

## A NEW SPECIES OF *ISCHNOCNEMA* (ANURA: LEPTODACTYLIDAE) FROM LA PAZ, BOLIVIA

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**ABSTRACT:** We describe a new species of *Ischnocnema* from upper montane rainforest in La Paz, Bolivia. Unlike its congeners, the new species possesses notched unguis flaps, a short dorsolateral fold, and a small axillary gland. The new species resembles *I. sanctaerucis* and is the third species of *Ischnocnema* known from Bolivia.

**Key words:** Anura; Bolivia; *Ischnocnema choristolemma* (new species); *Ischnocnema sanctaerucis*; Leptodactylidae

UNTIL the 1970's, the genus *Ischnocnema* was represented by *I. quixensis* from the Upper Amazon and *I. verrucosa* from the Atlantic rainforests of Brazil. Recently, additional species of *Ischnocnema* have been discovered in the Andean foothills. Lynch (1974) described *I. simmonsii* from the Cordillera del Condor, Ecuador, and Duellman (1990) discovered *I. saxatilis* in San Martín, Peru. Harvey and Keck (1995) first reported the genus from Bolivia when they described *I. sanctaerucis* from cloud forests of Parque Nacional Ambaró, Santa Cruz.

*Ischnocnema verrucosa* has rarely been collected (Lynch and Schwartz, 1971) and is known only from the Atlantic rainforests of Brazil. Duellman (1978, 1990), Lynch (1972, 1974), Lynch and Lescure (1980), and Toft and Duellman (1976) published distributional data for *I. quixensis* in upper Amazonia. Recently collected specimens extended the range of this species to Cusco and Madre de Dios in southern Peru (Harvey and Keck, 1995; Morales, 1997; Morales and McDiarmid, 1996; Rodríguez and Cadle, 1990; Rodríguez et al., 1993). De la Riva et al. (2000) reported *I. quixensis* from Pando in northern Bolivia, but did not give more precise locality information (the specimen came from San Sebastian; Reserva Tahuamanu; 11.40722° S, 69.0175° W, S. Reichle, I. De la Riva, personal communication). Additional specimens of *I. sanctaerucis* were later found in Cochabamba (Reichle, 1999), and Reichle (1999) described this species' call.

During the last ten years, M. B. Harvey and field parties from the Colección Boliviana de Fauna made several expeditions to the Serranía de Bella Vista, a humid ridge covered in upper montane rainforests in the foothills of La Paz, Bolivia. An earlier paper (Harvey and Noonan, 2005) reported centrolenids collected at this locality. Among the rocky seeps in rainforests on the lower slopes of the serranía, Harvey collected specimens of a distinctive new *Ischnocnema*, which we describe herein.

### MATERIALS AND METHODS

Specimens were fixed in 10% formalin and preserved in 70% ethanol. Measurements were taken with a dial caliper under a dissecting scope to the nearest 0.01 mm. To avoid pseudoprecision, we follow the recommendation of Hayek et al. (2001) and report values to 0.1 mm. We measured snout-vent length (SVL), head length (length of a chord from the rictus to the tip of the snout), head width (at the rictus), eye-nostril distance (shortest distance from the anterior border of the ocular aperture to the posterior border of the nostril), distance from the nostril to the tip of the snout, length and height of the tympanum including its annulus, eyelid width (maximum distance from the orbital margin to the edge of the eyelid), interorbital distance (shortest distance between the orbits), internarial distance (distance between the upper edges of the nostrils), hand length (from the proximal edge of the palmar tubercle to the distal margin of the third finger), foot length (from the proximal margin of the inner metatarsal tubercle to the

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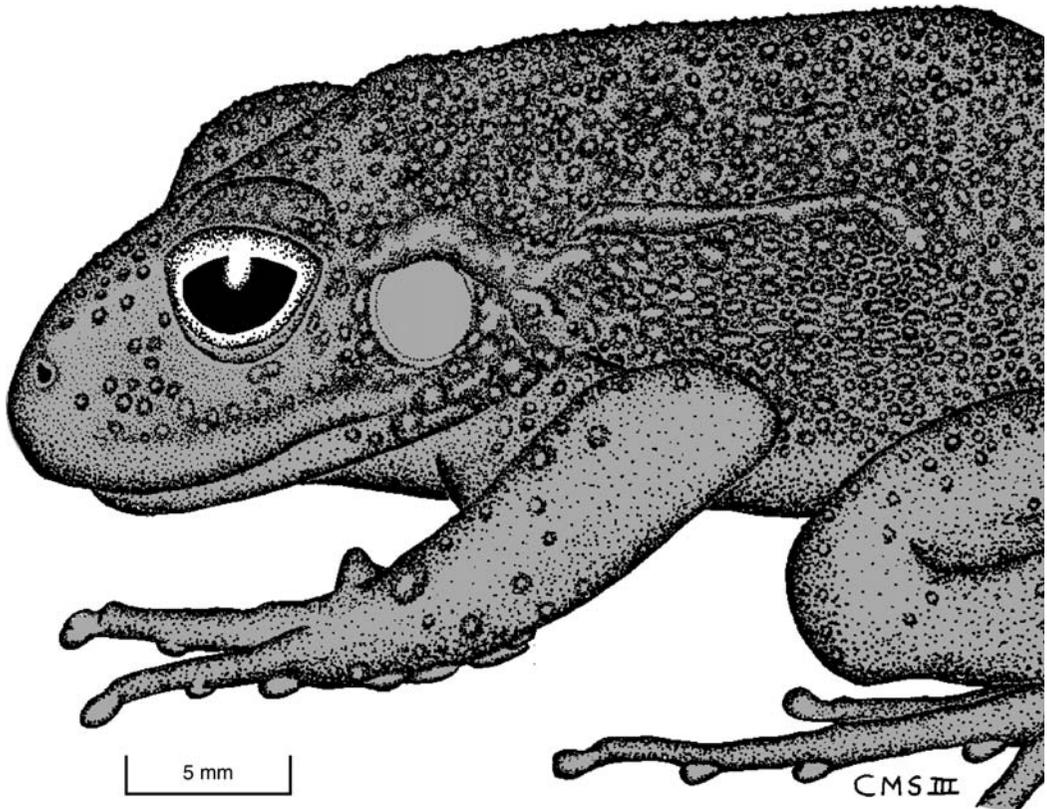


FIG. 1.—Adult female holotype (CBF 5611) of *Ischnocnema choristolemma*.

distal margin of the fourth toe), and length of the tibia. Eye diameter is reported, though we caution readers that Hayek et al. (2001) show this character to be both highly variable and prone to preservation artifacts. Our numbered diagnosis follows the standardized format used by J. D. Lynch and W. E. Duellman (updated and modified by them in 1997) for the closely related genus *Eleutherodactylus*. We determined adulthood by opening the coelom and inspecting the reproductive organs. In the description, colors characterized using Smith's (1975) color guide are capitalized and followed by his numbering system.

#### SPECIES ACCOUNT

##### *Ischnocnema choristolemma* sp.nov.

*Holotype*.—Colección Boliviana de Fauna (CBF; collector's tag M. B. Harvey 5753, Fig. 1) 5611, an adult female from the Serranía de Bella Vista, Caranavi province, La Paz

department, Bolivia, ca. 1000 m, found in rocky leaf litter near a stream on 1 January 1999 by M. B. Harvey.

*Paratype*.—A juvenile male topotype, Florida Museum of Natural History, University of Florida (UF) 142703, collected by M. B. Harvey on 1 January 1999.

*Diagnosis*.—*Ischnocnema choristolemma* may be distinguished from its congeners and all species of *Eleutherodactylus* by the following combination of characters: (1) skin of dorsum tuberculate, that on venter smooth; discoidal fold weak and far anterior on belly; dorsolateral fold tuberculate, not extending beyond anterior edge of sacrum; (2) tympanic membrane and its annulus prominent, their length about 2/3 of eye diameter; (3) snout subacuminate in dorsal view, rounded in profile; (4) upper eyelid lacking enlarged eyelid tubercle, slightly wider than interorbital distance; cranial crests absent; (5) dentigerous processes of vomers large, triangular, and



FIG. 2.—Adult female holotype (CBF 5611, SVL = 46.4 mm, left) and subadult male (UF 142703) *Ischnocnema choristolemma*.

posterior to choanae; (6) condition of vocal slits and nuptial excrescence in males unknown; (7) second finger longer than first; discs weakly developed on hands; digital pads absent; (8) fingers lacking lateral fringes; (9) ulnar tubercles low and inconspicuous, not forming fold or row; (10) heel and tarsal tubercles absent; (11) inner metatarsal tubercle oval and flat, larger than subconical outer metatarsal tubercle; supernumerary tubercles at base of toes; (12) lateral fringes, webbing, and digital pads absent from toes; fifth and third toes of equal length, their tips extending just beyond penultimate subarticular tubercle of fourth toe; ungual flaps indented or notched (= emarginate) on pedal digits 2–5; (13) dorsum brown with darker markings; lips and limbs barred; W-shaped mark in suprascapular region; venter drab brown with cream flecks; posterior thigh and groin unpatterned; (14) SVL in adult female 46.4 mm; adult males unknown.

*Description of holotype.*—Head wider than long (head width/head length 1.2; Fig. 2); snout subacuminate in dorsal view, bluntly rounded in profile; shallow notch present in upper lip (i.e., between premaxillae); canthus

distinct, rounded in transverse section, straight from nostril to orbit; loreal region weakly concave; lips slightly flared below eye; narial region protuberant; nares directed laterally; internarial region not depressed; eye large, its length greater than interorbital distance and approximately equal to eye–nostril distance (interorbital distance/eye–length 0.7, eye–nostril distance/eye–length 1.1); tympanic membrane and annulus prominent; tympanic membrane smooth and translucent; tympanum vertically ovoid (tympanum length/height 0.8), separated from corner of orbit by distance equal to about one-half length of tympanum; tympanum extending ventrally to overlap caudal portion of maxilla; dorsal edge of tympanic annulus partially overlapped by tuberculate supratympanic fold extending from posterior margin of orbit and angled posteriorly and ventrally toward insertion of arm.

Forelimbs long and slender; antibrachium with few, low ulnar tubercles, however tubercles not forming distinct rows or folds; fingers slender (Fig. 3); relative lengths of fingers when adpressed  $3 > 1 = 4 > 2$ , digit 4 approximately equal to digit 1, digit 1 much longer than digit 2; terminal discs weakly

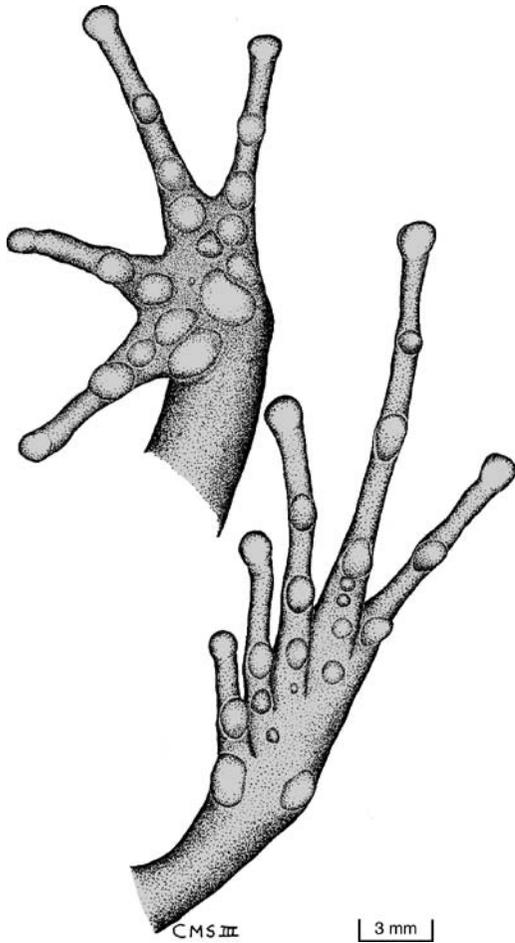


FIG. 3.—Plantar and palmar morphology of *Ischnocnema choristolemma* (CBF 5611).

developed; unguis flaps indented on digits 3 and 4, unguis flaps even and rounded on digits 1 and 2; digital pads absent, no trace of circumferential grooves; webbing and fleshy fringes absent; thenar tubercle ovoid and only slightly smaller than large divided palmar tubercle; subarticular tubercles large and subconical in profile, their bases oval; subconical supernumerary tubercles present between palmar tubercles and basal subarticular tubercles, two on each of digits 1 and 3, one on each of digits 2 and 4.

Hind limbs moderately robust; tibia relatively short (tibia length/SVL = 0.55); few cream tubercles (like those on dorsum) on ventral tarsus; tarsal folds absent; outer metatarsal tubercle subconical, smaller than flat

oval inner metatarsal tubercle; toes slender; digital pads, fleshy fringes, and webbing absent; terminal discs moderately well developed, half again as wide as toes; unguis flaps notched on digits 3 and 4, indented on digits 2 and 5, even and rounded on digit 1; when adpressed relative lengths of toes  $4 > 3 = 5 > 2 > 1$ ; toes 3 and 5 equal, their tips extending just beyond the penultimate subarticular tubercle; plantar subarticular tubercles large and subconical in profile, their bases oval; smaller supernumerary tubercles round, one on digit 1, two each on digits 2 and 3, four on digit 4, none on digit 5.

Dorsum of head, body, and limbs covered in small evenly spaced tubercles with few scattered, medium-sized tubercles restricted to dorsal body surfaces; tubercles on dorsum of head, body, and limbs with small clear tips; texture of eyelids as for body; eyelid tubercle (sensu Lynch and Duellman, 1997) absent; postriatal tubercle large and conical; smaller elongate tubercle on skin covering mandible directly below tympanum, remaining skin of mandible smooth; several tubercles of skin covering scapula irregularly fused; tuberculate lateral fold extending from posterior edge of suprascapula to anterior border of sacrum; flanks and postaxial surface of thigh aereolate; venter and remaining sides of limbs smooth; weak discoidal fold ending well anterior to groin; flat oval gland about as large as digital tip of fourth finger present in axillary (= post-humeral) region.

Dentigerous processes of vomers subtriangular, narrowly separated, positioned postero-medial to choanae, each with four or five teeth in a transverse row; choanae round, widely spaced, just medial to lingual shelf of maxilla; tongue slightly longer than wide, rounded without posterior notch, free posteriorly; vocal slits absent.

Color in preservative (terminology follows that of Smithe, 1975): Dorsal surface of body irregularly mottled Dusky Brown (19) and Raw Umber (23); irregular Dusky Brown and Raw Umber bands covering lips, arms, legs, hands, and feet; indistinct W-shaped Dusky Brown mark in scapular region; lateral surface of body irregularly mottled Dusky Brown and Pearl Gray (81); oval gland in axillary region cream; tympanum Raw Umber with irregular Dusky Brown blotch on dorsal half; venter of

body pale Drab (27); throat dark Drab; venter of hind legs Army Brown (219B); pad of digit 2 and finger distal to subarticular tubercle on digit 1 Pearl Gray.

In his field notes, Harvey described coloration of the holotype in life as follows: "Venter gray with scattered cream flecks in gular region and on thighs; groin gray; preaxial thigh gray; postaxial thigh like dorsum but darker; dorsum brown with black flecks; iris uniform bronze with black line perpendicular to pupil ventrally, yellow ring around pupil; palpebral membrane clear; tympanic membrane and annulus same color as dorsum."

*Variation.*—Vocal slits and nuptial excrescences are not present in the small, subadult male paratype. A low, glandular swelling is present dorsally at the level of the subarticular tubercle on digit 1. The structure may be associated developmentally with some form of nuptial excrescence but its true identity cannot be determined grossly. The female holotype lacks the structure.

Coloration of the paratype is a slightly lighter hue overall, but differs little in pattern. Ventrally, a cream patch is present on the posterior third of the venter and a similar though smaller cream patch lies below the pectoral girdle. Small cream spots cover the gular region.

Measurements (in mm) of the holotype are followed by those of the paratype in parentheses: SVL 46.4 (30.1), head length 13.3 (8.6), head width 20.1 (12.8), eye diameter 6.0 (3.9), eye-nostril distance 6.1 (3.7), distance from nostril to tip of snout 1.4 (1.1), tympanum length 3.8 (2.5), tympanum height 4.5 (2.8), distance from eye to tympanum 1.8 (1.0), eyelid width 4.8 (3.4), interorbital distance 4.0 (2.3), internarial distance 3.3 (3.0), hand length 15.3 (9.6), foot length 24.5 (15.5), length of tibia 25.6 (16.7).

*Distribution and natural history notes.*—Both specimens were found between 1900–2130 h at about 1000 m in deep forest. The specimens were found around rocky seeps along a densely forested hillside parallel to a large river flowing from the Serranía de Bella Vista past the small town of Kilómetro 52 (52 km from Caranavi on the road to Sapecho, Fig. 4). At this locality, *Epipedobates bolivianus*, *Lithodytes lineatus*, *Eleutherodactylus rhabdolaemus*, *E. platydactylus*, *Tripunargos com-*

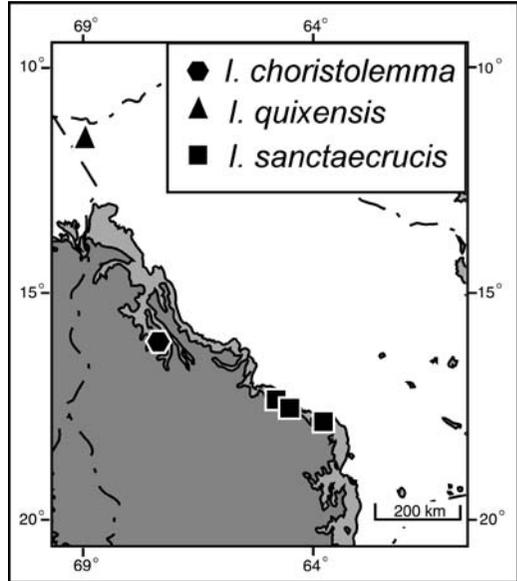


FIG. 4.—Distribution of *Ischnocnema* in Bolivia. Areas above 500 and 1000 m are shaded.

*pressus*, and *Epicrates cenchria* occur syntopically with *Ischnocnema choristolemma*. The specimens were immediately recognized as new; however, repeated visits by the senior author and other herpetologists (J. Padial, S. Reichle, and D. Ercken, personal communications) failed to produce additional specimens of this apparently rare and secretive frog.

Both specimens have a few dermal cysts produced by an unidentified parasite. The oviducts of the female are extensively convoluted and her ovaries are filled with mature, unpigmented eggs.

*Etymology.*—The specific epithet *choristolemma* is a feminine noun in apposition derived from the Greek words *choristos* meaning separated and *lemma* meaning sheath. The new name refers to this species' distinctive notched unguis flaps.

*Remarks.*—*Ischnocnema choristolemma* has two interesting morphological characters: notched unguis flaps (Fig. 5) and an axillary structure presumed to be a gland (Fig. 6). Lynch (1971) and Heyer (1975) describe the various kinds of glands of leptodactylid frogs; they do not describe glands like those in the new species. The axillary gland of *I. choristolemma* is small, flat, and hidden behind the forearm; had its cream coloration not

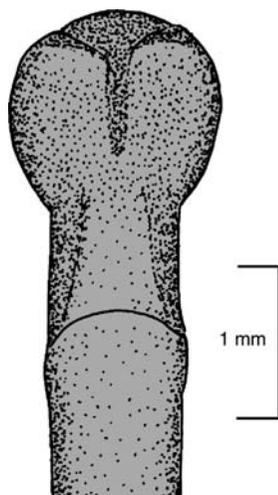


FIG. 5.—Emarginate unguis flap of the fourth toe of *Ischnocnema choristolemma* (CBF 5611, dorsal aspect).

contrasted so sharply with the adjacent skin, we might have overlooked it. Other *Ischnocnema* lack axillary glands, although the recently described *Eleutherodactylus cantitans* possesses a prominent, elevated axillary gland (Myers and Donnelly, 2001).

As in other *Ischnocnema*, digital pads are entirely absent in the new species. However, its digital tips are expanded and unguis flaps are notched on some digits. Harvey and Keck (1995) broadened the diagnosis of *Ischnocnema* when they included *I. sanctaerucis*. Previously, Lynch (1971) had defined the genus with a suite of morphological characters, most of which are osteological. Among the characters, he included toes with narrow digital tips containing knobbed terminal phalanges. Harvey and Keck (1995) noted that *I. sanctaerucis* possesses all of the external characters used by earlier authors (Duellman, 1990; Lynch, 1971, 1972, 1974; Lynch and Schwartz, 1971) to allocate species to *Ischnocnema*, except that its digital tips are slightly expanded and its plantar tubercles are subconical to round rather than conical. In the new species, digital tips are expanded to an even greater extent; otherwise, the plantar and palmar surfaces of *I. sanctaerucis* and *I. choristolemma* are about the same. Whereas Lynch (1971) defined *Ischnocnema* as lacking dermal glands, small axillary glands are present in *I. choristolemma*. Harvey and Keck (1995) called attention to the similar iris coloration among species of this genus. Where-

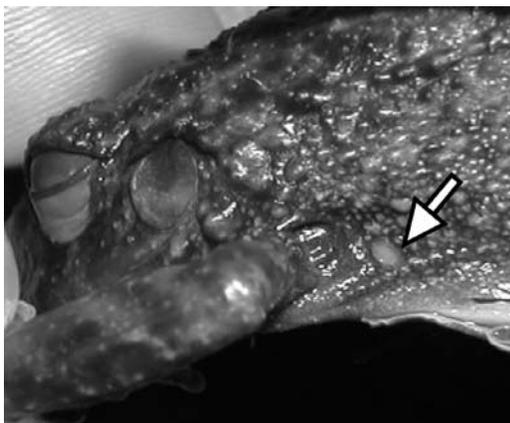


FIG. 6.—Axillary gland of *Ischnocnema choristolemma* (holotype, CBF 5611).

as, the iris of *I. quixensis*, *I. saxitilis*, and *I. sanctaerucis* is a darker color ventral to the pupil and uniformly reticulated in black, *I. choristolemma* differs from these species in having a reticulated though uniformly colored iris with a black bar below the pupil. Discovery of *I. choristolemma* further complicates the already unsatisfactory definitions of *Eleutherodactylus vis-a-vis Ischnocnema*. Generic allocation of the Bolivian species is clearly problematic, and the issue cannot be satisfactorily resolved until more specimens become available and investigators describe the species' internal anatomy. We include *choristolemma* in *Ischnocnema* because of its similarity to *I. sanctaerucis*. Unlike other congeners, *I. sanctaerucis* and *I. choristolemma* share poorly developed discs and have some subconical to round plantar subarticular and supernumerary tubercles. The remaining four species lack disks and have strongly conical plantar subarticular and supernumerary tubercles. Like other *Ischnocnema*, *I. choristolemma* and *I. sanctaerucis* are robust terrestrial eleutherodactylines with heterogenous dorsal tuberculation, prominent tympana, large eyes, weakly concave lores, banded limbs, divided palmar tubercles, long first fingers, and slender digits lacking digital pads. Morphometric ratios for *I. choristolemma* fall within ranges for other *Ischnocnema* (Harvey and Keck, 1995, their table 1). Characteristics distinguishing *I. sanctaerucis* and *I. choristolemma* are unique within the genus: the short dorsolateral fold,

axillary gland, and notched unguis flaps occur in no other *Ischnocnema*.

Lynch (1989) and Harvey and Keck (1995) noted the close similarity between members of the *Eleutherodactylus discoidalis* group and *Ischnocnema*. These frogs share the combination of long slender digits, smooth venters, and long first fingers. All species in the group occur in Bolivia, although *E. discoidalis* extends into Argentina and *E. cruralis* extends into southern Peru. Since 1995, two additional species of the *E. discoidalis* group have been named (Reichle and Köhler, 1997; Reichle et al., 2001), several others have been discovered and await description (Lavilla and Scrocchi, 1999; M. B. Harvey, unpublished), and the ranges of both *E. discoidalis* and *E. cruralis* have been expanded (De la Riva et al., 2000; Köhler et al., 1995). Márquez et al. (1995) described the call of *E. cruralis*.

Some species of the *Eleutherodactylus discoidalis* group are superficially similar to *Ischnocnema choristolemma*; however, no Bolivian *Eleutherodactylus* has notched unguis flaps. In addition, the species of the *E. discoidalis* group are generally more gracile. The lores are weakly concave in *I. sanctaerucis* and *I. choristolemma* but slope noticeably in *E. cruralis*, *E. ibischi*, and *E. zongoensis*. Dorsal tubercles of the new species are heterogenous and smaller than the uniformly large tubercles of *E. zongoensis*.

#### RESUMEN

Describimos una especie nueva de *Ischnocnema* procedente de bosque húmedo de montaña, Departamento La Paz, Bolivia. Se distingue de los demás especies del género por tener estuches ungulares con mellas, un pliegue dorsolateral corto, y una pequeña glándula axilar. La especie nueva se parece a *I. sanctaerucis*, y es la tercera especie de *Ischnocnema* registrado para Bolivia.

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## A NEW SPECIES OF *HETEROLIODON* (REPTILIA: SQUAMATA: COLUBRIDAE) FROM MONTAGNE DES FRANÇAIS, FAR NORTHERN MADAGASCAR

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A distinctive new species of the colubrid snake genus *Heteroliodon* is described from the deciduous dry forest of Montagne des Français, near the northern tip of Madagascar. The new species is characterized by stout habitus, low number of ventral scales, long relative tail length, high number of infralabial scales, and absence of a light colored vertebral stripe. The limestone massif of Montagne des Français appears to be an important center of endemism for Madagascan biota and should, therefore, be included in Madagascar's network of nature reserves.

**Key words:** Colubridae; *Heteroliodon fohy* new species; Madagascar; New species; Reptilia; Squamata; Systematics

THE COLUBRID snake genus *Heteroliodon* is endemic to Madagascar and probably closely

related to the genera *Pseudoxyrhopus*, *Exallodontophis*, *Pararhadinaea*, and *Liophidium* (Cadle, 1999; Raxworthy and Nussbaum, 1994). Nussbaum and Raxworthy (2000) re-

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FIG. 1.—*Heteroliodon foxy* sp. nov, holotype (ZSM 548/2000) in life.

cently revised *Heteroliodon* and described a new species, *H. lava*, from western and northwestern Madagascar. These authors also provided information on the nomenclatural history, distribution and systematics of this genus which is not repeated here. During a recent survey, we found a specimen of *Heteroliodon* at the northern tip of the island that differs distinctly from both known species of the genus (*H. occipitalis* and *H. lava*). In this paper, we describe the new species in order to provide a more complete view of the genus *Heteroliodon* and to call attention to the growing list of endemic species found at Montagne des Français.

#### MATERIALS AND METHODS

The snake was collected by hand, anesthetized by injection with chlorobutanol, fixed in formalin, stored in 70% ethanol, and deposited in the Zoologische Staatssammlung, München (ZSM). Snout–vent length (SVL) and tail length (TL) were measured to the nearest millimeter with calipers. To make comparisons easier, the terminology of characters and the

scheme of description follows Nussbaum and Raxworthy (2000). Geographical coordinates of localities were determined by global positioning instruments (GPS).

#### SYSTEMATICS

##### *Heteroliodon foxy* sp. nov.

*Holotype*.—ZSM 548/2000 (Figs. 1 and 2), male, most probably adult, obtained 13 March 2000 at Montagne des Français (12° 19' 17" S, 49° 20' 13" E, ca. 170 m elevation), Antsirana Province, northern Madagascar, by M. Landsberger, M. Vences, F. Glaw, and K. Schmidt.

*Other material*.—None.

*Diagnosis*.—A stout (ratio of width at midbody/SVL = 0.035) and apparently small (280 mm total length) *Heteroliodon* with 17 dorsal scale rows at midbody, a loreal scale, a uniformly dark colored dorsum, and a light colored complete nuchal collar. Differs from *H. occipitalis* by lack of light colored vertebral stripe, lower number of ventrals (136 versus 158–182), lower number of subcaudals (57 versus 61–72), longer relative tail length [TL/SVL] (0.32 versus

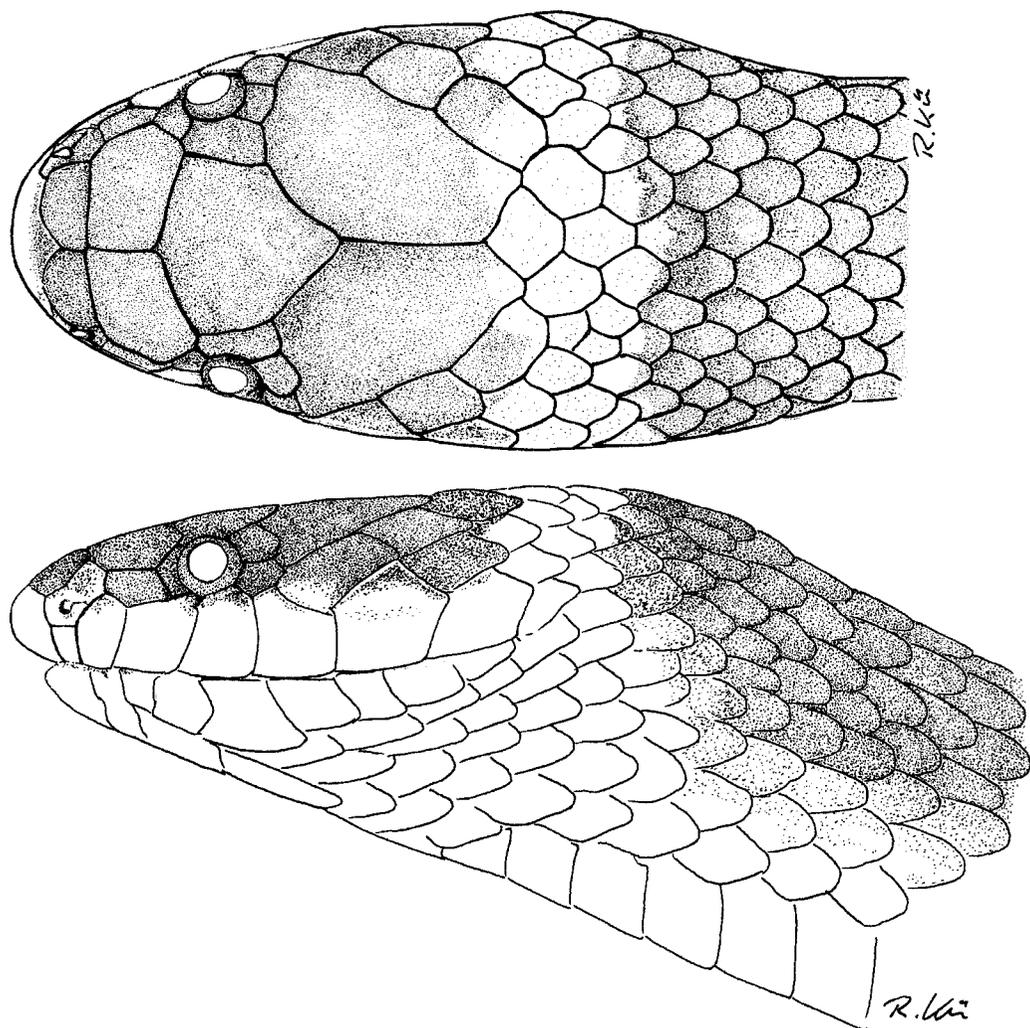


FIG. 2.—Dorsal and lateral views of *Heteroliodon fohy*, holotype.

0.25–0.31), higher number of infralabials (8–9 versus 7) of which the fifth is largest (versus fourth is largest), and much stouter habitus. Differs from *H. lava* by much lower number of ventrals (136 versus 214–224), lower number of subcaudals (57 versus 63–65), apparently smaller size (280 mm versus 441 mm total length), much longer relative tail length (0.32 versus 0.21–0.22), higher number of infralabials (8–9 versus 7) of which fifth is largest (versus fourth is largest), and much stouter habitus. The most important diagnostic characters of the three *Heteroliodon* species are summarized in Table 1. *H. fohy* is distinguished from other comparable Madagascan snakes with 17 dorsal

scale rows as follows: from *Exallodontophis albignaci* by lack of longitudinal stripes (see Raxworthy and Nussbaum, 1994) and much lower number of ventrals (136 versus 180–196), from *Pararhadinaea melanogaster* by light ventral coloration and unstriped dorsal coloration (see Cadle, 1999:408). In addition, *H. fohy* differs from both these species by presence of a loreal scale.

*Description of holotype*.—Specimen in relatively good condition; distinct ventro-lateral slit present; muscle tissue sample for DNA studies removed and stored in pure ethanol (genbank accession numbers of DNA sequences obtained from this specimen are AY188057,

TABLE 1.—Diagnostic characters of the three species of *Heteroliodon*. Data for *H. occipitalis* (numerous male and female specimens) and *H. lava* (one male and one female specimen) are from Nussbaum and Raxworthy (2000) and are based on specimens listed therein.

Variables	Species		
	<i>H. occipitalis</i>	<i>H. lava</i>	<i>H. fohy</i>
Snout-vent length [mm]	210–265	250–365	212
Tail length [mm]	60–77	56–76	68
Tail length/SVL length	0.25–0.31	0.21–0.22	0.32
Number of ventrals	158–182	214–224	136
Number of subcaudals	61–72	63–65	57
Number of infralabials	7	7	8–9
Width at midbody/SVL	0.025–0.033	0.023–0.024	0.035
Nasal groove from nostril to	1. supralabial	1. supralabial	2. supralabial
Eye diameter/head depth at midorbit	0.36–0.54	0.45–0.49	0.38
Dorsal coloration	with light band	uniform	uniform

AY188018, and AY187979, see also Nagy et al., 2003); male with partially everted hemipenes; right testis 4.7 by 2.0 mm, unpigmented.

Body slender, 212 mm SVL, width at midbody 7.4 mm; head width 6.7 mm, only slightly wider than neck (5.6 mm); snout bluntly rounded, slightly projecting; eye diameter 1.5 mm, 0.38 times head depth at mid-orbit; tail length 68 mm, complete, 0.32 times SVL, rounded at base, tapering to sharp point.

Scalation: Rostral much wider (3.1 mm) than tall (1.5 mm, ratio height/width 0.48), visible in dorsal view; nasal with horizontal groove passing from nostril opening to second supralabial; internasals 2; prefrontals 2; frontal single; parietals 2, large; loreal single, bordered anteriorly by nasal, dorsally by prefrontal, posteriorly by single large preocular, ventrally by second and third supralabials; preoculars 1–1 (left, right), large; supraoculars 1–1; postoculars 2–2; temporal formula 1–2–3 both sides; supralabials 7–7, third and fourth below eye; mental small, triangular, wider (2.5 mm, along the lower lip) than long (1.5 mm, from the tip of the angle touching the chin shields straight to the lower

lip, ratio length/width 0.6); chin shields in two pairs; mental groove between first infralabials and both pairs of chin shields; infralabials 8–9, fifth by far largest; dorsal scales smooth, without pits, in 17 rows along most of body; ventrals 136; anal plate divided; subcaudals 57, divided into two rows.

Dentition: Aglyphous. Not studied in detail due to the delicate nature of the teeth.

Coloration: The darker colors have apparently not faded after 12 months in alcohol and appear unchanged from life.

Dorsum of head and proximal neck dark brown, interrupted by yellow nuchal band 2–3 mm wide, covering distal tips of parietal scales and first three rows of neck scales; nuchal band continuous with white lip line and whitish ventral coloration; upper lips white, including most of supralabial scales and rostral scale; proximal edges of scales circling eye dark brown, iris black; dorsolateral portion of distal neck, body, and tail uniformly dark brown fading to lighter brown lateroventrally; faint, narrow, white, longitudinal lines running between scale rows on body, becoming more prominent lateroventrally; ventral surfaces of head, neck, body, and proximal portion of tail immaculate cream-white; distal portion of ventral tail white, slightly dusted with light brown.

*Etymology*.—The specific name “fohy” (pronounced “foo he”) is Malagasy for “short” and is used as an unlatinized specific epithet. Fohy is the opposite of “lava” (= long). *Heteroliodon fohy* has a stout habitus, possibly is the shortest species of the genus, and certainly belongs, together with its two congeners, to the smallest Malagasy colubrid snakes.

*Distribution and ecology*.—Only known from the type locality (Montagne des Français) near the northern tip of Madagascar. This limestone massif is a classified forest that, however, is not yet protected as a nature reserve. The holotype was collected at dusk on the ground, after several days of heavy rains. The specimen was crossing a small trail in dry deciduous forest, just at the border of eroded limestone formations (“tsingy”).

#### REMARKS

Among the 75 described species of Madagascan colubrids, *Heteroliodon fohy* is one of only five species which (at least occasionally) have a number of ventrals below 140, a char-

acter shared only with *Pseudoxyrhopus kely* (134–139), *P. quinquelineatus* (139–155), *Geodipsas boulengeri* (131–137), and *G. zeny* (132–137) (data from Cadle, 1996; Glaw and Vences, 1994; Raxworthy and Nussbaum, 1994). All of these species are small and largely terrestrial. The number of ventrals is variable intraspecifically in most snake species, but to a rather limited extent. In Madagascan colubrids, the maximum variation in the number of ventrals occurs in *Madagascarophis meridionalis* which has 196–232 ventrals (see Glaw and Vences, 1994:324–325). A difference of 78–88 ventrals as between *H. fohy* and *H. lava* is more than twice the maximum intraspecific variation in the number of ventrals found in Madagascan colubrids and is unusual between apparently closely related species.

Among the species of the genera *Pseudoxyrhopus*, *Heteroliodon*, *Pararhadinaea*, and *Exallodontophis*, *H. fohy* has the longest relative tail length (one third of SVL).

According to Cadle (1999:430), the number of dorsal scale rows may be the same posteriorly as at midbody in *Exallodontophis*, *Heteroliodon*, and *Pararhadinaea*, but may undergo posterior reduction in all species of *Pseudoxyrhopus*. *Heteroliodon fohy* does not show posterior reduction as well and, thus, confirms that this state is typical for its genus.

The relationships of *H. fohy* to *H. occipitalis* and *H. lava* appear entirely ambiguous according to available data. Regarding some morphological and meristic characters (SVL, number of ventrals, number of subcaudals, relative tail length), *H. fohy* is more similar to *H. occipitalis* than to *H. lava*. Similarities between *H. lava* and *H. fohy* include a uniform dorsal coloration and the habitat. Both known specimens of *H. lava* were found in limestone formations (“tsingy”), and the same is true for the single known specimen of *H. fohy*. In contrast, *H. occipitalis* is restricted to the drier southwestern habitats that include spiny-scrub, dry deciduous forests, and gallery forests, including non-tsingy limestone habitats (Nussbaum and Raxworthy, 2000). Similarities between *H. lava* and *H. occipitalis* include an elongated body, the number of infralabials (seven, with the fourth being the largest), and the position of the nasal groove. This mosaic distribution of shared characters between the

three species does not allow resolution of the relationships of these snakes.

Although only a few specimens of *H. lava* and *H. fohy* are available, it seems reasonable to assume that *H. fohy* and *H. lava* represent a pair of allopatric species and that the new species may be endemic to the region of Montagne des Français in far northern Madagascar. Recently, a variety of new herpetological taxa have been discovered at Montagne des Français, which were not found elsewhere and, therefore, appear to be endemic to this massif or the region, including the frog *Mantella viridis* (Pintak and Böhme, 1988), the colubrid *H. fohy* (described herein), and the recently described gecko *Paroedura lohatsara* (Glaw et al., 2001). Several other animals and plants are endemic in this region as well, among them a species of the famous Baobab trees (*Adansonia suarezensis*). Thus, there is sufficient evidence that Montagne des Français is an important center of endemism of Madagascan biota and should, therefore, be protected as a nature reserve. This massif apparently has rather close biogeographic relationships to the drier western and southern regions of Madagascar, whereas the rainforest of Montagne d’Ambre, just a few kilometres away, harbors many species with eastern relationships.

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## A NEW SPECIES OF *BUFO* (ANURA: BUFONIDAE) FROM THE ANDES OF BOLIVIA

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A new species of *Bufo* is described from cloud forests of the Cordillera de Apolobamba, La Paz, Bolivia. The new species has large glands on dorsal surfaces of shanks and forearms and is tentatively included in the *B. spinulosus* group.

*Key words:* Andes; Anura; Bolivia; *Bufo apolobambicus*; Bufonidae; New species

THE GENUS *Bufo* is a speciose group of toads in South America. In the Andes, this genus includes: (1) species belonging to primarily lowland groups, which reach elevations above 1000 m altitude (e.g., the *B. margaritifera* and *B. marinus* groups); (2) species belonging to a primarily Andean group (the *B. spinulosus* group); and (3) species belonging to an Andean endemic group (the *B. veraguensis* group) (Ceí, 1972; Duellman, 1979; Duellman and Schulte, 1992; Lynch, 1986). Situated in the middle of the South American sub-continent, Bolivia holds a diverse fauna of *Bufo*. De la Riva et al. (2000) reported 14 species for the country, eight of them occurring mostly or exclusively in the Andes. These authors recog-

nized several taxonomic problems among the Bolivian *Bufo* and predicted the description of several new species in the *B. margaritifera* and *B. veraguensis* groups, especially from cloud forests of the Cordillera Oriental. One of these species, *B. stanlani* (*B. margaritifera* group), was described later (Lötters and Köhler, 2000), and we are aware of other species in the *B. veraguensis* group awaiting description or deserving a taxonomic reassessment. For example, the Andes near the Argentinean border is an area of special interest because of the occurrence of poorly known forms of *Bufo*, which might be either conspecific with some Argentinean species or undescribed Bolivian endemics (De la Riva et al., 2000). Thus, it is anticipated that several species of *Bufo* will be discovered and described from Bolivia in the near future.

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FIG. 1.—Ventral (CBF 5491, holotype, 71.6 mm in SVL) and dorsal (CBF 5492) views of *Bufo apolobambicus* sp. nov.

In the last five years, several herpetological surveys have been done in the Área Natural de Manejo Integrado Apolobamba, which covers both the high puna (the former Reserva Nacional de Fauna Ulla Ulla) and the Andean slopes of the Bolivian section of the Cordillera de Apolobamba near the Peruvian border. One of the novelties found in this area is an undescribed, moderately large species of *Bufo*. The new species is distinctive, but not easily assignable to any of the species groups currently known in the Andes. Herein, we describe this toad and tentatively place it in the *B. spinulosus* group.

#### MATERIAL AND METHODS

Specimens were fixed with 10% formalin and preserved in 70% ethanol. Measurements were taken with digital calipers to the nearest 0.1 mm. The skin of the tympanic region of CBF 5490 was dissected to reveal the tympanic condition. Drawings were done using a camera lucida. The diagnosis and description follow Duellman and Ochoa (1991) with some modifications. Specimens examined are listed in the Appendix.

#### SYSTEMATICS

##### *Bufo apolobambicus* sp. nov.

(Figs. 1, 2 and 3)

*Holotype*.—CBF 5491, an adult female from Laitique on the banks of the river Pelechuco, ca. five hours downstream walking from the village of Pelechuco to Apolo, Provincia Franz Tamayo, La Paz, Bolivia, 14° 47' 09" S, 69° 01' 34" W, 2820 m, collected on 29 October 1999 by James Aparicio and Jehan Ninon Ríos.

*Paratypes*.—CBF 5490, 5492, and 5493, adult females collected with the holotype.

*Diagnosis*.—A moderately large species of *Bufo* attaining a snout-vent length (SVL) of 74.2 mm and distinguished from all other species of Andean *Bufo* by the following combination of characters: (1) cranial crests absent; interorbital region depressed, its skin co-ossified with underlying bone; (2) tympanic region covered by skin, tympanum and tympanic annulus absent; (3) parotoid gland large, moderately elongate; (4) paravertebral and dorsolateral rows of elongated glands; (5) dorsal surface of shanks and forearms completely covered by a large, elongate gland; a smaller

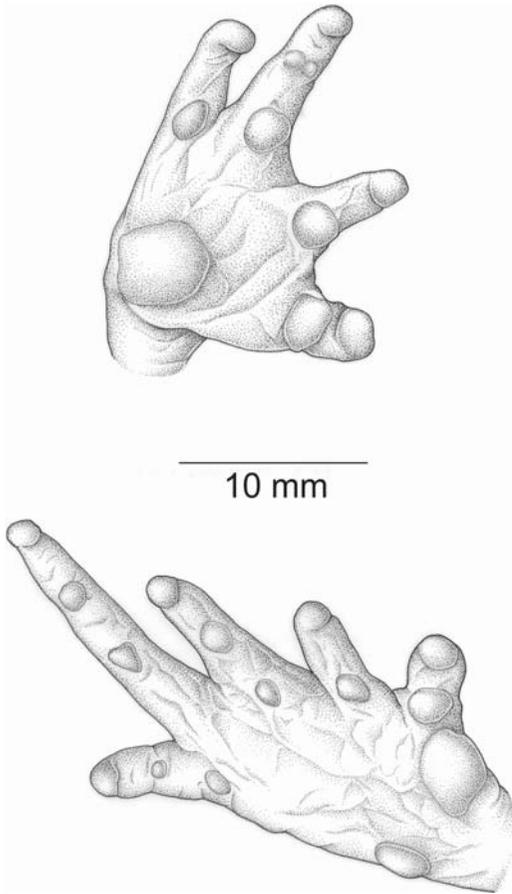


FIG. 2.—Plantar and palmar surfaces of *Bufo apolobambicus* sp. nov. (CBF 5492).

gland on the dorsal surface of tarsus; (6) tarsal fold absent; (7) hands and feet basally webbed.

*Bufo apolobambicus* is readily distinguished from any other species of Andean toad. The most similar species found in the Andes of Bolivia is *B. spinulosus*, from which *B. apolobambicus* differs by having elongate parotoid glands (round in *B. spinulosus*), a large gland covering the entire dorsal surface of the shanks and forearms (absent), head rounded with the interorbital region profoundly depressed (not depressed), tympanum absent (present), tarsal fold absent (present), and body color uniformly dark brown (brown or beige with irregular dark blotches). No species of Bolivian *Bufo* has a large gland covering the dorsal surface of the forearm. *Bufo schneideri* Werner, a large member of the *B. marinus* group occurring in the lowlands of Argentina, Bolivia, Brazil, Para-

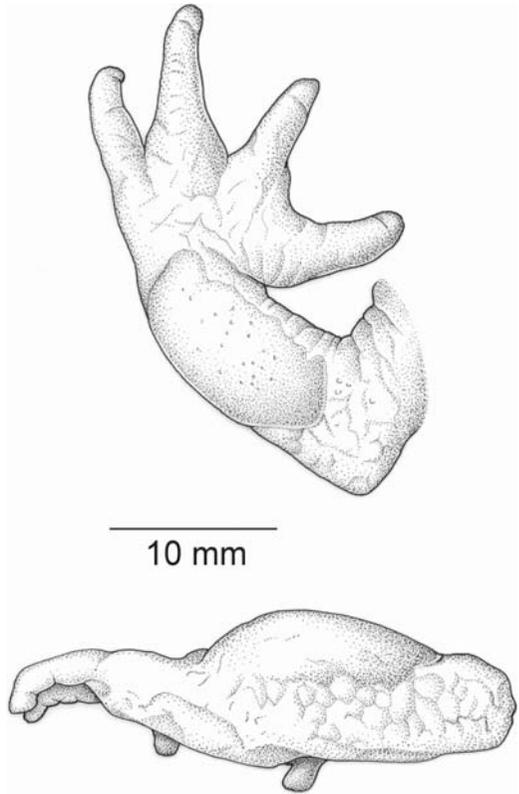


FIG. 3.—Antebrachial gland of *Bufo apolobambicus* sp. nov. (CBF 5492) in dorsal and lateral views.

guay, and Uruguay (Frost, 2004), possesses an enlarged longitudinal gland on the shank, but not on the forearm; furthermore, it is completely different from *B. apolobambicus* in many other respects, such as skin texture, color pattern, size, shape or parotoid glands, etc. Large glands on the tibia and forearm have been reported in two Peruvian species of *Bufo*, *B. chavin* Lehr, Köhler, Aguilar and Ponce, and *B. cophotis* Boulenger. *Bufo chavin*, from Department of Huánuco, is a species in the *B. veraguensis* group (Lehr et al., 2001) that has a tympanum and parotoids separated from the eye, whereas *B. apolobambicus* lacks a tympanum and the parotoids are directly in contact with the eye. *Bufo cophotis*, a member of the *B. spinulosus* group from Departments of Ancash, Cajamarca and La Libertad (Rodríguez et al., 1993) has the gland on the forearm not as developed as that of *B. apolobambicus*, and the tibial gland is rounded instead of elongate; additionally, *B. cophotis* has a con-

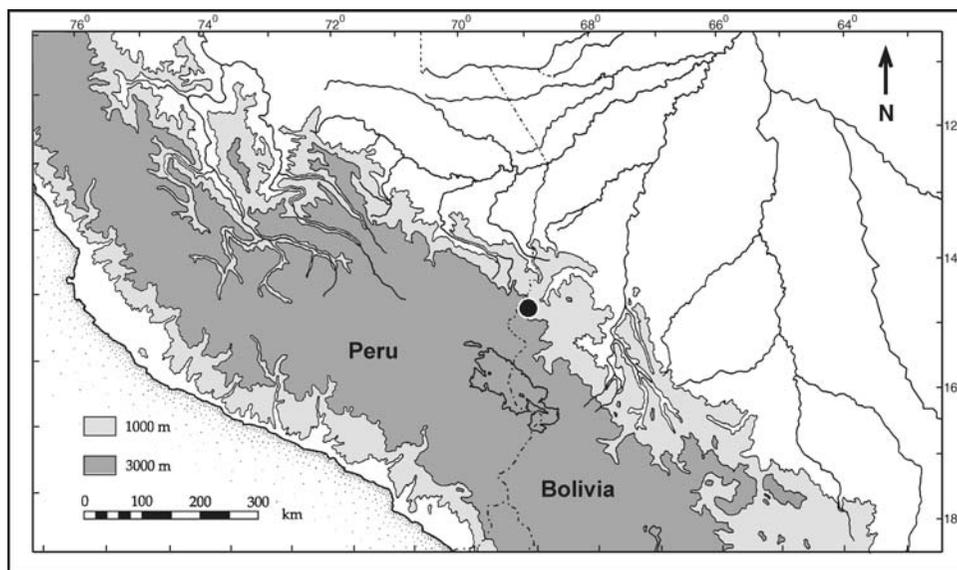


FIG. 4.—Map of the Andes of southern Peru and northern Bolivia showing the type locality of *B. apolobambicus* sp. nov.

trasting color pattern of yellow and brown patches and parotoid glands round, small, not larger than other dorsal glands, whereas *B. apolobambicus* is uniformly dark brown and possess large, elongate parotoid glands.

*Description of holotype.*—Body robust; head length (from rictus to tip of snout) 76.7% of head width (measured at level of rictus), head length 27.2% of SVL; snout acuminate in dorsal view, bluntly rounded in profile; top of head flat, depressed; no cranial crests; skin of frontoparietal region co-ossified with underlying cranial bones; internarial area convex; nostrils slightly protuberant, directed laterally; canthus rostralis angular, elevated posteriorly; loreal region concave; lip rounded; symphysis of upper jaw with notch; eye-nostril distance 80% of eye diameter; tympanum absent. Dorsal surface of forearm entirely covered by a single large, elevated gland (Fig. 3); relative lengths of fingers  $2 < 1 < 4 < 3$ ; palmar webbing fleshy, basal; lateral fringes absent from digits; tips of digits terminating in slightly broadened, indistinct discs; palmar tubercle low, indistinct, rounded, about three times size of ovoid, indistinct thenar tubercle; subarticular tubercles indistinct; supernumerary tubercles absent. Hind limbs short; tibia length 35.9% of SVL; tibia length 91.4% of foot length (from proximal border of inner metatarsal tubercle to tip of fourth toe); dorsal surface of shank entirely

covered by single large, elevated gland; tarsal fold absent; outer metatarsal tubercle rounded, low, indistinct; inner metatarsal tubercle ovoid, about twice size of outer tubercle; subarticular tubercles indistinct; supernumerary tubercles absent; relative lengths of toes  $1 < 2 < 3 = 5 < 4$ ; pedal webbing fleshy, basal; lateral fringes absent from toes; tips of toes terminating in indistinct discs.

Skin on dorsum granular with large, elongate glands forming a lateral row from parotoid gland to inguinal region; paravertebral glandular ridge extending from occipital region to mid-length of body; flanks with scattered, rounded glands; parotoid glands large, elevated, protruding laterally, elongately ovoid, about twice as long as wide, their lengths about three times eye diameter; numerous tubercles on dorsal surfaces of thighs and arms. Skin on throat and ventral surfaces of limbs granular; skin of venter with low tubercles and fine folds; plantar and palmar surfaces mostly smooth. Cloacal opening slightly protuberant, directed ventrally at midlevel of thighs.

Choanae small, round; vomerine odontophores absent; tongue about twice as long as wide, equal in width throughout its length, free at its posterior third; teeth absent.

*Measurements (in mm).*—SVL 71.6; tibia length 25.7; foot length 28.1; head length 19.5; head width 25.4; upper eyelid width 4.5; inter-

orbital distance 9.0; eye-nostril distance 4.4; inter-narial distance 4.8; eye length 5.5.

*Color.*—In preservative, dorsum uniformly dark grayish-brown; venter similar but with purplish hue and some diffuse, cream mottling barely visible; palmar and plantar surfaces gray with tubercles paler than background. In life, dorsum and head dark brown with diffuse whitish blotches posterior to eyes; iris dark gold; venter reddish-brown with small, diffuse pale cream blotches.

*Variation.*—Males of *Bufo apolobambicus* are unknown. The size and form of the dorsal glands show some variation. Specimen CBF 5492 has a large, round pustule in the middle of the scapular region (Fig. 1). Although superficially it looks like a gland, this structure may have been caused by a parasite. The longest specimen, CBF 5490, is not the largest. In fact, CBF 5492 is larger in some other measurements, but not SVL. This is because CBF 5490 has the region around the vent slightly more elongated than the other specimens.

Ranges of some morphometric ratios of the type series are (in parentheses, mean  $\pm$  SD): head length 74.8–76.7% (76.0  $\pm$  0.8%) of head width; head length 26.0–27.2% (26.7  $\pm$  0.5%) of SVL; eye–nostril distance 69.3–80.0% (75.3  $\pm$  5.4%) of eye length; tibia length 35.8–37.8% (36.8  $\pm$  0.9%) of SVL; tibia length 91.2–94.0% (91.9  $\pm$  1.3%) of foot length.

*Distribution and ecology.*—*Bufo apolobambicus* is known only from the type locality of Laitique, which is located among steep topography covered by “ceja de monte” vegetation (upper section of the cloud forest) (Aparicio, 1999) (Fig. 4). The type locality lies within the Área Natural de Manejo Integrado Apolobamba, a protected zone of 483,743 ha with an elevational range of 800–6200 m and encompassing puna to montane and lowland rainforest (SERNAP, 2000). The area around Laitique is secondary growth forest, the result of heavy subsistence agriculture, timber harvesting for house construction, firewood, cattle grazing, and traditional human movement between the old villages of Apolo and Pelechuco.

Almost nothing is known about the natural history and ecology of this species. Specimens were found active on the forest floor and on the path, both during day and night. Three out of the four females in the type series contain numerous mature, pigmented (cream and dark

brown), small (1.5 mm) eggs, and one has loose, dilated oviducts, indicating that a clutch had been laid before it was collected. The tadpole of *B. apolobambicus* is unknown.

*Etymology.*—The specific name refers to the Andean area where the type series was collected, the Cordillera de Apolobamba, which is shared by Peru and Bolivia.

#### DISCUSSION

Duellman and Schulte (1992) provided diagnoses of phenetic groups of South American *Bufo*. In general, these groups are well defined and every species of South American *Bufo* is easily assignable to one of these groups. Based on distribution and general morphology, we tentatively consider *B. apolobambicus* as a member of the *B. spinulosus* group (at least, it can be said with certainty that it belongs to none of the other groups as currently defined). However, the fact that the type series has no males precludes the confirmation of sexual dimorphism in skin texture, one of the defining characters of members of the *B. spinulosus* species group. Most species in this group are similar to the nominal species, *B. spinulosus*, and some of them (especially *B. arequipensis* Vellard, *B. atacamensis* Cei, *B. flavolineatus* Vellard, *B. rubropunctatus* Guichenot, and *B. trifolium* [Tschudi]) have been treated alternatively as valid species, subspecies, or synonyms of *B. spinulosus*, depending on the opinion of the authors (see for example Cei, 1972; Córdova, 1999; Duellman and Schulte, 1992; Frost, 2004; Haas, 2002; Henle, 1992; Lavilla, 1994; Morales, 1995; Morrison, 1992, 1994; Pramuk and Kadivar, 2003; Rodríguez, 1995; Rodríguez et al., 1993; Sinsch, 1990; Vellard, 1959). Exceptions to this rule are the well-defined species *B. cophotis* Boulenger, *B. corynetes* Duellman and Ochoa, and *B. variegatus* (Günther). These three distinctive forms of the *B. spinulosus* group share with *B. apolobambicus* the absence of a tympanum. However, these three species have a contrasting pattern of yellow and brown patches and dots, whereas *B. apolobambicus* is uniformly dark brown, both dorsally and ventrally. In addition, *B. apolobambicus* has a large gland on the forearms and the shanks, a feature shared in this group only with *B. cophotis*. For the moment, the relationships of *B. apolobambicus*

with other Andean *Bufo* are obscure and deserve future research.

## RESUMEN

Se describe una nueva especie de *Bufo* de la Cordillera de Apolobamba, en el Departamento de La Paz, Bolivia. La nueva especie, tentativamente incluida en el grupo de *B. spinulosus*, habita en bosques de niebla y se caracteriza por tener grandes glándulas cubriendo los antebrazos y la porción tibial de las patas traseras. No se conocen los machos ni las larvas.

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## APPENDIX

## Material Examined

- Bufo amoroensis*: BOLIVIA: Cochabamba: Río Chua Khocha, La Siberia (MNCN 41987).
- Bufo arborescandens*: PERU: Amazonas: 5 km N Mendoza, 06° 18' S, 77° 27' W, 2400 m (KU 209394–95).

*Bufo chavin*: PERU: Huánuco: Palma Pampa, 09° 53' 14" S, 75° 53' 21" W, 3010 m (MTD D 44318).

*Bufo cophotis*: PERU: Cajamarca: S slope Abra Quilsh, 26 km NNW Cajamarca, 3500 m (KU 196626; KU 211711); 55 km N Cajamarca, 3600 m (KU 211733); S slope Abra Comulica, 20 km NE Encanada, 3520 m (KU 211741).

*Bufo corynetes*: PERU: Cuzco: Abra Málaga, 50 km NW Ollantaytambo, 13° 09' S, 72° 20' W, 3780 m (KU 173229); San Luis, 13° 09' S, 72° 21' W, 3200 m (KU 212554).

*Bufo quechua*: BOLIVIA: Cochabamba. Tablasmontes (MNCN 41988).

*Bufo spinulosus*: BOLIVIA: La Paz: road Quime - Inquisivi, 16° 55' 49" S, 67° 09' 24" W, 3594 m (MNCN 41989); road Charazani -Curva 15° 08' 06" S, 69° 02' 03" W, 3700 m (MNCN 41990); Lahuachaca, 17° 23' S, 67° 40' W (CBF 00065). PERU: Arequipa: Yura (MNCN 41986)

*Bufo veraguensis*: BOLIVIA: Serranía Bellavista, 15° 42' 13" S, 67° 29' 15" W, 1450 m (MNCN 41991).

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## TWO NEW SPECIES OF *ELEUTHERODACTYLUS* (ANURA: LEPTODACTYLIDAE) OF THE *ALFREDI* GROUP FROM EASTERN GUATEMALA

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Two new species of frogs of the *Eleutherodactylus alfredi* group are described from Subtropical and Montane Wet Forests of the Montañas del Mico and the Sierra de Caral of the Caribbean slopes of Guatemala. They differ from other Guatemalan species in the group by having the fifth toe pad wider than the second, few melanophores on the abdominal area of the venter, and dorsal and ventral ground coloration. The species from the Sierra de Caral is larger in overall size and has smaller dentigerous fascicles than the one from the Montañas del Mico. These two species also differ between themselves in dorsal and ventral ground coloration.

*Key words*: Amphibia; Anura; *Eleutherodactylus campbelli* new species; *Eleutherodactylus nefrens* new species; Guatemala; Izabal; Leptodactylidae

OUR KNOWLEDGE of the diversity of the genus *Eleutherodactylus* in eastern Guatemala has increased by over 50% just in the last decade. Campbell and Vannini (1989) listed 13 species from this region, including two undescribed taxa. Campbell (1994a) described as *E. aphanus* those animals previously referred to *E. biporcatus* from Montañas del Mico. Campbell et al. (1994) described a new species of the *E. rugulosus* group, *E. psephosypharus*, which inhabits pristine rainforests throughout eastern Guatemala. Two more *Eleutherodactylus* from eastern Guatemala were described that same year. These were members of the *E. milesi* group, *E. trachydermus* from the western Sierra de Santa Cruz and *E. adamastus* from the northeastern Sierra de Las Minas, described by Campbell (1994b). This paper also mentioned two other populations of the

*E. milesi* group from eastern Guatemala that might represent undescribed taxa. Campbell and Savage (2000) described four new species belonging to the *E. rugulosus* group and inhabiting eastern Guatemala: *E. rivulus*, *E. inachus*, *E. sabrinus*, and *E. charadra*. Savage (2000) described a new species belonging to the *E. milesi* group from the Sierra de Xucaneb, *E. myllomyllon*, bringing the current number of eastern Guatemalan *Eleutherodactylus* to 22.

While sampling the herpetofauna of the wet forests of the Caribbean slopes of Guatemala, colleagues and I encountered two additional undescribed *Eleutherodactylus*. These are members of the *E. spatulatus* subgroup of the *E. alfredi* group (sensu Lynch, 1966, 1967; Campbell et al., 1989). The group is characterized by possessing greatly expanded and truncate digital pads on the outer two fingers (Campbell et al., 1989) and the fifth toe longer

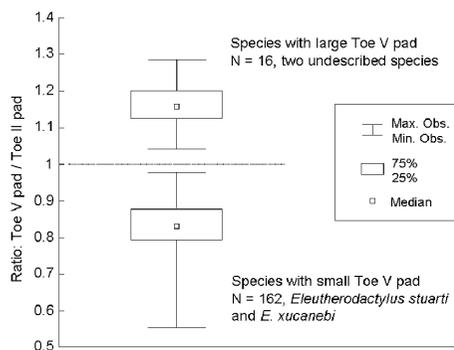


FIG. 1.—Distribution of ratios—Toe V pad width/Toe II pad width among Guatemalan species of the *Eleutherodactylus spatulatus* subgroup of the *E. alfredi* group with small and large outer toe pads.

than the third (Lynch, 2000). The *E. spatulatus* subgroup is characterized by having contrasting, usually bold, dorsal color patterns, and a tubercular dorsal skin (Lynch, 1966, 1967). The two new species are peculiar among *E. spatulatus* subgroup taxa in possessing the pad of the fifth toe very wide, as compared to previously known Guatemalan taxa, namely, *E. stuarti* and *E. xucanebi*. Comparison of the ratios of the fifth toe-pad width to the second reveals a significant difference between the new and the previously known Guatemalan frogs of this subgroup (Kolmogorov-Smirnov  $D_{\max} = 1, P < 0.001$ ) (Fig. 1). Additionally the new species occur isolated from each other and from the other species in the group by unsuitable lowland habitat. Description of these new forms is the purpose of this work.

#### MATERIALS AND METHODS

Measurements of tympanum and eye diameter, head, foot, tibia, and snout-vent (SVL) lengths follow those of Duellman (1970); measurements of eyelid and head widths, interorbital distance (IOD), and snout length (E-N, eye-nostril) follow those of Lynch and Duellman (1980), and toe and finger terminology follows Savage (1987). The following measurements also were included: internarial distance = distance between medial borders of nares; fascicular length = maximum length of longer axis of dentigerous fascicle (dentigerous process of vomer and associated oral lining projecting into buccal cavity); interfascicular distance = shortest distance between dentigerous fascicles; choana width = max-

imum width of choana; femur length = distance from tip of urostyle to distal end of femur; arm length = distance from proximal end of radio-ulna to proximal end of thenar tubercle; hand length = length from proximal border of palmar tubercle to tip of third finger; and tarsal length = distance from proximal border of inner metatarsal tubercle to proximal end of *tibiale*. Lengths were recorded from the left side of each specimen, unless otherwise stated. Measurements >10 mm were taken to the nearest 0.1 mm with digital calipers held under a dissecting microscope. Those <10 mm were taken using a stereoscope with an ocular micrometer. Specimens examined are listed in Appendix I.

Color descriptions of live specimens were made based on color transparencies deposited at the UTA Herpetological Slide Collection. Colors are taken from the *Naturalist's Color Guide* (Smithe, 1975). Color descriptions in the diagnoses refer to live specimens.

Specimens were fixed in the field with a 10% formalin solution and later transferred to 70% ethanol. The sex of preserved specimens was determined by the presence of white preopercular nuptial excrescences in adult males and their absence in females. Small individuals without nuptial excrescences were dissected to verify sex by directly observing the gonads.

#### DESCRIPTIONS OF NEW SPECIES

##### *Eleutherodactylus campbelli* sp. nov.

*Holotype*.—The University of Texas at Arlington (UTA) A-33452, an adult female (Fig. 2) from Torres de Guatel, Cerro San Gil, Montañas del Mico, Municipio de Puerto Barrios, Departamento de Izabal, Guatemala, 962 m, collected on 6 January 1991 by Michael B. Harvey, Jonathan A. Campbell, Dwight P. Lawson, William W. Lamar, E. N. Smith, and José Monzón (field no. JAC 17408). This locality is at approximately 15° 40' 10" N, 88° 41' 40" W.

*Paratypes* (10).—All from Cerro San Gil [Microhondas], Montañas del Mico, Municipio de Puerto Barrios, Departamento de Izabal, Guatemala. UTA A-33451, adult female, collected at approximately 12.0 km (by road) WSW Puerto Santo Tomás, 786 m, on 13 July 1990 by J. A. Campbell; KU 189805-06, males, adult and subadult, respectively, collected at



FIG. 2.—*Eleutherodactylus campbelli*, female holotype, 26.6 mm SVL, UTA A-33452. (Reproduced from UTA Slide No. 12855.)

approximately 11.8 km (by road) WSW Puerto Santo Tomás, 774 m, on 8 June 1981 by J. A. Campbell and W. W. Lamar; all from approximately 15° 40' 50" N, 88° 41' 00" W; UTA A-55228, 48531–32, juvenile female, and sub-adult female and male, respectively, collected at type locality, 900–905 m, on 27 December 1995 by Manuel Acevedo, Arturo Godoy, Hemeregildo Gil and E. N. Smith; approximately 15° 40' 18" N, 88° 41' 42" W; UTA A-48533, adult female collected on road to Torres de Guatel, 750 m, on 27 December 1995 by Manuel Acevedo, Arturo Godoy, Hemeregildo Gil and E. N. Smith; approximately 15° 40' 45" N, 88° 40' 56" W; UTA A-53034, juvenile female, collected above Las Escobas, Río San Ramoncito [near road to Torres de Guatel], ca. 260 m, on 7 June 1999 by Manuel Acevedo, J. A. Campbell, and E. N. Smith; approximately 15° 41' 25" N, 88° 39' 37" W; UTA A-53035–36, adult males, collected near road to Torres de Guatel, 860–870 m, on 9 June 1999 by Manuel Acevedo and E. N. Smith; approximately 15° 40' 06" N, 88° 41' 22" W.

**Diagnosis.**—A member of the *Eleutherodactylus spatulatus* subgroup of the *E. alfredi* group possessing no vocal sac or slits, a relatively large tympanum (55.3–75.0 % eye diameter, in adults), and sometimes having a fine tarsal ridge. It is most similar to *E. xucanebi* and the other species described in this paper. It may be distinguished from previously described Guatemalan members of the *E. spat-*

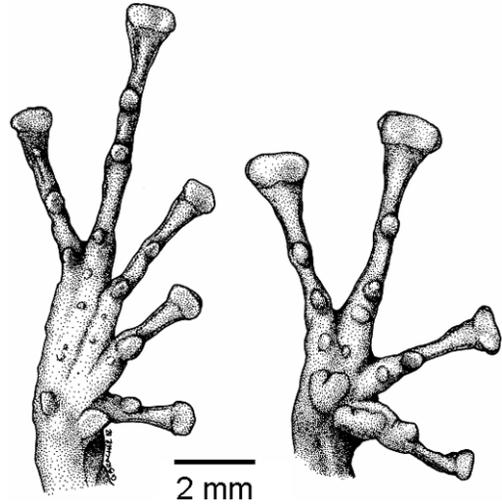


FIG. 3.—Ventral aspect of hand and foot of *Eleutherodactylus campbelli*, male paratype, KU 189806.

*ulatus* subgroup (*E. stuarti* and *E. xucanebi*) by possessing the pad of the fifth toe wider than that of the second (Fig. 3), a citrine or sulphur yellow dorsal ground color (versus brownish), a mauve to spectrum violet venter (versus vinaceous or bluish violet), and having no or few melanophores scattered on the belly. It differs from the species described hereafter by having moderately sized vomerine denticerous processes in adults (4–7 versus 0–3 teeth), a smaller body size (males 20.9–23.7 versus 24.0–26.8 mm in SVL), and in ventral and dorsal coloration. *Eleutherodactylus campbelli* differs from *E. bocourti*, the other member of the *E. alfredi* group (sensu Lynch, 2000) in the highlands of Guatemala, by lacking vocal slits. Additionally, possessing the pad of the fifth toe wider than that of the second differentiates *E. campbelli* from all members of the *E. alfredi* group (including *E. bocourti* [Lynch, 2000] and *E. galacticorhinus* [Canseco-Márquez and Smith, 2004]), except the species described hereafter.

**Description and variation.**—Holotype followed by variation of paratypes in parentheses (adult females [ $n = 2$ ], adult males [ $n = 3$ ], and juveniles [ $n = 5$ ], respectively). Measurements in mm: SVL 26.6 (26.9–29.3, 20.9–23.7, 15.0–20.4), head length 11.7 (11.3–12.3, 9.2–9.8, 6.4–9.0), head width 10.7 (10.3–11.3, 8.4–10.1, 6.2–8.1), eye diameter 3.8 (3.8–4.1, 3.2–3.7, 2.2–3.0), snout length 4.0 (3.9–4.1, 3.1–3.4, 2.9), internarial distance 2.2 (2.2–2.5, 2.0–2.1,

1.4–2.1), choana width 0.8 (0.7–0.9, 0.7–0.8, 0.4–0.7), tympanum diameter 2.3 (2.1–3.0, 2.3–2.4, 1.1–1.8), interfascicular distance 0.6 (0.4–0.6, 0.5–0.6, 0.3–0.5), fascicular length 0.8 (0.8–0.9, 0.5–0.6, 0.3–0.6), tarsal length 8.3 (8.4–9.6, 6.6–7.9, 4.7–6.6), hand length 9.7 (10.2–10.6, 7.7–9.2, 5.3–7.4), arm length 7.4 (7.3–9.0, 5.7–6.4, 3.9–5.7), tibia length 17.0 (16.0–18.3, 13.2–14.4, 9.1–12.2), foot length 12.5 (13.8–14.4, 10.6–11.9, 7.1–10.4), femur length 14.2 (14.8–18.2, 13.0–13.6, 8.2–12.3), upper eyelid width 2.4 (3.0–3.1, 1.9–2.6, 1.5–2.1), IOD 3.4 (3.1–4.0, 2.3–2.7, 1.7–2.6), pad width of Toe V 1.3 (1.3–1.4, 0.9–1.1, 0.6–0.9), pad width of Toe II 1.2 (1.1–1.2, 0.8–1.0, 0.4–0.8).

Head broader than body, about as long as wide, with a few large, scattered granules; head length 109.3 (108.9–109.9, 93.4–111.9, 103.2–111.8) % head width; head width 40.3 (38.3–38.5, 40.2–42.5, 38.8–41.4) % SVL; snout length 105.3 (100.0–101.3, 83.8–96.9, 80.4–100.0) % eye diameter, rounded to subacuminate in dorsal view, nearly truncate in lateral profile; canthus rostralis straight to weakly concave; loreal area slightly convex; lips not flared; interorbital distance 88.2 (81.6–97.6, 64.3–82.8, 72.5–86.7) % eye diameter; internarial distance 56.6 (57.9–61.0, 56.8–62.5, 54.9–71.2) % eye diameter; upper eyelid width 63.4 (74.9–78.9, 60.0–88.0, 50.2–76.0) % eye diameter, bearing granules; tympanum distinct, with a moderately developed supratympanic fold, 59.2 (55.3–73.2, 63.5–75.0, 43.1–60.0) % eye diameter; no cranial crests; choanae small; dentigerous fascicule 93.8 (94.4–114.3, 66.7–76.7, 43.5–85.7) % choana width, bearing 5/5 (6/5–7/7, 4/4–6/6–5/7, 2/2–3/3–4/4–6/6, left/right) clumped teeth, teardrop-shaped, round end directed postero-medially; interfascicular distance 68.8 (60.7–69.4, 69.0–83.3, 37.0–100.0) % choanae width; no vocal slits or sac; tongue lanceolate (ovoid to lanceolate), longer than wide.

Skin of dorsal surfaces smooth to finely shagreen with a few large, scattered granules, especially on upper eyelids and dorsum of head; no dorsolateral, paravertebral, or occipital folds; skin on venter smooth except for femoral surfaces which are areolate; scattered melanophores on chest, less densely arranged on belly.

Arm length 27.9 (27.2–30.7, 24.0–28.6, 24.0–28.7) % SVL; hand length 36.6 (36.0–38.1, 36.8–38.8, 33.9–36.6) % SVL; relative lengths of fingers I < II < IV < III; fingers bearing large, expanded disks, disk covers indented distally on Fingers II to IV; fingers with weak marginal keels; few small tubercles sometimes present in ulnar region; thumb with an enlarged thenar tubercle, almost as large as semidivided cordiform palmar tubercle; subarticular tubercles obtuse and projecting in lateral profile, rounded in basal outline, Fingers I and II with one, Fingers III and IV with two; accessory palmar tubercles globular to slightly conical in lateral profile, rounded in basal outline, Fingers II and IV with one, Finger I with one (two, one, two), Finger III with two (others with one); males with two white glandular nuptial pads—one on thenar tubercle and the other (reduced to absent in young adult), also on pollex, opposite and slightly lateral to distal subarticular tubercle (Fig. 3).

Femur length 53.5 (55.1–62.0, 55.0–62.7, 54.7–61.7) % SVL; tibia length 64.1 (59.6–62.5, 57.3–62.9, 56.1–61.6) % SVL; tarsal length 31.2 (31.4–32.6, 29.3–33.2, 29.5–32.2) % SVL; foot length 47.1 (49.1–51.2, 47.3–50.5, 43.8–51.0) % SVL; heels without or with only a few tubercles, overlapping when flexed; with (sometimes without) a fine tarsal ridge; inner metatarsal tubercle elongate and larger than outer metatarsal tubercle; subarticular tubercles globular to pungent in lateral profile, round in basal outline, Toes I and II with one, Toes III and V with two, Toe IV with three; plantar tubercles globular to conical in lateral profile, rounded in basal outline, Toe I with one (none, one, none), Toe II with one, Toe III with one (two, one, one), Toe IV with two, Toe V with none; toes with weak marginal keels; webbing basal; toe disks as large or smaller than those of fingers, disk covers indented distally on Toes II to V; Toe V pad width 104.0 (115.9–117.0, 112.8–120.0, 113.6–123.8) % Toe II pad width (Fig. 3).

In preservative, dorsum glaucous with fuscous blotches; tympanum cream; one to three prominent bars on lower arm; no well-defined bars on flanks; lips barred; bars on upper femoral, tibial, and tarsal areas; dark anal patch; venter white, except for cream to glaucous femoral area.

*Color in life.*—Dorsum of holotype sulphur yellow, that of paratypes citrine, with sepia

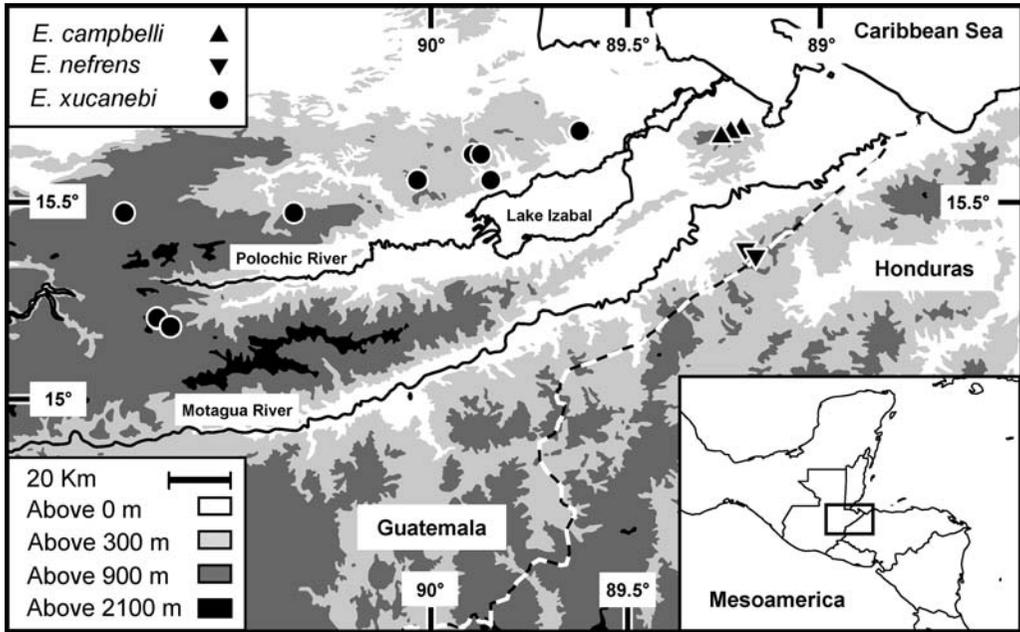


FIG. 4.—Distribution of frogs of the *Eleutherodactylus spatulatus* subgroup in eastern Guatemala.

markings; sepia bars on lips and limbs; iris silver below and copper-silver above with black reticulations; pupil surrounded by a thin pale copper or silver colored ring; supratympanic fold sepia; tympanum transparent or citrine; venter translucent with iridescent white markings on the chest and sides of the trunk, mauve to spectrum violet, somewhat darker on the sides; throat and ventral femoral area white; ventral surface of limbs citrine to sulphur yellow; dark sepia anal patch; fingers and toes sepia, with cream color disk covers possessing sepia indentations distally, and cream color or straw yellow articular areas.

*Etymology*.—The specific epithet is a patronym in honor of Jonathan A. Campbell, the most dedicated student of, and the foremost authority on, the Guatemalan herpetofauna.

*Distribution and natural history*.—*Eleutherodactylus campbelli* is known from elevations between 260 and 962 m in the Montañas del Mico (Fig. 4). The vegetation in this area is classified as Subtropical (Premontane) Wet Forest to Lower Montane Wet Forest (sensu Holdridge, 1959, 1967). The holotype was sitting on a leaf at approximately 0.75 m above the ground at the side of a small forest trail on a foggy night between 2150–2310 h at 20 C

ambient temperature. One of the adult female paratypes was sitting on a leaf in primary forest at 1915 h. The other adult female was sitting on a leaf 1 m above the forest floor at 2115 h and an ambient temperature of 21 C. An adult and a subadult male paratypes were on small palms approximately 2 m above the forest ground, between 2100 h and midnight, after a light rain. Two adult males were on low vegetation along a forest trail, ca. 2130 h. No calls were heard. Two subadults and one juvenile were found sitting on leaves between 0.25 and 1.65 m above the surface of large karstic rocks forming the forest floor, on a foggy night between 2125–2135 h at 20 C ambient temperatures. A single juvenile was found on low vegetation early at night, at the edge of forest and near a stream.

*Eleutherodactylus nefrens* sp. nov.

*Holotype*.—The University of Texas at Arlington (UTA) A-45279, an adult male from La Firmeza, Sierra de Caral, Municipio de Morales, Departamento de Izabal, Guatemala, 840 m, collected on 4 July 1994 by E. N. Smith, José Monzón, and Robin Schiele (field no. ENS 5255). This locality is at approximately 15° 22' 30" N, 88° 42' 30" W.

*Paratypes* (4).—UTA A-45278, adult male collected at the type locality, 800 m, on 3 July 1994; UTA A-45277, adult male (Fig. 5) collected at the type locality, 815 m, on 4 July 1994; UTA A-45280, adult male collected on trail between the type-locality and Cerro Pozo de Agua, 1000 m, on 9 July 1994, approximately 15° 22' 20" N, 88° 41' 40" W. All above paratypes collected by E. N. Smith. UTA A-51370, subadult female from trail between Finca Quebradas and Cerro Pozo de Agua [La Firmeza, near type locality], 890 m, collected on 17 July 1996 by E. N. Smith, José Monzón, and Karin Castañeda.

*Diagnosis*.—A member of the *Eleutherodactylus spatulatus* subgroup of the *E. alfredi* group possessing no vocal sac or slits, a relatively large tympanum (65.9–77.5 % eye diameter, in adults), and sometimes having a fine tarsal ridge. *Eleutherodactylus nefrens* is most similar to *E. xucanebi* and *E. campbelli*. It may be distinguished from other Guatemalan members of the *E. spatulatus* subgroup (*E. stuarti* and *E. xucanebi*) by possessing the pad of the fifth toe wider than that of the second, an olive-yellow dorsal ground color (versus brownish), a pale pink to lilac venter (versus vinaceous or bluish violet), and by having no or few melanophores scattered on the abdominal area of the venter. It differs from *E. campbelli* by having reduced or absent vomerine dentigerous processes (with 0–3 versus 4–7 teeth, in adults), a larger body size (males 24.0–26.8 versus 20.9–23.7 mm in SVL), and in ventral and dorsal coloration. *Eleutherodactylus nefrens* differs from *E. bocourti*, the other member of the *E. alfredi* group (sensu Lynch 2000) in the highlands of Guatemala, by lacking vocal slits. Additionally, possessing the pad of the fifth toe wider than that of the second differentiates *E. nefrens* from all members of the *E. alfredi* group (including *E. bocourti* [sensu Lynch, 2000] and *E. galacticorhinus* [Canseco-Márquez and Smith, 2004]), except *E. campbelli*.

*Description and variation*.—Holotype followed by variation of paratypes in parentheses (adult males [ $n = 3$ ], subadult female [ $n = 1$ ]). Measurements in mm: SVL 26.3 (24.0–26.8, 25.8), head length 11.1 (9.7–11.4, 10.6), head width 10.7 (10.0–11.3, 10.6), eye diameter 4.1 (3.4–4.0, 3.2), snout length 3.8 (3.3–3.6, 3.6), internarial distance 2.4 (2.1–2.4, 2.2), choana



FIG. 5.—*Eleutherodactylus nefrens*, male paratype, 26.8 mm SVL, UTA A-45277. (Reproduced from UTA Slide No. 17870.)

width 0.9 (0.7–0.9, 0.9), tympanum diameter 2.7 (2.5–3.1, 2.0), fascicular length 0.4 (0–0.4, 0.4), interfascicular distance 0.8 (0.8 or no dentigerous processes, 0.7), tarsal length 7.7 (6.7–7.9, 7.3), hand length 9.3 (8.9–9.7, 9.1), arm length 7.0 (6.5–7.8, 6.8), tibia length 15.9 (14.3–15.6, 15.1), foot length 13.5 (12.5–13.8, 12.2), femur length 14.9 (12.9–15.1, 13.5), upper eyelid width 2.3 (2.1–2.8, 2.35), IOD 3.0 (3.0–3.5, 2.8), pad width of Toe V 1.1 (1.0–1.1, 1.1), pad width of Toe II 1.0 (0.9–1.0, 0.9).

Head broader than body, about as long as wide, with a few scattered large granules; head length 104.1 (94.4–104.3, 100.0) % head width; head width 40.7 (41.6–42.1, 41.0) % SVL; snout length 91.5 (87.5–107.5, 114.3) % eye diameter, rounded to subacuminate in dorsal view, nearly truncate in lateral profile; canthus rostralis straight to weakly concave; loreal area slightly convex; lips not flared; interorbital distance 73.2 (87.5–89.6, 87.3) % eye diameter; internarial distance 57.3 (60.0–63.2, 68.3) % eye diameter; upper eyelid width 57.0 (62.7–71.5, 74.6) % eye diameter, bearing granules; tympanum distinct, with a moderately developed supratympanic fold, 65.9 (73.5–77.5, 63.5) % eye diameter; no cranial crests; choanae small; dentigerous fascicle 45.9 (0–40.5, 42.8) % choana width, bearing 3/2 (0/0–2/2, 3/1, left/right) clumped teeth, teardrop-shaped, round end directed posteromedially; interfascicular distance 81.1 (81.1 and two specimens without fascicules, 77.1) % choanae width; no vocal slits or sac; tongue lanceolate (rounded to lanceolate), longer than wide.

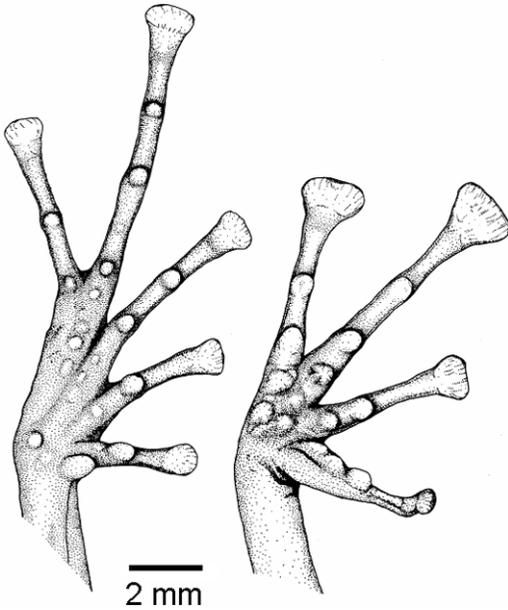


FIG. 6.—Ventral aspect of hand and foot of *Eleutherodactylus nefrens*, male holotype, UTA A-45279.

Skin of dorsal surfaces smooth to finely shagreen with a few large, scattered granules, especially on upper eyelids and dorsum of head; no dorsolateral, paravertebral, or occipital folds; skin on venter smooth except for femoral surfaces which are areolate; scattered melanophores on chest, less densely arranged on belly.

Arm length 26.6 (27.0–29.4, 26.3) % SVL; hand length 35.3 (36.2–36.8, 35.4) % SVL; relative lengths of fingers I < II < IV < III; fingers bearing large, expanded disks, disk covers indented distally on Fingers II to IV; fingers with weak marginal keels; few small tubercles sometimes present in ulnar region; thumb with an enlarged thenar tubercle, almost as large as semidivided cordiform palmar tubercle; subarticular tubercles obtuse and projecting in lateral profile, rounded in basal outline, Fingers I and II with one, Fingers III and IV with two; accessory palmar tubercles globular to slightly conical in lateral profile, rounded in basal outline, Fingers II and IV with one, Fingers I and III with two (one or two); with two white glandular nuptial pads—one on thenar tubercle and the other, also on pollex, opposite and slightly lateral to distal subarticular tubercle (Fig. 6).

Femur length 56.6 (53.6–58.0, 52.5) % SVL; tibia length 60.3 (58.2–60.4, 58.7) % SVL;

tarsal length 29.3 (27.9–29.7, 28.5) % SVL; foot length 51.4 (51.8–54.2, 47.2) % SVL; heels without (or with only a few) tubercles, overlapping when flexed; with (sometimes without) a fine tarsal ridge; inner metatarsal tubercle elongate and larger than outer metatarsal tubercle; subarticular tubercles globular to pungent in lateral profile, round in basal outline, Toes I and II with one, Toes III and V with two, Toe IV with three; plantar tubercles globular to conical in lateral profile, rounded in basal outline, Toe I with one (one or none), Toe II with one, Toe III with two, Toe IV with two (two or three), Toe V with none; toes with weak marginal keels; webbing basal; toe disks as large or smaller than those of fingers, disk covers indented distally on Toes II to V; Toe V pad width 110 (108–118, 128.6) % Toe II pad width (Fig. 6).

In preservative, dorsum glaucous with fuscous blotches; tympanum cream; one prominent bar on lower arm; no well-defined bars on flanks; lips barred; bars on upper femoral, tibial, and tarsal areas; dark anal patch; venter white, except for cream femoral area.

*Color in life*.—Dorsum of all individuals olive-yellow with sepia markings; sepia bars on lips and limbs; iris silver below and copper-silver above with black reticulations; pupil surrounded by a thin light copper or silver colored ring; supratympanic fold sepia; tympanum transparent to olive-yellow; venter pale pink with lilac sides, translucent with iridescent white markings on the chest and sides of trunk; throat and ventral femoral area white to pale pink; ventral surfaces of limbs pale olive-yellow; dark sepia anal patch; fingers and toes sepia, with cream color disk covers possessing sepia indentations distally, and cream color articular areas.

*Etymology*.—The specific epithet, *nefrens*, is a Latin adjective meaning toothless, in allusion to the reduced number of vomerine teeth characteristic of the species.

*Distribution and natural history*.—*Eleutherodactylus nefrens* is known from elevations between 800 and 1000 m in the Sierra de Caral (Fig. 4). It is the easternmost species of the *alfredi* group, and the only one occurring south of the Motagua Valley. The species may also occur in Honduras. The vegetation in this area is classified as Subtropical (Premontane) Wet Forest (sensu Holdridge, 1959, 1967). The

holotype was sitting on a *Cecropia* leaf 0.75 m above the ground at the edge of the forest along a small logging road at 2140 h with an ambient temperature of 25 C. Paratypes were collected on both rainy and clear nights (1908–2330 h) on low vegetation over the forest floor (0.3–2 m) near the buttresses of large trees or on a large elephant-ear plant, with ambient temperature between 18 and 26 C. One specimen appeared to be sleeping and the others were active. No calls were heard. Although extensive collections were made at slightly lower and higher elevations, no specimens were found at those elevations.

#### RESUMEN

Se describen dos nuevas especies de rana del género *Eleutherodactylus* pertenecientes al subgrupo *spatulatus* del grupo *alfredi*. Una de ellas, *E. nefrens*, es encontrada a elevaciones medias en el bosque lluvioso de la Sierra de Caral (Merendón), Guatemala. La otra especie, *E. campbelli*, es encontrada a elevaciones medias en el bosque lluvioso de las Montañas del Mico, Guatemala. *Eleutherodactylus nefrens* y *E. campbelli* difieren fácilmente de otras especies guatemaltecas en el subgrupo (*E. xucanebi* y *E. stuarti*) por poseer la almohadilla del quinto dedo del pie más grande que la del segundo, tener el vientre con ninguno o pocos melanóforos en la parte centro-posterior y por poseer coloración ventral y dorsal distinta. *Eleutherodactylus nefrens* se diferencia de *E. campbelli* por poseer un mayor largo hocico-cloaca y facículos dentíferos reducidos o ausentes (con 0 a 3 dientes vomerinos). *Eleutherodactylus campbelli* posee facículos dentíferos desarrollados (con 4 a 6 dientes vomerinos). Ambas especies difieren entre sí en aspectos de coloración.

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## APPENDIX I

### Specimens Examined

- Eleutherodactylus alfredi* (13).—MEXICO: *Oaxaca*: Cueva de Laguna Verde, 10 km SW Acatlán, KU 154636; Tolocito [Tolosita], 2 mi. S, 17.17° N 95.06° W, 70 m, KU 39673–74; Tolocito [Tolosita], 2 mi. E, KU 44550; La Esperanza, 17.63° N 96.36° W, MZFC 4585; *San Luis Potosí*: Xilitla region, KU 24036; *Tabasco*: Teapa, 2 mi. E, KU 41584; *Veracruz*: Cuautlapán, 18.87° N 97.02° W, 1000 m, KU 105494, 54068–69; Jesús Carranza, 35 km SE, 17.18° N 94.84° W, 106 m, KU 26926–28.
- Eleutherodactylus bocourti* (41).—GUATEMALA: *Baja Verapaz*: 2.0 km E, 2.5 km S Purullá; ca. 1700 m: UTA A-5987–88; Cerro Verde, UTA A-7993; Plantación Santa Teresa, 7.7 km SSE Purullá, 1600 m: UTA A-5538–39, 5581–82; Sierra de Las Minas, Chilascó, Finca San Jorge, 1900 m: UTA A-45395, 1875 m: UTA A-45396; *Izabal*: Sierra de Santa Cruz, Finca Semuc, S side Cerro Serujijá, 750 m: UTA A-33416; *Quiché*: Uspantán, 15° 30.72' N 90° 47.52' W, ca. 1500 m: UTA A-51242, ca. 1550 m: UTA A-51245, 1550–1635 m: UTA A-51247; Uspantán, Camino entre Camino El Chimele-San Pablo El Baldío y coordenadas 15° 30.72' N y 90° 47.52' W, 2040 m: UTA A-51219, 2070–2125 m: UTA A-51220–26, 2050 m: UTA A-51227–29, 2000–2005 m: UTA A-51230–31, 1980 m: UTA A-51232–33, 1950 m: UTA A-51234, 1940 m: UTA A-51235–37, ca. 1700 m: UTA A-51238, 1600–1670 m: UTA A-51239, 2125–2050 m: UTA A-51240–41, 1600–1670 m: UTA A-51243, 1500–1800 m: UTA A-51246, 51248, 1940 m: UTA A-51496, 1700–1715 m: UTA A-51244.
- Eleutherodactylus campbelli* (11).—See species description.
- Eleutherodactylus decoratus* (13).—MEXICO: *Hidalgo*: 45.7 km SW Huejutla, 1372 m, UTA A-12954; *Oaxaca*: Huautla, The Fissure, KU 125421; Huautla, Pit II, KU 125422–24; *Querétaro*: Municipio Jalpán de Serra, 1 km SE Juya del Maguey, MZFC 8958; *San Luis Potosí*: Sotano de la Linja, La Linja, KU 125417; In Cueva de Potrerillos, 2 km (by road and trail) W of village of Ahuacatlán, UTA A-52671–72; *Tamaulipas*: Sierra de Guatemala, small cave ca. El Refugio sawmill, KU 151936; Sotano Noventa-Dos, KU 154638; *Veracruz*: Tequila, KU 194598–99.
- Eleutherodactylus galacticorhinus* (1).—MEXICO: *Puebla*: 2 km E of Zoquitlán, Sierra Negra, 2155 m, MZFC-14461.
- Eleutherodactylus glaucus* (1).—MEXICO: Chiapas: 8.0 mi. E of Teopisca, UTA A-3570.
- Eleutherodactylus guerreroensis* (3).—MEXICO: *Guerro*: Agua del Obispo, 3 km N, 980 m, KU 86870–71; Chilpancingo, 31 km S, KU 86873.
- Eleutherodactylus megalotympanum* (1).—MEXICO: *Veracruz*: Bastonal, ca. Lago de Catemaco, 18.39° N 94.94° W, 950 m, KU 109978.
- Eleutherodactylus nefrens* (5).—See species description.
- Eleutherodactylus polynniae* (2).—MEXICO: *Oaxaca*: Sierra Juárez, 0.8 km N Vista Hermosa, 1420 m: UTA A-12976, 23511.
- Eleutherodactylus silvicola* (1).—MEXICO: *Oaxaca*: 12 air mi. NNE Zanatepec, 4900 feet; uncatalogued dorsal and ventral images of female holotype, LSU 7557.
- Eleutherodactylus spatulatus* (14).—MEXICO: *Oaxaca*: 27.0 mi. S of Valle Nacional, UTA A-2877–78; 33.9 km S Valle Nacional, UTA A-2899, 2902, 3711; 9.9 km NE Cerro Pelón, 32.5 mi. SSW Valle Nacional, UTA A-3079; N face Sierra Juárez, 4.8 km S Vista Hermosa, 1622 m, UTA A-12975; N slope Sierra de Juárez, 6.8 mi. (by road) N crest Cerro Pelón, 6720 ft., UTA A-5663; N slope Sierra Juárez, 20.1 km N Vista Hermosa, 610 m, UTA A-12974; Sierra Juárez, 9.9 km S Valle Nacional, 622 m, UTA A-12973; Sierra Juárez, vicinity of Metates (17.6 km S Valle Nacional); 902 m, UTA A-34149; Metates, vicinity, Sierra Juárez, 17.7° N 96.31° W, 914 m, MZFC 2263; Vista Hermosa, km 78 Carretera Oaxaca-Tuxtepec, 17.64° N 96.35° W, MZFC 4550; La Esperanza, 17.63° N 96.36° W, MZFC 4559.
- Eleutherodactylus stuarti* (46).—GUATEMALA: *Huehuetanango*: Montañas del Cuilco, Vicinity of Ojo de Agua, 1900 m, UTA A-52115; La Democracia, Cumbre entre Ojo de Agua y Hoja Blanca (Lado Este), 2070 m, UTA A-51371; 2085 m, UTA A-51372; 2105 m, UTA A-51380; 2135 m, UTA A-51373; 2175 m, UTA A-51379; 2245 m, UTA A-51378; ca. 1985 m, UTA A-51374–76; ca. 2200 m, UTA A-51377; La Democracia, Cumbre entre Ojo de Agua y Hoja Blanca, Lado Oeste, 2100 m, UTA A-51381. *Quezaltenango*: S. Slope Volcán Santa María, Finca El Faro, ca. 1467 m, UTA A-24499–500; 2200 m, UTA A-26209–10; 2250 m, UTA A-26211; 2000 m, UTA A-26212–13; Granja Lorena, 12.9 km NE Colomba, 1661 m, UTA A-45284. *San Marcos*: Aldea La Fraternidad, Finca La Esperanza, 1810 m, UTA A-45286; Entre Aldea Feria y Aldea Fraternidad, 1400–1900 m, UTA A-48178–79; Esquipulas Palo Gordo, Aldea Fraternidad, Finca La Esperanza, UTA A-50934–42; Esquipulas Palo Gordo, Aldea La Fraternidad, Finca La Esperanza, UTA A-50931–33; Municipio Esquipulas Palo Gordo, Aldea La Fraternidad, Finca La Esperanza, 1885 m, UTA A-48451; ca. 1880 m, UTA A-48452, 48457–58; 1910–1925 m, UTA A-48453–56; San Rafael Pie de La Cuesta, Aldea Feria, Finca América El Vergel, UTA A-50930. *Sololá*: 3.7 km S Santa María Visitación, 2000–2200 m, UTA A-33450; Santa María Visitación, Montaña El Poj (lado sur-oeste), 1945 m, UTA A-45285.
- Eleutherodactylus taylori* (1).—MEXICO: Chiapas: Rayón Mezcalapa, 6.2 km S, 1690 m, KU 58689.

*Eleutherodactylus yucatanensis* (5).—MEXICO: *Quintana Roo*: Pueblo Nuevo X-Can, 1.5 km S and 1 km E, 10 m, KU 71094; Pueblo Nuevo X-Can, 1.5 km S and 7 km E, 10 m, KU 71095-96; *Yucatán*: Chichén Itza, CM 36444; Felipe Carrillo Puerto, 25.43 km NE on Hwy 307, KU 171210.

*Eleutherodactylus xucanebi* (119).—GUATEMALA: *Alta Verapaz*: 5.1 mi. NE of Cobán on road to Chisec, 1250 m, UTA A-38468-69; Finca El Volcán, 1285-1380 m, UTA A-53026-33. *Baja Verapaz*: Cerro Verde, UTA A-5523; 7.7 km SSE Purullhá, Plantación Santa Teresa, UTA A-5579; between 1 km N and 1 km S entrance to Biotopo Mario Dary, UTA A-5942; 2.0 km E, 2.3 km S Purullhá, UTA A-5965-66, 7980, 7986-87, 17232; ca. 1600 m, UTA A-5991-92, 5994-96; 5300 ft., UTA A-6280; 1.9 km S Purullhá on Guat Hwy CA-14, UTA A-7985; 3.9 km SE Purullhá, UTA A-8015-18; 0.0-4.0 km SE Purullhá, UTA A-8248-49; 3.6 km SE Purullhá, UTA A-8254; 3.7 km SE Purullhá, UTA A-8258, 8263-64, 8267, 8278-81, 8287, 8289-92; 3.8 km SE Purullhá, UTA A-8304-08; 3.9 km SE Purullhá, UTA A-8016. *Huehuetenango*: Sierra de Los Cuchumatanes, Finca Chiblac Buena Vista (now Aldea Buenos Aires), 975

m, UTA A-51367; 960 m, UTA A-51368; 995 m, UTA A-51369. *Izabal*: Sierra de Santa Cruz, Finca Semuc, 500 m, UTA A-26454; Sierra de Santa Cruz, Finca Semuc, Cerro Serujijá, 875-925 m, UTA A-26455-59; 1150 m, UTA A-30113-14, 30119-30, 30225-28; 1140 m, UTA A-30115; 1150-1170 m, UTA A-30116-18; 1150-1200 m, UTA A-30131-34, 30229-30; 1145 m, UTA A-30224; Sierra de Santa Cruz, Finca Semuc, [Cerro] Serujijá (lado Sur), 750 m, UTA A-33416; Sierra de Santa Cruz, Cerro 1019, 960 m, UTA A-30231; 975 m, UTA A-30232; 1000 m, UTA A-30233-34; 975-1000 m, UTA A-30235-37; Sierra de Santa Cruz, Xiacam, 950-975 m, UTA A-30238-39; Sierra de Santa Cruz, no other data, UTA A-30240; Sierra de Santa Cruz, Finca Semuc, S side Cerro Serujijá, 890-990 m, UTA A-33453-64; Sierra de Santa Cruz, Cerro 1019, 935 m, UTA A-45281; Sierra de Santa Cruz, Cerro 1019, 945 m, UTA A-45282; Sierra de Santa Cruz, Cerro 1019, 1000 m, UTA A-45283. *Quiché*: Uspantán, ca. 15° 30' 43" N y 90° 47' 31" W, 1550-1635 m, UTA A-51366; Uspantán, Camino entre Camino El Chimmel-San Pablo El Baldío y coordenadas 15°30'43" N y 90°47'31" W, 1635 m, UTA A-51364; 1940 m, UTA A-51363; 1715 m, UTA A-51365.

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## MARSUPIAL FROGS (ANURA: HYLIDAE: GASTROTHECA) FROM THE ANDES OF NORTHERN PERU WITH DESCRIPTIONS OF TWO NEW SPECIES

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Nine species of *Gastrotheca* primarily have allopatric distributions in the Andes of northern Peru. A new species with integumentary-cranial co-ossification is described from montane forest in the northern part of the Cordillera Central in the Departamento de Amazonas, Peru. A second new species from the same area lacks integumentary-cranial co-ossification and differs from all other members of the genus by having a black venter with white spots.

*Key words:* Anura; *Gastrotheca ossilaginis* new species; *Gastrotheca phalarosa* new species; Patterns of distribution in Andes of Peru

EXPLORATION of the Andes in northern Peru has resulted in the discovery of a diversity of anurans of the genus *Bufo* (Duellman and Schulte, 1992), family Centrolenidae (Cadle and McDiarmid, 1990; Duellman and Schulte,

1993); the dendrobatid genus *Colostethus* (Duellman, 2004); the leptodactylid genera *Eleutherodactylus* (summarized by Duellman and Pramuk, 1999), *Phyllonastes* (Duellman, 1991), *Phrynopus* (Cannatella, 1984; Duellman, 2000), and *Telmatobius* (Wiens, 1993); and the hylid genera *Gastrotheca* (Duellman, 1987; Duellman and Trueb, 1988; Trueb and

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Duellman, 1978), *Hyla* (Duellman, 1982), *Phyllomedusa* (Cannatella, 1982), and *Scinax* (Duellman and Wiens, 1993).

Including the two new species described herein, nine species of *Gastrotheca* are now known to occur at elevations greater than 1500 m in the northern parts of the Cordillera Occidental and Cordillera Central and in the smaller ranges, Cordillera Colán, Cordillera del Cóndor, and Cordillera Huancabamba in northern Peru. Another species is endemic to a small area in the Cordillera Oriental in adjacent Ecuador. The two new species bring the total number of species of *Gastrotheca* in Peru to 19. Herein we describe the two new species from the northern part of the Cordillera Central, provide a key to the species of *Gastrotheca* in the Andes of northern Peru, and summarize the distributions of the species in that region.

#### MATERIALS AND METHODS

The 16 morphological measurements, external descriptive characters, and numbered diagnostic features are those that have been used in earlier descriptions by Duellman and Pyles (1980), Duellman and Hillis (1987), Duellman and Trueb (1988), Duellman et al. (2001) and Duellman et al. (2004). All measurements are in mm; snout-vent length is abbreviated SVL. Sex was determined by the presence of brood pouches or by examination of gonads. Webbing formula was determined by the method proposed by Savage and Heyer (1967), as modified by Myers and Duellman (1982). Stages of tadpoles are those defined by Gosner (1960). Color photographs of the new species will be available on AmphibiaWeb (<http://elib.cs.berkeley.edu/aw/>). Osteological data were obtained from radiographs. Abbreviations of museum collections are those given by Leviton et al. (1985), with the addition of QCAZ (Museo de Zoología, Pontificia Universidad Católica, Quito, Ecuador), and the exceptions that the Museo de Historia Natural Universidad Mayor de San Marcos, Lima, Peru, is noted as MHNSM and the Staatliches Museum für Tierkunde, Dresden, Germany is noted as MTD. Specimens used in comparisons and distributional analysis are listed in Appendix I.

#### DESCRIPTION OF NEW SPECIES

##### *Gastrotheca ossilaginis* sp. nov.

*Holotype*.—MHNSM 19486, an adult female, from Lago Quindecocha (06° 51' 18.1" S, 77° 42' 18.9" W, 3100 m), Juanjui, Provincia de Huallaga, Departamento de San Martín, Peru obtained by Pablo Venegas on 19 November 2003.

*Paratypes*.—KU 272293, an adult male, and KU 272294, an adult female collected with the holotype. MHNSM 19488, an adult male, from Ullilen (06° 50' 32" S, 77° 41' 50" W, 3000 m), Juanjui, Provincia de Huallaga, Departamento de San Martín, Peru; obtained by Pablo Venegas on 30 November 2003.

*Diagnosis*.—A medium-sized species of *Gastrotheca* (to 53.3 mm) having: (1) tibia length  $\pm 50\%$  of SVL, slightly shorter than foot; (2) interorbital distance about twice width of eyelid; (3) skin on dorsum finely shagreen, co-ossified with skull, lacking transverse ridges; (4) supraciliary processes absent; (5) heel lacking calcar, bearing low tubercles; (6) tympanic annulus smooth; (7) Finger I < II, with discs slightly wider than digits; (8) finger unwebbed; (9) toes about one-fourth webbed; (10) dorsum green or tan; (11) head markings absent; (12) pale dorsolateral stripe absent; (13) flanks colored like dorsum; (14) venter creamy gray; (15) brood pouch single, dorsal.

The skin is co-ossified with underlying cranial elements in nine other species of *Gastrotheca*. Of these five species (*G. fissipes*, *galeata*, *nicefori*, *ovifera*, and *weinlandi*) differ by having a bony transverse occipital ridge, which has four dorsal projections in *G. ovifera*. *Gastrotheca galeata* differs from all of the others and *G. ossilaginis* by having the premaxillae and maxillae flared so as to create a spatulate skull. *Gastrotheca antomia*, *bufona*, and *guentheri* differ from *G. ossilaginis* by having supraciliary processes, much longer hind limbs (tibia length  $>60\%$  of SVL), and prominent projections on the heels (two conical tubercles in *G. antomia* and triangular calcars in *G. bufona* and *G. guentheri*). The remaining species, *G. trachyceps*, differs from *G. ossilaginis* by having Fingers I and II equal in length (I < II in *G. ossilaginis*), by lacking low tubercles on the heel, and in coloration—pale

labial and dorsolateral stripes present in *G. trachyceps* and absent in *G. ossilaginis*.

Among the species of *Gastrotheca* known from high elevations in Departamento de Amazonas, Peru, *G. abdita* differs by lacking integumentary-cranial co-ossification and in preservative having a color pattern consisting of a dull grayish brown dorsum with a darker brown middorsal mark beginning in the occipital region, bifurcating just posterior to the scapula, and coalescing just anterior to its terminus at the anterior border of the opening to the brood pouch. *Gastrotheca lateonota* and *G. monticola* also lack integumentary-cranial co-ossification and differs in coloration in preservative; the dorsum is bluish gray or tan with darker markings consisting of a large middorsal blotch, paravertebral blotches, or smaller, irregular blotches; pale labial and dorsolateral stripes usually are present, and the venter is pale cream with dark gray or black spots or mottling. The only other species of *Gastrotheca* in the Andes in northern Peru are *G. phalarosa* and *G. peruana*, which also lack integumentary-cranial co-ossification; these species differ further from *G. ossilaginis* by having pustular skin on the dorsum, Fingers I and II equal in length or Finger I > II, and the interorbital distance about equal to the width of the upper eyelid.

*Description of holotype*.—An adult female; body moderately robust; head wider than long, as wide as body; head width 36.7% of SVL; head length 32.5% of SVL; snout narrowly truncate in dorsal view, bluntly rounded above and inclined anteroventrally in profile; canthus rostralis not elevated, straight, rounded in section; loreal region slightly concave; lips rounded; top of head slightly depressed between elevated lateral edges of frontoparietals forming low cranial crests extending posteriorly nearly to posterior end of skull; interorbital distance 229% of width of upper eyelid; internarial area flat; nares slightly protuberant, directed laterally at level slightly posterior to anterior margin of lower jaw; diameter of eye about equal to eye–nostril distance; tympanum nearly round, its diameter 66.7% of diameter of eye, separated from eye by distance nearly half again length of tympanum; tympanic annulus distinct, smooth; supratympanic fold inclined posteroventrally

from posterior end of supratympanic crest, obscuring upper edge of tympanum.

Arm moderately robust; ulnar tubercles absent; hand large; fingers long, bearing small, rounded discs; width of disc on Finger III three-fourths diameter of tympanum; relative lengths of fingers 1 < 2 < 4 < 3; fingers unwebbed; palmar tubercle small, low, ovoid; prepollical tubercle large, elliptical; subarticular tubercles small, round, none bifid; supernumerary tubercles large, prominent, present only on proximal segments of digits. Hind limb moderately slender; when hind limbs adpressed, heels overlap by about one-fourth length of tibia; tibia length 51.0% of SVL; foot length 53.0% of SVL; calcar absent; heel bearing two low, diffuse tubercles; three low tubercles on outer edge of tarsus; inner tarsal fold absent; outer metatarsal tubercles absent; inner metatarsal tubercle large, flattened, ovoid, barely visible from above; toes long, bearing rounded discs about same size as those on fingers; relative lengths of toes 1 < 2 < 3 < 5 < 4; toes about one-fourth webbed; webbing formula **I** 2–2<sup>+</sup> **II** 2–3 **III** 2–3<sup>+</sup> **IV** 3<sup>+</sup>–2<sup>+</sup> **V**; subarticular tubercles small, round; supernumerary tubercles prominent, subconical, present only on proximal segments of digits.

Skin on dorsum of body and limbs finely shagreen, with a few small, tubercles on forearms and hind limbs; skin on head co-ossified with underlying nasals, frontoparietals, and zygomatic and otic rami of squamosal; skin on flanks weakly areolate; skin on throat, chest, belly, and ventral surfaces of forelimbs and thighs coarsely areolate; skin on ventral surfaces of shanks and tarsi smooth; opening of brood pouch U-shaped at level of sacrum. Vomerine odontophores prominent, narrowly separated medially, nearly transverse between ovoid choanae, each bearing five teeth.

Coloration in preservative: Flanks and dorsal surfaces of body and limbs nearly uniform pale gray; narrow lines forming incomplete, irregular black circles, one each on left side of body in scapular region and on posterior part of left flank; anterior and posterior surfaces of thighs dark gray; throat, chest, and anterior part of belly creamy gray; posterior part of belly and ventral surfaces of thighs grayish tan.



FIG. 1.—Holotype of *Gastrotheca ossilaginis* in life, female, SVL 53.3 mm, MHNSM 19486.

Coloration in life: Dorsal surfaces of head, body, and limbs pale brown with darker brown broad middorsal mark originating in occipital region, bifurcating just posterior to scapula, and coalescing just anterior to opening of brood pouch; loreal and tympanic regions pale brown; all ventral surfaces uniform pale gray; it is coppery brown with fine dark reticulations (Fig. 1).

Measurements of holotype (in mm): SVL 53.3, tibia length 26.1, foot length 27.8, head length 17.3, head width 19.5, interorbital distance 7.8, width of upper eyelid 3.4, internarial distance 3.0, length of eye 4.5, length of tympanum 3.0, eye–nostril distance 4.6, orbit–jaw distance 3.3, nostril–jaw distance 3.8, thumb length 10.2, Finger III length 18.1, width of disc on Finger III 2.3.

*Variation.*—In addition to the female holotype, the type series consists of one female (SVL 44.5 mm) and two males (SVLs 36.7 and 38.5 mm). Little variation in proportions exists among the four specimens (mean in parentheses): tibia length/SVL 49.0–50.4 (50.1), foot length/SVL 49.3–53.2 (51.3), head length/SVL 32.5–36.4 (35.1), head width/SVL 36.7–39.8 (38.0), interorbital distance/eyelid width 185.7–229.4 (200.9), eye length/eye–nostril distance 90.6–97.8 (95.8), tympanum length/eye length 63.9–69.2 (66.2). Structurally, all specimens are alike with respect to skin texture and webbing. The degree of integumentary–cranial co-ossification is slightly greater in the largest individual than in the two smaller males.

In life, MHNSM 14989, male, was colored like the holotype, except that the branches of the middorsal mark coalesced just anterior to the cloacal opening, small black spots were present on the dorsum and dorsolateral surfaces of the body, and a dark brown post-tympanic stripe was present. In life, MHNSM 19490, an adult female, all dorsal surfaces were bright green; a yellow patch was present in the inguinal region.

*Cranial osteology.*—Radiographs reveal some aspects of cranial structure. The dermal roofing bones (nasals, dermal sphenethmoid, and frontoparietals) are deeply sculptured and co-ossified with the overlying skin. The nasals broadly articulate medially; their borders are not distinct from the dermal sphenethmoid. The frontoparietals are completely articulated medially and in broad contact with the dermal sphenethmoid; each bears an extensive supra-orbital flange that is broadest at the level of the posterior part of the orbit. The otic flange of the frontoparietal does not articulate with the squamosal; a temporal arcade is absent. The otic and zygomatic rami of the squamosal are robust, and the latter appears to articulate with the maxilla.

*Life history.*—On the morning of 20 November 2003, 21 froglets (each about 7.4 mm SVL) emerged from the pouch of the Holotype while in captivity; about half of the babies were green, and the other half were brown. Another brown female produced 14 brown froglets on 26 November 2003.

*Distribution and ecology.*—*Gastrotheca ossilaginis* is known only from two localities at elevations of 3000–3100 m in the vicinity of Lago de Los Condores in the northern part of the Cordillera Central in northern Peru. At the type locality, three individuals were found at night on low bushes and a spiny terrestrial bromeliad. The individual from Ullilen was under a rock in a pasture by day. Sympatric anurans include *Eleutherodactylus melanogaster*, *E. nephophyllus*, *E. patailos*, *E. schultei*, *Telmatobius atahualpai*, and *T. truebae*.

*Etymology.*—The specific name is a Latin adjective meaning bony hardness; the name refers to the bony nature of the integumentary–cranial co-ossification.

*Remarks.*—The skull of *Gastrotheca abdita* is similar to that of *G. ossilaginis* by having

large nasals in median contact, nasals and frontoparietals in broad contact with the dermal sphenethmoid, and frontoparietals with supraorbital flanges. However, they differ in that the dermal roofing bones of *G. abdita* are not co-ossified and the supraorbital flanges are narrower than those in *G. ossilaginis*.

*Gastrotheca phalarosa* sp. nov.

*Holotype*.—MHNSM 19487, an adult male, from Esperanza (06° 49' 10.1" S, 77° 43' 21.7" W, 3435 m, Juanjui, Provincia de Huallaga, Departamento de San Martín, Peru, obtained on 18 November 2003 by Pablo Venegas.

*Paratype*.—MHNSM 19472, an adult male, with same data as holotype.

*Diagnosis*.—A medium-sized species of *Gastrotheca* (to 43.3 mm in SVL) having (1) tibia length <50% of SVL, shorter than foot; (2) interorbital distance slightly greater than width of eyelid; (3) skin on dorsum smooth with scattered prominent pustules, not co-ossified with skull, lacking transverse ridges; (4) supraciliary processes absent; (5) heel lacking calcar and tubercles; (6) tympanic annulus smooth; (7) Finger I > II, with discs barely wider than digits; (8) fingers unwebbed; (9) toes about one-fifth webbed; (10) dorsum grayish tan with black paravertebral marks; (11) narrow white canthal stripe and white spots on lips; (12) pale dorsolateral stripe absent; (13) flanks black with white spots; (14) venter black with white spots; (15) nature of brood pouch unknown.

Among other short-legged Andean species of *Gastrotheca* in which the skin is not co-ossified with underlying cranial elements, only two are like *G. phalarosa* in having Finger I > II. Both of these, *G. espeletia* and *G. ruizi*, are like *G. phalarosa* in having inclined, protruding snouts in profile, digits on the fingers barely wider than adjacent segments of digits, and interorbital distances that are equal to, or only slightly greater than width of the eyelids; however, they differ from *G. phalarosa* by having smooth skin on the dorsum without pustules. Furthermore, the venter is uniformly dark gray in *G. ruizi*, a species known only from southern Colombia (Duellman and Burrowes, 1986); the venter is cream with dark gray flecks or weak mottling in *G. espeletia*, a species known only from the Andes of extreme northern Ecuador and adjacent

Colombia (Duellman and Hillis, 1987). *Gastrotheca peruana* is like *G. phalarosa* in having a convexly inclined, protruding snout in profile, interorbital distance about equal to width of eyelid, and pustular skin on the dorsum. However, *G. peruana* differs from *G. phalarosa* (conditions in parentheses) by having the snout acutely rounded in dorsal view (nearly truncate), nostrils at level of anterior margin of lower jaw (posterior to margin), tympanic annulus distinct and granular (barely evident, smooth), tarsal fold extending full length of tarsus (evident only distally), and features of coloration—broad black canthal stripe (narrow white stripe), pale labial stripe (absent), and tan venter with brown flecks (black with white spots).

Among the species of *Gastrotheca* known from high elevations in the Andes of northern Peru, *G. galeata* and *G. ossilaginis* differ by having the skin co-ossified with underlying cranial elements; neither has a black venter with white spots. *Gastrotheca abdita* differs by having in preservative a color pattern consisting of a dull grayish brown dorsum with a darker brown middorsal mark beginning in the occipital region, bifurcating just posterior to the scapula, and coalescing just anterior to its terminus at the anterior border of the opening to the brood pouch; the venter is pale tan. *Gastrotheca lateonota* and *G. monticola* also lack integumentary-cranial co-ossification and have Finger I = II, bluntly rounded snouts in profile, and interorbital distances that are much greater than the width of the upper eyelids. They also differ in coloration in preservative; the dorsum is bluish gray or tan with darker markings consisting of a large middorsal blotch, paravertebral blotches, or smaller, irregular blotches. Pale labial and dorsolateral stripes usually are present, and the venter is pale cream with brown flecks (*G. lateonota*) or cream with dark gray or black spots or mottling (*G. monticola*).

*Description of holotype*.—An adult male; body robust; head wider than long, not as wide as body; head width 37.9% of SCL; head length 36.3% of SVL; snout nearly truncate in dorsal view, convexly inclined anteroventrally and protruding in profile; canthus rostralis not elevated, slightly curved, rounded in section; loreal region noticeably concave; lips rounded; top of head flat; interorbital distance slightly

greater (107.5%) than width of upper eyelid; internarial area slightly depressed; nostrils barely protuberant, directed laterally with slight anterior inclination at level well posterior to anterior margin of lower jaw; diameter of eye equal to eye-nostril distance; tympanum nearly round, its diameter 51.2% of diameter of eye, separated from eye by distance 1.3 times diameter of tympanum; tympanic annulus barely evident, smooth; supratympanic fold weak, rounded above tympanum, enlarged, almost globular posteroventral extension obscuring posterior edge of tympanum.

Arm moderately robust; forearm more stout than upper arm; ulnar tubercles absent; hand moderately large; fingers moderately long, bearing narrow, fleshy lateral fringes and small terminal discs; width of disc on third finger 68.2% of diameter of tympanum; relative lengths of fingers  $1 > 2 < 4 < 3$ ; fingers unwebbed; palmar tubercle absent; prepollical tubercle, low, wide and diffuse proximally, bluntly elliptical distally; nuptial excrescences absent; subarticular tubercles moderately large, subconical; supernumerary tubercles small, subconical, present on proximal segments of Fingers III and IV. Hind limb short, moderately robust; when hind limbs adpressed, heels barely overlap; tibia length 42.7% of SVL; foot length 45.8% of SVL; heel lacking calcar or tubercles; outer tarsal fold and tarsal tubercles absent; inner tarsal fold barely evident on distal fifth of tarsus; inner metatarsal tubercle elevated, ovoid, visible from above; outer metatarsal tubercle absent; toes long, slender, with fleshy lateral fringes; terminal discs small, no wider than adjacent phalangeal segments; relative lengths  $1 < 2 < 3 = 5 < 4$ ; outer toes about one-fifth webbed; webbing formula **I** 21-3<sup>+</sup> **II** 2<sup>+</sup>-3<sup>+</sup> **III** 3<sup>-</sup>-4 **IV** 4-21 **V**; subarticular tubercles low, rounded; supernumerary tubercles low, rounded, present only on proximal segments of Toes II-IV.

Skin on dorsal surfaces of head, body, and limbs smooth with scattered small pustules on eyelids and large and small pustules on body; skin on flanks shagreen; skin on venter smooth except granular on posterior part of belly and proximal posteroventral surfaces of thighs; supraciliary processes and transverse dermal ridges absent. Cloacal sheath short; cloacal opening directed posteriorly at upper level of thighs; enlarged paracloacal tubercles absent.

Vomerine odontophores narrowly separated medially, transverse between ovoid choanae, bearing 3/0 teeth. Tongue broadly cordiform, shallowly notched posteriorly, free behind for about one-third of its length; vocal slits narrow, at midlateral base of tongue; vocal sac single, median subgular.

Coloration in preservative: Dorsum of head, body, and limbs grayish tan with black markings narrowly outlined with white consisting of ovoid spot on each upper eyelid, broad paravertebral markings from occipital region to upper inguinal region, narrowly connected posteriorly to narrowly triangular median postsacral mark with apex anteriorly, broad transverse marks on each thigh and shank, and irregular transverse mark on each forearm; other dorsal surfaces of limbs, including hands, feet, and digits, black with small irregular white spots; small, irregular black marks middorsally on head and body; flanks black with white spots. Narrow white canthal stripe; loreal region black; labial and tympanic regions black with irregular white dashes and small spots. Anterior surfaces of thighs black, each with two narrow, vertically transverse white lines and a few small black spots; posterior surfaces of thighs black; tubercles ventrolateral to cloacal opening tipped with white. Throat and belly black with white spots, smaller on throat than on belly (Fig. 2); palmar and plantar surfaces grayish tan; other ventral surfaces black with irregular white markings. Iris mottled gray and white; lower eyelid gray with black edge.

Coloration in life: Dorsum creamy tan with dark brown markings corresponding to those visible in preservative; venter black with creamy white spots; iris pale bronze with reddish-brown flecks (Fig. 3).

Measurements of holotype (in mm): SVL 43.3, tibia length 18.5, foot length 15.7, head length 15.7, head width 16.4, interorbital distance 4.3, width of upper eyelid 4.0, internarial distance 4.0, length of eye 4.3, length of tympanum 2.2, eye-nostril distance 4.3, orbit-jaw distance 2.5, nostril-jaw distance 3.5, thumb length 7.8, Finger III length 13.4, width of disc on Finger III 1.5.

*Variation.*—A second specimen, an adult male, has the same coloration as the holotype and the following measurements (in mm): SVL 45.2, tibia length 19.5, foot length 31.3, head



FIG. 2.—Venter of Holotype of *Gastrotheca phalarosa*, MHNSM 19487.



FIG. 3.—Holotype of *Gastrotheca phalarosa* in life, male, SVL 43.3 mm, MHNSM 19487.

length 15.0, head width 17.8, interorbital distance 2.4, width of upper eyelid 4.2, internarial distance 3.5, length of eye 4.5, length of tympanum 3.1, eye–nostril distance 4.1, orbit–jaw distance 2.8, nostril–jaw distance 3.7, thumb length 8.2, Finger III length 11.3, width of disc on Finger III 1.4.

*Cranial osteology.*—Radiographs reveal that the dermal roofing bones are not co-ossified with the overlying skin. The dermal sphenethmoid is weakly sculptured. The nasals narrowly articulate medially; their borders are distinct from the sphenethmoid. The frontoparietals have an incomplete articulation medially; each frontoparietal bears a narrow supraorbital flange, and a temporal arcade is absent. The otic and zygomatic rami are narrow; it appears as though the zygomatic ramus articulates with the maxilla.

*Life history.*—The only known adults of this species are males. Several tadpoles found in a small pool with a depth of 40 cm and a mud substrate at the type locality on 18 November 2003 were feeding on a dead earthworm. Some of these tadpoles were raised in captivity and metamorphosed into *Gastrotheca phalarosa*.

*Description of tadpole.*—One tadpole in Stage 34 has a body length of 23.9 mm, and a total length of 51.9 mm. A second tadpole in

Stage 39 has a body length of 29.4 mm and a total length of 65.5 mm. Both specimens are catalogued as MHNSM 19498; the individual in Stage 39 was used in the following description.

Body ovoid, robust in dorsal view blunt posteriorly, abruptly narrowing anterior to orbits to rounded snout, without visible indentations posterior to orbits and at mid-length, its greatest width (11.9 mm) at level of orbits and in midgut region; body highest (10.1 mm) at point slightly less than its midlength, gradually diminishing in height to level of orbits, abruptly decreasing in height from level of nares to snout; throat slightly concave. Eyes small (1.6 mm in diameter), situated more dorsally than laterally, not visible from below, slightly inclined anterolaterally; interorbital distance 3.4 mm; distance from snout to anterior edge of orbits 6.1 mm. Nares large with low rim, about midway between tip of snout and orbits, situated dorsolaterally, protuberant anterolaterally; internarial distance 2.7 mm. Spiracle sinistral, its base just left of midventral line, curved posterolaterally, attached to body wall throughout its length; spiracle opening directed dorsolaterally well below midheight of body, situated 13.9 mm posterior to tip of snout; vent dextral, elongately cone-shaped, with transverse aperture, attached throughout its length to ventral fin.

Caudal musculature massive, gradually tapering from base to pointed tip 1.5 mm proximal to end of fin; dorsal fin originating on base of caudal musculature, increasing in height on proximal one-fourth of tail, maintaining equal height throughout middle half of tail, gradually diminishing to rounded tip; ventral fin originating on body wall, highest

at about one-third length of tail; height at midlength of tail 8.5 mm, height of dorsal fin less than half of caudal musculature, height of ventral fin about one-fourth height of caudal musculature.

Oral disc directed more anteriorly than ventrally, its width (3.9 mm) 32.7% of greatest width of body. Single row of large conical marginal papillae on labia, largest laterally; those on anterior labium visible from above; 5–7 small submarginal papillae on lateral and ventrolateral parts of the anterior and posterior labia. Jaw sheaths moderately massive with rough appearance, finely serrate; anterior sheath broadly arch-shaped; posterior sheath broadly V-shaped, wider than anterior sheath. Labial tooth row formula 2/3; tooth rows long, extending to marginal papillae; denticles long, slender, those on P-3 smaller than others.

In life and preservative, tadpoles black dorsally and ventrally; viscera not visible; fins translucent gray.

*Distribution and ecology.*—This species is only known from the type locality at an elevation of 3435 m in the vicinity of Laguna de Los Cóndores in the northern part of the Cordillera Central in northern Peru. The frogs were found by day in areas of bunch grass and *Baccharis* sp., with spiny terrestrial bromeliads and scattered shrubs. *Telmatobius atahualpai*, *Telmatobius truebae*, and *Proctoporus ventrimaculatus* also were found at the type locality.

*Etymology.*—The specific name is a Greek adjective, *phalaros*, meaning white spotted; the name refers to distinctive ventral coloration.

*Remarks.*—The skull of *Gastrotheca phalarosa* is like that of *G. peruana*.

- calcar absent on heel; tubercle usually absent on heel ..... 3
- 2. Skin on head co-ossified with skull; triangular calcar on heel ..... *G. weinlandi*
- Skin on head not co-ossified with skull; small tubercle on heel ..... *G. testudinea*
- 3. Skin of head co-ossified with skull ..... 4
- Skin on head not co-ossified with skull ..... 5
- 4. Head spatulate with flared lips ..... *G. galeata*
- Head not spatulate with rounded lips .....  
..... *G. ossilaginis*
- 5. Small, conical tubercle of heel ..... *G. abdita*
- No tubercle on heel ..... 6
- 6. Snout convexly inclined anteroventrally in profile; interorbital distance about equal to width of upper eyelid; disc on Finger III barely wider than distal part of digit; skin on dorsum with distinct, elevated pustules ..... 7
- Snout rounded to nearly truncate in profile; interorbital distance at least 50% greater than width of upper eyelid; disc on Finger III noticeably wider than distal part of digit; skin on dorsum smooth to weakly granular, lacking elevated pustules ..... 8
- 7. Snout acutely rounded in dorsal view; tympanic annulus granular; tarsal fold extending full length of tarsus; venter uniform pale gray .....  
..... *G. peruana*
- Snout nearly truncate in dorsal view; tympanic annulus smooth; tarsal fold present only distally; venter black with white spots *G. phalarosa*
- 8. Inner tarsal fold extending two-thirds length of tarsus; width of disc on Finger III equal to diameter of tympanum; interorbital distance about 1.75 times width of upper eyelid; temporal arcade complete ..... *G. monticola*
- Inner tarsal fold extending full length of tarsus; width of disc on Finger III about 1.3 times diameter of tympanum; interorbital distance about 1.5 times width of upper eyelid; temporal arch incomplete ..... *G. lateonota*

NOTE: The nature of the temporal arch can be ascertained by moving a blunt probe posterolaterally around the posterior margin of the orbit.

KEY TO THE SPECIES OF *GASTROTHECKA* IN THE ANDES OF NORTHERN PERU

The following key includes those species known from elevations >1500 m in the departments of Amazonas, Cajamarca, Piura, and San Martín in northern Peru.

- 1. Tibia length >50% SVL; disc on Finger III much wider than distal part of digit; Finger I > Finger II; tubercle or calcar on heel ..... 2
- Tibia length <50% SVL; disc on Finger III no more than slightly wider than distal part of digit; relative lengths of fingers variable;

PATTERNS OF DISTRIBUTION

Of the nine species of *Gastrotheca* known from the Andes in northern Peru, two species, *G. testudinea* and *G. weinlandi*, are arboreal inhabitants of cloud forest at elevations of 550–2775 m principally on humid slopes in the Amazonian drainage of the Andes (Table 1, Fig. 4). Both species are widely distributed on the slopes of the Cordillera Oriental in Ecuador and the Cordillera Oriental and northern part of the Cordillera Central in Peru; they also inhabit the outlying ranges—

TABLE 1.—Elevational distributions (in meters) of species of *Gastrotheca* in different mountain ranges in northern Peru and adjacent Ecuador.

Species	Cordillera Occidental, Ecuador	Cordillera Oriental, Ecuador	Cordillera de Cucutú, Ecuador	Cordillera del Cóndor, Ecuador	Cordillera de Colán, Peru	Cordillera Central, Peru	Cordillera Occidental, Peru	Cordillera Huancabamba, Peru
<i>G. abdita</i>	—	—	—	—	2970–3330	—	—	—
<i>G. galeata</i>	—	—	—	—	—	—	—	1740–3130
<i>G. lateonota</i>	—	—	—	—	—	—	—	2180
<i>G. monticola</i>	2100–2500	—	—	—	—	2180–3440	2560–2700	1900–2620
<i>G. ossilaginis</i>	—	—	—	—	—	3000–3100	—	—
<i>G. peruana</i> <sup>1</sup>	—	—	—	—	—	—	2500–3600	—
<i>G. phalarosa</i>	—	—	—	—	—	3435	—	—
<i>G. psychrophila</i>	—	2770–2850	—	—	—	—	—	—
<i>G. testudinea</i> <sup>2</sup>	—	550–2590	1700	1800	—	1585–2180	—	—
<i>G. weinlandi</i> <sup>3</sup>	—	1100–2370	1700	1830	2000	1500	—	—

<sup>1</sup> Also occurs at elevations of 3090–3450 m farther south in the Cordillera Occidental and at elevations of 2530–4600 m in the central part of the Cordillera Oriental in Peru.

<sup>2</sup> Also occurs at elevations of 1560–2775 m farther south on the Amazonian slopes of the Cordillera Oriental in Peru and at 1600 m in Bolivia.

<sup>3</sup> Also occurs at elevations of 1750–2000 m on the Amazonian slopes of the Cordillera Oriental in southern Colombia.

the Cordillera de Cucutú in Ecuador and the Cordillera del Cóndor in Ecuador and Peru—and *G. weinlandi* is known from the Cordillera Colán in Peru. Although their geographic and elevational ranges broadly overlap, the two species have been found sympatrically only at Abitagua, 1300 m, Provincia Pastaza, Ecuador.

The other species of *Gastrotheca* are primarily terrestrial. Of these, *G. monticola* has the widest distribution; it occurs in humid montane forest and above tree line at elevations of 2180–3440 m in the Cordillera Central, 2560–2700 m in the Cordillera Occidental in Peru, 1900–2620 m in the Cordillera de Huancabamba, and 2100–2500 m in the southern part of the Cordillera Occidental in Ecuador. It also inhabits subhumid intermontane basins and the valleys of the Río Marañón and Río Zamora at elevations of 1000–2700 m (Fig. 4). The only other species of *Gastrotheca* in northern Peru that has an extensive distribution is *G. peruana*, which occurs to the south of *G. monticola* in the Cordillera Occidental at elevations of 2500–3600 m, mostly above tree line. To the south, *G. peruana* is known from elevations of 4000–4600 m in the northern headwaters of the Río Mantaro on the southern slope of the Nudo de Pasco in central Peru, at elevations of 2300–3350 m in the upper valley of the Río Marañón, and from elevations 2300–3520 m on the Pacific slopes of the Cordillera Occidental.

The other terrestrial species have restricted distributions (Table 1). *Gastrotheca abdita* occurs above tree line on the western slopes of the Cordillera Colán at elevations (2970–3330 m), higher than the record of *G. weinlandi* in cloud forest (2000 m) on the same slope. On the western slopes of the Cordillera de Huancabamba, *G. galeata* is known from dry montane forest and cloud forest at elevations of 1740–3230 m. *Gastrotheca lateonota* is known only from an elevation of 2180 m on the same slope, but it and *G. galeata* have not been found sympatrically. The known distributions of *G. ossilaginis* and *G. phalarosa* are parapatric at elevations of 3000–3100 m and 3435 m, respectively, above tree line in the northern part of the Cordillera Central. An outlier seems to be *G. psychrophila*, which is known only from elevations of 2770–2850 m at the Abra de Zamora in the southern part of the Cordillera Oriental in Ecuador (Fig. 4).

The phylogenetic relationships of the species of *Gastrotheca* are unknown. Phenetically, three allopatric pairs of species exist: *G. lateonota*–*G. monticola*, *G. peruana*–*G. phalarosa*, and *G. abdita*–*G. ossilaginis*. Two reproductive modes are known among the species of *Gastrotheca* in the Andes of Ecuador and Peru. In three terrestrial species—*G. abdita*, *G. galeata*, *G. ossilaginis*—and the two arboreal cloud-forest inhabitants, *G. testudinea* and *G. weinlandi*, the eggs undergo direct development into froglets in

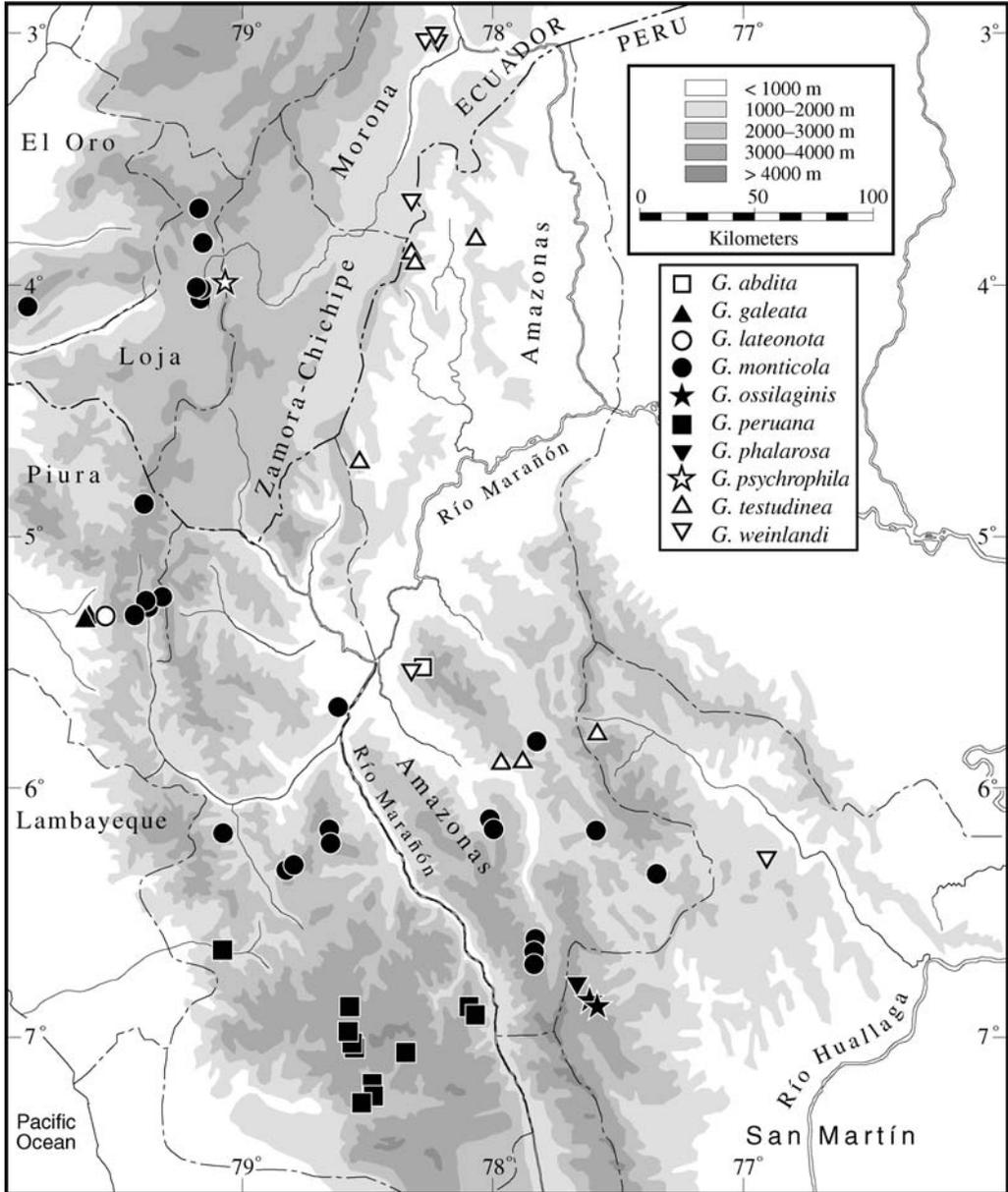


FIG. 4.—Physiographic map of northern Peru and adjacent Ecuador showing localities of occurrence of 10 species of *Gastrotheca*. Based on Mapa Físico Político del Perú, 1:1,000,000, 1973, Instituto Geográfico Militar del Perú, and Mapa de Ecuador, 1:1,000,000, 1974, Instituto Geográfico Militar, Quito, Ecuador.

the brood pouches. In five of the other terrestrial species (*G. lateonota*, *monticola*, *phalarosa*, *peruana*, and *psychrophila*), the eggs hatch as tadpoles that are released from the brood pouches to develop in ponds.

*Gastrotheca monticola*, as now recognized, may consist of more than one species. Some

individuals from high elevations (e.g., KU 212078 from 27 km SSW Leimebamba, 3440 m) are notable in the extent of black markings ventrally. However, multivariate analyses of data from series of specimens from the Loja Basin in southern Ecuador, the vicinity of Huancabamba in north-central Peru, and from

the northern part of the Cordillera Central in Peru reveals that these samples are indistinguishable morphometrically and in structural characters and coloration; results from these analyses are not shown here. Comparisons of DNA sequences now underway may reveal genetic differences among populations of this highly variable species.

#### DISCUSSION

Despite extensive collecting in the Cordillera Central in northern Peru during the past three decades, probably many species of anurans remain to be found. Currently 30 species are known from moderate to high elevations (>1500 m) in the Cordillera Central; nine species are known from the Cordillera Colán, of which *Eleutherodactylus serendipitus* has been recorded from both cordilleras. Endemism is high in both cordilleras—67% in the Cordillera Colán and 83% in the Cordillera Central. In addition to the foregoing *Eleutherodactylus*, non-endemics in the Cordillera Central include four species (*E. bromeliaceus*, *Gastrotheca testudinea*, *Hyla aperomea*, and *Scinax oreites*) that also occur in the Cordillera Oriental in central Peru; the first two also occur in the Cordillera Oriental in Ecuador, and *E. percnopterus* also inhabits the Cordillera del Cóndor to the north. The other nonendemic, *G. monticola*, also occurs in the Huancabamba Depression and in the Cordillera Occidental in northern Peru and in southern Ecuador. In addition to *E. serendipitus*, the nonendemics in the Cordillera Colán include *E. galdi*, which occurs in the Cordillera Oriental in Ecuador, and *Gastrotheca weinlandi*, which is widespread on the Amazonian slopes of the Andes from southern Colombia to Roque, Departamento de San Martín, Peru.

#### RESUMEN

Se describen dos nuevas especies de *Gastrotheca* para los bosques montanos de la parte norte de la Cordillera Central, en el Departamento de San Martín, Perú. La primera nueva especie se caracteriza por tener una co-osisificación craneal integumentaria y la segunda nueva especie, de la misma área sin co-osisificación craneal integumentaria, se diferencia de todos los demás miembros del género

por poseer el vientre negro con puntos blancos. Siendo nueve las especies de *Gastrotheca*, con una distribución principalmente alopátrica, las que habitan en los Andes del norte de Perú.

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- Gastrotheca antomia*: COLOMBIA: Chocó: El Boquerón, at border of Valle de Cauca on El Cairo–Las Amarillas road, 1900–2250 m, KU 289245.
- Gastrotheca bufona*: COLOMBIA: Antioquia: Ventanas, 50 km NW (by road) Yarumal, MLS 344 (holotype).
- Gastrotheca fissipes*: BRAZIL: Espírito Santo: Vila Velha, KU 193297, 193298 (skeleton).
- Gastrotheca galeata*: PERU: Piura: 15 km (by road) E Canchaque, 1740 m, KU 174361–64, 174365 (skeleton), 181700, LSUMZ 32058 (holotype), 32059; 15.8 km (by road) E Canchaque, 1890 m, KU 219765–66, MHNSM 15416; 16 km (by road) E Canchaque, 1900 m, MHNSM 15417; 33 km (by road) SW Huancabamba, 2130 m, LSUMZ 32052–53.
- Gastrotheca guentheri*: COLOMBIA: Nariño: Reserva Natural La Planada, 7 km S Chucunés, 1650–1780 m, KU 195628, 200259–60. ECUADOR: Pichincha: Quebrada Zapadores, 5 km ESE Chiriboga, 2010 m, KU 164224–26, 164227 (skeleton), 164228, 173112, 178464.
- Gastrotheca lateonota*: PERU: Piura: El Tambo, 31.5 km E Canchaque, 2180 m, KU 181729, 181730 (holotype), 181731–39, 181836–37 (skeleton), MHNSM 1635.
- Gastrotheca monticola*: ECUADOR: Loja: Celica, 2130 m, BMNH 1931.11.3.3–4; Loja, 2150 m, BMNH 1931.2.12.10–13, 1933.6.3.18–44, 1935.11.3.26–32, 1947.2.31.6–12, 1931.2.31.13 (holotype of *G. lojana*), 1931.2.31.14–18, KU 120673–74, USNM 258851–58; 5 km N Loja, 2150 m, KU 138235–36, 138237 (skeleton); 42 km N Loja, QCAZ 3846 (tadpoles); 2 km E Loja, 2200 m, KU 120675; 6.8 km E Loja, 2640 m, KU 217511–12; 9 km E Loja, 2660 m, KU 121387 (tadpoles); 10 km E Loja, 2600 m, KU 178470–76; 2 km S Loja, CAS 93898; 3 km W Loja, 2150 m, KU 138233; 5.2 km W Loja, 2310 m, KU 202688, 5.5 km W Loja, 2330, KU 142603–08, 148549–51; 10 km W Loja, 2500 m, KU 138234; Saraguro, 2500 m, KU 138404–09, 138410 (skeleton), 148568. PERU: Amazonas: N slope Abra Barro Negro, 27 km WSW Leimebamba, 3440 m, KU 212078; Chachapoyas, 2340 m, KU 138238–41; 20.5 km WSW Leimebamba, 3130 m, KU 181741; 24 km WSW Leimebamba, 3370 m, FSM 30080; 5 km N Levanto, 2850 m, KU 212021; 6 km NW Mendoza, 2200 m, KU 209421; Molinopampa, 2400 m, KU 212022–3, MHNSM 6116–21; Pomacochas (Florida), 2180 m, KU 181742–70, 181838–39 (skeletons), 212032–36, MHNSM 1040 (5), 6122–31. Cajamarca: Bellavista. BMNH1947.2.22.47–48, 1947.2.25.77–78; Cutervo, 2620 m, KU 212055–66, NMW 6483; 8 km NW Cutervo, 2560 m, KU 212067, 212492 (tadpoles); Hacienda Taulis, 1500 m, SMF 81730–31; Quercotillo, MCZ 5328–30. Piura: Ayabaca, 2700 m, MHNSM 702 (2); W slope Cerro Chinguela on Huancabamba–San Ignacio trail, 2620 m, KU 196819; Huancabamba, 1960 m, AMNH 7551, KU 219771, MCZ 5290 (holotype), 5291–93, 5296–97, 5299–300, 5302, 5304–07, 5309, 5312–25, 5317, 5329, 5328–30; 1.8 km N Huancabamba, 1980 m, KU 219767–68, MHNSM 15418–19; 4 km N Huancabamba, 1900 m, KU 209769–70, MHNSM 15420–21; 18.5 km WSW Huancabamba, 2740 m, KU 181874 (tadpoles); San Andres de Cutervo, KU 221705; Súcota, KU 221704.
- Gastrotheca nicefori*: COLOMBIA: Antioquia: Medellín, 1490 m, KU 192401, 192402 (skeleton). Huila: Parque

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## APPENDIX I

### Specimens Examined

*Gastrotheca abdita*: PERU: Amazonas: Cordillera Colán, 2970–3330 m, E La Peca, KU 196833 (holotype),

Arqueológico San Agustín, 3 km SW San Agustín, 1750 m, KU 169416-17; Peak near Cano Sardinata, ca. 35 km WSW Vista Hermosa, Serranía de Macarena, 1140 m, KU 153485, 153486 (skeleton). PANAMA: *Darién*: Cerro Citurio, Serranía de Pirre, 1100 m, KU 101538-39; ridge between Río Jaque and Río Imamadó, 800 m, KU 111991. VENEZUELA: *Táchira*: 11 km S Delicias, 1750 m, KU 181071. *Trujillo*: 3 km NE Boconó, 1575 m, KU 133392.

*Gastrotheca ossilaginis*: PERU: *San Martín*: Lago Quindecocha, 3100 m, MHNSM 19486 (holotype), 19489-90; Ullilen, 3000 m, MHNSM 19488.

*Gastrotheca ovifera*: VENEZUELA: *Aragua*: Paso Portochuelo, 1170 m, KU 185733; Rancho Grande, 1100 m, KU 133388-89, 166760-64, 185732, 185785, 209587-90 (cleared and stained). *Distrito Federal*: Caracas, KU 125372, 125373 (skeleton).

*Gastrotheca peruana*: PERU: *Ancash*: Chavín de Huántar, 3230 m, KU 138514-26; Chiquián, 3200-3400 m, KU 138495-512; Huaráz, 3250 m, KU 138513; 5 km N Recuay, 3450 m, KU 138527-44. *Cajamarca*: E slope Abra Gelic, 20 km E Celendín, 2740 m, KU 212071, 212679 (tadpoles), MHNSM 6115, 6275 (tadpoles); S slope Abra Quilsh, 26 km NNW Cajamarca, 3500 m, KU 212068, MHNSM 6114; S slope Abra Quilsh, 28 km NNW Cajamarca, 3520 m, KU 212069, 215628 (tadpoles), MHNSM 6290 (tadpoles); Cajamarca, 2800 m, KU 138494 55 km N Cajamarca, 3600 m, KU 212072-75; 8 km S Cajamarca, 3050 m, KU 212070, MHNSM 6182; Celendín, Poyunte, 2400 m, QCAZ 7013; 23 km SW Celendín, 3050 m, KU 181740; Cutervo, 2620 m, KU 212055-57, 212058-59 (young), 212060-66, 212498 (tadpoles), MHNSM 264 (tadpoles), 269; 6188-92, 6295 (tadpoles); 8 km NW Cutervo, 2560 m, KU 212492 (tadpoles), MHNSM 6302 (tadpoles); 3 km SW Encanada, 2980 m, KU 215631 (tadpoles); 4 km W Llama, 2500 m, KU 212497 (tadpoles), MHNSM 6299 (tadpoles). *Huánuco*: 5 km NE La Unión, 3100 m, KU 138411-52. *Junín*: between Casa Pato and Anascancha, ca. 10 km S Carhuamayo, 4050 m, KU 139189-90; Odonores, 4115 m, KU 207815. *La Libertad*: Huamachuco, 3350 m, KU 138453-59; Laguna Sacsacocha, 12 km E Huamachuco, 3200 m, KU 138460-91, 138492-93 (skeletons); Otuzco, 2730 m, KU 138545-46.

*Gastrotheca phalarosa*: PERU: *San Martín*: Esperanza, 3435 m, MHNSM 19472, 19487 (holotype), MHNSM 19498 (tadpoles).

*Gastrotheca psychrophila*: ECUADOR: *Loja*: Loja, 2150 m (?), QCAZ 2365-67. *Loja-Zamora-Chinchipec*: 13-15 km E Loja, 2770-2850 m, KU 120760 (holotype), 120761-62, 141585 (skeleton), 141586, 141595 (young), 142631-37, 148599, 164233-34, 166182 (tadpoles), 166308 (skeleton), 203596-600 (young), 203601 (tadpoles); QCAZ 896, 898, 900, 903, 2379 (tadpoles).

*Gastrotheca trachyceps*: COLOMBIA: *Cauca*: Cerro Munchique, 2170 m, KU 144122, 144123 (holotype), 144124 (skeleton), 144125-26; west slope Cerro Munchique, 2530 m, KU 181188-93.

*Gastrotheca testudinea*: BOLIVIA: *La Paz*: Serranía Bellavista, 35 km (by road) N Caranavi, 1650 m, KU 197083. ECUADOR: *Morona-Santiago*: Agua Rica, SW Limón, 1910 m, USNM 258754; Yapitya, E slope Cordillera Cutucú, 1700 m, ANSP 29223; 18.6 km WSW Plan de Milagro, 2275 m, KU 202701; 0.5 km E Sapote, between Limón and Gualaceo, 2420 m, USNM 258755; 2 km W Sapote, between Limón and Gualaceo, 2590 m, USNM 258756 San Vicente, USNM 260787. *Napo*: Loreto, 550 m, USNM 258757; San José de Moti, MNCN 155 (holotype). *Pastaza*: Abitagua, 1300 m, CAS-SU 5073, UMMZ 90243-44. *Tunguarhua*: Baños, 1800 m, CAS-SU 5080, FMNH 27605-14, 28001-02, 28009-10, 28014, 28017, 23093-98, 36698, NHRM 1964 (10) (syntypes of *Nototrema viviparum*). PERU: *Amazonas*: E slope Abra Pardo Miguel, 2180 m, KU 212077; 15 km NE Ingenio (road to Laguna Pomacochas), 1585 m, KU 196818; 33 km NE Ingenio (road to Laguna Pomacochas), 2180 m, KU 206146; 3 km N Vista Alegre (SE spur Cordillera del Cóndor), 1800 m, KU 217305. *Ayacucho*: Río Piene, Tutumbaro, 1840 m, KU 163271-74, 163275 (skeleton), 163276-78. *Cusco*: Marcapata, 2775 m, FMNH 81370; Quincemil, FMNH 141109; Río Cosñipata, 4 km SW Santa Isabel, 1700 m, KU 163270. *Huánuco*: base of Bosque Zapata-Cocha, above Acamayo, 2545 m, KU 196815, LSUMZ 31969-70; Huaylaspampa, 2590 m, KU 196817, LSUMZ 31972; Pozuzo, BMNH 81.5.13.65; Río Huaylaspampa, 2530 m, KU 196816. *Junín*: Serranía de Sira, 1560 m, NHMW (Aichinger 4683); Yano Mayo, Río Tarma, 2620 m, BMNH 1926.1.21.1. *Pasco*: Yaupi, MTD 45907. *San Martín*: E slope Abra Patricia above Venceremos, 1700 m, KU 209422; Venceremos, 1630 m, KU 212076.

*Gastrotheca weinlandi*: COLOMBIA: *Cauquetá*: 10.3-12.5 km E Alto de Gabinete, 1750-1900 m, ICN 23368, 24449-50. *Huila*: Cueva de los Guácheros, 2000 m, ICN 31588, 47899. ECUADOR: *Morona-Santiago*: El Cruzado, between Limón and Gualaceo, 2220 m, USNM 258752; trail between Logroño and Yaupi, Cordillera de Cutucú, 1700 m, ANSP 29229; 8.8 km WSW Plan de Milagro, 2370 m, KU 202702; Río Piuntza, Cordillera del Cóndor, 1830 m, KU 146041-42. *Napo*: Río Azuela, 1740 m, KU 143103; 7 km SW Río Azuela (Quito-Lago Agrio road), KU 155468; 16.5 km NNE Santa Rosa, 1700 m, KU 143104, 143105 (skeleton), 143106. *Pastaza*: Abitagua, 1300 m, FMNH 27620; between Abitagua and Río Pastaza, 1100 m, UMMZ 90245-48; Río Villano, CAS 149430. *Sucumbios*: S slope Cordillera del Dué, above Río Coca, 1150 m, KU 122600. PERU: *Amazonas*: Cordillera Colán, ca. 20 km E La Peca, 2000 m, KU 196820. *San Martín*: Roque, NHMG 472 (holotype of *Hyla pusilla*).