E. cerasinus*, *E. cruentus*, and *E. ridens* as three easily confused frogs, we do not think that these three are members of the same species group. We view *E. cruentus* and *E. ridens* as closely related, but think that *E. cerasinus* is allied to several species found in the northern Andes.

THE MONTANE (ANDEAN) SPECIES

Cochran and Goin (1970) named a subspecies of *Eleutherodactylus latidiscus* on the basis of a single female from a cloud-forest locality along the frontier between the departamentos of Caquetá and Huila. Although

Lynch (1976a) treated the taxon as a species in 1976, it was not until 1989 that additional material of the species was acquired from cloud-forest localities on the eastern flank of the Cordillera Oriental of Colombia in Departamento Caquetá. *Eleutherodactylus tamsitti* is distinct from *E. latidiscus* and probably is not closely allied to it. (They are placed in separate species groups.)

Eleutherodactylus tamsitti Cochran and Goin

Figure 3

Eleutherodactylus latidiscus tamsitti Cochran and Goin, 1970:418.—Holotype: FMNH 69735, an adult female from near San Adolfo along Río Suaza, Municipio Acevedo, Departamento Huila, Colombia, 1400 m. *Eleutherodactylus tamsitti*—Lynch, 1976a:17.

Diagnosis.—(1) Skin of dorsum tuberculate, that of venter areolate; dorsolateral folds absent; (2) tympanum depressed, its length 17–26% that of eye; (3) snout subacuminate (males) to round (females) in dorsal view, round in profile; lips not flared; canthus rostralis weakly concave; (4) interorbital space narrower than upper eyelid; cranial crests absent; one or two subconical tubercles on upper eyelid; (5) vomerine odontophores elevated, subtriangular in outline; (6) males lacking vocal slits; males with glandular nuptial pads on thumbs; (7) first finger slightly shorter than second; broad disks on Digits II–IV; (8) fingers bearing lateral keels; (9) small ulnar tubercles present; (10) large tubercle on heel, small tubercles on outer edge of tarsus; short, thick fold on inner edge of tarsus (distal); (11) two metatarsal tubercles; inner oval, about eight times size of round outer; low supernumerary tubercles at bases of Toes II–IV; (12) toes bearing narrow lateral fringes, coalescing at bases of toes; toe disks smaller than those of fingers; (13) dorsum gray with dark brown markings, tubercles and occipital folds edged with rust; no canthal stripe; narrow labial stripe; throat and chest pale, venter off-white, heavily marbled with black; posterior surfaces of thighs black with white spots; (14) adults moderate sized, males 32.7–37.8 (\bar{x} = 35.3 \pm 0.4, n = 14) mm SVL, females 47.5–54.7 (\bar{x} = 49.9 \pm 0.8, n = 9) mm SVL.

In coloration, *Eleutherodactylus tamsitti* resembles *E. cremnobates* Lynch and Duellman. The two species share a peculiar feature of ventral coloration (probably a synapomorphy); in each, the throat is pale in preserved specimens with a feeble reticulum, whereas the venter is heavily spotted or marbled (*E. cremnobates*) or reticulated (*E. tamsitti*). The paler throat and darker venter are separated by a diffuse to prominent line of brown pigment extending from just anterior to the forearm insertion posteromedially to the area above the sternum. The throat of *E. cremnobates* is dull yellow in life, whereas in *E. tamsitti*, it is orange to salmon.

Eleutherodactylus tamsitti is distinguished from *E. cremnobates* because it has nuptial pads in males (none in *E. cremnobates*), more tuberculate skin of the dorsum, larger heel tubercle, is larger in size (*E. cremnobates* males 28.4–32.5 mm, females 41.6–51.7 mm SVL), and has bold black and bright yellow markings on the concealed surfaces of the limbs (brown with cream flecks in *E. cremnobates*). Last, *E. cremnobates* has a longer snout than does *E. tamsitti*. *Eleutherodactylus tamsitti* is easily differentiated from *E. latidiscus* using the morphology of the hands (Fig. 1). In *E. tamsitti*, the digital discs are narrower than in *E. latidiscus* and the thumb is obviously shorter than in *E. latidiscus*.

Description.—(See Table 1 for proportions.) Head as wide as body, as long as wide; snout round to subacuminate in dorsal view, rounded in lateral profile; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis weakly concave, edge not sharp; loreal region concave, sloping abruptly to lips; lips not flared; numerous small tubercles on upper eyelid, plus one or two larger, subconical tubercles on posterolateral edge of eyelid; cranial crests absent; supratympanic fold obscured by tubercles, obscuring upper and posterior edge of tympanum; postriatal tubercles not prominent, conical; tympanum in cavity, annulus distinct along anterior and ventral borders, separated from eye by distance equal to twice length of tympanum; choanae moderate sized, 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, each about 1.5 times size of a choana, oval to subtriangular in outline, separated on midline by distance equal to 25–33% odontophore width in larger females, each bearing a transverse row of eight or nine teeth; vocal slits absent in males.

Skin of dorsum bearing many close-set, subconical warts, those on flanks becoming flatter (skin nearly smooth on posterior flank surfaces); limbs less tuberculate than dorsum; skin of throat smooth, of venter areolate; discoidal folds well anterior to groin; anal sheath absent; four ulnar tubercles, antebrachial best developed; palmar tubercle bifid, twice size of oval thenar tubercle; numerous small, low, supernumerary palmar tubercles; subarticular tubercles round, nonconical; fingers bearing lateral keels; disks dilated on all digits, disks of outer fingers truncate in outline, of thumb round; disks of Fingers III–IV 2.5–3 times width of digit below disk, of II about twice width of digit, of thumb about 1.5 times width; circumferential grooves complete about pads, pads broader than long; tip of I reaches to base of disc of II when inner fingers equally adpressed (Fig. 1); white glandular nuptial pad on top of I (approximately above joint between metacarpal and phalanges) in males.

Large subconical tubercle on heel; two or three tubercles along outer edge of tarsus; short, thick, inner tarsal fold on distal fifth of tarsus; inner

metatarsal tubercle 2.5 times as long as wide; outer metatarsal tubercle round, subconical, one-eighth size of inner; low supernumerary plantar tubercles at bases of Toes II–IV; toes with narrow lateral fringes, coalescing at bases of toes as “webbing”; toe “webbing” does not incorporate basal subarticular tubercles except on Toes IV–V; pads and discs of toes like those of hand, but smaller; toes long, slender; fifth toe much longer than third when each is adpressed against fourth; tip of fifth toe reaches to distal edge of distal subarticular tubercle of Toe IV, whereas tip of third toe reaches just beyond distal border of penultimate subarticular tubercle of Toe IV; heels overlapping when flexed hind legs held perpendicular to sagittal plane.

Color in preservative: Dorsum gray with dark brown markings (chevrons, occipital W, interorbital bar, snout bar) narrowly separated by creamy gray; many warts are reddish brown giving rusty cast to dorsum; folds (or series of tubercles) forming occipital W usually rust-red; snout bar extends onto lip as first labial bar; three or four labial bars; canthal stripe absent; edge of upper lip bearing narrow, orange labial stripe (lip stripe developing ontogenetically); shank bars reddish brown, transverse, broader than interspaces; three or four bars across thighs; edges of thigh bars sometimes outlined with white (extending up from concealed surfaces of thighs); throat washed orange with indistinct reticulum; paler throat area extends onto breast and undersides of arms, bordered posteriorly by incomplete brown line; venter off-white with heavy black reticulum (extending onto flanks and anterior surfaces of thighs); ventral surfaces of thighs gray-brown with darker brown mottling; ventral surfaces of shank, tarsus black with white bands (or rows of white spots); posterior surfaces of thighs black with white spots; posterior flank, anterior surfaces of thighs reticulated black and white (or black with large white spots); vague slanted bars on flanks. Smallest specimens having gray venters (no black reticulation, throat not pale) appear distinctive because the black and white reticulum is confined to the flanks, concealed surfaces of shanks, and anterior and posterior surfaces of the thighs.

Color in life: Dorsal surfaces brown with dark brown or black markings; bold black bands across tops of thighs, usually outlined in yellow; labial stripe salmon; throat and inner digits salmon; venter marbled black on dirty cream or yellow ground color; black and yellow marbling in groin, concealed surfaces of limbs; iris dark chocolate-brown. Juveniles have black throats with tiny white flecks; concealed limb surfaces banded black and white; venter dark with darker mottling; labial stripe absent.

Cranium.—The nasals are narrowly separated in *Eleutherodactylus tamsitti*, although the separation is greater on the posterior third (Fig. 5E, F). The frontoparietals effectively cover the fontanelle and are slightly narrower at midorbit than elsewhere. The frontoparietals do not extend so

far forward as in *E. cruentus* and, therefore, expose a larger expanse of the sphenethmoid. The sphenethmoid is more extensively ossified than in *E. cruentus*. Low ridges are evident posteriorly on the frontoparietals, but these are not so large as to be considered cranial crests. The median portions of the neopalatines are spatulate in contrast to the condition in *E. cruentus*. The cultriform process of the parasphenoid is long, lanceolate anteriorly, and extends to the level of the planum antorbitale. The parasphenoid alae of *E. tamsitti* are more slender than those of *E. cruentus* (Fig. 5). The otic plate of the otic ramus of the squamosal is better developed than that of *E. cruentus*.

The cranium of *Eleutherodactylus tamsitti* is very similar to that of *E. cremnobates*, but the latter has a thin zygomatic ramus of the squamosal, shorter cultriform process of the parasphenoid, and the vomers are stockier. (The odontophores are not so close to the neopalatines as those of *E. tamsitti*.)

Distribution.—The type locality of *Eleutherodactylus tamsitti* is in the headwaters of the Río Magdalena Drainage, but all recently collected material has come from moderate to intermediate elevations (1350–2040 m) on the eastern slopes of the Cordillera Occidental in extreme western Departamento Caquetá, Colombia (Fig. 4). Individuals are relatively common, being found at night perched on twigs and broad leaves along the margins of small streams and in the spray zones of waterfalls.

Remarks.—In describing *Eleutherodactylus cremnobates*, Lynch and Duellman (1980) did not compare it to *E. tamsitti*, but instead, to a taxon described below as *E. labiosus*. Their comments about the similarities and differences between *E. cruentus* and *E. tamsitti* actually concern *E. latidiscus* and *E. tamsitti*. *Eleutherodactylus cremnobates* occurs on the eastern slopes of the Ecuadorian Andes (Prov. Napo) at 1410–1700 m and *E. tamsitti* occurs at comparable elevations (1350–2040 m) some 300 km to the northeast. Collections along the Colombian-Ecuadorian frontier (Santa Bárbara Road), as well as above Mocoa (Depto. Putumayo), Colombia, in this altitudinal band did not reveal either species (or an equivalent).

When Lynch (1980) named *Eleutherodactylus supernatis*, he included specimens from the departamentos of Antioquia, Caldas, and Tolima of Colombia, and noted that the Colombian specimens are larger and have with slightly different proportions and a different color pattern on the concealed surfaces of the limbs. During fieldwork in 1980, many *E. supernatis* were collected in the departamentos of Cauca and Huila in southern Colombia. These specimens do not differ from topotypic material in any significant way.

Beginning in 1981, we had the opportunity to collect and observe frogs from the northern populations. At that time, we expected a transition between the distinctive northern populations and those from southern Colombia and northern Ecuador. Fieldwork during the past decade has

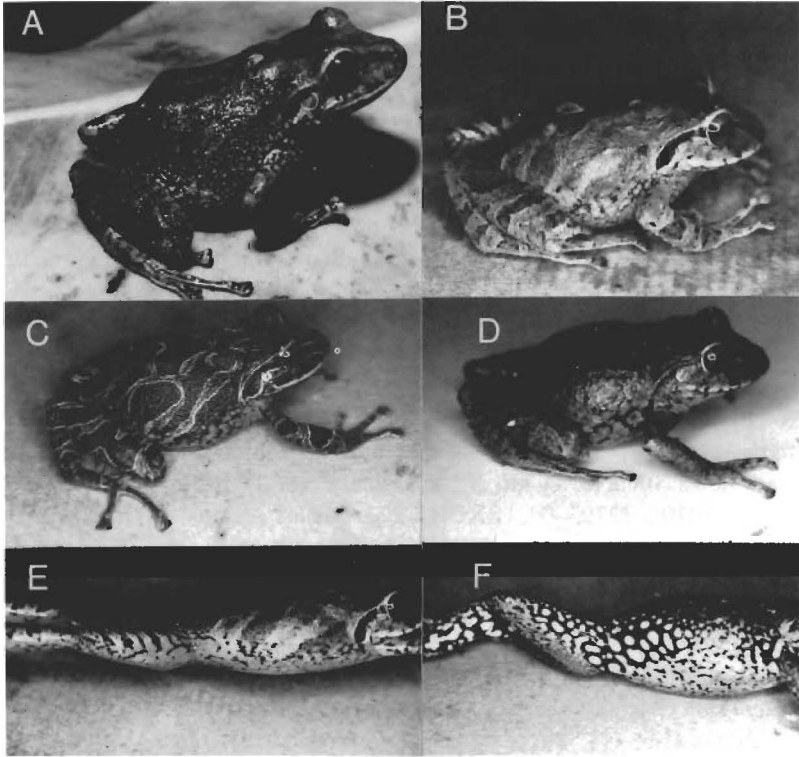


Fig. 6. *Eleutherodactylus permixtus*. A. ICNMHN 23334, female, 44.6 mm SVL. B. ICNMHN 8798, female, 35.0 mm SVL. C. ICNMHN 8861, female, 41.4 mm SVL. D. ICNMHN 8908, female, 34.3 mm SVL. E. ICNMHN 8798. F. ICNMHN 8907, female, 40.4 mm SVL.

permitted definition of distributions and the discovery that Lynch's assignment of material from the northern Cordillera Central (and adjacent Cordillera Occidental) to *E. supernatis* is in error.

The northern populations are most easily distinguished from the southern populations (traits for *Eleutherodactylus supernatis* in parentheses) in having white testes (black), no nuptial pad in males (glandular nuptial pads in males), and in lacking cranial crests (low crests present, best developed in females). (Rivero and Serna [1987:391] first called attention to the absence of cranial crests in Antioquian specimens.) Each species has (1) a labial stripe; (2) a dark reticulation enclosing pale spots in the groin and on the concealed surfaces of the thighs; (3) a small (nonconical or subconical) tubercle on each eyelid and the heel; and (4) absence of vocal slits in the males. Superficially, they are quite similar and may be each other's nearest relative; however, they do not share a known exclusive synapomorphy.

Eleutherodactylus permixtus sp. nov.

Figure 6

Eleutherodactylus latidiscus latidiscus (part)—Cochran and Goin, 1970:416–18.

Eleutherodactylus supernatis (part)—Lynch, 1980:415–417.

Holotype.—ICNMHN 8798, one of a series collected between “El Silencio” and “El Rancho” along the Río Combeima, corregimiento Inspección de Policía Las Juntas, Municipio Ibagué, Departamento de Tolima, Colombia, 2400–2650 m, on 26 May 1981 by P. Bernal, J. Lynch, V. Rueda, and P. Ruíz.

Paratypes.—(178) ICNMHN 8799–802, 8804–11, 8813–28 (topotypes), 22618–21, 22628–50, 22660–77, 22680–87, “EXCHANGE” females (topotypes collected between 2590–2700 m); ICNMHN 8849–59, Casa de El Silencio, 11 km N Las Juntas, 2600 m; ICNMHN 22688–89, 22693, 22700, 22703–04, “EXCHANGE” males, arriba de El Silencio por carretera, 2830–2980 m; ICNMHN 8829–42, 8845–46, arriba de El Silencio, Río Combeima, 2800–2820 m; ICNMHN 8861–62, 8864–65, 8867–75, 8877, 8879, 8886, 8895, 22591–600, Departamento Tolima, Municipio Cajamarca, “La Linea,” Km 109–113, carretera Cajamarca a Calarcá, 3040–3300 m; ICNMHN 22601–15, Departamento Tolima, Municipio Cajamarca, corregimiento Anaime, 3480 m.

Diagnosis.—(1) Skin of dorsum very finely shagreen (coarser on lower back), of venter areolate; dorsolateral folds absent; (2) tympanum distinct, superficial, its length 25–50% eye length; (3) snout subacuminate in dorsal view, rounded in lateral profile; canthus rostralis sharp; (4) IOD broader than upper eyelid; cranial crests and furrow absent; one or two nonconical tubercles on upper eyelid; (5) vomerine odontophores oblique and oval; (6) males lacking vocal slits and nuptial pads; (7) first finger slightly shorter than second; Digits II–IV bearing moderate sized disks; (8) fingers bearing lateral keels; (9) antebrachial tubercle prominent; (10) nonconical tubercle on heel; indistinct outer tarsal tubercles; thickened tubercle on inner edge of tarsus; (11) two metatarsal tubercles, inner oval, about four times size of round outer tubercle; numerous supernumerary plantar tubercles; (12) toes bearing lateral keels, no webbing; disks of toes smaller than those of fingers; (13) dorsal pattern polymorphic (see below); dorsum pale brown with brown markings; facial markings distinct, dark; cream labial stripe; venter cream with few brown flecks to reticulated with brown; groin and posterior surfaces of thighs cream with brown reticulum to black with small white spots (geographically variable, see below); (14) adults moderate sized, males (southern) 21.9–30.5 mm (\bar{x} = 25.4 \pm 0.5, n = 28) or males (Antioquia) 23.2–31.4 mm (\bar{x} = 26.7 \pm 0.5, n = 17), females (southern)

32.4–42.1 mm ($\bar{x} = 37.3 \pm 0.5$, $n = 40$) or females (Antioquia) 34.3–45.4 mm ($\bar{x} = 39.7 \pm 0.6$, $n = 30$).

Eleutherodactylus permixtus is most similar to *E. supernatis* (with which Lynch confused it in 1980), but it differs in lacking cranial crests and a frontoparietal furrow (thin crests [upturned edges of frontoparietals] and shallow furrow), in having white testes (black) and in lacking nuptial pads (present), and in having feebly developed outer tarsal tubercles (absent).

Description.—(See Table 1 for proportions.) Head as wide as body, longer than wide; snout acuminate to subacuminate in dorsal view, rounded in lateral profile; nostrils directed dorsolaterally, weakly protuberant; canthus rostralis sharp, feebly concave; loreal region concave, sloping abruptly to lips; lips not flared; cranial crests absent, edges of frontoparietals of largest females not upturned; supratympanic fold thick, obscuring uppermost edge of tympanum; tympanum superficial, annulus distinct, round to slightly higher than long, separated from eye by distance equal 1.5 times length of tympanum; postrictal tubercles small; choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posteriad to choanae, oval, each only slightly larger than a choana, separated on midline by distance equal to one odontophore width, bearing two to four teeth in adult females; in males, odontophores more oblique, median separation 1.5–2 times odontophore breadth, bearing one to three teeth; tongue slightly longer than wide, posterior half not adherent to floor of mouth, posterior edge bearing shallow notch; vocal slits absent in males.

Skin of dorsum nearly smooth on top of head and anterior back, becoming finely shagreen and more coarse on lower back, with occasional round tubercles on upper flank; skin of upper surfaces of limbs smooth; skin of lower flanks and venter coarsely areolate; no dorsolateral folds or ridges; skin of side of head smooth; discoidal folds well anteriad to groin; no anal sheath; antebrachial tubercle prominent; sometimes one or two smaller ulnar tubercles; palmar tubercle bifid, twice size of oval thenar tubercle; numerous supernumerary palmar tubercles; subarticular tubercles round, subconical; fingers bearing lateral keels; disks on Fingers II–IV much broader than digit below disk (of III–IV, twice as wide); all digits bearing ventral pads (broader than long); first finger slightly shorter than second (Fig. 1); thumb of male swollen but no nuptial pad evident.

Nonconical tubercle on heel; indistinct tubercles along outer edge of tarsus; inner edge of tarsus bearing thickened tubercle or short fold immediately proximal to inner metatarsal tubercle; inner metatarsal tubercle 2.5 times as long as wide, about four times size of round outer; numerous supernumerary plantar tubercles, largest at bases of Toes II–IV; toes with lateral keels (no fringes), no webbing; toe disks smaller than those of fingers; subarticular tubercles round, subconical; fifth toe much longer than

third when each is adpressed against fourth; tip of fifth toe reaches to distal edge of distal subarticular tubercle of Toe IV, whereas tip of third toe reaches just beyond distal border of penultimate subarticular tubercle of Toe IV; heel of adpressed hind limb reaches to just in front of eye; heels overlapping when flexed hind legs held at right angles to sagittal plane.

Color in preservative: Dorsum pale brown to dark gray-brown with brown to reddish-brown markings (viz., interorbital bar, sacral chevron, suprascapular lines, blotch above coccyx, all of which may anastomose into a complex figure); frequently with a pale (cream to silver) spot (edged with black) on midline at level of arms; dark markings on dorsal surfaces usually edged with cream halos, the most constantly so marked is a cream line across the anterior edge of interorbital bar; snout usually paler than dorsum and bearing pale brown snout spot; canthal-supratympanic stripe dark brown (edged with cream); only traces of labial bars evident; cream labial stripe; venter cream with few to many brown flecks, sometimes forming loose reticulation; fewest flecks on throat, undersides of legs; axilla, groin, anterior (Fig. 6) and posterior surfaces of thighs, ventral surface of shank bearing black reticulum (an open reticulum, "enclosing" large pale "spots"); posterior surfaces of thighs black with pale spots (as large as disks of thumb); anal triangle poorly developed; limb bands complete, narrower than interspaces, edged with cream, those on shanks slightly oblique; black bands on tops of thighs continuous with black field on posterior surfaces of thighs.

Specimens from Antioquia have the black field in the axilla, groin, on the anterior and posterior surfaces of the thighs, and concealed shanks enclosing small white spots (mostly smaller than disk of thumb); in females from these populations, the field is blackest and the spots are smallest (Fig. 6). A few specimens having the "open reticulum" in the groin and concealed limb surfaces occur as far north as Medellín, but most specimens from every locality in the Cordillera Central from Antioquia have small white spots on a black field.

Color in life: Departamentos Caldas and Tolima.—Dorsum tan, reddish brown, or brown with brown or nearly black markings; labial stripe cream-yellow to bronze; throat and venter cream to dull yellow-cream (rarely gray), throat flecked with brown or all ventral surfaces reticulated with brown; groin and posterior surfaces of thighs orange with black reticulation in females; axilla of large females orange; in most males, these surfaces are orange-yellow with brown flecks (sometimes boldly reticulated); iris bright copper with few brown flecks (or reticulations) and brown horizontal streak (JDL field notes, May 1981, June 1984). Departamento Antioquia.—Males: dorsum brown, tan, or olive with brown markings; venter yellow with pale orange or brown markings to a dirty cream without markings; reddish-orange line demarking upper area of posterior surfaces of thighs

and groin; below that, black fading to gray with cream spots; some black marbling along lower flanks; iris dark rusty copper with black flecks and brown streak (to almost orange-brown with flecks and streak). Females: mostly brown (pale to dark) above; venter dirty cream with black flecks (some with yellow wash to venter); black with white spots in axilla, groin, and concealed surfaces of hind limbs; iris bright copper with black reticulum and brown horizontal streak (JDL field notes, 6 June 1981). At other localities, males have red or yellow spots in the groin and on the concealed surfaces of the thighs, but females have white spots except when venter is red or orange, in which case, the lowermost spots are red or yellow (JDL field notes, 8–9 June 1981).

Cranium.—The nasal bones are narrowly separated medially along their anterior halves (Fig. 10, left) and more widely separated posteriorly.

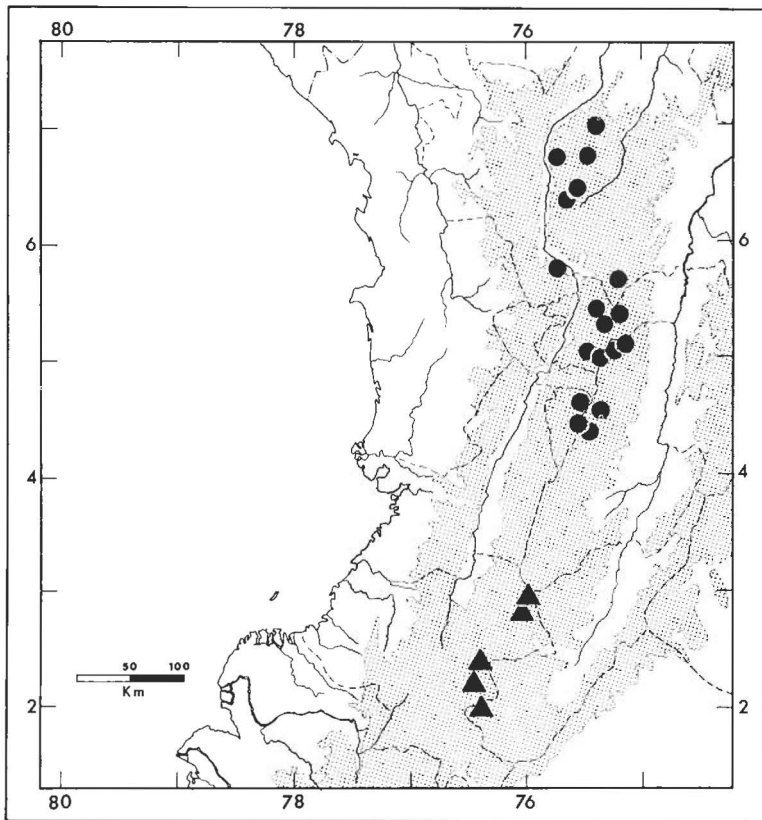


Fig. 7. Map of locality records in Colombia of *Eleutherodactylus permixtus* (●) and *E. supernatis* (▲).

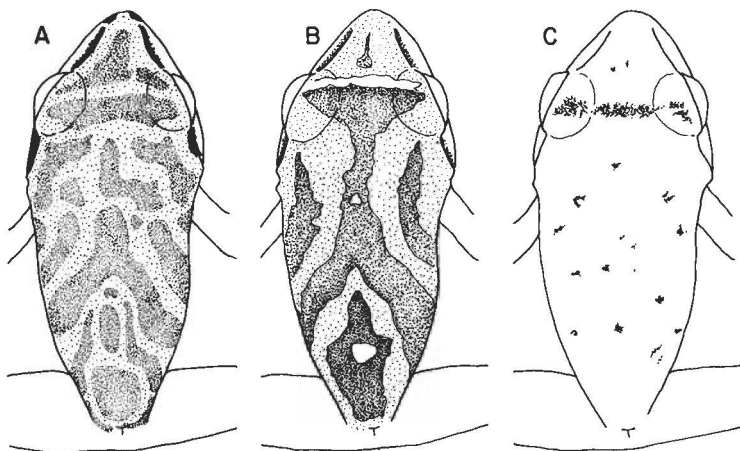


Fig. 8. Pattern polymorphism in *Eleutherodactylus permixtus*. A. Mottled, ICNMHN 22599. B. Mottled, ICNMHN 22691. C. Brown flecks, ICNMHN 22665.

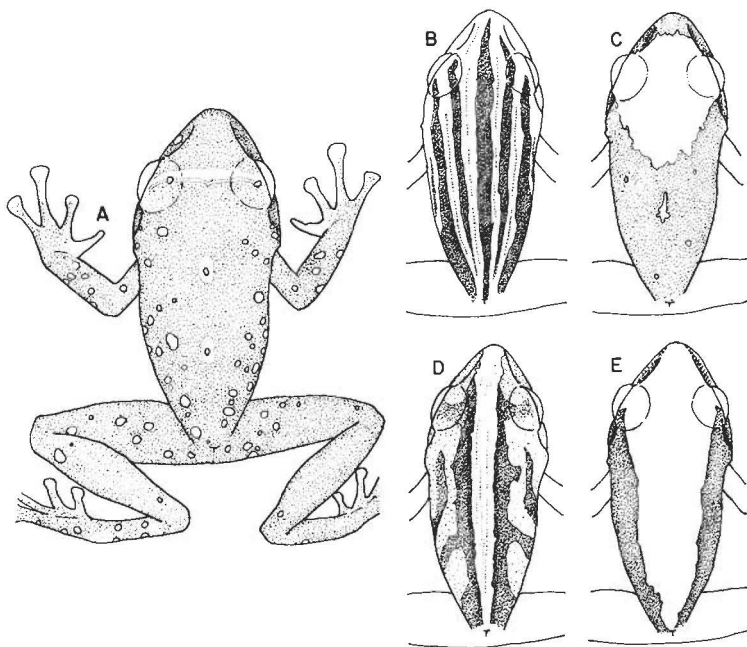


Fig. 9. Pattern polymorphism in *Eleutherodactylus permixtus*. A. Yellow flecks, ICNMHN 22621. B. Lineate, ICNMHN 22612. C. Silver cap, ICNMHN 4279. D. Median raphe, ICNMHN 22650. E. Dorsosconcolor, ICNMHN 18813.

The frontoparietal fontanelle is covered completely, and the nasals and frontoparietals separated only moderately. The frontoparietals are slightly broader anteriorly than at midorbit and lack crests. The alary processes of the premaxillae are directed dorsally and the palatal shelf is dissected deeply. The vomers are elongate (comparable to those of *E. tamsitti*; see Fig. 5). The neopalatines are narrow medially. The cultriform process of the parasphenoid is short (not reaching level of planum antorbitale), blunt anteriorly, and tapers anteriorly. The alary processes are deflected slightly posteriorly (not perpendicular to cultriform process) and distally are expanded slightly. The zygomatic ramus of the squamosal is thick and slightly shorter than the otic ramus. The otic plate is well developed.

Eleutherodactylus supernatis (Fig. 10, right) differs in the form of the nasals (not widely separated posteriorly), frontoparietals (bearing crests, borders parallel through orbit), separation of frontoparietals and nasals (less widely separated), vomers (dentigerous processes overlies neopalatines), parasphenoid (cultriform process pointed anteriorly, reaching to level of planum antorbitale, alary processes more expanded distally), and squamosal (zygomatic ramus larger and otic plate larger).

Measurements of holotype in mm.—SVL 33.2; tibia 18.2; HW 13.6; HL 12.7; chord HL 13.7; eyelid 2.7; IOD 3.8; tympanum 1.3; eye 3.9; E-N 4.2.

Etymology.—Latin, *per* (very) + *mixtus* (mixed), in reference to the confusion that has surrounded this common frog.

Distribution.—*Eleutherodactylus permixtus* is found in upper cloud forest and subpáramo (2400–3700 m) of the Cordillera Central of Colombia south to the southern edge of the Los Nevados district and on at least the eastern slopes of the northern portion of the Cordillera Occidental (Fig. 7). These frogs are abundant by day beneath rocks and logs. At night, individuals are found on low vegetation and the ground where males call.

The record from Jericó, Antioquia (MCZ 24896–97), is the only record of the species from the Cordillera Occidental. While there are species of *Eleutherodactylus* in common with the two cordilleras (Lynch, 1992), this record requires verification because the habitats in the vicinity of Jericó are dissimilar to those where *E. permixtus* is found.

The MLS record for Municipio Remedios (Antioquia) is not plotted. Finca El Amparo is in the lowlands and we suspect that the locality data were confounded either by the collector or by personnel at the Museo La Salle.

Variation.—As is in many species of *Eleutherodactylus*, *E. permixtus* is pattern polymorphic (Figs. 8–9). Most individuals bear a mottled or spotted pattern (Fig. 8A–B), which may be simplified by fusion (Fig. 8 B). Most mottled frogs have white outlines to some of the dark markings and may have a chalky white spot (or blotch) on the lower back. The mottled pattern

accounts for three fourths of all individuals, but in most populations, it is exhibited by 66–90% (Table 2). The population found on the Serranía de Sonsón is distinctive in that only 34% of the individuals possess the mottled morph.

On the Serranía de Sonsón, 56% of the individuals have a reduced pattern of dark flecks on a brown ground color (Fig. 8C). This morph is found throughout the distribution of *E. permixtus*, but usually is uncommon (1–8%).

A lineate pattern (Fig. 9B) is uncommon overall, but can be locally abundant (23% at Ucumarí, Depto. Risaralda). The equally distinctive median raphe (Fig. 9D) is only about half as common. The remaining morphs are rare. The yellow-flecks morph (brown with yellow flecks Fig. 9A), the yellow-tan morph (uniform color), and the silver cap morph (Fig. 9C) occur in 1–2% of the individuals and their rarity probably explains why some are not found in some populations (the silver cap morph excepted). A dorsoconcolor morph (Fig. 9E) is found in several species of *Eleutherodactylus*, but is the rarest morph in *E. permixtus*.

The Cajamarca, Letras, and Nevado Tolima localities are narrowly separated and represent three entry points into what is surely a contiguous habitat band. If we consider these entry points as samples drawn from a single population, Cajamarca has fewer than expected lineate frogs, whereas Letras has more than expected. Nevado Tolima has fewer brown flecks frogs and more yellow-tan frogs than expected. Otherwise, these three localities appear to be different samplings of the same population.

Remarks.—*Eleutherodactylus cremnobates*, *E. permixtus*, *E. supernatis*, and *E. tamsitti* are assigned here to the *Eleutherodactylus devillei* group recognized by Flores (1988) and Lynch (1983). Flores' (1988) assignment of *E. alberchi* to this group is in error and will be addressed in a forthcoming study of the *Eleutherodactylus* of western Ecuador (Lynch and Duellman, in prep.). Lynch and Duellman (1980) proposed the group (as an assembly) and Lynch (1983) added a Colombian (*E. anolirex*) and a Venezuelan species (*E. briceni*) and Lynch (1984) another Colombian species (*E. spilogaster*) to the phenetic cluster. We concur with Flores that *E. thymalopsoides* is a member of the *devillei* group and suspect that several other taxa belong here as well.

As a working hypothesis, treating these 11 species as members of a single species group is an improvement to the current dispersement of these taxa, although no synapomorphy is available to support the conjecture. Within the group, *E. cremnobates* and *E. tamsitti* seem to be sister species because they share a synapomorphy (transverse line separating throat and venter coloration) as do *E. permixtus* and *E. supernatis*. All species are residents of intermediate-elevation cloud forests (ca. 2000–3400 m) except for *E. cremnobates* and *E. tamsitti*, which occur lower at 1400–2200 m.

Table 2. Pattern polymorphism in *Eleutherodactylus permixtus*. $n = 387$. Pattern morphs are identified using Figures 8 and 9.

Locality	Pattern								n
	8AB	8C	9A	9B	9C	9D	9E	Yellow-tan	
Medellín-Yarumal	36	2	0	1	2	0	0	0	41
Sonsón	14	23	1	0	0	2	1	0	41
Ucumarí	22	1	0	7	0	0	0	0	30
Letras	42	5	4	7	1	4	0	0	63
N. Tolima	126	2	3	9	0	6	0	4	150
Cajamarca	54	5	0	1	0	2	0	0	62

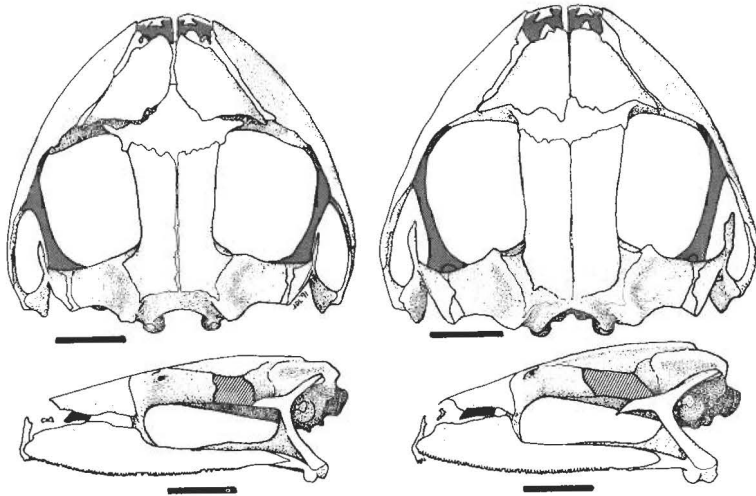


Fig. 10. Crania of *Eleutherodactylus permixtus* (left, ICNMHN 635) and *E. supernatis* (right, ICNMHN 8032). Scales = 3 mm.

THE *ELEUTHERODACTYLUS CERASINUS* SPECIES GROUP

We propose the recognition of a small species group, primarily distributed about the Andes of Colombia and Ecuador at moderate and low elevations. One species of the group, *E. cerasinus*, occurs in Middle America along the Atlantic versant of Nicaragua to central Panama and on the Pacific versant in central and western Panama at elevations between 40 and 1300 m (Savage, 1981). *Eleutherodactylus cerasinus* has not been treated monographically, but Savage's (1981) summary and Taylor's (1952) detailed description enable easy recognition. Nevertheless, we here provide a comparable diagnosis of *E. cerasinus*.

Eleutherodactylus cerasinus (Cope)

Diagnosis.—(1) Skin of dorsum very finely shagreen, bearing occipital folds, of venter areolate; dorsolateral folds absent; (2) tympanum superficial, its length 25.7–44.1% (\bar{x} = 38.0) eye length; (3) snout subacuminate in dorsal view, round in profile; canthus rostralis concave; upper lips flared, especially in adult females; (4) upper eyelid slightly narrower than IOD, lacking enlarged tubercles; cranial crests absent; (5) vomerine odontophores small, elevated, oval to triangular in outline (oblique in small individuals); (6) males with vocal slits, white glandular nuptial pads; (7) first finger slightly shorter than second; fingers with large disks, largest on II–IV; (8) lateral keels or fringes absent on fingers; (9) ulnar tubercles low, antibrachial largest; (10) conical tubercle on heel, smaller tubercles along outer edge of tarsus, inner edge of tarsus bearing tubercle or low fold of semi-separated tubercles; (11) two metatarsal tubercles, inner oval, two to three times size of outer; numerous supernumerary plantar tubercles; (12) toes not bearing lateral fringes, webbing absent; toe disks about as large as those of outer fingers; (13) dorsum variable, usually blotched; posterior surfaces of thighs uniform brown (red in life); venter cream, usually with brown flecks and vermiculations; (14) adults moderate sized, males 16.9–22.2 (\bar{x} = 19.8 \pm 0.3, n = 22) mm SVL, females 25.1–34.9 (\bar{x} = 29.7 \pm 0.5, n = 22) mm SVL.

Savage (1981) seems to have erred in reporting that this species lacks nuptial pads in males, because we find nuptial pads in all adult males from Costa Rica and Panama (KU). Taylor's (1952) description and Savage's (1981) summary of characteristics neglect to point out the presence of an inner tarsal tubercle in *Eleutherodactylus cerasinus*. *Eleutherodactylus cerasinus* usually is compared with *E. cruentus* (Savage, 1981) because the two species co-occur, sometimes have been confused with one another, and have similar coloration. However, we consider *E. cerasinus* to be the Central American representative of an otherwise Andean group. *Eleutherodactylus cerasinus* is easily distinguished from the Andean taxa because it is the smallest species and has an inner tarsal tubercle.

Over a 20-yr period, Lynch confused a broad-disked species found at low elevations in western Colombia and Ecuador with *E. latidiscus* (Boulenger). This species, described below as *E. labiosus*, has large digital disks, but lacks the lateral fringes found in *E. latidiscus* (and *E. cruentus*).

Two apparently closely related species have been described. Lynch (1976b) named *E. crenunguis* from Pichincha Province of Ecuador, and Lynch and Burrowes (1990) named *E. ocellatus* from Departamento Nariño, Colombia. The only other species having pervasive similarities are *E. cerasinus* (Cope) from lower Central America (Savage, 1981) and *E. rubicundus* (Jiménez de la Espada) from the eastern slopes of the Andes in

Table 3. Comparison of species of the *Eleutherodactylus cerasinus* Group.

Character	Species of <i>Eleutherodactylus</i>					
	<i>cerasinus</i>	<i>crenunguis</i>	<i>labiosus</i>	<i>ocellatus</i>	<i>orpacobates</i>	<i>rubicundus</i>
Eyelid tubercle	No	No	Yes	No	Yes	No
Heel tubercle	Yes	Yes	Yes	No	Yes	Yes
Vocal slits	Yes	Yes	Yes	?	No	No
Nuptial pad	Yes	No	No	?	Yes	No
Fingers I/II	Less	Greater	Less	Less	Less	Greater
Skin texture	Fine shagreen	Shagreen	Shagreen	Shagreen	Granular	Tuberculate
Male size	17–22	35–49	36–50	?	24–36	32–36
Female size	25–35	59–64	48–52	46	36–51	46–51

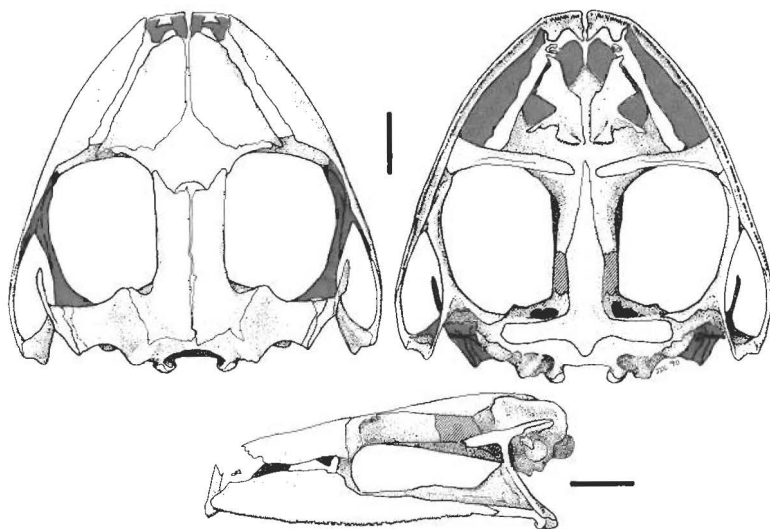


Fig. 11. Cranium of *Eleutherodactylus rubicundus*, KU 177452. Scales = 3 mm.

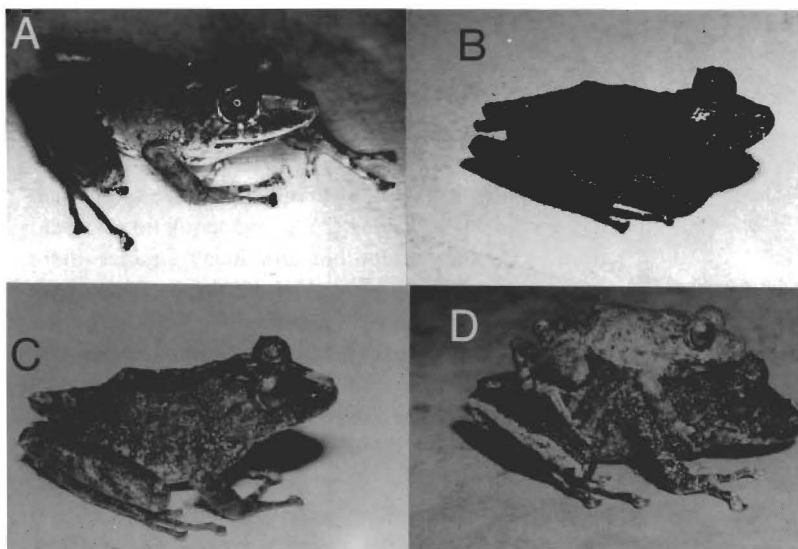


Fig. 12. *Eleutherodactylus labiosus* (A) KU 131612, holotype and (B) ICNMHN 13243, male, 36.0 mm SVL. *Eleutherodactylus orpacobates* (C) ICNMHN 20249, female, 43.9 mm SVL and (D) amplexant pair, ICNMHN (JDL 18805-06), female 47.2 mm SVL.

Ecuador (redescribed by Lynch and Duellman, 1980).

Eleutherodactylus cerasinus, *E. crenunguis*, *E. ocellatus*, *E. rubicundus*, the undescribed frog Lynch confused with *E. latidiscus*, and another species from western Colombia form a small phenetic group—a group that we consider to include the nearest relatives of all the taxa. These animals superficially resemble the large-disked *E. cruentus* and *E. latidiscus*, but have longer legs and lack lateral fringes on the digits. Aside from some slight differences in color, these animals differ from one another in terms of expression of eyelid and heel tubercles, shagreen versus tuberculate skin of the dorsum, presence of nuptial pads and vocal slits in males, and the lengths of the inner digits of the hand (Table 3). Osteologically, the species (aside from *E. ocellatus* which has not been studied) are very similar as well. The shapes and sizes of skull bones agree among the five species for which skeletal material has been prepared and are distinguishable (as a group) from the species once confused with *E. latidiscus* (*E. cruentus*, *E. permixtus*, *E. supernatis*, *E. tamsitti*).

Cranium.—(Based on *Eleutherodactylus rubicundus*) The nasals are long (Fig. 11) in comparison to those of *E. cruentus*, *E. permixtus*, *E. supernatis*, and *E. tamsitti*, and are closely juxtaposed along the anterior half to two thirds of their length. Posteriorly, the nasals are widely separated. The sphenethmoid is well ossified and extends well anterior beneath the nasals, reflecting the elongate snouts of species of this group. The frontoparietals are of equal width through the length of the orbit and nearly cover the frontoparietal fontanelle. No cranial crests are evident in large females. The crista paroticae are more slender than those seen in *E. permixtus* or *E. supernatis* (Fig. 10). The alary processes of the premaxillae are directed dorsally (with a slight posterior vector) and the palatal shelf is dissected moderately. The vomers are large and narrowly separated in their posterior half. The odontophores are well anterior of the neopalatines. The neopalatines are somewhat spatulate medially. The cultriform process is long, acuminate, and extends between the neopalatines. The alary processes are perpendicular to the cultriform process and are narrowly overlapped by the median rami of the pterygoids. The pars facialis of the maxilla is only moderately high, but the posterior end of the maxilla (and quadratojugal) are low. The zygomatic ramus of the squamosal is nearly as long as the otic ramus and relatively high. The otic plate is narrow.

Eleutherodactylus labiosus sp. nov.

Figure 12

Eleutherodactylus latidiscus—Lynch, 1979:502–03; Lynch and Duellman, 1980:23–24, 64; Lynch and Miyata, 1980:6, 11.

Holotype.—KU 131612, a juvenile (but see Remarks) female from La

Palma (junction of Highways 28 and 30), Provincia Pichincha, Ecuador, 920 m, obtained 8 August 1970 by John D. Lynch.

Paratypes.—ICNMHN 13242–43, Colombia, Departamento de Valle del Cauca, Municipio Restrepo, Vereda Alegre, Campo Las Vegas, 200 m, ICNMHN 13241, Vereda Alegre, Río Calima; AMNH 102759, MCZ 90049–50, Hotel Tinalandia, 15 km SE Santo Domingo de los Colorados, Provincia Pichincha, Ecuador, 800 m.

Diagnosis.—(1) Skin of dorsum shagreen, bearing low occipital folds, that of venter areolate; dorsolateral folds absent; (2) tympanum distinct, higher than long, its length 24–39% eye length; (3) snout subovoid in dorsal view, rounded in lateral profile; lips flared in adult females; canthus rostralis well defined, straight to weakly concave; (4) IOD narrower than upper eyelid; low cranial crests in adult females; conical tubercle on upper eyelid; (5) vomerine odontophores prominent, triangular in outline; (6) males with vocal slits, nuptial pads absent; (7) first finger slightly shorter than second; Fingers II–IV bearing broad discs; (8) fingers lacking lateral fringes; (9) ulnar tubercles absent; (10) small conical tubercle on heel, row of tubercles along outer edge of tarsus; (11) two metatarsal tubercles, inner oval, about four times size of rounded outer tubercle; supernumerary tubercles only at bases of toes; (12) lateral fringes and toe webbing absent; toes with broad discs, smaller than those of fingers; (13) brown above with darker markings; venter cream with brown reticulation; posterior surfaces of thighs dark brown with cream flecks; (14) adults moderate sized, males 35.4–50.8 ($\bar{x} = 44.3 \pm 1.6$, $n = 12$) mm, females 48.5–52.3 ($\bar{x} = 50.4$, $n = 2$) mm SVL.

Eleutherodactylus labiosus is most similar to *E. crenunguis*, but differs in having prominent tubercles on the upper eyelid and a shorter thumb.

Description.—Head as broad as body, slightly wider than long; HW 37.7–40.2% ($\bar{x} = 39.1 \pm 0.2$, $n = 12$) SVL in males, 36.7–41.4% ($\bar{x} = 39.3 \pm 0.4$, $n = 10$) in females; snout suboval in dorsal view, rounded in lateral profile, long; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis well defined, edge rounded, straight to weakly concave; loreal region concave, sloping to flared lips; E–N 85.4–116.4% ($\bar{x} = 100.3 \pm 2.4$, $n = 12$) eye length in males, 87.9–110.2% ($\bar{x} = 98.1 \pm 2.4$, $n = 10$) in females; large, sometimes conical tubercle on posterolateral part of upper eyelid (anterior end of occipital W); edges of frontoparietals upturned, producing shallow furrow; interorbital space broad; upper eyelid 91.1–137.9% ($\bar{x} = 119.7 \pm 13.6$, $n = 12$) IOD in males, 93.8–143.2% ($\bar{x} = 123.6 \pm 4.9$, $n = 10$) in females; supratympanic fold low; tympanum distinct, superficial, higher than long, separated from eye by 1.5 times its length; tympanum length 23.6–36.7% ($\bar{x} = 30.6 \pm 1.3$, $n = 12$) eye length in males, 25.0–38.8% ($\bar{x} = 31.1 \pm 1.2$, $n = 10$) in females; postrectal tubercles present, subconical, not prominent; choanae relatively small, longer than wide, not

concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, triangular in outline, each approximately twice size of a choana, separated medially by distance about one-sixth odontophore width, bearing a transverse row of 9–11 teeth; tongue longer than wide, its posterior border not notched, posterior one third to two fifths not adherent to floor of mouth; males with long vocal slits posterolateral to tongue.

Skin of dorsum shagreen (closely packed flattened granules), least evident on top of head and upper surfaces of limbs; low folds forming occipital **W**; apices of **W** extend anteriorly in form of **X**; dorsolateral folds absent, but low, indistinct folds beginning at posterior edge of head extending short distances down flanks; flanks shagreen above, becoming areolate near venter; discoidal folds well anterior to groin; venter finely areolate, throat more obviously areolate; skin below vent coarsely areolate; skin on undersides of limbs smooth; anal sheath absent; ulnar tubercles absent; palmar tubercle bifid, much larger than oval thenar tubercle; numerous low supernumerary palmar tubercles; subarticular tubercles elevated, round; no lateral keels on fingers; fingers long and slender bearing large expanded disks (disk of III–IV about 3 times widths of digits below disks, of I–II about twice); disks truncate with slight emargination; disk of third finger 1.75–2 times length of inner metatarsal tubercle; all disks bearing broad ventral pads; if Fingers I and II are adpressed equally, tip of I reaches two-thirds distance up the disk of II (inner two fingers approximately equal in length); nuptial pad absent on thumb of male.

Small conical tubercle on heel; row of up to five smaller nonconical tubercles along outer edge of tarsus; folds and tubercles absent on inner edge of tarsus; inner metatarsal tubercle slightly more than twice as long as wide, outer metatarsal tubercle round, not elevated, about 25% size of inner; supernumerary plantar tubercles at bases of Toes II–IV; subarticular tubercles round, elevated, nonconical; toes with slight lateral keels, no webbing; disks and pads broad, smaller than those of fingers; fifth toe slightly longer than third toe when each is adpressed against fourth; tip of fifth toe reaches about half way between distal and penultimate subarticular tubercles of Toe IV, whereas tip of third toe reaches to distal border of penultimate subarticular tubercle of Toe IV; heels overlapping when flexed hind limbs held at right angles to sagittal plane; shank 52.7–64.2% ($\bar{x} = 58.6 \pm 1.0$, $n = 12$) SVL in males, 56.2–64.0% ($\bar{x} = 60.0 \pm 0.9$, $n = 10$) in females.

Color in preservative: Dorsum brown with pale occipital **W**, edged with dark brown, brown sacral chevron, interorbital bar; limb bars vague on thighs, bolder on other parts of limbs; bars narrower than interspaces, weakly oblique on shanks; posterior surfaces of thighs rich brown with few cream flecks to several small spots (KU 145000); faint canthal-

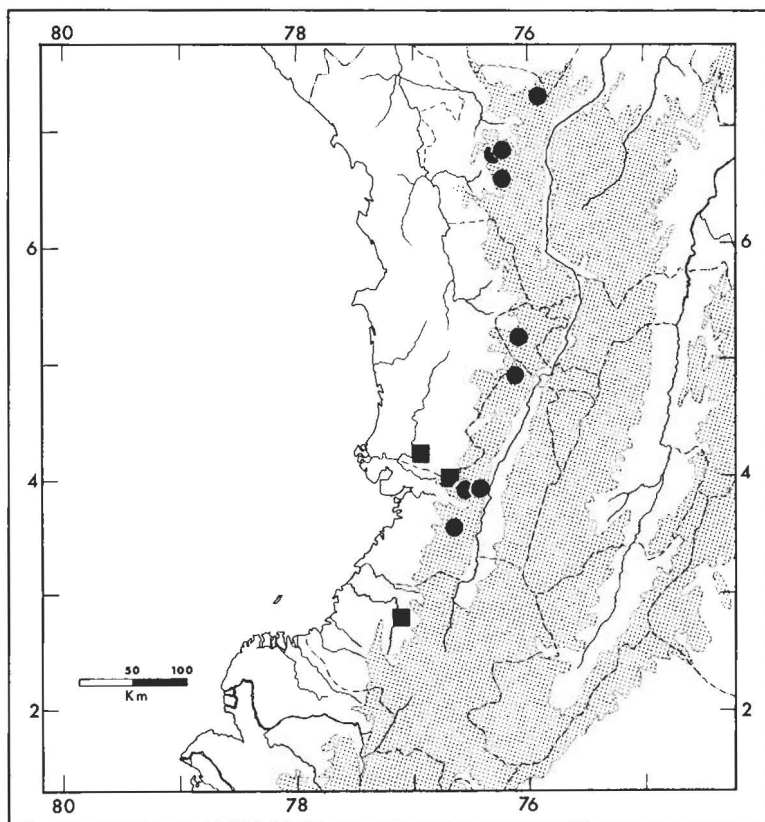


Fig. 13. Map of Colombian locality records of *Eleutherodactylus labiosus* (■) and *E. orpacobates* (●).

supratympanic stripe; cream line along upper lip with dark brown patches above it; dorsal pigmentation set off from venter by heavy brown reticulation on nearly white background of flank; some individuals having brown flanks enclosing large white spots; this brown reticulum extending along anterior surfaces of thighs as an irregular line and along postaxial edge of underside of shank; ventral surfaces cream with few brown vermiculations on anterior belly, breast, throat.

Color in life: Dorsal surfaces brown to dark brown with rust to orange highlights on warts and ridges; venter off-white to dirty cream with brown flecking to black marbling; throat usually darker than venter; labial bar cream to dull yellow; posterior surfaces of thighs fleshy-brown; iris pale green above, gray below, with a brown horizontal streak and black reticulation. (JDL field notes, May–June 1983). The iris of the holotype was

described as “bright reddish rust in upper quarter, gray over remainder, all reticulated with black” (JDL field notes, 8 August 1970).

Etymology.—Latin, meaning large-lipped, in reference to the flaring of the lips in adult females.

Distribution.—Found at low and moderate elevations from the Río San Juan, Colombia, south to west-central Ecuador (Fig. 13). In general, *Eleutherodactylus labiosus* and *E. crenunguis* replace one another geographically. The former occurs primarily at elevations below 1000 m, whereas the latter occurs at elevations of 800–1600 m. The two species are found sympatrically at Tinalandia and La Florida in Provincia Pichincha, Ecuador, but the lower cloud forests have been poorly collected in Ecuador and scarcely at all in southwestern Colombia.

Remarks.—Only two adult females have been examined (AMNH 110871, ICNMHN 13241). The other females are anatomical juveniles (straight oviducts with only small ovarian eggs) despite the fact that some are larger than the “adults” (e.g., KU 145000 is 55.6 mm SVL). The holotype is a juvenile female 45.4 mm SVL and KU 145001 is approximately the same size (45.5 mm SVL). The absence of females having moderate convolutions of the oviducts (what JDL terms “young females”) suggests that this species may not exhibit a normal eleutherodactyline pattern of oviductal morphology (thin, straight oviducts in juveniles, some bending of the oviducts in larger females, and extensive convolution and expansion in adult females, gravid or not). The absence of such a pattern is found in some other frog species (e.g., *Rana blairi* and *Rana pipiens*) in which convolutions occur during the reproductive season, but then regress.

Eleutherodactylus orpacobates sp. nov.

Figure 12

Holotype.—ICNMHN 20249, adult female from Quebrada Agudelo, Parque Nacional Natural Las Orquídeas, Vereda Calles, Municipio Urrao, Departamento Antioquia, Colombia, 1410–1430 m, one of a series obtained 24 May 1988 by M. C. Ardila, J. D. Lynch, P. M. Ruíz, and R. Sánchez.

Paratypes.—ICNMHN 20250–63, collected with holotype; ICNMHN 20264–74, Quebrada de las Canoas, Vereda Calles, Municipio Urrao, 1770–1870 m; ICNMHN 20244–48, Quebrada El Silencio, Vereda Calles, Municipio Urrao, 1480–1540 m; ICNMHN 20278–82, Quebrada Vironda, Parque Nacional Natural Las Orquídeas, Vereda Calles, Municipio Urrao, 1400–1450 m; ICNMHN 20275–77, vicinity INDERENA cabaña “Río Calles,” Parque Nacional Natural Las Orquídeas, 1410–1525 m; CSJMHN 1922, 1925, 1929, 1933–34, 1940, Quebrada Sabaletas, Antadó, Municipio Ituango, Antioquia, Colombia, 1420 m.

Diagnosis.—(1) Skin of dorsum granular, with scattered larger tubercles, that of venter areolate; dorsolateral folds absent; (2) tympanum distinct, round, 22–37% eye length; (3) snout subacuminate in dorsal view, rounded in lateral profile; lips slightly flared in adult females; canthus rostralis straight or weakly concave; (4) interorbital space narrower than upper eyelid; low cranial crests in females; one to three subconical tubercles on upper eyelid; (5) vomerine odontophores elevated, triangular in outline; (6) males with white nuptial pad on thumb, lacking vocal slits; (7) first finger shorter than second; Fingers II–IV bearing large discs; (8) fingers without lateral fringes; (9) ulnar tubercles small, nonconical; (10) nonconical tubercle on heel, row of tubercles along outer edge of tarsus; (11) two metatarsal tubercles, inner oval, three to four times size of outer; supernumerary tubercles only at bases of toes; (12) toes without lateral fringes or webbing, discs broad, smaller than those of fingers; (13) brown above with darker markings; venter off-white with gray spots or reticulum; posterior surfaces of thighs dark brown with minute white spots; (14) size geographically variable, in most populations, males 24.3–35.6 ($\bar{x} = 30.1 \pm 0.7$, $n = 18$), females 43.6–48.4 ($\bar{x} = 45.9 \pm 0.4$, $n = 16$) mm SVL; in southern Departamento Valle del Cauca, Colombia, males 25.7–29.7 ($\bar{x} = 27.7 \pm 0.2$, $n = 21$) mm, females 35.8–41.5 ($\bar{x} = 39.6$, $n = 6$) mm SVL.

Eleutherodactylus orpacobates most closely related to *E. cerasinus*, *E. crenunguis*, *E. labiosus*, *E. ocellatus*, and *E. rubicundus*, but differs from *E. crenunguis* and *E. labiosus* in having nuptial pads in the male (vs. absent) and in lacking vocal slits (present in those species). Those species have shagreen skin of the dorsum, rather than the more granular skin with scattered tubercles of *E. orpacobates*. *Eleutherodactylus orpacobates* has conical eyelid tubercles as does *E. labiosus* (absent in *E. crenunguis*, *E. ocellatus*, and *E. rubicundus*), but is a smaller frog (comparable in size to *E. ocellatus* and *E. rubicundus*). *Eleutherodactylus cerasinus* is markedly smaller (Savage, 1981) and has obvious inner tarsal tubercles.

Description.—(For proportions, $n = 18$ for males, 16 for females.) Head as broad as body, longer than wide; HW 38.1–41.2% ($\bar{x} = 39.7 \pm 0.2$) SVL in males, 38.7–41.7% ($\bar{x} = 40.1 \pm 0.2$) in females; snout subacuminate in dorsal view, rounded in lateral profile; E–N 77.8–100.0% ($\bar{x} = 90.8 \pm 1.5$) eye length in males, 92.1–113.7% ($\bar{x} = 105.8 \pm 1.6$) in females; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis straight, evident but edge rounded; loreal region concave, sloping relatively gradually to lip; lips slightly flared in larger females; one to three conical tubercles on tuberculate upper eyelid; interorbital space broad, low cranial crests (up-turned edges of frontoparietals) in females; upper eyelid width 100.0–139.4% ($\bar{x} = 118.3 \pm 2.4$) IOD in males, 100.0–139.1% ($\bar{x} = 111.2 \pm 2.5$) in females; heavy supratympanic fold obscuring upper edge of tympanum; tympanum superficial, not prominent, separated from eye by distance equal

1.5–2 times tympanum length; tympanum length 22.4–31.1% ($\bar{x} = 27.6 \pm 0.5$) eye length in males, 24.5–37.2% ($\bar{x} = 31.3 \pm 0.8$) in females; one or two conical postrictal tubercles; choanae not concealed by palatal shelf of maxillary arch, moderately large; vomerine odontophores median and posterior to choanae, about size of a choana, separated on midline by distance nearly equal width of an odontophore; odontophores elevated, bearing transverse row of seven to nine teeth; tongue longer than wide, posterior third not adherent to floor of mouth, posterior edge notched; vocal slits absent in males.

Skin of dorsum granular but beset with more pungent tubercles on lower back and flanks; dorsolateral folds absent; skin of venter areolate; discoidal folds well antieriad to groin; anal sheath absent; three to five nonconical ulnar tubercles; palmar tubercle bifid, much larger than oval thenar tubercle; supernumerary palmar tubercles numerous, low, diffuse; subarticular tubercles distinct, round, nonconical; indistinct lateral keels on III–IV; fingers bearing expanded disks, largest on III–IV, round apically; ventral pads broader than long, surrounded by grooves; first finger shorter than second; males bearing large, compact, white nuptial pad atop each thumb.

Nonconical tubercle on heel; row of four or five outer tarsal tubercles; indefinite tubercle on distal portion of inner tarsal surface (otherwise, no inner tarsal folds or tubercles); inner metatarsal tubercle twice as long as wide, three to four times size of low outer metatarsal tubercle (longer than wide); low, indistinct supernumerary plantar tubercles at bases of Toes II–IV; subarticular tubercles round, nonconical; no lateral keels on digits; digits long, slender, bearing expanded disks; disks round apically, smaller than those of fingers; fifth toe longer than third when each is adpressed equally against fourth; tip of fifth toe not reaching base of distal subarticular tubercle of Toe IV, whereas tip of third toe reaches distal border of penultimate subarticular tubercle of Toe IV; heels overlapping when flexed hind legs held perpendicular to sagittal plane; shank 53.6–63.1% ($\bar{x} = 57.5 \pm 0.6$) SVL in males, 51.9–58.7% ($\bar{x} = 55.4 \pm 0.6$) in females.

Color in preservative: Dorsum brown with darker brown head and shoulders, some dark brown chevrons on lower back, continuing across thighs onto shanks; limb bars oblique on shanks, narrower than interspaces; indistinct pale postocular ridges; white flecks in oblique rows across upper flanks onto lower flanks; white flecks on upper surfaces of limbs; belly off-white with spots and short dashes of dark gray, forming a loose reticulum on anterior surfaces of thighs, lowest flanks; throat more heavily stippled with brown; dense reticulum (of dark gray or brown) on undersides of shank, anterior surfaces of thighs, flanks; posterior surfaces of thighs dark brown or black with small (much smaller than pad of thumb) white spots.

Color in life: Dorsum pale to dark brown with brown markings and

cream (or yellow) flecks; some ridges and warts with rust highlights; throat washed with brown; crural stripe (when present) salmon to dull pale orange; venter dirty cream to off-white with gray to brown flecks, spots, or reticulum; posterior surfaces of thighs brown to black with cream to white flecks; underside of shank banded black and white; iris bright copper to rich brown with black flecks; concealed tunic of eye blue.

Eleutherodactylus orpacobates exhibits considerable metachrosis. The color description given above is for animals observed during the day. At night, these animals are quite pale with the predominant ground color being cream (markings are brown).

Measurements of holotype in mm.—SVL 44.1; tibia 24.9; HW 17.7; HL 16.9; chord of HL 18.7; upper eyelid width 5.0; IOD 4.4; tympanum length 1.5; eye length 5.5; E-N 5.8.

Etymology.—Greek (*orpacos* + *bates*), meaning one who frequents twigs. Most specimens have been found perched on twigs in cloud forests where they assume a *Gastrotheca*-like stance.

Natural history.—Amplectant pairs are relatively common in this species. Each pair has been found perched on a liana or twig. No vocalization or other reproductive activity has been seen. Adults and juveniles are found at night perched on twigs (very occasionally on leaves) in wet cloud forest.

Distribution.—Known from moderate elevations (1140–2000 m) along the western flank of the Cordillera Occidental of Colombia from Paramillo (Antioquia) to northern Valle del Cauca (Fig. 13).

Remarks.—Specimens from the most southern populations (Lago Calima and Yotoco, Valle del Cauca) are smaller than those over the remainder of the distribution. Even specimens from northern Valle del Cauca (Charco Azul, Mcpio, El Cairo) are as large as those from Antioquia. The small frogs from southern Valle del Cauca are larger than *E. cerasinus*, the smallest member of the group, and lack the inner tarsal tubercles of that species.

Eleutherodactylus orpacobates has three pattern polymorphisms. The normal morph is described above (and see Fig. 12C, as well as male in Fig. 12D). One variant (female, Fig. 12D) has a crural stripe (the outer edge of the shank bears an orange stripe that obliterates bars on the shank). This variant is seen in 15 individuals (9 from the Lago Calima site, 1 from Charco Azul, 1 from the Orquídeas samples, and 4 from Murri). The third variant is the middorsal stripe (a thin cream line from the tip of the snout to the vent) and is seen in 12 individuals (5 from Lago Calima, 2 from Pueblorico, 2 from Orquídeas, 1 from Murri, and 2 from Ituango). One individual (KU 168087) has both the crural stripe and middorsal stripe.

The Lago Calima site (1230 m) is near the Yotoco site (1590 m) and each sample consists of 47 specimens. Only the common variant is seen in the Yotoco sample. The difference in polymorph frequency between these

two sites suggests the absence of gene flow (an observation in agreement with Lynch's, 1992, conclusion for the better-collected *E. erythropleura*).

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APPENDIX: SPECIMENS EXAMINED

Eleutherodactylus cerasinus (80)

- COSTA RICA: Prov. Cartago: Turrialba, KU 28341–45. Prov. Heredia: Puerto Viejo, KU 36956. Prov. Limón: Estrella, KU 35373; La Lola, KU 37487; Suretka, KU 36945, 36957–64, 37036–38.
- PANAMA: Prov. Bocas del Toro: 4.8–12.9 km W Almirante, KU 114067–71; Cayo Nancy, 2–40 m, KU 114058; Isla de Colón, La Gruta, 20 m, KU 114059–61; S

end Isla Popa, 10 m, KU 114062; mainland, NW Isla Split Hill, KU 114063; mouth of Río Cahuita, 1 m, KU 114056–57; Río Changena, 650–830 m, KU 114013–55; Río Claro at Río Changena, 910 m, KU 114012; Peninsula Valiente, 10 m, KU 114064–66.

Eleutherodactylus cruentus (36)

COLOMBIA: Depto. Antioquia: Mcpio. Dabeiba, Campamento “Pantanos,” Río Amparradó, 805 m, ICNMHN 10565–72, 10580–83, 10612–17, 10619–20, 10634–39, 13869–74. Depto. Chocó: Mcpio. Istmina, Quebrada Peradó, ICNMHN 3218 (ID questionable, possibly = *E. latidiscus*); Mcpio. San José del Palmar, Alto de Oso, 10 km W La Italia (Valencia), 1000 m, UVC 8257–58, 8260.

Eleutherodactylus labiosus (85)

COLOMBIA: Depto. Cauca: Mcpio. El Tambo, La Costa, 1000 m, KU 145000–02. Depto. Chocó: Quebrada Pangalá, east bank lower Río San Juan (ca. 17 km airline NE Palestina), AMNH 110871. Depto. Valle del Cauca: Mcpio. Dagua, Río Anchicayá, 300 m, KU 168136; Mcpio. Restrepo, Vereda Alegre, Campo Las Vegas, 200 m, ICNMHN 13242–43, Río Calima, ICNMHN 13241.

ECUADOR: Prov. Carchi: cabeceras del Río Baboso, near Lita, MECN LAC 138. Prov. Cotopaxi: on frontier of Bolívar province, ca. 7 km airline SSW El Corazón, 800 m, AMNH 104961. Prov. Pichincha: Centinela, 14.1 km SE Patricia Pilar, 550–600 m, MCZ 97575–91; Centro Científico Río Palenque, 47 km S Santo Domingo de los Colorados (road to Quevedo), KU 165895, MCZ 90053–54, 91954–56, 92113, 94461, 94866; along Highway 28 (old road to Quito), 16 km from junction with Highway 30, 1500 m, MCZ 90006; [Hotel] Tinalandia, 15–16 km SE Santo Domingo de los Colorados, 800 m, AMNH 102759, MCZ 88392–93, 88891–93, 89974–92, 89993–90004, 90049–52, 91953; La Florida, near Alluriquin, QCAZ 569–70, MECN LAC 210; Las Palmas, junction Highways 28 & 30, 920 m, KU 131612, 165894, 165896.

Eleutherodactylus latidiscus (76)

COLOMBIA: Depto. Cauca: Mcpio. El Tambo, Río Munchique, 800 m, KU 145006, 1000 m, KU 145008; Mcpio. Timbiquí, Quebrada Guanguí, AMNH 88947, 88950–53; Depto. Chocó: Mcpio. Istmina, Quebrada Docordó, AMNH 87028–33; Mcpio. Tadó, 2 km above Playa de Oro, AMNH 87034–42, upper Río San Juan, AMNH 87044–50; Depto. Valle del Cauca: Mcpio. Dagua, Bajo Anchicayá, 300 m, UVC 5611, 5757–61, 5763–65, 6612, 6827; Mcpio. Darién, 1.5 km W Lago Calima, 1230 m, KU 168010–11; Mcpio. Restrepo, Vereda Alegre, Campo Agua Bonita, 300 m, ICNMHN 13338, Campo Chanco, 460 m, ICNMHN 13335–36, 13343, Campo Las Vegas, 200 m, ICMNH 13339–42.

ECUADOR: Prov. Carchi: cabeceras del Río Baboso, near Lita, MECN LAC 33, 74–75; Prov. Esmeraldas: Cachabí, 16 km SE Concepción, 200 m, BMNH 1947.2.15.66–67. Prov. Pichincha: Centinela, 14.1 km SE Patricia Pilar, 550–600 m, MCZ 97555, 97557, 97574; Centro Científico Río Palenque, 47 km S

Santo Domingo de los Colorados, MCZ 88391, 90014–16, 92111–12, 94455, 94457–58; [Hotel] Tinalandia, 15–16 km SE Santo Domingo de los Colorados, 800 m, MCZ 88422, 90017, 90330–33, 91221; La Florida, near Alluriquin, MECN LAC 206, 208; Santo Domingo de los Colorados, 500 m, KU 109059.

Eleutherodactylus orpacobates (186)

COLOMBIA: Depto. Antioquia: Mcpio. Frontino, Corregimiento de Nutibara, Km 14 carr. Nutibara a La Blanquita, 2000 m, ICNMHN 16495–96, Km 16 Nutibara a La Blanquita, 1960 m, ICNMHN 16472, 16579, Km 18 Nutibara a La Blanquita, 1940 m, ICNMHN 16475–86, Km 16.5–17 Nutibara a La Blanquita, 1900 m, ICNMHN 16473–74, Km 23 Nutibara a La Blanquita, 1430 m, ICNMHN 16487–90, Km 27 Nutibara a La Blanquita, 1140 m, ICNMHN 16492–94; Mcpio. Ituango, Antadó, Quebrada Sabaletas, 1420 m, MHNCSJ 1922, 1925, 1929, 1933–34, 1940, 2382, 2384–85, 2388, 2393, 2395, 2598, 2603, 2605; Mcpio. Urrao, Vereda Calles, Parque Nacional Natural Las Orquídeas, vic. cabaña Río Calles, 1410–1525 m, ICNMHN 20275–77, Quebrada Aquelero, 1410–1430 m, ICNMHN 20249–63, Quebrada de las Canoas, 1770–1870 m, ICNMHN 20264–74, Quebrada El Silencio, 1480–1540 m, ICNMHN 20244–48, Quebrada Vironda, 1400–1450 m, ICNMHN 20278–82. Depto. Risaralda: Mcpio. Pueblorico, 15 km NE Pueblorico, vic. La Trinidad, 1600 m, ICNMHN 27501; Km 1–4 carr. Pueblorico–Villa Claret, Quebrada San José, 1520 m, ICNMHN (MC 3379, 3403); Vereda Tatamá, Río Tatamá, 1800 m, ICNMHN (MC 3531–34); carr. Pueblorico a Villa Claret, Vereda La Trinidad, near La Trinidad, 1510 m, ICNMHN (MC 3748, 3751). Depto. Valle del Cauca: Mcpio. La Cumbre, Vereda Chicoral, corregimiento de Bitaco, Finca La Cataisa, 1900 m, ICNMHN 21580, 21582, 21585–86; Mcpio. Darién, 1.5 km W Lago Calima, Río Calima, 1230 m, KU 168083–99, 168101–31; Mcpio. Yotoco, Reserva forestal de Yotoco, Km 18, Buga-Loboguerrero Road, 1590 m, ICNMHN (JDL 11129–75).

Eleutherodactylus permixtus (526)

COLOMBIA: Depto. Antioquia: Mcpio. Angelópolis, MLS 167; Mcpio. Belmira: El Yermal, 6 km N Belmira, 2720 m, ICNMHN 8932–35; Vereda Los Patos, Quebrada Los Patos, 3.7 km N Belmira, 2620 m, ICNMHN 8936–37; Mcpio. Jericó: MCZ 24896–97; Mcpio. Medellín: Medellín, AMNH 38831–35, ICNMHN 4113; Medellín Valley, AMNH 38784, 38787; Serranía de las Valdías, Boquerón, 2800–3000 m, ICNMHN 4278–81, 6353–57; Corregimiento San Félix, 2400 m, ICNMHN 14263–73; 5.6–5.7 km WSW San Félix, 2860–2940 m, ICNMHN 23329–33; 6.6–8.1 km WSW San Félix, 2820–3100 m, ICNMHN 8929–31; Mcpio. San Pedro: AMNH 38757, 38759–60, 38762, 38763–64, MCZ 24903–06 (reported as “Sampedro,” Cochran and Goin, 1970), MLS 138, 143, 145, 400(3), 425(3), 426(2); Vereda La Lana, Finca La Montañita, ca. 4 km E El Tambo, 2510 m, ICNMHN 23334–38; Mcpio. Santa Rosa de Osos: AMNH 14073, 38817 (Cochran & Goin, 1970, reported this specimen as being from Santa Rosa de Aso, Depto. Caldas), 39456–58; 7.3 km S Llanos de Cuiva, 2770 m, ICNMHN 8915; El Chaquiro, MLS 69; Mcpio. Remedios: Finca El Amparo, MLS 454; Mcpio. Sonsón: MLS 186; 8 km E Sonsón, 2780 m, ICNMHN 8938–

42; 12–12.5 km E Sonsón, 2540–2560 m, ICNMHN 8943–44; Páramo de Sonsón, 17 km E Sonsón, 2800 m, ICNMHN 18685–716, 18813; Páramo de Sonsón, 22 km E Sonsón, 2540 m, ICNMHN 18717; Mcpio. Yarumal: 3.5 km N Llanos de Cuiva, 2700 m, ICNMHN 8907–14; 5 km N Llanos de Cuiva, 2650 m, ICNMHN 8916–28; Ventanas, MLS 347, 445. Depto. Caldas: Mcpio. Manizales: 17 km E Manizales, 2520 m, ICNMHN 22491–97; between crest of Cordillera Central and 5 km toward Manizales, 3700 m, ICNMHN 2024, 2026, 4734; MLS 155 (“Páramo Las Letras, Caldas,” is probably from this locality); Mcpio. Marulanda: Alto de las Cruces, MLS 189a, 322–323; Mcpio. Pensilvania: MLS 424; Mcpio. Salamina: MLS 325–26, 328–29, Montañita, MLS 365, 372. Depto. Quindío: Mcpio. Calarcá: Cerro Campanario, 1 km S Cajamarca-Calarcá Road, 3240 m, ICNMHN 8896–8906; Mcpio. Salento: Carretera Salento-Cocora, Hda. Alaska, Finca Rincón Santo, 6 km N road, UVC 6993–7007, 7322. Depto. Tolima: “Quindío Mountains,” MCZ 8220–21, 8223; “Carretera Fresno-Manizales” (probably = Páramo Letras, Mcpio. Herveo), MLS 318–20; Mcpio. Cajamarca: Corregimiento Anaime, 3190 m, ICNMHN 22752; Corregimiento Anaime, 3480 m, ICNMHN 22601–17; “La Línea,” Km 111–112 Carretera Cajamarca a Calarcá, 3040–3080 m, ICNMHN 8861–95; “La Línea,” Km 113–109 Carretera Cajamarca a Calarcá, 3070–3340 m, ICNMHN 22784, 22591–600; Mcpio. Herveo: Páramo de Letras, 3050 m, ICNMHN 945, 948–49, 952, UVC 6759; Páramo de Letras, 0.5 km above “El Paisa,” 3100 m, ICNMHN 635–40, 642–49, 651–53, 2581–83, 2585–92, 2594–95; Páramo de Letras, Vereda Albania, 3200 m, ICNMHN 760–65, 771, 774, 3187–96, 3491–93, 6226–28, 6230–35, 6242–48, 6250–52; Páramo de Letras, Km 77–79 Carretera Mariquita a Manizales, 3310–3340 m, ICNMHN 18826–37; 15 km W Padua, 2420 m, ICNMHN 22498; Mcpio. Ibagué: Nevado del Tolima, Inspección de Policía Las Juntas a El Rancho, 2400–2750 m, ICNMHN 4782–93; 11 km N Juntas, El Silencio, 2600 m, ICNMHN 8849–60; along Río Combeima, between El Silencio and El Rancho, 2590–2750 m, ICNMHN 8798–8828, 22618–87, 22813–28; El Rancho, 2750 m, ICNMHN 3256–60, 3262–65, 3267–69, 3272–73; Nevado del Tolima, by road, above El Silencio, 2830–2980 m, ICNMHN 22829–32; 1.5 hr by foot above El Rancho, 2800–2820 m, ICNMHN 8829–8848.

Eleutherodactylus supernatis (63)

COLOMBIA: Depto. Cauca: Mcpio. Coconuco, Paletará, 3030 m, ICNMHN 8036–52, 8064–67, between Paletará and Quebrada Bujíos, 2960 m, ICNMHN 8073–75, Quebrada Ullucos, 27 km SSE Coconuco, 2930 m, ICNMHN 8053–63, Río Negro, 23 km SSE Coconuco, 2960 m, ICNMHN 8068–71, Vereda Bellavista, ca. 2000 m, UVC 5589; Mcpio. Páez, Km 34–35, carretera Belalcázar-Tacueyó, 2265–2400 m, ICNMHN 6485, 8381, Km 40–41, carretera Belalcázar-Tacueyó, 2780–2820 m, ICNMHN 6427–28, 6451, 6480, 6510, 6512–13, 6607, 6984, 7063–64, Km 46–49.5, carretera Belalcázar-Tacueyó, 3200–3300 m, ICNMHN 6839–40, 6842–44. Depto. Huila, Mcpio. San José de Isnos, Chupallal de Perico, 29.4 km by road NW San José de Isnos, 2600 m, ICNMHN 8031–32, 39 km by road NW San José de Isnos, 2880 m, ICNMHN 8033–35.

For localities in Ecuador, see Lynch (1980).

Eleutherodactylus tamsitti (53)

COLOMBIA: Depto. Caquetá: Mcpio. Florencia, Vereda Gabinete, 8.6 km E Alto de Gabinete, 2040 m, ICNMHN 22948, Vereda La Portada, 35.2 km NW Florencia, 1230 m, ICNMHN 23818, 37.4 km NW Florencia, 1350 m, ICNMHN 23850–58, Vereda Tarqui, 12.5 km E Alto de Gabinete, 1750 m, ICNMHN 22949–51, Km 48–49 carretera Altamira–Florencia, 1655 m, ICNMHN 23632, Km 53–54 carretera Altamira–Florencia, 1350 m, ICNMHN 23633–41, 38.8 km NW Florencia, 1370 m, ICNMHN 23819–23, 23848, 39.3 km NW Florencia, 1410 m, ICNMHN 23824–28, 41.1 km NW Florencia, 1470 m, ICNMHN 23829–47, 41.8 km NW Florencia, 1530 m, ICNMHN 23849. Depto. Huila: Mcpio. Acevedo, near San Adolfo, on Río Suaza, 1400 m, FMNH 69735, 69737.