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## Frogs of the Genus *Eleutherodactylus* (Leptodactylidae) in the Cordillera Occidental in Peru with Descriptions of Three New Species

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**ABSTRACT** Three new species of *Eleutherodactylus* are described from the Río Zaña Valley in the Pacific versant of the Cordillera Occidental in the Departamento de Cajamarca, Peru. One of the species is a member of the *Eleutherodactylus conspicillatus* Group, and two are members of the *Eleutherodactylus unistrigatus* Group. We recognize 15 species of *Eleutherodactylus* in the Cordillera Occidental; 10 of these species are reported for the first time from the Cordillera Occidental. Four of these species are shared with the Cordillera Occidental in Ecuador, and five are shared with the Cordillera de Huancabamba in northern Peru.

**KEY WORDS:** Leptodactylidae; *Eleutherodactylus*; Cordillera Occidental, Peru; Taxonomy; Biogeography.

**RESUMEN** Se describen tres nuevas especies de *Eleutherodactylus* del Valle de Río Zaña en la vertiente pacífica de la Cordillera Occidental en el Departamento de Cajamarca, Perú. Una de las especies es una miembro del grupo *Eleutherodactylus conspicillatus*, y dos especies son miembros del grupo *Eleutherodactylus unistrigatus*. Reconocemos 15 especies de *Eleutherodactylus* en la Cordillera Occidental; 10 de ellas se reportano por primera vez para la Cordillera Occidental. Cuatro de estas especies ocurren también en la Cordillera Occidental en Ecuador, y cinco ocurren también en la Cordillera de Huancabamba en el norte de Perú.

**PALABRAS CLAVES:** Leptodactylidae; *Eleutherodactylus*; Cordillera Occidental, Perú; Taxonomía; Biogeografía.

## INTRODUCTION

In their review of the frogs of the genus *Eleutherodactylus* in northern Peru, Duellman and Pramuk (1999) reported only five species from the Cordillera Occidental (exclusive of the northern extension, the Cordillera de Huancabamba), but noted that more species might be discovered as previously uncollected areas were investigated. Subsequently we have undertaken a comprehensive review of the eleutherodactyline frogs of Peru and have "discovered" several undescribed species in various museums (e.g., Duellman et al., 2006, Lehr and Duellman, 2007). Among these are series of three new species collected in the Cordillera Occidental in Peru by John E. Cadle in 1987. Unfortunately, with the exception of one brief statement on coloration in the catalogue in the Field Museum of Natural History, we have been unable to obtain data on the coloration, behavior, or habitats of the new species.

The three new species, along with series of *Eleutherodactylus cajamarcensis* and *E. lymani*, were collected in the valley of the Río Zaña. Cadle (1989) and Cadle and McDiarmid (1990) briefly described the area. They noted the presence of cloud forest at elevations above 1500 m and emphasized the disparate occurrence of humid forests on the western slopes of the Cordillera Oriental, which becomes progressively drier from north to south.

In what was purported to be "The amphibian tree of life," Frost et al. (2006) proposed many taxonomic changes based on molecular evidence of relatively few taxa. They considered *Eleutherodactylus* to be in the Brachycephalidae and elevated all of the subgenera recognized by Lynch and Duellman (1997) to genera. Their phylogeny of "eleutherodactyline" frogs, like that of other groups of frogs was based on so few taxa so as to be unacceptable

(Wiens, 2007). Even so, the new taxa described herein are members of the nominal genus *Eleutherodactylus*, as defined by Lynch and Duellman (1997). The subgenera and species groups also are those of Lynch and Duellman (1997) as modified by Duellman and Pramuk (1999), with the inclusion of *Eleutherodactylus danae* Duellman 1978 and *E. mercedesae* Lynch and McDiarmid 1987 in the *Eleutherodactylus conspicillatus* Group.

## ACKNOWLEDGMENTS

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## MATERIALS AND METHODS

The format for the description follows that of Lynch and Duellman (1997), except that the term dentigerous processes of vomers is used instead of vomerine odontophores (Duellman et al., 2006). Specimens were sexed externally and by examination of gonads. Measurements were taken with digital calipers and rounded to the nearest 0.1 mm; snout-vent length is abbreviated SVL, and interorbital distance is abbreviated IOD. Comparative lengths of Toes III and V were determined by addressing both toes against Toe IV; lengths of Fingers I and II were

determined by addressing the fingers against each other. Drawings were prepared by E. Lehr, who used a stereomicroscope and camera lucida (Nikon SMZ 1000). Photos were taken by Lehr of specimens immersed in ethanol. Geographic coordinates were approximated from the map provided by Cadle and McDiarmid (1990). Specimens examined are listed in the appendix; codes of collections are those of Leviton et al. (1985) with the addition of MHNSM = Museo de Historia Natural Universidad Nacional Mayor de San Marcos, Lima, Peru.

## DESCRIPTIONS OF NEW SPECIES

*Eleutherodactylus phalaroinguinis* new species

**Holotype.**—FMNH 232328, a gravid female, from the Río Zaña, ca. 06°51' S, 79°06' W, 1800 m, Departamento de Cajamarca, Peru, obtained on 29 May 1987 by John E. Cadle.

**Paratopotypes.**—KU 307069, an adult female; 232329 and 232725, adult males; 232292 and 232297, subadult males, all collected between 8 May and 20 June 1987 by John E. Cadle.

**Diagnosis.**—A member of the *Eleutherodactylus* (*Eleutherodactylus*) *conspicillatus* Group having (1) skin on dorsum and venter smooth; discoidal fold evident; dorsolateral folds absent; (2) tympanic membrane smooth; tympanic annulus prominent, slightly higher than long, its length about 50% length of eye; (3) snout moderately long, rounded in dorsal view and in profile; (4) upper eyelid lacking tubercles, narrower than IOD; cranial crests absent; (5) dentigerous processes of vomers low, oblique; (6) males lacking vocal slits and nuptial pads; (7) Finger I shorter than II; discs on outer fingers expanded, truncate, more than twice width of digit proximal to pad; (8) fingers lacking lateral fringes; (9) ulnar tubercles absent; (10) heel and outer edge of tarsus lacking tubercles; inner edge of tarsus lacking fold distally; (11) inner metatarsal tubercle elevated, ovoid, about 2× rounded outer metatarsal tubercle; supernumerary plantar tubercles low, diffuse; (12) toes lacking lateral fringes; webbing absent; Toe V slightly longer than Toe III; discs smaller than those on fingers; (13) dorsum brown with small, diffuse dark brown spots; belly tan reticulated with brown; groin and anterior surfaces of thighs dark brown with white spots; (14) SVL 26.0–31.4 mm in two males, 31.4–36.7 mm in two females.

Only four other members of the *Eleutherodactylus conspicillatus* Group in Peru have Finger I shorter than Finger II. Three of these (*E. danae*, *mercedesae*, and *meridionalis*, a

newly described species from Departamento de Ancash) differ from *E. phalaroinguinis* by having areolate skin on the venter, and the last two species also differ by having small tubercles on the upper eyelids, and basal webbing between the outer toes. The fourth species, *E. ornatus*, is like *E. phalaroinguinis* in having a smooth venter, no tubercles on the upper eyelids, and no webbing between the toes, but it differs from that species by having a cream groin with small brown spots. *Eleutherodactylus muscosus* is like *E. phalaroinguinis* in having brown reticulations on the venter and white spots in the groin and on the anterior surfaces of the thighs, but *E. muscosus* differs by having areolate skin on the venter, tubercles on the upper eyelids, and Toe V much longer than Toe III.

Among the sympatric species, *Eleutherodactylus lymani* is like *E. phalaroinguinis* by having smooth skin on the venter; but the former is much larger (SVL in males to 45.3 mm, in females to 69.3 mm) and lacks markings on the belly, whereas the latter has a brown groin and thighs with distinct, round white spots. Other sympatric species differ from *E. phalaroinguinis* by having areolate skin on the venter and by having Toe V much longer than Toe III. Furthermore, *E. cajamarcensis* differs from *E. phalaroinguinis* by having a gray belly, rose-red groin, and the posterior surfaces of thighs black with white or red spots; *E. vermiculatus* differs by having, brown vermiculations on the venter, and a dark spot in the groin, and *E. amydrotus* by having an unmarked groin and posterior surfaces of the thighs.

**Description of holotype.**—Adult female with slender body; head narrow, about as wide as body, slightly wider than long; head width 32.4% of SVL; head length 31.8% of SVL, 98.4% of head width; snout moderately long, rounded in dorsal view and in profile (Fig. 1A and B); diameter of eye slightly greater than eye-nostril distance; nostrils barely protuberant laterally; canthus rostralis curved in

dorsal view, rounded in section; loreal region concave; lips rounded; upper eyelid lacking tubercles; width of upper eyelid 77.8% of IOD; tympanic annulus and membrane distinct, slightly higher than long; dorsal part of annulus obscured by weak supratympanic fold; diameter of tympanum 52.8% of diameter of eye, separated from eye by distance slightly greater than diameter of tympanum; one low postrictal tubercle. Choanae small, triangular, not concealed by palatal shelf of maxillae; dentigerous processes of vomers low, oblique, bearing two and three teeth; tongue nearly round, free behind for about one-fourth of its length.

Skin on all dorsal and ventral surfaces smooth; dorso-lateral folds absent; discoidal fold evident; cloacal sheath short; ornamentation in cloacal region absent.

Ulnar tubercles absent; palmar tubercle elevated, bi-

fid, about twice as large as elliptical thenar tubercle; sub-articular tubercles prominent, round in ventral view and rounded in section; supernumerary tubercles few, low, subconical, much smaller than subarticular tubercles; fingers lacking lateral fringes; Finger I shorter than Finger II; disc on Finger I slightly expanded; discs on Fingers II–IV expanded, truncate, twice as wide as digit proximal to disc; ventral digital pads well defined by circumferential grooves (Fig. 1C).

Hind limbs moderately slender; tibia length 48.5% of SVL; foot length 45.9% of SVL; heel and outer edge of tarsus lacking tubercles; inner tarsal fold absent; inner metatarsal tubercle elevated, ovoid, about 2× nearly round outer metatarsal tubercle; toes unwebbed, lacking lateral fringes; discs on toes slightly smaller than those on fingers; all toes having ventral pads well defined by circumferential grooves; relative lengths of toes  $I < II < V < III < IV$ ; Toe V slightly longer than Toe III; disc on Toe V reaching proximal edge of distal subarticular tubercle on Toe IV; disc on Toe III not reaching proximal edge of distal subarticular tubercle on Toe IV (Fig. 1D).

Coloration of holotype in preservative: Dorsum and flanks brown with small faintly darker diffuse brown spots; no dark interorbital bar, labial bars, canthal and supratympanic stripes, or transverse bars on limbs; broad tan band between outer edges of upper eyelid and onto base of snout; groin and proximal parts of anterior and posterior surfaces of thighs dark brown with distinct creamy-tan round spots; venter tan; belly having brown reticulations enclosing tan spots; palmar and plantar surfaces pale brown (Fig. 2A and B).

Coloration of holotype in life: "Groin, thighs, and ventral surfaces of hind limbs brown with white spots" (J. E. Cadle, field notes in FMNH catalog).

Measurements of holotype in mm: SVL 37.7, tibia length 18.3, foot length 17.3, head length 12.0, head width 12.3, IOD 4.5, width of upper eyelid 3.5, eye-nostril distance 3.3, diameter of eye 3.6, diameter of tympanum 1.9.

**Variation.**—All individuals have Toe V slightly longer than Toe III and are like the holotype in structural features. Snout-vent lengths of the paratypes are: adult female 36.7 mm, adult males 25.0 and 32.7 mm, and subadult males 21.0 and 23.5 mm. All specimens are like the holotype in having pale spots on brown ground color in the groin and on the thighs, but the pattern is faint in FMNH 232335. The holotype has the boldest reticulated pattern on the belly, and it is the only specimen with a pale transverse band on the head. The female paratype (FMNH 232335) has narrow tan dorsolateral stripes from the occiput just posterior to the eyelids to the sacrum. Two individuals have faint W-shaped marks in the scapular region, and one of these (FMNH 232715) also has a pair of longitudinal brown marks in the sacral region. That specimen

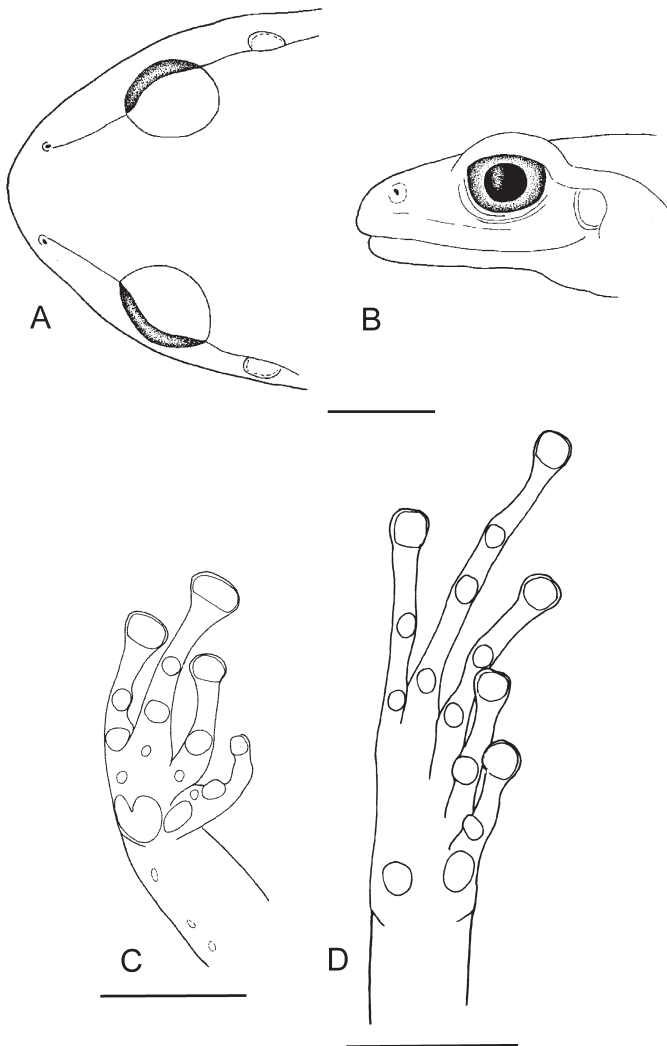


Fig. 1. Holotype of *Eleutherodactylus phalaroinguinis* (FMNH 232328): A. Dorsal view of head. B. Lateral view of head. C. Palmar view of hand. D. Plantar view of foot. Scale bars = 5 mm.

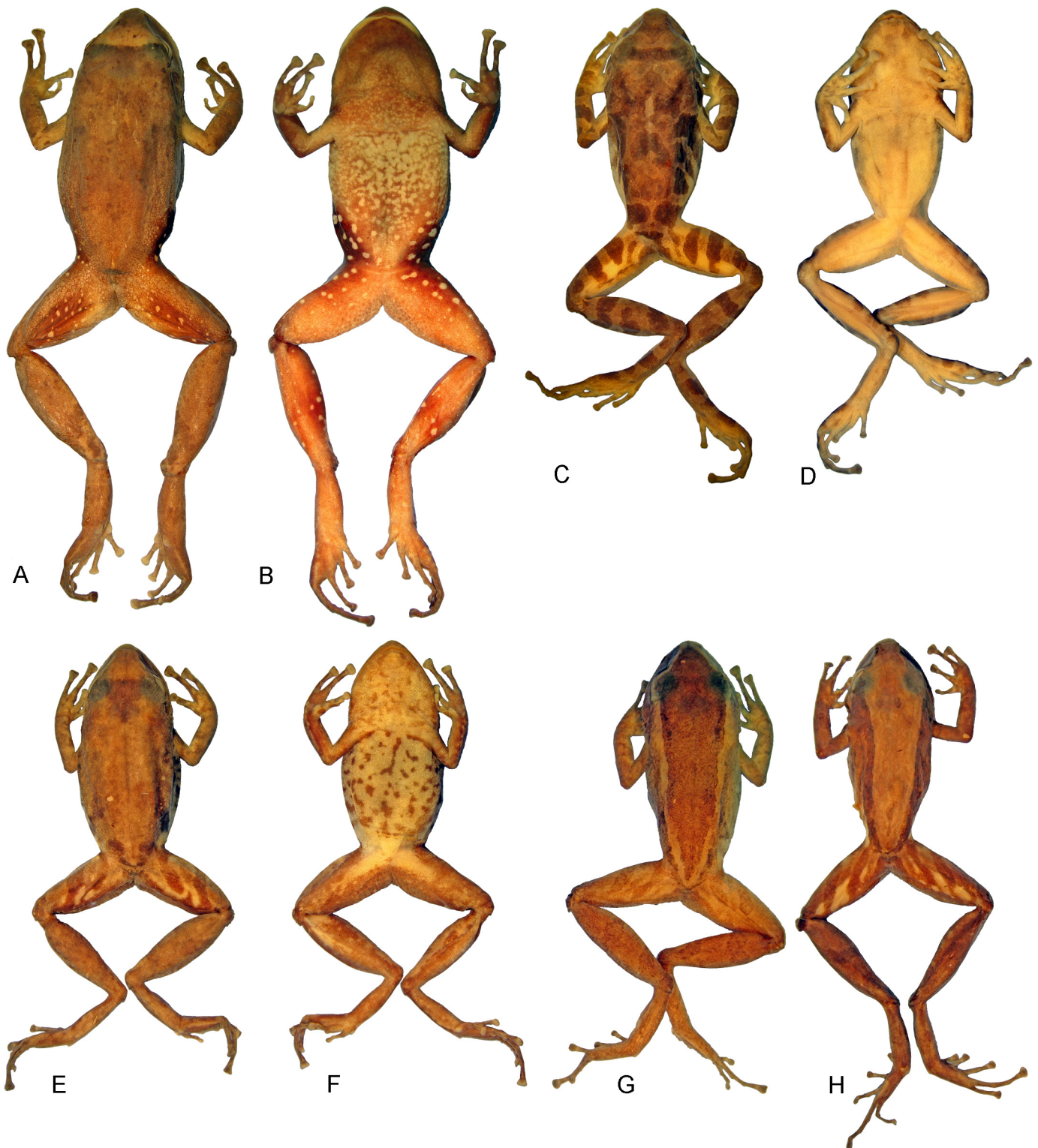


Fig. 2. Preserved specimens of three species of *Eleutherodactylus*: A and B. Dorsal and ventral views of the holotype (FMNH 232328) of *E. phalaroinguinis*. C and D. Dorsal and ventral views of the holotype (FMNH 231949) of *E. amydotus*. E and F. Dorsal and ventral views of the holotype (FMNH 232330) of *E. vermiculatus*. G. Dorsal view of *E. vermiculatus* (FMNH 232332). H. Dorsal view of *E. vermiculatus* (FMNH 231937). See text for sexes and SVLs.

and FMNH 232292 have minute flecks, instead of reticulations, on the belly, and the latter has a brown occipital blotch. One subadult male (FMNH 232277) has irregular brown mottling on the chest and an unmarked belly.

**Etymology.**—The specific name is an adjective derived from the Greek *phalaros* meaning white-spotted and the Latin *inguinis* meaning groin. The name refers to the distinctive white spots in the groin and on the hind limbs.

**Remarks.**—Nearly all other South American *Eleutherodactylus* that have Toe V shorter than Toe III are members of the *Eleutherodactylus discoidalis*, *nigrovittatus*, and *sulcatus* groups and the Middle American subgenus *Craugastor*; an exception is *E. simonsii*, a member of the *Eleutherodactylus orestes* Group. This same toe condition is common among West Indian species of *Eleutherodactylus* and members of the subgenera *Euhyas* and *Syrrhophus* (Lynch and Duellman, 1997).

*Eleutherodactylus amydrotus* new species

**Holotype.**—FMNH 231949, an adult male, from the ridge above the base camp near Chorro Blanco, ca. 4.5 km (airline) NE Monte Seco, ca. 06°51' S, 79°06' W, ca. 1500 m, Departamento de Cajamarca, Peru, obtained on 2 June 1987 by John E. Cadle.

**Paratopotype.**—FMNH 231948, an adult male, collected with the holotype.

**Diagnosis.**—A member of the *Eleutherodactylus* (*Eleutherodactylus*) *unistrigatus* Group having (1) skin on dorsum smooth with a few minute tubercles dorsolaterally; that on venter areolate; discoidal fold barely evident posteriorly; dorsolateral folds absent; (2) tympanic membrane not differentiated; tympanic annulus distinguishable under skin, round, its length about one third length of eye; (3) snout long, rounded in dorsal view and in profile; (4) upper eyelid lacking tubercles, narrower than IOD; cranial crests absent; (5) vomerine teeth absent; (6) vocal slits and nuptial pads absent; (7) Finger I shorter than II; discs on outer fingers elliptical, about twice width of digit proximal to pad; (8) fingers lacking lateral fringes; (9) ulnar tubercles absent; (10) heel and outer edge of tarsus lacking tubercles; inner edge of tarsus lacking tubercles and fold; (11) inner metatarsal tubercle elevated, ovoid, about 3× subconical outer metatarsal tubercle; supernumerary plantar tubercles absent; (12) toes lacking lateral fringes; webbing absent; Toe V much longer than Toe III; discs nearly as large as those on outer fingers; (13) dorsum brown with darker brown markings; venter and posterior surfaces of thighs cream; (14) SVL 26.0–25.8 mm in two males; females unknown.

Seven other species have no differentiated tympanic membrane, but most of the circumference of the tympanic annulus is visible through the skin. Of these, *Eleuthero-*

*dactylus nebulanastes* differs from *E. amydrotus* by having a smooth (instead of areolate) venter and narrow, rounded terminal digits (instead of expanded), Toes III and V equal in length (instead of Toe V much longer than Toe III), and Finger I longer than Finger II (instead of I shorter than II). *Eleutherodactylus aureolineatus* differs in lacking transverse bars on the limbs and having distinctive yellow dorsolateral stripes connected to a yellow interorbital bar. The groin in *E. amydrotus* is cream, in contrast to a large yellow spot in *E. carvalhoi* and red and yellow mottling in *E. rufioculis*, which also differs from *E. amydrotus* by having a red iris, yellow throat, and brown mottling on the belly. *Eleutherodactylus ockendeni* differs from *E. amydrotus* by having more broadly expanded, elliptical discs on the fingers, and dorsolateral folds. *Eleutherodactylus infraguttatus* differs from *E. amydrotus* by having small tubercles on the upper eyelid, dark mottling on the belly, and no labial bars. *Eleutherodactylus ardalonychus* is most similar to *E. amydrotus* but differs by having vomerine teeth, lateral fringes on the digits, much more pigmentation ventrally, and vocal slits and nuptial pads in males.

Among the sympatric species of *Eleutherodactylus*, *E. lymani* and *E. phalaroinguinis* differ from *E. amydrotus* by having smooth skin on the venter; also, the former is much larger (SVL in males to 45.3 mm, in females to 69.3 mm) and lacks markings on the belly, whereas the latter has a brown groin and thighs with distinct, round white spots. *Eleutherodactylus cajamarcensis* differs from *E. amydrotus* by having a gray belly, rose-red groin, and the posterior surfaces of thighs black with white or red spots; *E. vermiculatus* differs by having a distinct tympanic annulus, brown vermiculations on the venter, and a dark spot in the groin.

**Description of holotype.**—Adult male with slender body; head slightly wider than body, not as wide as long; head width 36.8% of SVL; head length 38.3% of SVL; head width 96.0% of head length; snout moderately long, rounded in dorsal view and in profile (Fig. 3A and B); diameter of eye less than eye-nostril distance; nostrils slightly protuberant laterally; canthus rostralis curved in dorsal view, nearly angular in section; loreal region concave; lips rounded; upper eyelid lacking tubercles; width of upper eyelid 77.1% of IOD; tympanic membrane not differentiated; tympanic annulus visible under skin, slightly higher than long; dorsal part of annulus obscured by weak supratympanic fold; diameter of tympanum 38.5% of diameter of eye, separated from eye by distance 2.5× diameter of tympanum; no postrictal tubercles. Choanae small, nearly round, not concealed by palatal shelf of maxillae; vomerine teeth absent; tongue broadly cordiform, shallowly notched posteriorly, free behind for about one-third of its length.

Skin on dorsum smooth with an irregular line of min-

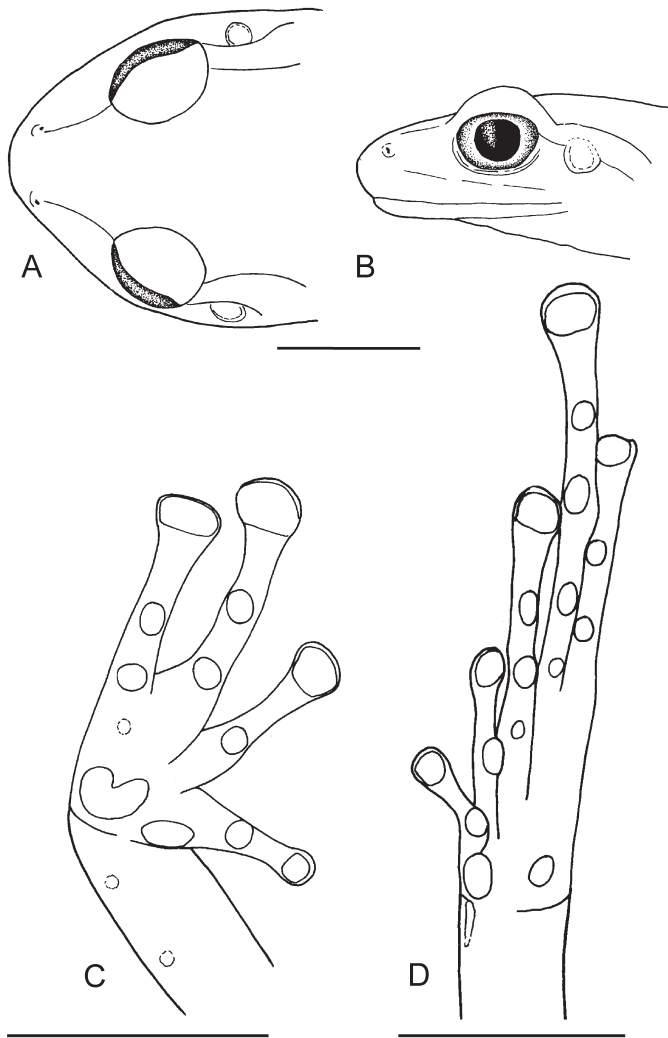


Fig. 3. Holotype of *Eleutherodactylus amydrotus* (FMNH 231949): A. Dorsal view of head. B. Lateral view of head. C. Palmar view of hand. D. Plantar view of foot. Scale bars = 5 mm.

ute tubercles dorsolaterally on body; skin on belly areolate; that on other ventral surfaces smooth; dorsolateral folds absent; discoidal fold barely evident posteriorly; cloacal sheath short; ornamentation in cloacal region absent.

Ulnar tubercles absent; palmar tubercle elevated, bifid, about twice as large as ovoid thenar tubercle; subarticular tubercles prominent, round in ventral view and rounded in section; supernumerary tubercles absent; fingers lacking lateral fringes; Finger I shorter than Finger II; disc on Finger I slightly expanded; discs on Fingers II–IV expanded, elliptical, twice as wide as digit proximal to disc; ventral digital pads well defined by circumferential grooves (Fig. 3C).

Hind limbs moderately slender; tibia length 51.9% of SVL; foot length 52.3% of SVL; heel and outer edge of tarsus lacking tubercles; inner tarsal fold absent; inner meta-

tarsal tubercle elevated, ovoid, about 3× subconical outer metatarsal tubercle; toes unwebbed, lacking lateral fringes; discs on toes slightly smaller than those on fingers; all toes having ventral pads well defined by circumferential grooves; relative lengths of toes  $I < II < III < V < IV$ ; Toe V much longer than Toe III; disc on Toe V reaching distal edge of distal subarticular tubercle on Toe IV; disc on Toe III not reaching proximal border of distal subarticular tubercle on Toe IV (Fig. 3D).

Coloration of holotype in preservative: Dorsum grayish brown with dark brown markings consisting of narrow internarial bar, interorbital bar, labial bars, canthal and supratympanic stripes, transverse bars on limbs (three each on thigh, shank, and tarsus; two on forearm) and variously shaped marks on body—W-shaped mark in scapular region, roughly chevron-shaped mark at mid-length of body, pair of small spots in sacral region, and pair of larger square marks postsacrally. Flanks and anterior and posterior surfaces of thighs cream; two dark brown diagonal bars on anterior part of each flank; venter cream with minute brown flecks on throat, chest, and belly (Fig. 2 C and D).

Coloration of holotype in life: Unknown.

Measurements of holotype in mm: SVL 25.8, tibia length 13.4, foot length 13.5, head length 9.9, head width 9.5, IOD 3.5, width of upper eyelid 2.7, eye-nostril distance 2.9, diameter of eye 2.6, diameter of tympanum 1.0.

**Variation.**—The paratype, a male, has a SVL of 25.0 mm. Structurally, it is nearly identical to the holotype in having the head slightly longer than wide, eye-nostril distance greater than diameter of the eye, and foot slightly longer than the tibia. Minor differences exist in coloration. The paratype has a rather diffuse W-shaped mark in the scapular region, no chevron or sacral spots on the back, only two dark bars on each tarsus, and minute brown flecks only on the throat and chest.

**Etymology.**—The specific name is derived from the Greek *amydros* meaning indistinct and the Greek *otos* meaning ear. The name alludes to the undifferentiated tympanum and barely distinguishable tympanic annulus in this species.

*Eleutherodactylus vermiculatus* new species

**Holotype.**—FMNH 232330, adult female, from the Río Zaña, ca. 06°51' S, 79°06' W, 1800 m, Departamento de Cajamarca, Peru, on 9 May 1987 by John E. Cadle.

**Paratypes.**—FMNH 232296, an adult male, 231762, 231879, 231914, 231917, 231937, 232293–94, 232299, 232331–33, 232334, 232724, 232726–28, KU 307070–71, adult females, from the type locality, collected between 5 May and 25 June 1987 by John E. Cadle.

**Diagnosis.**—A member of the *Eleutherodactylus* (*Eleutherodactylus*) *unistrigatus* Group having (1) skin on dor-

sum smooth with or without a few minute tubercles; that on venter areolate; discoidal fold evident; dorsolateral folds absent; (2) tympanic membrane and tympanic annulus distinct, round, its length about one third length of eye; (3) snout moderately long, rounded in dorsal view, sloping anteroventrally and rounded terminally in profile; (4) upper eyelid with or without low tubercles, narrower than IOD; cranial crests absent; (5) vomerine teeth absent; (6) vocal slits present; nuptial pads absent; (7) Finger I shorter than II; discs on outer fingers elliptical, nearly truncate about twice width of digit proximal to pad; (8) outer fingers bearing lateral fringes distally; (9) one or two ulnar tubercles; (10) heel and outer edge of tarsus lacking tubercles; inner edge of tarsus lacking tubercles, bearing distinct fold distally; (11) inner metatarsal tubercle elevated, ovoid, about 2× ovoid outer metatarsal tubercle; supernumerary plantar tubercles minute, low; (12) toes lacking lateral fringes; webbing absent; Toe V much longer than Toe III; discs smaller than those on outer fingers; (13) dorsum brown with darker brown markings; venter cream with small irregular dark brown marks; (14) SVL 19.7 mm in one male; 20.8–35.3 mm in 18 females.

Among the Peruvian species of *Eleutherodactylus* that have a snout that slopes anteroventrally in profile, only *E. variabilis* and *E. vermiculatus* have expanded discs on the fingers and Toe V much longer than Toe III; *E. variabilis* differs from *E. vermiculatus* by having more truncate discs on the outer fingers, an acuminate (versus rounded) snout in dorsal view, and a prominent, large yellow spot bordered by black in the groin. The other species with anteroventrally sloping snouts (*E. atrabracus*, *flavomaculatus*, *lucida*, *stictoboubonus*, and *sulcatus*) have narrow, rounded discs on the fingers; in all of these except *E. lucida*, Toe V is only slightly longer than, or equal in length to, Toe III. Furthermore, *E. flavomaculatus* and *E. sulcatus* differ from *E. vermiculatus* by having cranial crests.

Many other Peruvian species of *Eleutherodactylus* have dark mottling on the belly that may form reticulations. Among these species, the tympanic annulus is either visible beneath the skin (*E. ardalonychus*, *infraguttatus*, and *rufioculis*) or absent (*E. ventrimaculatus*), in contrast to an externally prominent in *E. vermiculatus*. Several species with dark mottling or reticulations on the belly differ from *E. vermiculatus* by having Toe V only slightly longer than Toes III; these include *E. atrabracus*, *avicuporum*, *corrugatus*, *cuneirostris*, *infraguttatus*, *mercedesae*, *pinguis*, and *rufioculis*. In contrast to the barren heel in *E. vermiculatus*, the heels in *E. cryptomelas*, *diadematus*, *mucosus*, and *nephophilus* bear tubercles. The groin in *E. vermiculatus* has a single large dark spot, whereas that in *E. lindae* has black reticulations like those on the belly.

Among the sympatric species of *Eleutherodactylus*, *E. lymani* and *E. phalaroinguinis* differ from *E. vermiculatus*

by having smooth skin on the venter; also, the former is much larger (SVL in males to 45.3 mm, in females to 69.3 mm) and lacks markings on the belly, whereas the latter has a brown groin and thighs with distinct, round white spots. *Eleutherodactylus cajamarcensis* differs from *E. vermiculatus* by having a gray belly, rose-red groin, and the posterior surfaces of thighs black with white or red spots; *E. amydrotus* differs by having an indistinct tympanic annulus, minute brown flecks on the venter, and a cream groin and posterior surfaces of the thighs.

**Description of holotype.**—Adult male with slender body; head as wide as body, not as wide as long; head width 37.0% of SVL; head length 39.6% of SVL; head width 93.5% of head length; snout moderately long, rounded in dorsal view, sloping anteroventrally to rounded terminus in profile (Fig. 4A and B); diameter of eye more than eye-nostril distance; nostrils barely protuberant laterally; canthus rostralis shallowly curved in dorsal view, rounded in section; loreal region concave; lips rounded; upper eyelid bearing low tubercles; width of upper eyelid 75.0% of IOD; tympanic membrane and tympanic annulus distinct; annulus smooth, round; dorsal edge of annulus partially obscured by weak supratympanic fold; diameter of tympanum 34.5% of diameter of eye, separated from eye by distance slightly less than diameter of tympanum; two low, subconical postrictal tubercles. Choanae small, nearly round, not concealed by palatal shelf of maxillae; vomerine teeth absent; tongue narrowly cordiform, deeply notched posteriorly, free behind for about one-half of its length.

Skin on dorsum smooth a few minute tubercles dorsolaterally on body; skin on belly and lower posterior surfaces of thighs areolate; that on other ventral surfaces smooth; dorsolateral folds absent; discoidal fold evident; cloacal sheath short; ornamentation in cloacal region absent.

Two low ulnar tubercles; palmar tubercle elevated, divided longitudinally, inner part smaller than elevated, elliptical thenar tubercle; subarticular tubercles low, round; supernumerary tubercles numerous, about one-half size of subarticular tubercles; lateral fringes present on outer edge of Finger IV and on penultimate section of Finger III; Finger I shorter than Finger II; disc on Finger I slightly expanded; discs on Fingers II–IV expanded, elliptical, nearly truncate, twice as wide as digit proximal to disc; ventral digital pads well defined by circumferential grooves (Fig. 4C).

Hind limbs moderately slender; tibia length 54.2% of SVL; foot length 46.2% of SVL; heel and outer edge of tarsus lacking tubercles; inner tarsal fold distinct on distal third of tarsus; inner metatarsal tubercle elevated, ovoid, about 2× ovoid outer metatarsal tubercle; plantar supernumerary tubercles minute, low; toes unwebbed, lacking



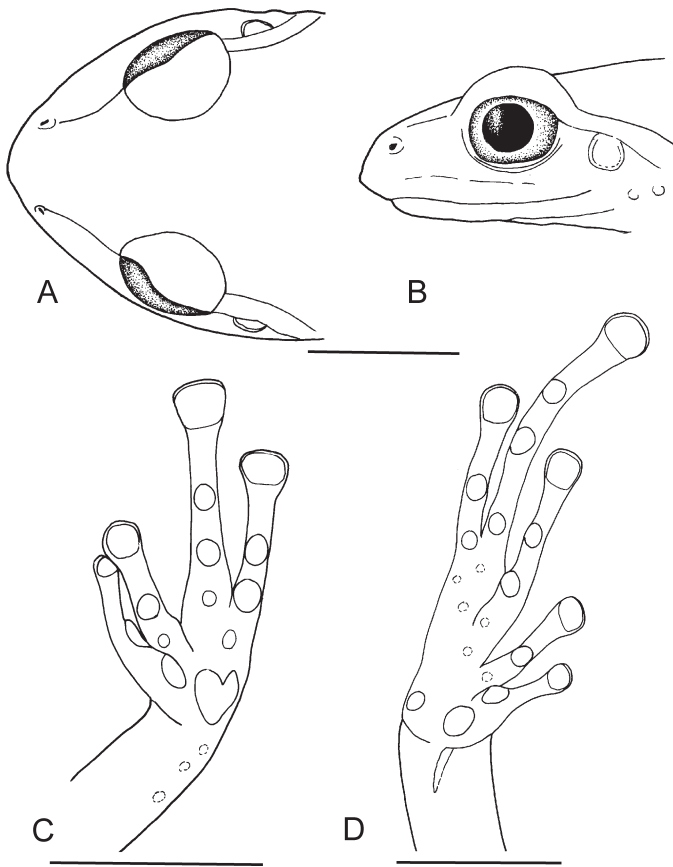


Fig. 4. Holotype of *Eleutherodactylus vermiculatus* FMNH 232330: A. Dorsal view of head. B. Lateral view of head. C. Palmar view of hand. D. Plantar view of foot. Scale bars = 5 mm.

lateral fringes; discs on toes slightly smaller than those on fingers; all toes having ventral pads well defined by circumferential grooves; relative lengths of toes I < II < III < V < IV; Toe V much longer than Toe III; disc on Toe V reaching distal edge of distal subarticular tubercle on Toe IV; disc on Toe III not reaching proximal border of distal subarticular tubercle on Toe IV (Fig. 4D).

Coloration of holotype in preservative: Dorsum pale brown with dark brown markings consisting of broad interorbital bar with median posterior extension, faint labial bars, supratympanic stripe, pair of small postsacral spots, and two transverse bars on shank and one on tarsus. Flanks and anterior and dorsal surfaces of thighs cream; large dark brown spot posteriorly on flank; two diagonal brown bars on dorsal surface of each shank; venter cream with irregular small brown marks on throat, chest, and belly (Fig. 2E and F).

Coloration of holotype in life: Unknown.

Measurements of holotype in mm: SVL 27.3, tibia length 14.8, foot length 12.6, head length 10.8, head width 10.1, IOD 2.8, width of upper eyelid 2.1, eye-nostril distance 2.7, diameter of eye 2.9, diameter of tympanum 1.0.

**Variation.**—Structurally, all of the paratypes are essentially like the holotype. Coloration in most specimens is like that of the holotype. All but two individuals have well-defined vermiculations on the chest and belly; the exception have small brown dots. A discrete interorbital bar is present in 11 specimens; in six of these there is a posteromedial extension giving a triangular appearance to the interorbital bar. Faint labial bars are present in only six specimens, but a supratympanic stripe is evident in all specimens. The dorsal markings on the body vary from a few small dark brown spots to several larger spots, but no individuals have chevrons or a W-shaped mark in the scapular region. All specimens have diagonal brown bars on the dorsal surfaces of the thighs, and with the exception of the two specimens described below, all individuals have one to three diagonal dark marks on the flanks.

Two specimens have distinctly different dorsal color patterns, but the ventral color pattern is like the others. One individual (FMNH 232332) has a pale brown dorsum bordered by dark brown dorsolateral stripes extending from the posterior corner of the orbit to the groin; there is a narrow brown middorsal line (Fig. 2G). This individual has a triangular interorbital bar, faint labial bars, and a distinct supratympanic stripe. Another individual (FMNH 231937) has a brown dorsum with broad, pale tan dorsolateral stripes that are continuations of a narrower cream stripe that encircles the snout; these stripes extend to the groin and are bordered above by a narrow brown line (Fig. 2H). The flanks are dark brown. A broad ventrolateral cream stripe extends from the angle of the jaw to the groin. This individual has an interorbital bar and supratympanic stripe but lacks labial bars.

The following measurements (in mm) are for the single male followed by those of 18 females with the mean and one standard deviation in parentheses: SVL 19.7, 20.8–35.3 (25.2 ± 3.1); tibia length 10.6, 12.1–17.3 (14.2 ± 1.1); foot length 9.3, 9.6–15.2 (12.1 ± 1.3); head length 7.8, 8.8–12.3 (10.0 ± 0.8); head width 7.2, 7.4–13.1 (9.5 ± 1.2); IOD 2.4, 2.5–4.1 (3.0 ± 0.4); eyelid width 1.7, 1.8–2.7 (2.2 ± 0.2); eye-nostril distance 1.6, 2.2–3.7 (2.8 ± 0.3); eye diameter 2.5, 2.4–3.7 (2.9 ± 0.3); tympanum diameter 0.7, 0.9–1.6 (1.1 ± 0.2). All proportions for the single male are within the range of variation of the 18 females; these ranges are: tibia length/SVL 0.49–0.62, foot length/SVL 0.43–0.53, head length/SVL 0.35–0.44, head width/SVL 0.35–0.40, head width/head length 0.84–1.07, eyelid width/IOD 0.57–1.00, eye-nostril distance/eye diameter 0.59–1.08, tympanum diameter/eye diameter 0.35–0.50.

**Etymology.**—The specific name, *vermiculatus*, is a Latin adjective meaning worm-like and is used in reference to the brown marks on the venter.

## ELEUTHERODACTYLUS IN THE CORDILLERA OCCIDENTAL

Two species of *Eleutherodactylus* (*E. cajamarcensis* and *E. lymani*) have extensive ranges in the Cordillera Occidental in Peru; both also extend northward into the Huancabamba Depression and the southern part of the Cordillera Occidental in Ecuador. Many specimens of both of these species were collected by Cadle in the Río Zaña Valley. The species of *Eleutherodactylus* in the Cordillera Occidental in Peru include the two aforementioned species with broad distributions and 13 species with more limited distributions, including *E. amydrotus*, *phalaroinguinis*, and *vermiculatus* described herein (Fig. 5).

*Eleutherodactylus lymani* occurs at elevations of 130–1800 m on the Pacific slopes of the Cordillera Occidental in Peru, at an elevation of 725 m in the upper Río Marañón Valley, at elevations of 610–1600 m on the Pacific slopes of the Cordillera Occidental in Ecuador, and up to 3000 m in subparamo in Provincia Loja in southern Ecuador. The

range of this species extends southward into the Departamento de Lambayeque; it extends farther south than any other species on the lower Pacific Slopes, where it is most commonly found near streams in thorn forest.

*Eleutherodactylus cajamarcensis* has nearly as extensive a distribution as *E. lymani*. It is known from elevations of 1800–2500 m on the Pacific slopes of the Cordillera Occidental in Peru, 2500–2800 m in the interior of the Cordillera Occidental in Peru, 1800 m on the Pacific slopes of the Cordillera Occidental in Ecuador, and from 1870–3100 m in the Huancabamba Depression to subparamo in the Andes of southern Ecuador and the Cordillera de Huancabamba in northern Peru (Fig. 6). The valley of the Río Zaña is the southernmost known locality for the species, which inhabits subparamo, humid montane forest, and thorn forest. Individuals are frequently found in arboreal bromeliads.

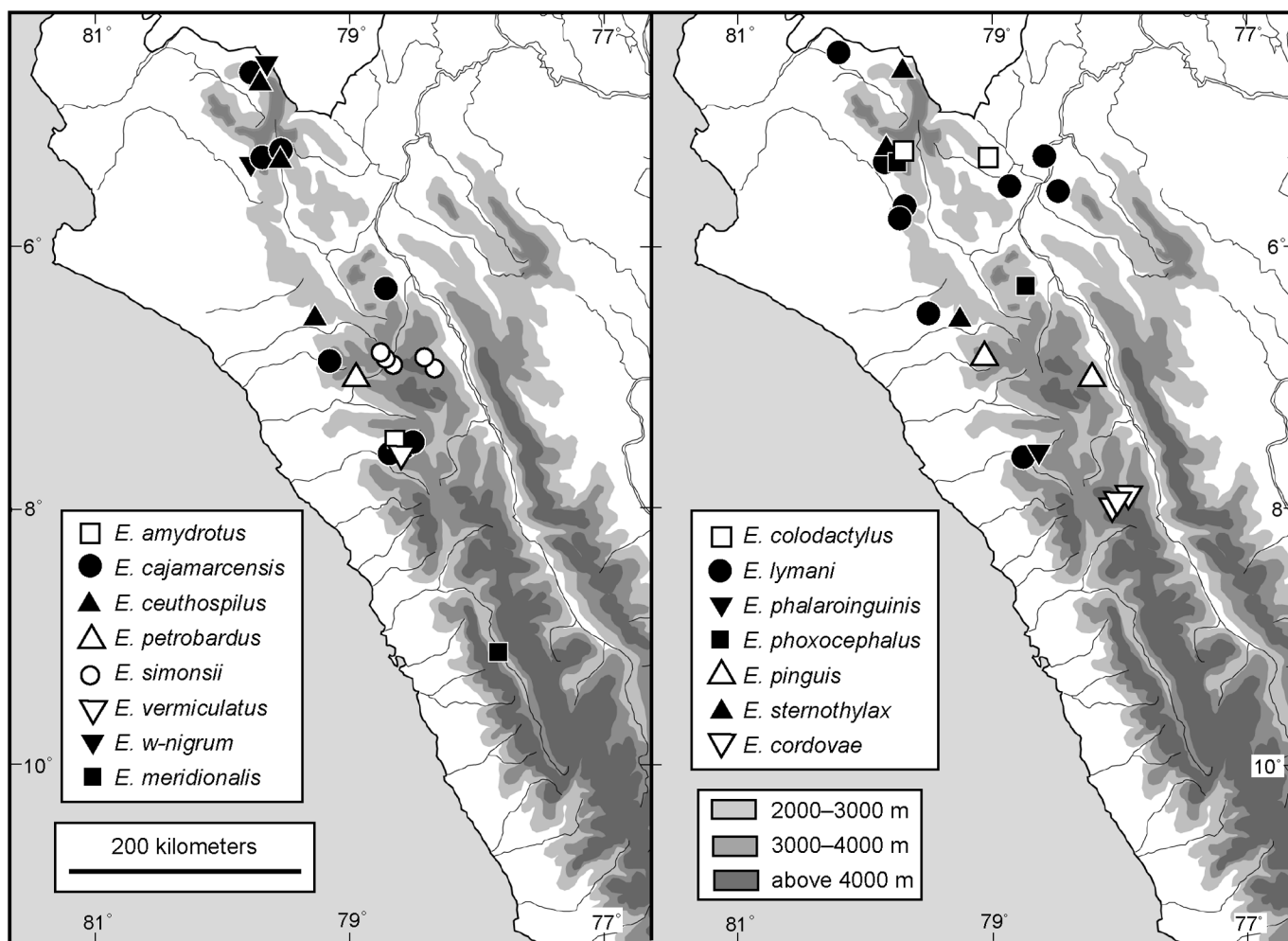


Fig. 5. Localities of occurrence of 15 species of *Eleutherodactylus* in the Cordillera Occidental and Cordillera de Huancabamba in northwestern Peru.

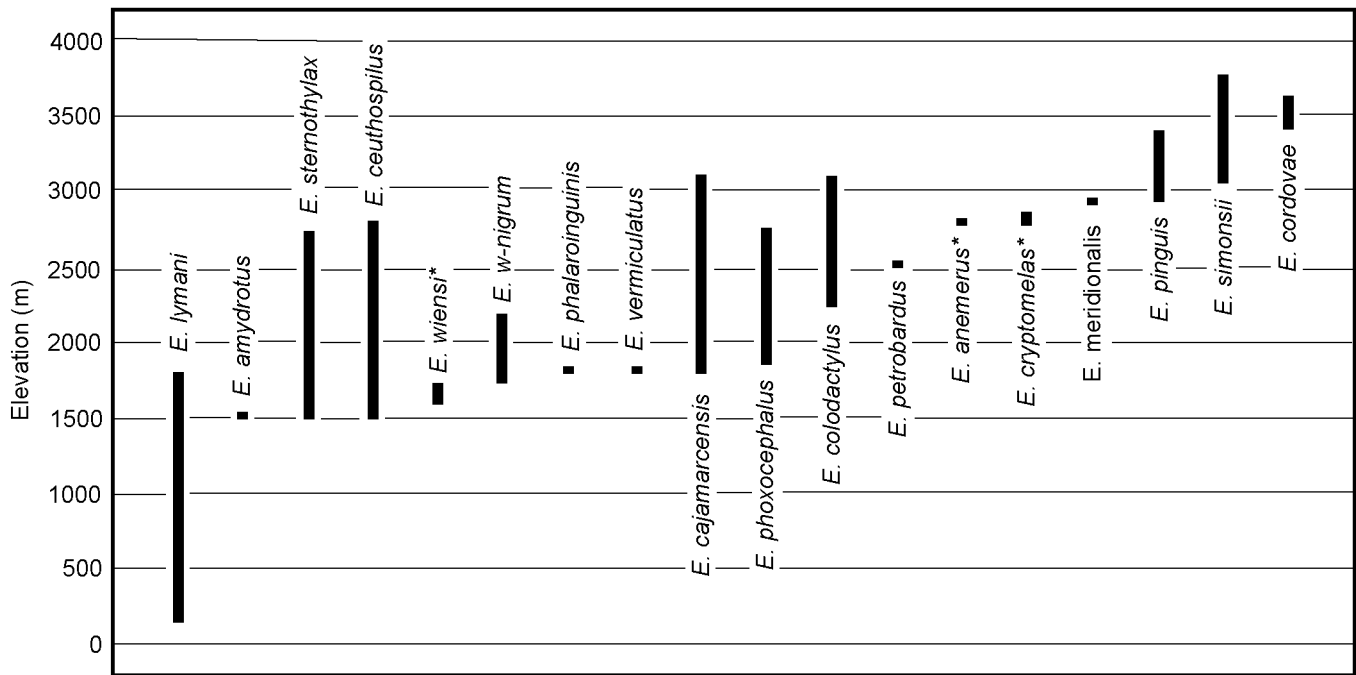


Fig. 6. Altitudinal distribution of 18 species of *Eleutherodactylus* on the Pacific Versant of the Cordillera Occidental and the Cordillera de Huancabamba in northwestern Peru. An asterisk denotes species known in Peru solely in the Cordillera de Huancabamba.

*Eleutherodactylus ceuthospilus* is known from elevations of 1735–2870 m in humid montane forest on the western slopes of the Cordillera de Huancabamba and from thorn forest at an elevation of 1500 m on the Pacific slope of the Cordillera Occidental (Duellman and Pramuk, 1999).

*Eleutherodactylus colodactylus*, which occurs in humid montane forest at elevations of 2195–3140 m in the Andes of southern Ecuador, previously has been known in Peru only from humid montane forest at elevations of 2870–3100 m in the Cordillera de Huancabamba. Herein we report it from the ridge above San José de Lourdes, ±2250 m, in the Cordillera Occidental in Departamento de Cajamarca, LSUMZ 47797.

*Eleutherodactylus cordovae* is known from three localities at elevations of 3400–3642 m in the Cordillera Occidental in the Departamento de Libertad (Lehr and Duellman, 2007).

*Eleutherodactylus meridionalis*, known from a single locality at 2900 m in the Río Santa Ana Valley in Departamento de Ancash, is the southernmost record for the genus in the Cordillera Occidental (Lehr and Duellman, 2007).

*Eleutherodactylus petrobardus* is known only from one locality in dry scrub forest at an elevation of 2500 m on the Pacific slope of the Cordillera Occidental in the Departamento de Cajamarca (Duellman, 1991).

*Eleutherodactylus phoxocephalus* is widespread at elevations of 1800–3100 m in the Cordillera Occidental in central and southern Ecuador. It remains known from only

1850–2770 m in the Cordillera de Huancabamba, and a single locality, San Andres de Cutervo, ±2500 m, in the Cordillera Occidental.

*Eleutherodactylus pinguis* has been reported previously only from an elevation of 3050 m south of Celendín in eastern Departamento de Cajamarca (Duellman and Pramuk, 1999). Twelve additional specimens are from two localities on the high western slopes of the Cordillera Occidental in Departamento de Cajamarca—near Chugur, 2900–3000 m, SMF 81763–65, and Hacienda Taulis, ca. 6° 50' S, 79° 10' W, 3100–3400 m, SMF 81754–62.

*Eleutherodactylus simonsii*, formerly in the genus *Phrynosus*, was transferred to *Eleutherodactylus* by Lehr et al. (2005) and assigned to the *Eleutherodactylus orestes* Group by Duellman et al. (2006). This species is widespread in humid puna at elevations of 3050–3760 m in the northern part of the Cordillera Occidental in the Departamento de Cajamarca (Duellman, 2000).

*Eleutherodactylus sternothylax* previously was known only from elevations of 1735–1840 m in humid montane forest on the western slopes of the Cordillera de Huancabamba (Duellman and Pramuk, 1999). Herein we report the species from three localities in the Cordillera Occidental—Chota, 12 km [by road] W Llama, 1500 m, Departamento de Cajamarca, MHNSM 6198 and two localities in Departamento de Piura: Cerro Aypate, 2710 m, MHNSM 17068–77, and Toronche, 16 km SE Ayabaca, 1950–2100 m, MHNSM 17079.

*Eleutherodactylus w-nigrum* is widespread in humid

montane forests and subparamo at elevations of 800–3300 m in the Cordillera Occidental and the Cordillera Oriental in Ecuador and extends well into Colombia. In Peru, it is known from two localities in humid montane forest at elevations of 1740 m in the Cordillera de Huancabamba and 2200 in the northern part of the Cordillera Occidental in the Departamento de Piura (Lehr and Aguilar, 2004).

Thus, in contrast to the summary by Duellman and Pramuk (1999), who recorded only five species of *Eleutherodactylus* from the Cordillera Occidental in Peru, we record 15 species. Four of these species (*E. cajamarcensis*, *lymani*, *phoxocephalus*, and *w-nigrum*) are shared with the Cordillera Occidental in Ecuador, and five species (*E. cajamarcensis*, *ceuthospilus*, *colodactylus*, *phoxocephalus*, and *sternothylax*) are shared with the Cordillera de Huancabamba. No species is shared with either the Cordillera Central or Cordillera Oriental in Peru.

The collections made by Cadle in the Río Zaña Valley reveal that the two geographically widespread species, *Eleutherodactylus cajamarcensis* and *E. lymani* have broad elevational ranges in the valley, 1555–2630 m and 1250–2240 m, respectively. Their elevational ranges encompass those of the other three species—*E. amydrotus* at 1500 m and *E. phalaroinguinis* and *E. vermiculatus* at 1800 m. Therefore, it seems that the largest community of *Eleutherodactylus* is composed of four species at 1800 m.

Four species also are sympatric at El Tambo at an elevation of 2770 m on the western slopes of the Cordillera de Huancabamba and at 1700 m on the western slope of the Cordillera Colán (Duellman and Pramuk, 1999). *Eleutherodactylus* communities are slightly larger on the Amazonian slopes of the Andes—five species each at Abra

Tangarana, 1080 m and Río Cosñipata (Duellman and Pramuk, 1999, and Duellman, 1978a, respectively).

To anyone who has worked extensively with these frogs in the field in western South America, it is obvious that *Eleutherodactylus* communities contain more species in wetter environs than in drier ones. For example, in contrast to the Peruvian sites mentioned above, communities on the Pacific slopes of the Ecuadorian Andes are composed of 6–16 species (Lynch and Duellman, 1997) and those of the Amazonian slopes of 8–14 species (Lynch and Duellman, 1980). Likewise, there is a north-south gradient in rainfall in the Amazon Basin. At Santa Cecilia on the equator in Ecuador, there are 16 species of *Eleutherodactylus* (Duellman, 1978b), whereas there are 14 species at the Río Lullapichis in central Peru (Schlüter, 2005) and only eight at Cusco Amazónico in southern Peru (Duellman, 2005).

Although most of the Pacific slopes of the Cordillera Occidental in Peru are relatively dry and provide a rather harsh environment for anurans, there are pockets of humid habitats that do harbor *Eleutherodactylus* and other kinds of anurans (e.g., centrolenids [Cadle and McDiarmid, 1990] and *Colostethus* [Duellman, 2004]). These pockets of humid habitats presumably are relicts of former more widespread and contiguous environments that were disrupted during Pleistocene climatic changes, resulting in vicariant speciation as proposed for *Eleutherodactylus* in Ecuador by Lynch and Duellman (1997). We strongly suspect that investigation of these relictual habitats in the Cordillera Occidental will reveal additional new species of anurans.

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## APPENDIX SPECIMENS EXAMINED

### *Eleutherodactylus cajamarcensis*

ECUADOR: AZUAY: Luz María, 1800 m, KU 217853–56. LOJA: 5 km NE Cariamanga, 1870 m, KU 141896–909; 12 km NE Catacocha, 2060 m, KU 141890–95; 9 km E Loja, 2660 m, KU 119949–50; 12.5 km S Loja, 2250 m, KU 165190–92; 6 km N San Lucas, 2760–2900 m, KU 120007–15, 165193–99; 7–8 km N San Lucas, 2940–3000 m, KU 119951–909, 120006 (5); 13 km E Veracruz, 2250 m, KU 141860–89.

PERU: CAJAMARCA: Pre-Incan ruins near Huambos, MCZ 5407; Quebrada Cachil, 3 km SW Contumaya, 2550 m, MHNSM 17063–64, 17090–97; Quebrada Chorro Blanco, 2530–2650 m, MHNSM 17065–66; San Andres de Cutervo, 2800 m, KU 221706–09, MHNSM 16567. PIURA: between Canchaque and Huancabamba, 3100 m, KU 135495, 135502; Cerro Aypate, 2710–2800 m, MHNSM 17062, 17067, 17087–89; 25.5 km [by road] SW Huancabamba, 3010 m, KU 181250–61; 26 km [by road] SW Huancabamba, 3050 m, KU 196508; 29.3 km [by road] SW Huancabamba, 3100 m, KU 181244–49; Toronche, Cerro Aypate, 16 km SE Aypate, 1950–2100 m, MHNSM 17080, 17081–86.

### *Eleutherodactylus ceuthospilus*

PERU: CAJAMARCA: 12 km [by road] W Llama, 1500 m, KU 212215–18. PIURA: 15–16 km [by road] E Canchaque, 1735–1840 m, KU 181270, 181272–78, 196492–98, 219775 (holotype), 219776–85, LSUMZ 32321–31, MHNSM 15387–07; 29 mi (46 km) [by road] E Canchaque, 9200 ft (2840 m), UF 34103.

### *Eleutherodactylus lymani*

ECUADOR: AZUAY: 4 km SW Cataviña, 1600 m, USNM 212019; 55.4 km E Pasaje, 1000 m, KU 152009; Río Minas, 20 km W Santa Isabel, 1250 m, USNM 212020. EL ORO: Cordillera de Chilla, Llanos de Guavos, AMNH 13738; El Chiral, AMNH 13961, 13964; Guainche, AMNH 13256; Piñas, AMNH 16257; Porto Velo, 610 m, AMNH 16334. 16339, 16341–44. LOJA: Loja, 2150 m, KU 119502; 2 km E Loja, 2210 m, 119504–12; 7 km E Loja, 2100 m, 2500 m, KU 119503; 7.6 km S Loja, 2210 m, KU 141962–64; 9 km S Loja, 2230 m, KU 165539–40; 12.2 km S Loja, Río Malacatos Valley, 2275 m, KU 141292; 17 km NE Macará, 1240 m, KU 141965; Pta. Santa Ana, 1100 m, AMNH 13734, 13966, 13973; Río Puyango, AMNH 16211–15, 16224.

PERU: AMAZONAS: 6.1 km NW Bagua Grande, TCWC 28767; 15.5 km W Bagua Grande, LACM 49175–79. CAJAMARCA: Bellavista, USNM 118189; 0.5 km E Bellavista, 1725 m, LACM 49162–74, 49277–79; TCWC 28747–66, 28921; Perico, AMNH 7552, 83923; 2.5 mi S Puerto Tautorapa, 617 m, MVZ 92868; San José de Lourdes, MHNSM 597; 28 km [by road] N Santa Cruz, 725 m, KU 196464, 196509. LAMBAYEQUE: Chongoyape, Quebrada Chaparri, 451 m, MHNSM 21905; near Molino, 7 km N, 21 km E Olmos, 710 m, MVZ 82517; 16 km N, 25 km E Olmos, 133 m, MVZ 82512–16; 20 km E Olmos, LACM 122812; San Isidro, 500 m, LSUMZ 52563. PIURA: 15 km [by road] E Canchaque, 1740 m, KU 181266–67, 196465–69. TUMBES: Los Naranjos, 620 m, MHNSM 17621–38, 17643–44, 17646–48, 17650–54, 17696.

### *Eleutherodactylus petrobardus*

PERU: CAJAMARCA: ca. 2 km W Huambos, 2500 m, KU 212292 (holotype), 212293–06, MHNSM 6196–97.

### *Eleutherodactylus phoxocephalus*

ECUADOR: AZUAY: 10 km SW Victoria del Portete, 2700 m, KU 131281–82. CAÑAR: 18 km NW El Tambo, 2960 m. COTOPAXI: Pilaló, 2460 m, KU 131404–78, 131480–88, 131698–716, 142075–103. IMBABURA: La Delicia, 2710 m, KU 179387. LOJA: Saraguro, 2500 m, 135460–62; Río Zamora, 6.5 km N Loja, 2060, KU 142113. PICHINCHA: 7.7 km E Chiriboga, 2120 m, KU 142063–71; Quebrada Zapadores, 5 km ESE Chiriboga, 2010, KU 165556–58. ZAMORA-CHINCHIPE: 15 km E Loja, 2710 m, KU 142104–12.

PERU: CAJAMARCA: San Andres de Cutervo, 3520 m, KU 221710–13. PIURA: 15 km [by road] E Canchaque, 1740 m, KU 181271.

### *Eleutherodactylus pinguis*

PERU: CAJAMARCA: 23 km [by road] SW Celendín, 3050 m, KU 181282, 181283 (holotype), 181284; near Chugur, 2900–3000 m, SMF 81763–65; Hacienda Taulis, ca. 6° 50' S, 79° 10' W, 3100–3400 m, SMF 81754–62.

### *Eleutherodactylus simonsii*

PERU: CAJAMARCA: Abra Comulica, 20 km [by road] NE Encanada, 3520 m, KU 181391, 212368–402; south slope Abra Quilsh, 26 km [by road] NNW Cajamarca, 3500 m, KU 212346–47; south slope Abra Quilsh, [by road] 28 km NNW Cajamarca, 3520 m, KU 212348–67, MHNSM 6036–42; 55 km [by road] N Cajamarca, KU 212403–10; 57 km [by road] N Cajamarca, 3760 m, UF 104018–19; 30 km [by road] NNW Cajamarca, 3640 m, UF 103998–409; 45 km [by road] NNW Cajamarca, 3640 m, UF 104010–17; Celendín, 3200 m, MHNSM 1526–27, 1546–48; 23 km [by road] SW Celendín, 3050 m, KU 181357–60; 33 km SW [by road] Celendín, 3200 m, KU 181361–90; 15 km [by road] NE Encanada, 3540 m, UF 104020–25; 19 km [by road] NE Encanada, 3650 m, UF 104026–28; 23.5 km [by road] NE Encanada, 3510 m, MHNSM 1163–79; 26 km [by road] NE Encanada, 3650 m, UF 104029–31; 28 km [by road] NE Encanada, 3540 m, ROM 16403, 16414, 16394, 16396, 16402, 16404–06, 16409–10.

### *Eleutherodactylus sternothylax*

PERU: CAJAMARCA: Chota, 12 km [by road] W Llama, 1500 m, MHNSM 6198. PIURA: Cerro Aypate, 2710 m, MHNSM 17068–77; 15 km [by road] E Canchaque, 1735 m, KU 196479–91, LSUMZ 32439–42; 16 km [by road] E Canchaque, 1840 m, KU 219793 (holotype), 219794; Toronche, Cerro Aypate, 16 km SE Ayabaca, 1950–2100 m, MHNSM 17079.





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