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# Eleutherodactyline Frogs (Anura: Leptodactylidae) from the Cordillera Yanachaga in Central Peru

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**A small collection of anurans from the Cordillera Yanachaga in central Peru revealed the presence of 10 species of *Eleutherodactylus*. Four of these species are unknown elsewhere and are described herein. Three of the new species are members of the immense *Eleutherodactylus unistrigatus* group, and one belongs with the smaller, South American *Eleutherodactylus conspicillatus* group. The 83 described species of *Eleutherodactylus* known in Peru belong to six species groups that have different patterns of distribution. Most species in the cloud forest in the Cordillera Oriental, Cordillera Central, and associated ranges have small latitudinal and elevational distributions.**

**Una pequeña colección de anuros de la Cordillera Yanachaga en el centro del Perú ha revelado la presencia de 10 especies de *Eleutherodactylus*. Cuatro de estas especies son únicas de esta región y se describen en este trabajo. Tres de las especies nuevas pertenecen al inmenso grupo *Eleutherodactylus unistrigatus* y la especie adicional pertenece al grupo *Eleutherodactylus conspicillatus*. Las 83 especies de *Eleutherodactylus* conocidas en el Perú están incluídas en seis grupos de especies que tienen diferentes patrones de distribución. La mayoría de las especies que habitan los bosque nublados de la Cordillera Oriental, Cordillera Central y serranías asociadas presentan rangos de distribución latitudinal y altitudinal restringidos.**

THREE genera of Eleutherodactylinae (*sensu* Duellman, 2003, and Frost, 2004) are conspicuous members of the anuran fauna in the Andes from Bolivia northward. Of these, frogs of the genus *Eleutherodactylus* are a major component of the anuran faunas in the humid montane forests in the Andes of Colombia, Ecuador, and Peru. Diversity is highest on the Pacific versant of the Cordillera Occidental in Colombia, where Lynch (1998) reported 76 species at elevations of 1000–3000 m. Fifty-one species are known from elevations of 1000–3000 m on the western slopes of the Andes in Ecuador (Lynch and Duellman, 1997), and 45 species are known from the same elevations on the Amazonian slopes of the Andes in Ecuador (Lynch and Duellman, 1980). The number of species seems to dwindle to the south. Duellman and Pramuk (1999) reported 45 species in all of the Andean cordilleras in northern Peru; 16 of these occur on the Amazonian slopes of the northern part of the Cordillera Central. Farther south the Amazonian slopes seem to have even fewer species, but this may be an artifact of inadequate sampling.

In central Peru, the Cordillera Yanachaga is an isolated mountain range to the east of the Andes and rising to over 4000 m (Hedges, 1990: Fig. 2). Much of the upper elevations are within Parque Nacional Yanachaga Chemillén. In late June and early July 1987, one of us (SBH) made a small collection of anurans in the vicinity of Oxapampa (ca. 1900–2000 m), in humid montane forest on the higher slopes (ca. 2600 m) of the Cordillera Yanachaga just to the east of Oxapampa, and in forest at a lower elevation (900–1200 m) to the southeast near Cacazú along the Río Cacazú. Most frogs were collected from concealed locations, even at night, and few anuran vocalizations were heard, presumably because of the seasonally dry conditions. Nonetheless, these limited collections contained a variety of eleutherodactyline frogs, including *Phrynopus bracki* described by Hedges (1990), *Eleutherodactylus sagittulus* named by Lehr at al. (2004a), and *Eleutherodactylus bromeliaceus* reported by Morales and Icochea (2000). Jars containing at least four undescribed species of *Eleutherodactylus* have gathered dust in the offices of the authors for 17 years. We now provide descriptions of these new species and a brief summary of the eleutherodactyline fauna of the Cordillera Oriental in central Peru.

## MATERIALS AND METHODS

Treatment of animals in the field followed the standardized guidelines (Anonymous, 1987). Color photographs of living frogs were taken. Subsequently, frogs were euthanized in ice water, tissues were removed and stored in liquid nitrogen, and specimens were fixed in

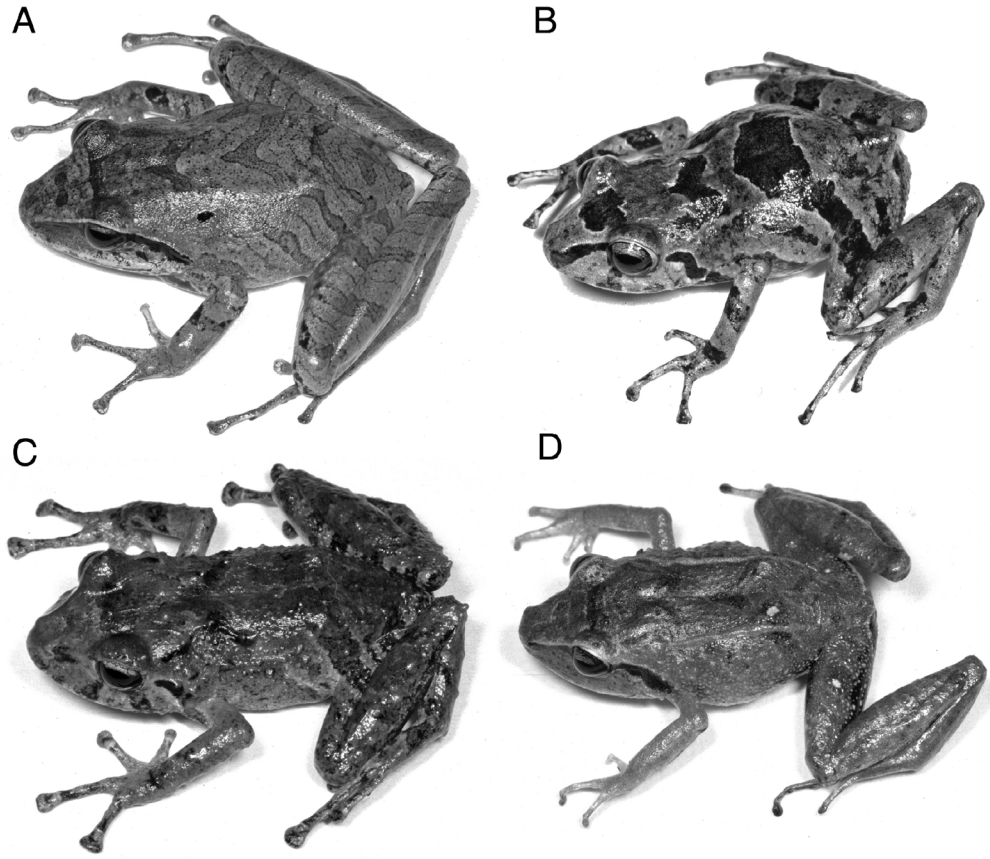


Fig. 1. New species of *Eleutherodactylus*. (A) *E. bipunctatus*, KU 291638, female, 35.5 mm SVL. (B) *E. aniptopalmatus*, KU 291626, female, 22.0 mm SVL. (C) *E. rhabdocnemus*, KU 291646, female, 24.5 mm SVL. (D) *E. stictogaster*, KU 291659, female, 20.5 mm SVL. Photographs by S. Blair Hedges.

10% formalin (4% formaldehyde); specimens were later transferred to 70% ethanol. Tissue samples were taken from some of the specimens and frozen in liquid nitrogen. A portion of the mitochondrial 12S rRNA gene (~350 nucleotides) was sequenced and compared in samples from Peru and in several species from elsewhere in South America. A phylogenetic tree was constructed with minimum evolution (Tamura-Nei model), using bootstrapping (2000 replications) and rooted with a sequence of *Rana pipiens* (Genbank accession Y10945). Genbank numbers for the eleutherodactyline frogs mentioned herein are Y964066–89. Detailed methods are described elsewhere (Feller and Hedges, 1998).

The format of species diagnoses and descriptions follow those of Lynch and Duellman (1997). Measurements were taken with dial calipers and rounded to the nearest 0.1 mm. Snout-vent length is abbreviated SVL throughout. Abbreviations of museum depositories are KU = Natural History Museum, University of Kansas; MTD = Museum für Tierkunde, Dresden; NHMG = Naturhistoriska Museet, Göteborg; and USNM = National Museum of Natural History.

## Results

### *Eleutherodactylus bipunctatus*, new species
Figure 1A

*Holotype.*—KU 291638, an adult female, Peru, Departamento de Pasco, Provincia de Oxapampa, 0.7 km south and 4.5 km east (airline) of Oxapampa, approximately 10°34′S, 75°24′W, 2120 m elevation, S. B. Hedges, 2 July 1987.

*Referred specimens.*—All juveniles, KU 291639–43 collected with the holotype, and KU 291644–45 from about 1 km SE of La Suiza, 2060 m elevation, S. B. Hedges, 11 July 1987.

*Diagnosis.*—A member of the *Eleutherodactylus* (*Eleutherodactylus*) *conspicillatus* group having (1) skin on dorsum finely shagreen, that on venter weakly areolate; discoidal fold evident; dorsolateral folds present; (2) tympanic membrane smooth; tympanic annulus prominent, round, its length about two-thirds length of eye; (3) snout long, bluntly rounded in dorsal view, nearly truncate in profile; (4) upper eyelid lacking tubercles, narrower than IOD; cranial crests absent; (5) vomerine odontophores prominent, oblique; (6) vocal slits present; nuptial pads absent; (7) Finger I about equal in length to Finger II; discs on outer fingers expanded, broadly rounded, more than twice width of digit proximal to pad; (8) fingers lacking lateral fringes; (9) ulnar tubercles absent; (10) heel and tarsus lacking tubercles and folds; (11) inner metatarsal tubercle, elevated, elliptical, about 3× subconical outer metatarsal tubercle; supernumerary plantar tubercles absent; (12) toes lacking lateral fringes; basal webbing between Toes IV and V; Toe V slightly longer than Toe III; discs slightly smaller than those on fingers; (13) dorsum tan with faint narrow brown chevrons and pair of black spots in scapular region venter cream with faint brown mottling on throat; posterior surfaces of thighs brown with cream flecks; (14) SVL 35.5 mm in female.

The definition of the *Eleutherodactylus conspicillatus* group by Lynch and Duellman (1997) was modified slightly by Duellman and Pramuk (1999) by the inclusion of five additional species from Peru; the addition of *E. bipunctatus* does not change the definition of the group, which is made up of frogs having long snouts, relatively narrow heads, and Toe V only slightly longer than Toe III.

There are now 24 species of the *Eleutherodactylus conspicillatus* group known from the Amazonian slopes of the Andes in Colombia, Ecuador, Peru, and Bolivia, and in the Amazonian-Guianan region. Fifteen of these species (*E. caliginosus*, *citriogaster*, *condor*, *conspicillatus*, *fenestratus*, *gutturalis*, *lanthanites*, *lymani*, *malkini*, *metabates*, *peruvianus*, *samaipatae*, *vilarsi*, *w-nigrum*, and *zeuctotylus*) differ from *E. bipunctatus* by having smooth skin on the belly and Finger I longer than Finger II. Three other species (*E. cuneirostris*, *savagei*, and *skydmainos*) are like *E. bipunctatus* in having Fingers I and II equal in length, but they differ from *E. bipunctatus* by having smooth skin on the belly. The other five species of the group are like *E. bipunctatus* in having weakly areolate skin on the belly. Of these, Fingers I and II are equal in length in *E. karcharias*, which is unique among members of the group by having a finlike middorsal tubercle and low cranial crests (Flores and Rodríguez, 1997). *Eleutherodactylus buccinator* differs from *E. bipunctatus* by having Finger I longer than Finger II, an X-shaped ridge the scapular region, a subacuminate snout in dorsal view, and pink spots in the groin and on the hidden surfaces of the thighs (Rodríguez, 1994). In two other species with areolate venters, Finger I is slightly longer than Finger II; of these, *E. avicuporum* differs from *E. bipunctatus* by having scattered tubercles on a smooth dorsum, many small tubercles on the upper eyelids, lateral fringes on the fingers, and a low tarsal fold, whereas *E. medemi* differs by small tubercles on the upper eyelids and lateral fringes on the fingers and toes (Lynch, 1994). *Eleutherodactylus carranguerorum* differs from *E. bipunctatus* by having short dorsolateral folds and lateral fringes on the fingers and toes.

As emphasized by Lynch (1980), the distinctiveness of *Eleutherodactylus conspicillatus* (Günther) and *E. peruvianus* (Melin) is questionable. Accordingly, we compared diagnostic features of *E. bipunctatus* with the diagnosis of *E. peruvianus* based on the holotype (NHMG 490) by Köhler (2000). The holotype of *E. peruvianus*, an adult female with a SVL of 41.5 mm, differs from *E. bipunctatus* by having the skin on the venter smooth, snout subacuminate in dorsal view and rounded in profile, Finger I much longer than Finger II, and fingers and toes bearing narrow lateral fringes.

*Description.*—Head as wide as body; head width 35.8% of SVL; head length 40.0% of SVL; snout long, shallow, bluntly rounded in dorsal view, nearly truncate in profile, protruding slightly beyond margin of lower lip; eye-nostril distance 102.3% of length of eye; nostrils barely protuberant, directed laterally at level well behind anterior margin of lower lip. Canthus rostralis straight, acutely rounded in section, not elevated; loreal region slightly concave; lips rounded; internarial region and top of head flat; upper eyelid lacking tubercles, its width 82.9% of interorbital distance; supratympanic fold elevated, curved from posteroventral edge of orbit to point above insertion of arm, barely obscuring dorsal edge of tympanum; tympanic annulus distinct, smooth; tympanum nearly round, 59.5% of diameter of eye, separated from eye by distance equal to diameter of tympanum; enlarged postrictal tubercles absent. Choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores prominent, oblique, narrowly separated medially, at level behind posterior margins of choanae, each odontophore bearing six teeth; tongue about

twice as long as wide, notched behind, posterior one-third not adherent to floor of mouth.

Skin on dorsum shagreen with small tubercles in scapular region and on posterior part of body; skin on flanks finely granular; skin on belly weakly areolate; skin on other ventral surfaces smooth; dorsolateral folds low, originating in scapular region; discoidal fold evident; cloacal sheath short; large tubercles in cloacal region absent. Ulnar tubercles absent; thenar tubercle elevated, elliptical, about same size as bifid palmar tubercle; subarticular tubercles prominent, subconical; few minute supernumerary tubercles on proximal segments of digits; fingers lacking lateral fringes; Finger I = II; discs on Fingers III and IV rounded terminally, expanded laterally, more than twice width of digit proximal to pad; all fingers having ventral pads well defined by circumferential grooves. Hind limbs slender; when hind limbs flexed perpendicular to axis of body heels overlap by about two-fifths length of shank; tibia length 65.6% of SVL; foot length 60.8% of SVL; heel lacking tubercles and calcar; tarsal tubercles and fold absent; inner metatarsal tubercle elevated, elliptical, about thrice size of subconical outer metatarsal tubercle; toes slender, lacking lateral fringes, bearing rounded terminal discs smaller than those on fingers; basal webbing between Toes IV and V; other toes unwebbed; relative lengths of toes 1 < 2 < 3 < 5 < 4; Toe III slightly shorter than Toe V; Toe III extending to base of antepenultimate subarticular tubercle on Toe IV; Toe V extending to middle of antepenultimate subarticular tubercle on Toe IV; subarticular tubercles small, subconical; supernumerary tubercles weakly defined on proximal segments of digits.

*Coloration in life.*—Dorsum greenish-tan with most other markings (e.g., chevrons, etc.) medium brown, except for dark brown canthal and postorbital stripes, scapular spots, and small blotches on front of arms and legs; iris coppery-tan (Fig. 1A).

*Coloration in preservative.*—Dorsum of head, body, and limbs reddish-brown; two faintly darker brown chevrons on back; pair of small black spots laterally in scapular region at level of arms; dark brown transverse bar on forearm; faint evidence of brown transverse bars on dorsal surfaces of thighs; three brown transverse bars on each shank, two on each tarsus; anterior surfaces of thighs reddish-tan; posterior surfaces of thighs reddish-brown with many pale cream spots. Facial markings consisting of dark brown canthal and posteroventrally curved postorbital stripes; upper lip reddish-tan with faint brown labial bars extending onto margin of lower lip. Flanks reddish-brown gradually fading into cream belly; ventral surfaces of limbs cream with small, diffuse brown spots; throat pale brown with cream spots.

*Measurements of holotype (in mm).*—SVL 35.5; tibia length 23.3; foot length 21.6; head length 14.2; head width 17.7; interorbital distance 4.1; upper eyelid width 3.4; eye-nostril distance 4.3; eye diameter 4.2; tympanum diameter 2.5.

*Variation.*—Eight juveniles have SVLs of 14.0–19.3 mm ($\bar{x}$ = 16.8). In preservative, these small specimens have a tan to pale reddish-brown dorsum; each has a pair of black spots in the scapular region, and two individuals have faint brown interorbital bars. The lips are tan and lack labial bars; no pale spots are evident on the posterior surfaces of the thighs.

*Distribution and habitat.—Eleutherodactylus bipunctatus* is known from two localities at elevations of 2060–2120 m on the western slopes of the Cordillera Yanachaga in central Peru. All were under logs along trails.

*Remarks.*—The holotype weighed 3.7 g in life.

*Etymology.*—The specific name is derived from the Latin *bi* meaning two and the Latin *punctum* meaning dot. The name refers to the pair of dark dots in the scapular region of this species.

### ***Eleutherodactylus aniptopalmatus*, new species**

Figure 1B

*Holotype.*—KU 291626, an adult female, Peru, Departamento de Pasco, Provincia de Oxapampa, 2.9 km north and 5.5 km east (airline) of Oxapampa, 10°32′38″S, 75°21′10″W, 2600 m elevation, S. B. Hedges, 2 July 1987.

*Paratypes.*—KU 291627 and 291631, adult females with the same data as holotype; KU 206102, an adult male, Peru, Departamento de Pasco, Provincia de Oxapampa, 12 km east of Oxapampa, Cumbre de Ollón, 2300 m elevation, T. S. Schulenberg, 26 March 1982.

*Referred specimens.*—KU 291628–29, 291630, and 291632 from the type locality.

*Diagnosis.*—A member of the *Eleutherodactylus* (*Eleutherodactylus*) *unistrigatus* group having (1) skin on dorsum and venter smooth; discoidal fold barely evident; dorsolateral folds absent; (2) tympanic membrane smooth; tympanic an-

nulus weak, slightly higher than long, its length about one-half length of eye; (3) snout long, bluntly rounded in dorsal view and in profile; (4) upper eyelid usually with single tubercle posteriorly, about half as wide as interorbital distance; cranial crests absent; (5) vomerine odontophores elliptical, oblique; (6) vocal slits present; nuptial pads absent; (7) Finger I shorter than II; discs on outer fingers expanded, bluntly rounded, about twice width of digit proximal to pad; (8) fingers bearing narrow lateral fringes; (9) ulnar tubercles absent; (10) heel and tarsus lacking tubercles and folds; (11) inner metatarsal tubercle, elevated, elliptical, about 4X subconical outer metatarsal tubercle; supernumerary plantar tubercles present; (12) toes lacking lateral fringes; basal webbing between Toes IV and V; Toe V much longer than Toe III; discs slightly smaller than those on fingers; (13) dorsum tan, usually with variable brown markings, labial bars present; venter cream with minute brown flecks; palmar and plantar surfaces dark brown; posterior surfaces of thighs brown with pale tan diagonal streaks proximally; (14) SVL to 16.5 mm in males, to 22.0 mm in females.

*Eleutherodactylus aniptopalmatus* is like many other species in the *Eleutherodactylus unistrigatus* group on the Amazonian slopes of the Andes of Ecuador and Peru in having one or more tubercles on the upper eyelid, but it differs from many of those species by lacking tubercles on the heel. Small tubercles are present on the heels of *E. bromeliaceus*, *colodactylus*, *cryptomelas*, *lirellus*, *nephophilus*, *ockendeni*, *pecki*, *rhodoplichus*, and *schultei*, whereas larger conical tubercles are present on the heels in *E. galdi*, *muscosus*, and *quaquaversus*. *Eleutherodactylus exoristus* and *percnopterus* differ from *E. aniptopalmatus* by lacking lateral fringes on the fingers and toes; *E. versicolor* differs by lacking lateral fringes on the fingers, and *E. proserpens* differs by having basal webbing between the toes. In *E. aniptopalmatus* the snout is bluntly rounded in dorsal view and in profile; the snout is acutely rounded in dorsal view and in profile in *E. ceuthophilis* and acuminate in dorsal view and posteroventrally inclined in profile in *E. rhodostichus*. *Eleutherodactylus infraguttatus* differs from *E. aniptopalmatus* by having prominent ulnar tubercles and ventral coloration–throat brown with cream mottling and belly cream with dark brown mottling.

*Description.*—Head not as wide as body; head width 34.5% of SVL; head length 40.9% of SVL; snout moderately long, bluntly rounded in dorsal view and in profile, slightly protruding beyond margin of lower lip; eye-nostril distance 1.08% length of eye; nostrils not protuberant, directed laterally at level slightly behind anterior margin of lower lip. Canthus rostralis straight, angular in section, not elevated; loreal region slightly concave; lips rounded; internarial region and top of head flat; upper eyelid with single low tubercle posteriorly, its width 50.0% of interorbital distance; supratympanic fold low, angling downward behind tympanum, obscuring upper and posterior edges of tympanum; tympanic annulus weak, smooth; tympanum slightly higher than long, 40.9% of diameter of eye, separated from eye by distance equal to twice diameter of tympanum; enlarged postrictal tubercles absent. Choanae small, elliptical, not concealed by palatal shelf of maxillary arch; vomerine odontophores oblique, widely separated medially, at level between posterior margins of choanae, each odontophore bearing three teeth; tongue about twice as long as wide, notched posteriorly, posterior one-half not adherent to floor of mouth.

Skin on dorsum, flanks, and venter smooth; dorsolateral folds absent; discoidal fold barely evident; cloacal sheath short; large tubercles in cloacal region absent. Ulnar tubercles absent; thenar tubercle slightly elevated, elliptical, about equal in size to ovoid palmar tubercle; subarticular tubercles prominent, subconical; supernumerary tubercles minute, present only on proximal segments; fingers bearing narrow lateral fringes; Finger I < II; discs on Fingers III and IV bluntly rounded, subtruncate, about twice width of digit proximal to pad; all fingers having ventral pads well defined by circumferential grooves. Hind limbs slender; when hind limbs flexed perpendicular to axis of body heels overlap by about two-fifths length of shank; tibia length 53.6% of SVL; foot length 44.1% of SVL; heel lacking tubercles and calcar; tarsal tubercles and fold absent; inner metatarsal tubercle elevated, elliptical; outer metatarsal tubercle small, subconical; toes slender, lacking lateral fringes; webbing basal between Toes IV and V, absent between others; toes bearing subtruncate terminal discs slightly smaller than those on fingers; relative lengths of toes 1 < 2 < 3 < 5 < 4; Toe III shorter than Toe V; Toe III extending to base of antepenultimate subarticular tubercle on Toe IV; Toe V extending to point midway between antepenultimate and penultimate subarticular tubercles on Toe IV; subarticular tubercles small, round; supernumerary tubercles minute, present only on proximal segments.

*Coloration in life.*—In the holotype, the dorsum was coppery-tan with dark brown markings (e.g., chevrons, limb bars, etc.; Fig. 1B). In a paratype (KU 291627), the dorsal ground color

was predominantly grayish-red, although the flanks and limbs were mostly grayish-tan; the dorsal markings were dark brown. In both individuals, the dorsal markings were edged by a narrow, pale gray line, making the marking more noticeable, and the iris was grayish-white.

*Coloration in preservative.*—Dorsum of head, body, and limbs pale tan with brown markings consisting of large quadrangular mark between orbits, massive roughly W-shaped mark in scapular region, broad mark in sacral region with diagonal extensions into inguinal regions, one broad transverse bar on each forearm, two diagonal bars on each thigh, two transverse bars on each shank, and three narrow diagonal bars on each foot. Anterior surface of upper arm brown; anterior surfaces of thighs pale brown; posterior surfaces of thighs brown with two creamy tan diagonal streaks proximally (extensions of dorsal ground color). Flanks creamy tan with two diffuse brown marks; canthal and supratympanic stripes dark brown; upper lip with three vertical bars on each side; second bar entering orbit. Plantar and palmar surfaces dark brown; other ventral surfaces creamy tan with brown flecks, some coalesced to form diffuse spots laterally on throat and chest.

*Measurements of holotype (in mm).*—Holotype measurements followed by those of female and male paratypes KU 291626, 291631, and KU 206102, respectively: SVL 22.0, 14.6, 16.5; tibia length 11.8, 8.3, 8.4; foot length 9.7, 6.5, 8.0; head length 9.0, 7.7, 6.2; head width 7.6, 5.0, 4.9; interorbital distance 2.8, 2.0, 2.0; upper eyelid width 1.4, 1.3, 1.3; eye-nostril distance 2.6, 1.9, 1.8; eye diameter 2.2, 1.8, 1.7; tympanum diameter 0.9, 0.9, 0.7.

*Variation.*—Structurally, the paratypes (KU 291627–32) are like the holotype (KU 291626), except that there are 1–3 teeth on each odontophore, but two females have no discernable vomerine teeth. However, there are differences in coloration. All individuals have dark brown labial bars and canthal-postorbital stripes; likewise, interorbital bars of varying widths are present in all specimens. Six of eight specimens have distinct dark marks in the scapular and sacral regions. One individual (KU 291628) has a massive V-shaped scapular mark and a broad blotch in the sacral region. Another individual has a narrow V-shaped mark in the scapular region, and another has a narrow middorsal streak posteriorly. A juvenile essentially lacks dorsal markings on the body. With the exception of that juvenile, other individuals have proportionately darker throats and bellies than the holotype, and in the male paratype the flecks on the venter are coalesced into distinct brown spots, especially numerous on the throat.

*Distribution and habitat.*—*Eleutherodactylus aniptopalmatus* is known from elevations of 2300–2600 m on the western slopes of the Cordillera Yanachaga in central Peru. The frogs were found under moss on tree trunks and under moss on the ground in cloud forest.

*Remarks.*—The holotype weighed 0.6 g in life; one female paratype (KU 291628) weighed 0.5 g and contained small ova, and the other female paratype (KU 291631) weighed 0.7 g and contained 16 eggs.

*Etymology.*—The specific name is derived from the Greek *aniptos* meaning unwashed and the Greek *palmatos* meaning sole of foot. The name refers to the dark coloration of the palmar and plantar surfaces of this species.

### ***Eleutherodactylus rhabdocnemus*, new species**

Figure 1C

*Holotype.*—KU 291646, an adult female, Peru, Departamento de Pasco, Provincia de Oxapampa, 2.9 km north and 5.5 km east (airline) of Oxapampa, 10°32′38″S, 75°21′10″W, 2600 m elevation, S. B. Hedges, 2 July 1987.

*Paratype.*—KU 291651, adult female collected with the holotype.

*Referred specimens.*—KU 291647–50, 291652–56, juvenile and subadults collected with the holotype; MTD 45073, Peru, Departamento de Pasco, Cillapata, 2900 m elevation.

*Diagnosis.*—A member of the *Eleutherodactylus* (*Eleutherodactylus*) *unistrigatus* group having (1) skin on dorsum shagreen with or without scattered small tubercles; that on venter areolate; discoidal fold not evident; dorsolateral folds absent; (2) tympanum absent; (3) snout moderately long, rounded in dorsal view and in profile; (4) upper eyelid lacking tubercles, slightly narrower than IOD; cranial crests absent; (5) vomerine odontophores absent; (6) condition of vocal slits and nuptial pads unknown; (7) Finger I shorter than II; discs on outer fingers broadly expanded, rounded, about twice width of digit proximal to pad; (8) fingers bearing narrow lateral fringes; (9) ulnar tubercles absent; (10) heel with single tubercle; inner tarsal fold absent; (11) inner metatarsal tubercle,

large, elevated, ovoid, about 8× subconical outer metatarsal tubercle; supernumerary tubercles present proximally; (12) toes bearing lateral fringes; webbing absent; Toe V much longer than Toe III; discs slightly smaller than those on fingers; (13) dorsum brown with darker brown markings including V-shaped marks in scapular region; labial bars present; venter pale tan with brown flecks and small brown spots; posterior surfaces of thighs dark brown; (14) SVL 24.5–19.5 mm in females; males unknown.

Four other species on the eastern slopes of the Andes in Ecuador and Peru and in the upper Amazon Basin of Peru lack a tympanum. All of these differ from *Eleutherodactylus rhabdocnemus* by lacking a tarsal tubercle. *Eleutherodactylus colodactylus*, *lirellus*, and *pugnax* also differ by having vomerine odontophores; furthermore, *E. colodactylus* and *E. pugnax* differ from *E. rhabdocnemus* by having the toes webbed basally, and *E. lirellus* also differs by having small tubercles on the upper eyelid and two small tubercles on the heel. The small (SVL to 14 mm in males and 20 mm in females) Amazonian *E. imitatrix* is like *E. rhabdocnemus* in lacking vomerine odontophores, but it differs by having distinct ulnar tubercles and inner tarsal fold and by lacking a tubercle on the heel. Moreover, the bluish-white venter with black reticulations is distinctly different from that of *E. rhabdocnemus*.

*Description.*—Head as wide as body and as wide as long; head width and length 39.2% of SVL; snout moderately long, rounded in dorsal view and in profile, protruding slightly beyond margin of lower lip; eye-nostril distance equal to length of eye; nostrils barely protuberant, directed laterally at level slightly behind anterior margin of lower lip. Canthus rostralis curved, acutely rounded in section, not elevated; loreal region concave; lips rounded; internarial region and top of head flat; upper eyelid smooth, its width 76.9% of interorbital distance; supratympanic fold and tympanum absent; enlarged postrictal tubercles absent. Choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores absent; tongue about twice as long as wide, shallowly notched behind, posterior one-half not adherent to floor of mouth.

Skin on dorsum and flanks shagreen with short diagonal ridge posterior to orbit; skin on belly coarsely areolate; skin on other ventral surfaces smooth; dorsolateral folds absent; discoidal fold not evident; cloacal sheath short; large tubercles in cloacal region absent. Ulnar tubercles absent; thenar tubercle barely elevated, elliptical, larger than small round palmar tubercle; subarticular tubercles small, round; supernumerary tubercles prominent of proximal segments of digits; fingers with narrow lateral fringes; Finger I < II; discs on Fingers II and IIII rounded terminally; disc on Finger IV truncate, more than about twice width of digit proximal to pad; all fingers having ventral pads well defined by circumferential grooves. Hind limbs slender; when hind limbs flexed perpendicular to axis of body heels overlap by about one-fourth length of shank; tibia length 55.1% of SVL; foot length 49.8% of SVL; heel bearing single prominent tubercle; single low tubercle on outer edge of tarsus at about two-thirds of its length; inner tarsal fold absent; inner metatarsal tubercle large, elevated, ovoid, about 8X subconical outer metatarsal tubercle; toes slender, lacking webbing, bearing narrow lateral fringes and subtruncate terminal discs smaller than those on fingers; relative lengths of toes 1 < 2 < 3 < 5 < 4; Toe III much shorter than Toe V; Toe III extending to distal edge of antepenultimate subarticular tubercle on Toe IV; Toe V extending to middle of penultimate subarticular tubercle on Toe IV; subarticular tubercles prominent, subconical; supernumerary tubercles low, indistinct, present only on proximal segments of digits.

*Coloration in life.*—Ground color tan on sides of head, forearms, and posterior flanks, reddish-brown on upper surfaces of head, body, and hind limbs; most dorsal markings dark brown to black, including broad area on anterior surfaces of flanks; reddish-brown dorsal color partially obscuring much of dorsal markings; iris grayish-tan (Fig. 1C).

*Coloration in preservative.*—Dorsal ground color pale tan; pair of distinct dark brown V-shaped marks (apex medially) in scapular region with anterior arm originating on dermal ridge behind orbit; irregular transverse dark brown mark in sacral region and a narrow mark at posterior end of body; dark brown markings on head consisting of broad interorbital bar, diagonal stripe in tympanic region, spot on canthus rostralis and adjacent loreal region, and three labial bars. Flanks brown above and cream below with diagonal brown streaks. Dorsal surfaces of limbs pale tan with narrow broad transverse dark brown bar on forearm, slightly diagonal dark brown bars on hind limbs–four on thighs, three on shanks, and two on feet; anterior and posterior surfaces of thighs brown with darker brown triangular mark below cloacal opening. Venter pale tan with minute brown flecks on all surfaces and small brown spots on belly; narrow

dark brown longitudinal streak extending length of ventral edge of forearm.

*Measurements of holotype (in mm).*—Holotype measurements followed by those of female paratype: SVL 24.5, 29.5; tibia length 13.5, 14.0; foot length 12.1, 13.4; head length 9.6, 10.5; head width 9.6, 10.3; interorbital distance 2.6, 3.5; upper eyelid width 2.0, 2.2; eye-nostril distance 2.8, 2.9; eye diameter 2.8, 2.9.

*Variation.*—Scattered small tubercles on the dorsum are present in the female paratype and in some of the small males. In preservative, the dorsal color pattern of the 11 specimens is remarkably uniform, except that in KU 291652 only the apexes of the V-shaped marks are present in the scapular region; in KU 291648 a broad orange-tan middorsal stripe extends from the occiput to the posterior end of the body. In two small juveniles (6.9 and 7.3 mm SVL) the throat and chest are dusky brown. The only specimens having brown spots on the belly are the two adult females; KU 291650, a male with a SVL of 15.3 mm, has a pair of brown spots on the throat. In most of the small individuals, the diagonal streaks on the flanks and longitudinal streak on the ventral surfaces of the forearms are indistinct or absent. In life, coloration in KU 219647 was similar to that of the holotype, except that there was almost no reddish-brown dorsal wash and the iris was gray. In KU 291648, the entire dorsum was black except for a white middorsal stripe beginning behind the head and extending to the vent; narrow gray bands were present near the digital tips, and the iris was tan.

*Distribution and habitat.—Eleutherodactylus rhabdocnemus* is known only from elevations of 2600–2900 m on the western slopes of the Cordillera Yanachaga in central Peru. Individuals were found at approximately 0.3 m above the ground on leaves of plants along a trail in cloud forest.

*Remarks.*—The paratype weighed 2.2 g and contained 27 eggs. Four males having small white testes weighed 0.25–0.50 g ($\bar{x}$ = 0.34). One specimen (KU 291652), with a SVL of 21.4 mm, possibly is an adult male. Because of their relative small SVLs (14.5–15.7 mm, $\bar{x}$ = 15.0, n = 7) and small size of their testes, these males probably are not adults.

*Etymology.*—The specific name is derived from the Greek *knemos* meaning shoulder and the Greek *rhabdotos* meaning striped. The name refers to the distinctive dark V-shaped marks in the scapular region of this species.

### *Eleutherodactylus stictogaster*, new species

Figure 1D

*Holotype.*—KU 291659, a subadult female, Peru, Departamento de Pasco, Provincia de Oxapampa, 2.9 km north and 5.5 km east (airline) of Oxapampa, 10°32′38″S, 75°21′10″W, 2600 m elevation, S. B. Hedges, 3 July 1987.

*Diagnosis.*—A member of the *Eleutherodactylus* (*Eleutherodactylus*) *unistrigatus* group having (1) skin on dorsum tuberculate; that on venter areolate; discoidal fold barely evident; dorsolateral folds present; (2) tympanic membrane smooth; tympanic annulus prominent, slightly higher than long, its length about one-half length of eye; (3) snout long, truncate in dorsal view and in profile; (4) upper eyelid with numerous small, low tubercles, much narrower than IOD; cranial crests absent; (5) vomerine odontophores low, elliptical, transverse; (6) condition of vocal slits and nuptial pads unknown; (7) Finger I shorter than II; discs on outer fingers moderately expanded, rounded, about 1.5X width of digit proximal to pad; (8) Fingers III and IV bearing narrow lateral fringes; (9) ulnar tubercles absent; (10) heel and tarsus lacking tubercles and folds; (11) inner metatarsal tubercle, low, flat, elliptical, about 6× subconical outer metatarsal tubercle; supernumerary plantar tubercles absent; (12) toes lacking lateral fringes; webbing absent; Toe V much longer than Toe III; discs slightly smaller than those on fingers; (13) dorsum brown with darker brown W-shaped mark in scapular region and chevrons posteriorly; broad, white labial stripe in life; belly and lower flanks white with conspicuous dark brown spots; groin brown with white spots; posterior surfaces of thighs dark brown; (14) SVL 20.5 mm in female; males unknown.

The dark brown groin with white spots and white belly with brown spots is unique among the *Eleutherodactylus* on the Amazonian slopes of the Andes. The only other members of the *Eleutherodactylus unistrigatus* group in the Andes of Peru that have pale spots in the groin are *E. cajamarcensis*, *ceuthospilus*, *lirellus*, *muscosus*, and *rufioculis*, but none of these has dark brown spots on the belly. In all of these except *E. cajamarcensis* and *E. stictogaster*, the spots in the groin are not set in a dark field. Furthermore, the larger *E. muscosus* differs from *E. stictogaster* by having a conical tubercle on the heel and white spots on the flanks. *Eleutherodactylus rufioculis* also differs from *E. stictogaster* by having the

tympanic annulus beneath the skin, cream spots on the flanks, and lacking tubercles on the upper eyelid, and *E. lirellus* lacks a tympanum and tympanic annulus. *Eleutherodactylus cajamarcensis* also has small pale spots on the posterior surfaces of the thighs; these and the spots in the groin are red in life.

*Description.*—Head as wide as body; head width 35.1% of SVL; head length 40.9% of SVL; snout long, shallow, truncate in dorsal view, bluntly rounded in profile, barely protruding beyond margin of lower lip; eye-nostril distance equal to length of eye; nostrils protuberant, directed laterally at level slightly behind anterior margin of lower lip. Canthus rostralis straight, acutely rounded in section, not elevated; loreal region slightly concave; lips rounded; internarial region depressed; top of head flat; upper eyelid with small tubercles, its width 68.2% of interorbital distance; supratympanic fold diffuse, barely obscuring posterodorsal edge of tympanum; tympanic annulus distinct, smooth; tympanum slightly higher than long, 51.9% of diameter of eye, separated from eye by distance equal to diameter of tympanum; enlarged postrictal tubercles absent. Choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores small, low, transversely elliptical, widely separated medially, at level behind posterior margins of choanae, each odontophore bearing two teeth; tongue about thrice as long as wide, not notched posteriorly, posterior two-thirds not adherent to floor of mouth.

Skin on dorsum and flanks shagreen with small scattered tubercles; skin on belly areolate; skin on other ventral surfaces smooth; dorsolateral folds low; discoidal fold barely evident; cloacal sheath short; large tubercles in cloacal region absent. Ulnar tubercles absent; thenar tubercle barely elevated, elliptical, larger than small round palmar tubercle; subarticular tubercles small, round; supernumerary tubercles absent; Fingers III and IV with narrow lateral fringes; Finger I < II; discs on Fingers III and IV rounded terminally, expanded laterally, about twice width of digit proximal to pad; all fingers having ventral pads well defined by circumferential grooves. Hind limbs slender; when hind limbs flexed perpendicular to axis of body, heels overlap by about one-third length of shank; tibia length 51.2% of SVL; foot length 45.4% of SVL; heel lacking tubercles and calcar; tarsal tubercles and fold absent; inner metatarsal tubercle small, elliptical; outer metatarsal tubercle absent; toes slender, lacking lateral fringes and webbing, bearing rounded terminal discs smaller than those on fingers; relative lengths of toes 1 < 2 < 3 < 5 < 4; Toe III much shorter than Toe V; Toe III extending to base of antepenultimate subarticular tubercle on Toe IV; Toe V extending to middle of penultimate subarticular tubercle on Toe IV; subarticular tubercles small, round; supernumerary tubercles absent.

*Coloration in life.*—Dorsum coppery-tan with faint, medium brown, traces of markings (e.g., chevrons, etc.), except for black supratympanic stripe and two cream spots (on back and upper thigh); upper eyelid with narrow bluish-white edge; forearms tan without markings, except for black along posterior edge; chin mostly dark gray, but slightly mottled with paler gray; belly bluish white with distinctive black spots; undersides of hind limbs mostly dark gray with some bluish-white and black spotting; iris greenish-tan and brown (Fig. 1D).

*Coloration in preservative.*—Dorsal surfaces of head, body, and limbs tan with faintly darker brown markings consisting of slender interorbital bar, W-shaped mark in scapular region; chevron with apex anteriorly in sacral region, smaller chevron postsacrally, and transverse bars on limbs–three each on thigh and shank, two each on foot and forearm. Dark brown postorbital stripe extending from posteroventral edge of orbit to base of forelimb; upper lip pale tan; dark canthal stripe and labial bars absent; anterior and posterior surfaces of thighs tan; throat and ventral surfaces of limbs pale tan; chest and belly cream with prominent dark brown irregularly shaped spots.

*Measurements of holotype (in mm).*—SVL 20.5; tibia length 10.5; foot length 9.3; head length 8.4; head width 7.2; interorbital distance 2.2; upper eyelid width 1.5; eye-nostril distance 2.7; eye diameter 2.7; tympanum diameter 1.4.

*Distribution and habitat.*—*Eleutherodactylus stictogaster* is known only from the type locality at an elevation of 2600 m on the western slopes of the Cordillera Yanachaga in central Peru. The only known specimen was under moss on the ground.

*Remarks.*—The holotype weighed 0.6 g in life. This is a distinctively patterned species of *Eleutherodactylus* in central Peru. Thus, we have no qualms about naming it on the basis of a single specimen.

*Etymology.*—The specific name is derived from the Greek *stiktos* meaning spotted and the

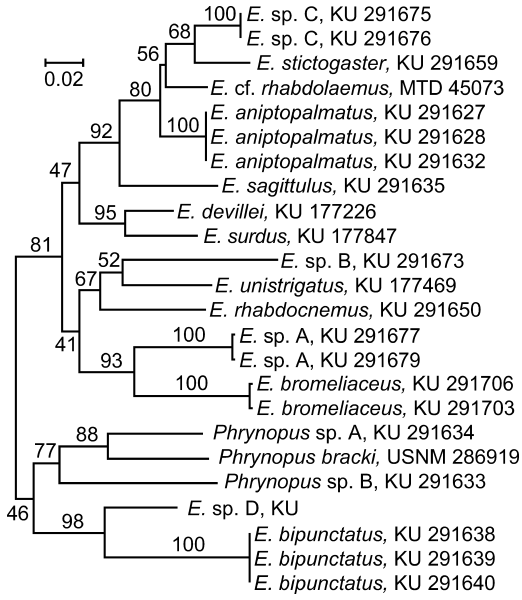


Fig. 2. Phylogenetic tree of some South American species of *Eleutherodactylus* and *Phrynopus* showing relationships of specimens collected in the region of Oxapampa, Peru, including new species described herein. Numbers on nodes are bootstrap confidence values. The tree was rooted with *Rana pipiens* (not shown). The scale bar indicates percent sequence divergence.

Greek *gaster* meaning belly. The name refers to the distinctive dark spots on the belly of this species.

## Discussion

Our preliminary sequence analysis was used as a forensic tool in sorting and allocating specimens to species and not for constructing a robust phylogeny of *Eleutherodactylus*. The latter will require longer sequences and additional taxa to address questions such as the relationships of *Phrynopus* and *Eleutherodactylus* (S. B. Hedges, in prep.). The tree (Fig. 2) shows support for the recognition of the four new species described in this paper, in that specimens of each species, defined morphologically, also have similar or identical sequences (indicated by vertical lines at the terminal branches of the tree) within a species but differ considerably between species. At the same time, the analysis has revealed at least four additional species of *Eleutherodactylus* (labeled A–D), and two of *Phrynopus* (labeled A–B), that apparently are undescribed. Those species will be the subject of future morphological comparisons.

Updating the taxonomic lists of Peruvian amphibians by Rodríguez et al. (1993) and Lehr (2002) reveals the known existence of 83 named species of *Eleutherodactylus*, 18 of *Phrynopus*, and five of *Phyllonastes* in Peru (exclusive of *Eleutherodactylus* A–D and *Phrynopus* A and B identified in Fig. 2). Fifty-nine of the species of *Eleutherodactylus* are assigned to the immense *Eleutherodactylus unistrigatus* group, 17 to the *Eleutherodactylus conspicillatus* group, four to the *Eleutherodactylus orestes* group, two to the *Eleutherodactylus nigrovittatus* group, and one each to the *Eleutherodactylus discoidalis* and *sulcatus* groups, as defined by Lynch and Duellman (1997). Three juveniles in the collection from Oxapampa lack expanded digital discs and have Toe III longer than Toe IV; they possibly belong to either the *Eleutherodactylus nigrovittatus* or *discoidalis* groups. Of members of these groups, only *E. cruralis* (*E. discoidalis* group) is known from the central part of the Cordillera Oriental in Peru (Lynch, 1989).

Phylogenetic relationships among eleutherodactyline frogs are only now beginning to be unraveled. Morphologically, *Phyllonastes duellmani* is intermediate between *Phrynopus* and *Phyllonastes* (Lehr et al., 2004b). According to Duellman and Pramuk (1999), there is no substantial evidence that any of the three genera, as well as *Ischnocnema*, are monophyletic, and *Eleutheroactylus* may be paraphyletic with respect to the other genera, as is shown in the phylogenetic tree of eleutherodactylines from central Peru (Fig. 2).

Among the eleutherodactyline genera in the central and northern Andes, *Phrynopus*, *Phyllonastes*, and the six groups of *Eleutherodactylus* have different patterns of diversity in Peru (Table 1). *Phrynopus* is widespread in the Andes from Colombia to Bolivia; in Peru, the greatest diversity is in Cordillera Occidental (including the Cordillera de Huancabamba) and in the northern part of the Cordillera Oriental (Duellman, 2000; Lehr and Aguilar, 2003 and papers cited therein). *Phyllonastes* is more limited in its distribution in the Andes–southern Ecuador to central Bolivia–and has one species in the upper Amazon Basin (Duellman, 1991; Lehr et al., 2004b). The *Eleutherodactylus orestes* group consists of seven species distributed at high elevations in the Andes of southern Ecuador and northern Peru (Duellman and Pramuk, 1999). The *Eleutherodactylus sulcatus* group consists of seven species in Andean cloud forests in Ecuador and Colombia, plus *E. laticorpus* in extreme eastern Panama (Myers and Lynch, 1997) and one species, *E. sulcatus*, in the upper Amazon Basin (Lynch, 1997). The *Eleutherodactylus discoidalis* group, as defined by Lynch (1989), has

TABLE 1. DIVERSITY OF SPECIES IN DIFFERENT GROUPS OF *Eleutherodactylus* IN PERU.

| Group/genus | Amazon Basin | Huancabamba Depression | Andean Cordilleras | | | | |
|---|---|---|---|---|---|---|---|
| | | | Occidental[a] | Cóndor[b] | Central | Oriental (N)[c] | Oriental (S)[d] |
| *E. conspicillatus* | 8 | 2 | 0 | 2 | 3 | 3 | 1 |
| *E. discoidalis* | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| *E. nigrovittatus* | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *E. orestes* | 0 | 0 | 1 | 0 | 3 | 0 | 0 |
| *E. sulcatus* | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *E. unistrigatus* | 20 | 1 | 10 | 17 | 13 | 7 | 9 |
| *Phrynopus* | 0 | 0 | 5 | 0 | 2 | 8 | 4 |
| *Phyllonastes* | 1 | 0 | 1 | 2 | 2 | 1 | 0 |
| Total | 32 | 3 | 17 | 21 | 24 | 20 | 14 |

[a] Includes Cordillera de Huancabamba.
[b] Includes Ecuadorian part of the range.
[c] Departamento Huánuco northward.
[d] Departamento Ayacucho southward.

been expanded to include four species on the eastern Andean slopes from central Peru to northern Argentina and the Amazonian lowlands of southern Peru and northern Bolivia (Reichle and Köhler, 1997; Reichle et al., 2001). The *Eleutherodactylus nigrovittatus* group is made up of six species–four in the Andes from northern Peru to Colombia and one, *E. nigrovittatus*, in the upper Amazon Basin (Duellman and Pramuk, 1999; Lynch, 1989, 2003). The *Eleutherodactylus conspicillatus* group, with 35 species, ranges from Costa Rica and Suriname to Bolivia; the greatest number of species are on the Amazonian slopes of the Andes and in the upper Amazon Basin (Lynch and Duellman, 1997; Duellman and Pramuk, 1999). With at least 170 species, the *Eleutherodactylus unistrigatus* group is most diverse in montane forests in the Andes of Colombia, Ecuador, and Peru; the group also is speciose in the upper Amazon Basin and ranges northward into Costa Rica and southward into Bolivia (Lynch and Duellman, 1997; Duellman and Pramuk, 1999).

All of the species of *Phrynopus* and *Phyllonastes* and most species of *Eleutherodactylus* inhabiting the Andes have small latitudinal and altitudinal distributions. Most species of *Phrynopus* in Peru occur at elevations in excess of 3000 m, which is beyond the upper limits of most *Eleutherodactylus* in the country. In the Cordillera Oriental in central Peru, only three of the eight described species of *Phrynopus* are known from elevations of less than 3000 m. Sympatry among *Phrynopus* has been documented only for *P. cophites* and *P. peruvianus* at 3450 m at Abra Acanacú, Departamento de Cusco (Lynch, 1975) and for *P. nebulanastes* and *P. parkeri* at 2770 m in the Cordillera de Huancabamba, Departamento de Piura (Duellman and Wild, 1993). The elevational ranges of *E. atrabatrachus*, *cajamarcensis*, and *colodactylus* extend above 3000 m, and the ranges of two members of the *Eleutherodactylus orestes* group (*E. melanogaster* and *E. pataikos*) are at 3300–3470 m (Duellman and Pramuk, 1999). The species of *Phyllonastes* in the Andes are known from elevations of 1250–3160 m.

On the Amazonian slopes of the northern part of the Cordillera Central, seven species of *Eleutherodactylus* are known from 1800–2200 m; only one of these descends to 1080 m, and six other species occur at elevations of 800–1200 m (Duellman and Pramuk, 1999). The Cordillera de Cólan is a northern extension of the Cordillera Central; none of the four species of *Eleutherodactylus* in that cordillera is known from Cordillera Central. Of the five species of *Eleutherodactylus* known from the Cosñipata Valley in Departamento de Cusco, only one is known in the Tambo-Valle de Apurimac area of Departamento de Ayacucho, about 300 km northeast in the Cordillera Oriental (Duellman, 1978; Lynch and McDiarmid, 1987). This species, which has a broad elevational range of 1020–2650 m also ranges southeastward into Bolivia (De la Riva et al., 2000).

To the uninitiated, the recognition of so many species of eleutherodactyline frogs with restricted ranges may be difficult to comprehend. The complex topography with essentially isolated mountain ranges, such as the Cordillera del Cóndor in northern Peru and the Cordillera Azul in central Peru, provide great opportunities for allopatric speciation. The apparent small latitudinal distributions may be real or an artifact of collecting. Significant herpetological collections have been made only along five of the nine roads that traverse the approximately 1500 km stretch of the Amazonian slopes of the Andes in Peru. Further collecting in the extensive unsampled regions probably will extend the

ranges of some species and certainly will reveal the presence of many more unnamed species.

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