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A NEW SPECIES OF *HYLOSCIRTUS* (ANURA: HYLIDAE) FROM COLOMBIA, WITH A REDIAGNOSIS OF *HYLOSCIRTUS LARINOPYGION* (DUELLMAN, 1973)

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ABSTRACT: Hyloscirtus larinopygion is rediagnosed, and a new species formerly confused with that species is described from the highlands of the Central Cordillera in the Andes Mountains of Colombia. The new species differs from the other species of the *H. larinopygion* group by its color pattern, iris coloration, and presence of a nuptial pad with dark-brown epidermal projections. We discuss variation and diversity of nuptial pads, the calcar tubercle, and some aspects related to the swollen cloacal region in the *H. larinopygion* group. Finally, we discuss reproductive biology and problems involving the definition of a putative synapomorphy of *Hyloscirtus*.

Key words: Andes Mountains; Cophomantini; Systematics; Taxonomy; Tree Frog

THE HYLID genus *Hyloscirtus* includes 32 species (Frost, 2013) of stream-dwelling treefrogs whose monophyly is supported both by molecular and morphological data (Faivovich et al., 2005; Sánchez, 2010; Wiens et al., 2010; Pyron and Wiens, 2011). Its species are divided in three species groups—the *H. armatus*, *H. bogotensis*, and *H. larinopygion* groups. The monophyly of each of these groups is mostly supported by molecular data (Faivovich et al., 2005; Wiens et al., 2010), and larval morphological synapomorphies further support the monophyly of the *H. armatus* group (Duellman et al., 1997; Faivovich et al., 2005; Lötters et al., 2005).

The Hyloscirtus larinopygion group currently comprises 13 colorful species distributed in the Andes Mountains of Colombia and Ecuador: *H. caucanus* (Ardila-Robayo et al., 1993), *H. criptico* (Coloma et al., 2012), *H. larinopygion* (Duellman, 1973), *H. lindae* (Duellman and Altig, 1978), *H. pacha* (Duellman and Hillis, 1990), *H. pantostictus* (Duellman and Berger, 1982), *H. princecharlesi* (Coloma et al., 2012), *H. psarolaimus* (Duellman and Hillis, 1990), *H. ptychodactylus* (Duellman and Hillis, 1990), *H. sarampiona* (Ruiz-Carranza and Lynch, 1982), *H. stauf-ferorum* (Duellman and Coloma, 1993), *H. tapichalaca* (Kizirian et al., 2003), and *H. tigrinus* Mueses-Cisneros and Anganoy-Criollo, 2008.

Species included in the *H. larinopygion* group have relatively restricted ranges, although *H. larinopygion* is widely distributed in the Cordillera Central and Occidental in Colombia and is present in Provincia de Carchi in northern Ecuador. While studying material identified in collections as *H. larinopygion* from the northern Cordillera Central, in the Departamento de Antioquia, Colombia, it became evident that the specimens actually correspond to a different and new species. The goals of this paper are to rediagnose *Hyloscirtus larinopygion*, describe the new species, and discuss some taxonomic characters of the *H. larinopygion* group.

MATERIALS AND METHODS

Specimens were fixed in 10% formaldehyde and stored in 70% ethanol. Measurements are those established by Duellman (1970) and Heyer et al. (1990). All measurements were taken with digital calipers and rounded to the nearest 0.1 mm. Abbreviations are SVL

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(snout-vent length), HL (head length), HW (head width), ED (eye diameter), END (nostril-eye distance), NSD (nostril-tip-ofsnout distance), IND (internostril distance), AMD (distance between the anterior margins of eyes), TD (tympanum diameter), TL (tibia length), FL (foot length), TFD (third-finger disc diameter), and FTD (fourth-toe disc diameter). Webbing formulae follow the terminology of Savage and Heyer (1967) as modified by Myers and Duellman (1982). The description of nuptial pads follows the terminology of Luna et al. (2012). Sex was determined by examination of secondary sexual characters (nuptial pads, vocal slits, and expansion of the vocal sac) or, when in doubt, by examination of gonads. Color pattern in life was described from field notes and color photographs. Drawings were made using a Zeiss stereomicroscope with a drawing tube. Information on other species was taken from preserved specimens (Âppendix), notes and photographs of living specimens, and literature. Institutional abbreviations used throughout this paper are MHUA-A (Museo de Herpetología, Universidad de Antioquia, Medellín, Colombia), ICN (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia), QCAZ (Museo de Zoología, Pontificia Universidad Católica del Ecuador), and DHMECN (División de Herpetología, Museo Ecuatoriano de Ciencias Naturales).

RESULTS

Hyloscirtus larinopygion (Duellman, 1973) (Figs. 1–3,6)

Diagnosis.—The following characters distinguish Hyloscirtus larinopygion from the other species of the H. larinopygion group: dorsal coloration that varies from light brown to dark brown, sometimes with a dark-brown reticulated pattern; white-grayish or bluegrayish flanks with black stripes, sometimes anastomosed or reticulated; iris gold or silver (see below), with black reticulation; nuptial pad large, creamy white, covering medial margin of prepollex and matacarpal II, and with a distal component that partially covers the dorsal surface of the finger; broad

elliptical prepollex, not modified as a projecting spine. Hyloscirtus larinopygion has been formerly confused with *H. psarolaimus* (Duellman and Hillis, 1990), H. criptico (Coloma et al., 2012), and the new species described below. It differs from *H. psarolaimus* in that the latter has a dull bronze iris with black reticulations (golden or silver in H. larinopygion), has a middorsal line in most individuals (absent in *H. larinopygion*), and lacks nuptial pads in adult males (present in H. larinopygion). Hyloscirtus criptico differs from H. *larinopygion* in having small orange flecks and stippling on the dorsum and venter (absent in H. larinopygion), having a dark gray iris (golden or silver with black reticulation in *H*. *larinopygion*), and lacking nuptial pads in adult males (present in *H. larinopygion*). The new species described below differs from H. *larinopygion* in having a reddish-brown dorsum with orange markings that turn to yellow toward the black flanks and are delimited with blue or pale gray outline (dorsum light brown to dark brown, sometimes with a dark-brown reticulated pattern; white-gravish or bluegravish flanks with black stripes, sometimes anastomosed or reticulated in H. larinopygion); iris gray with burgundy reticulation (golden or silver, with black reticulation in H. *larinopygion*); nuptial pad with dark-brown epidermal projections and with a larger distal component (creamy white in *H. larinopygion*, with the distal component covering a smaller area). See Table 1 for a summary of diagnostic characters of all species of the Hyloscirtus *larinopygion* group.

Description.—The description provided by Duellman (1973) is adequate; however, it was based only on a female individual, and more specimens (including several males) have been collected in the past 20 yr. These new specimens indicate that males of this species have a large creamy-white nuptial pad. It covers the medial margin of prepollex and Metacarpal II, with a distal component that partially covers the dorsal surface of the finger. Male SVL 53.6–60.5 (n = 10), female SVL 62.0–68.4 (n = 4). See below for further comments.

Remarks.—Hyloscirtus larinopygion was described from near the city of Popayan in the Departmento del Cauca, Cordillera Cen-

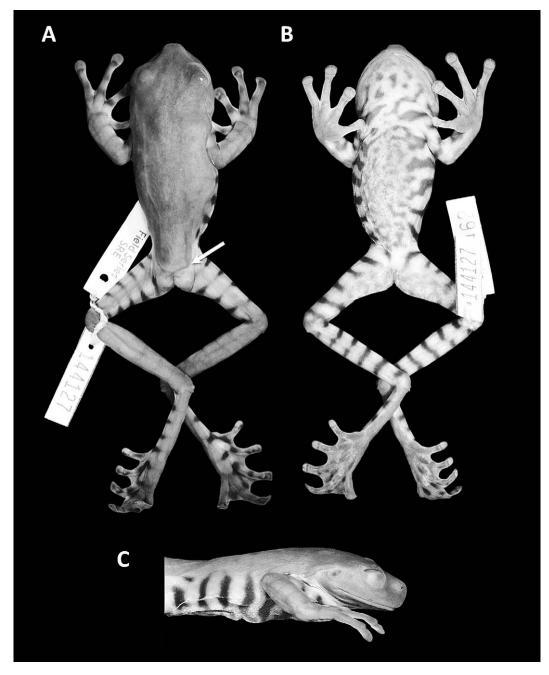


FIG. 1.—Holotype of *Hyloscirtus larinopygion*, KU 144127, SVL 53.6 mm; (A) dorsal view; (B) ventral view; (C) lateral view. The arrow indicates an artifactual fold above the cloaca. Photo: M. Bustamante.

tral of Colombia (see Duellman, 1973). Duellman and Altig (1978) identified as *H. larinopygion* specimens from San Francisco (Departmento del Putumayo, Colombia) and Papallacta (Provincia de Napo, Ecuador). Subsequently, Duellman and Hillis (1990) described these populations as *Hyla psarolai*ma (now *Hyloscirtus psarolaimus*). Ardila-

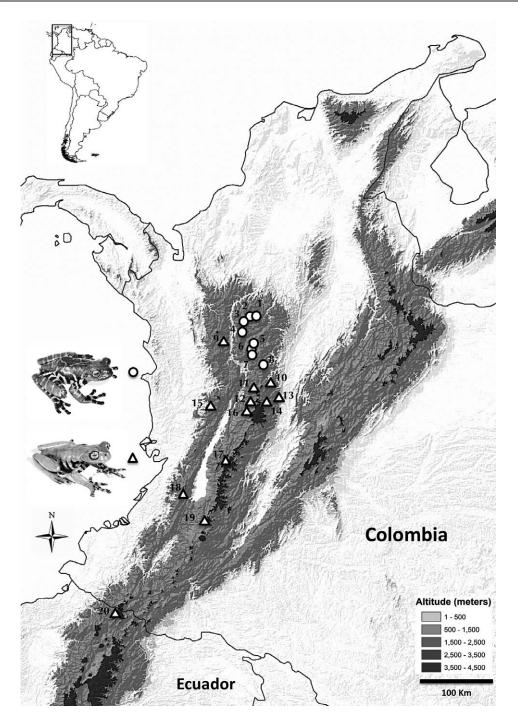


FIG. 2.—Geographic distribution of *Hyloscirtus antioquia* sp. nov. (circles), and *H. larinopygion* (triangles). *Hyloscirtus antioquia*: (1) San Antonio del Río, Yarumal; (2) Llanos de Cuivá, Santa Rosa de Osos; (3) Páramo de Belmira, Belmira; (4) Serranía Las Baldías, Bello (holotype locality); (5) Santa Elena, Medellín; (6) Loma El Escobero, Envigado; (7) Alto de San Miguel, Caldas; (8) Páramo de Sonsón, Sonsón. *Hyloscirtus larinopygion*: (9) Páramo de Frontino, Antioquia; (10) Pensilvania, Caldas; (11) Villamaría, Caldas; (12) Ucumari, Risaralda; (13) Murillo, Tolima; (14) Juntas, Tolima; (15) Serranía de los Paraguas, Chocó-Valle del Cauca; (16) Salento, Quindío; (17) Parque Natural Las Hermosas, Tolima-Valle del Cauca; (18) Parque Natural Farallones de Cali, Valle del Cauca; (19) Popayan, Cauca (type locality); (20) Carchi, Ecuador.



FIG. 3.—(A) *Hyloscirtus antioquia* sp. nov. in life (MHUA-A 7230, paratype, adult male, SVL 53.4 mm); (B) *H. larinopygion* in life (QCAZ 41826, adult male, SVL 55.2 mm). Photos: M Rivera-Correa and S. Ron. (A color version of this figure is available online.)

Robayo et al. (1993) considered some populations from Departmento de Antioquia (i.e., localities in the municipalities of Bello, Belmira, and Sonsón), as the most-northern records of *H. larinopygion* along the Central Cordillera in Colombia; however, these populations belong to the new species described below. In addition, some populations in the provinces of Carchi and Imbabura (northern Ecuador) that were traditionally assigned to *H. larinopygion* (Duellman and Coloma, 1993; Toral et al., 2002) have recently been described as *H. criptico* by Coloma et al. (2012).

Duellman (1973) described a fold above the cloaca in the holotype (KU 144127). We find that this fold is very likely an artifact of the position of preservation (legs extended in a posterior direction; Fig. 1A); in 26 examined specimens of *H. larinopygion*, we did not observe this structure. Duellman (1973) described the iris color as being silver with fine black reticulations. However, several

specimens collected along in the range of *H. larinopygion* and photographs of many living specimens (i.e., ICN, MHUA, and QCAZ specimens), did not show this color pattern, and no color slides of the type specimen are available (W. Duellman, personal observation). Nevertheless, differences in iris coloration had already been described by Mueses-Cisneros and Perdomo-Castillo (2011) in *H. tigrinus*, another species of the *H. larinopygion* group. Until more observations on iris coloration become available, we consider the iris of *H. larinopygion* to be golden or silver with black reticulation.

Coloma et al. (2012) recently presented a phylogenetic hypothesis based on mitochondrial DNA evidence (12S and 16S sequences) for most of the currently known species. Their results indicated that *Hyloscirtus larinopygion* is the sister taxon of *H. lindae* plus *H. pantostictus*. They also described the tadpole and ontogenetic changes for a population from Ecuador. Bernal et al. (2004) briefly described the advertisement call of *H. larinopygion* from Municipio de Ibagué, Departamento del Tolima, Colombia, without providing information on the number of individuals or voucher specimens.

Distribution.—Hyloscirtus larinopygion is the most widely distributed species of the group, and is currently known from the Cordillera Central and Occidental of Colombia to northern Ecuador, approximately between 2000 m and 2800 m elevation (Fig. 2).

> Hyloscirtus **antioquia** sp. nov. (Figs. 2–6; Tables 1, 2)

- *Hyla larinopygion*, Ardila-Robayo et al. (1993:564; part).
- *Hyloscirtus larinopygion*, Palacio et al. (2006:72; part).
- Hyloscirtus larinopygion, Mueses-Cisneros and Anganoy-Criollo (2008:135, Fig. 6A; part).

Holotype.—MHUA-A 7227, adult male, Colombia, Antioquia, Municipio de Bello, Serranía Las Baldías, Corregimiento de San Félix, Vereda Las Huertas, Quebrada El Hato (6°19'53.93"N, 75°38'10.10"W, 2660 m, datum = WGS84), km 5 along San Félix road— Truchera San Félix. Collected on 5 June 2010 TABLE 1.—Comparison of some diagnostic characters in species of the *Hyloscirtus larinopygion* group. In addition to the characters shown, *H. tapichalaca* differs from all other species in the group for having the prepollex modified as a spine, and absence of the omosternum (Kizirian et al., 2003). Sources: (1) Ardila-Robayo et al. (1993); (2) Coloma et al. (2012); (3) Duellman (1973); (4) Duellman and Altig (1978); (5) Duellman and Berger (1982); (6) Duellman and Hillis (1990); (7) Duellman and Coloma (1993); (8) Kizirian et al. (2003); (9) Mueses-Cisneros and Anganoy-Criollo (2008); (10) Mueses-Cisneros and Perdomo-Castillo (2011); (11) Ruiz-Carranza and Lynch (1982); (°) this study.

Species	Dorsal pattern	Flanks	Iris color	
H. antioquia	Reddish-brown; with or without scattered orange blotches	Gray or black with yellow markings delimited with blue or pale-gray outline	Gray with burgundy reticulations	
H. caucanus	Brown or reddish-brown with dark-brown scattered blotches; with or without middorsal stripe	Black or brown with orange spots and thick black stripes with tiny white dots	Pale yellow with brown reticulations	
H. criptico	Grayish-brown, densely stippled with minute cream flecks and bright-orange blotches	Black with white and brown markings with tiny orange blotches	Dark gray	
H. larinopygion	Light brown to dark brown; with or without dark-brown reticulation	White or light bluishgray with black vertical bars or blotches	Golden or silver with black reticulations	
H. lindae	Dark metallic brown	Dark metallic brown and dirty gray	Dull bluish-gray with minute black flecks	
H. pacha	Dark brown with metallic orange flecks	Brown with creamy white blotches	Olive brown	
H. pantostictus	Olive-brown with small orange spots	Olive-brown with small orange spots	Dark gray	
H. princecharlesi	Black with many round-oval orange blotches	Black with large, round, orange blotches	Dark gray	
H. psarolaimus	Grayish brown with dark-brown and minute cream flecks; with or without middorsal stripe	Cream with dark brown spots	Dull bronze with black reticulation	
H. ptychodactylus	Orange-tan to reddish brown with minute orange-tan flecks enclosed in black markings; with or without middorsal stripe	Uniform black or with reddish- brown extensions of the ground dorsal color	Pale blue	
H. sarampiona	Pale olive with orange spots	Black	Gold with thin black reticulation	
H. staufferorum	Uniform dark brown	Uniform dark with white bars	Metallic brown	
H. tapichalaca	Gray or dark brown	Gray brown with diffuse pink- orange marks more conspicuous in axillary and inguinal regions	Yellow-gold with black reticulation	
H. tigrinus	Yellow-green or yellowish-brown with transverse black stripes, sometimes reticulated; with or without middorsal stripe	Yellow-green with black reticulation	Light gray or yellow with black reticulation	

by Mauricio Rivera, Alejandro Montoya, and Felipe Duarte (Fig. 4).

Paratypes.—All adults. MHUA-A 7228–9 (males): collected with the holotype. MHUA-A 5707 (female) and MHUA-A 5708 (male): collected at the type locality on 11 May 2008 by Laura Bravo. MHUA-A 7230–32 (males): collected at the type locality on 5 June 2012 by Mauricio Rivera, Esteban Alzate, Felipe Duarte, Diego Rivera, and Carlos Botéro.

ICN 9384–86 (three adult males) and ICN 9387 (one adult female): Colombia, Antioquia, Municipio de Bello, Corregimiento de San Félix, Serranía Las Baldías, 6.6–8.1 km along San Felix road—Antenas, 2820–3100 m, collected 9 July 1981 by John Lynch and Pedro Ruiz-Carranza. ICN 9388–93, 9401 (males): Colombia, Antioquia, Municipio de Belmira, Vereda Los Patos, Quebrada Los Patos, 3.7 km N of Belmira, 2620 m, collected

TABLE	1.—Extend	led.
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Vomerine teeth series	Nuptial pad	Calcar tubercle	Ulnar tubercles	Source
In contact or not, 12–20 teeth each	Medial and distal component; dark-brown epidermal projections	Present	Present rounded	* (1)
In contact, 10–14 teeth each	Distal component only; creamy white	Present or Absent	Present, acute, white pigmented	* (1)
In contact or not, 8–15 teeth each	Absent	Present	Absent	* (2)
In contact or not, 8–15 teeth each	Medial and distal component; creamy white	Present or absent	Present rounded or acute	* (3)
In contact, 11–13 teeth each	Distal component; creamy white	Present or absent	Present rounded or absent	* (2, 4)
In contact, 11–15 teeth each	Absent	Present	Present rounded or absent	* (2, 6)
In contact or not, 10–14 teeth each	Medial and distal component, light-brown epidermal projections	Present or absent	Present rounded	* (2, 4)
In contact or not, 11–15 teeth each	Medial and distal component; creamy white	Absent	Absent	* (2)
In contact, 10–18 teeth each	Absent	Present	Present, rounded or absent	* (2, 6)
In contact, 11–15 teeth each	Absent	Present	Present	* (2, 6)
In contact or not, 8–16 teeth each	Medial and distal component; dark-brown epidermal projections	Present or absent	Present, rounded or acute	* (11)
In contact, 16–25 teeth each	Creamy white	Present	Present, acute or absent	* (2, 7)
No contact, 4–6 teeth each	Absent	Present	Absent	* (8)
In contact, 10–15 teeth each	Absent	Present	Absent	* (9, 10)

on 10 July 1981 by John Lynch and José V. Rueda. MHUA-A 6139 (female): Colombia, Antioquia, Municipio de Belmira, Vereda Río Arriba, Alto el Morro, finca Quebradona (6°38'17.0"N, 75°39'49.0"W, 2917 m), collected on 28 November 2008 by Alejandro Montoya. MHUA-A 7449–50, 7453, 7568 (males) and MHUA-A 7451–52 (females): Colombia, Antioquia, Municipio de Belmira, Vereda Montañitas, Reserva de Corantioquia (6°36′49.0″N, 75°39′13.10″W, 2820–2875 m), collected during 9–18 June 2012 by Esteban Alzate, Felipe Duarte, and Laura Pinto. MHUA-A 2645, 2647 (males) and MHUA–A 2646 (female): Colombia, Antioquia, Municipio de Envigado, Loma El Escobero, Parque Ecólogico San Sebastian—La Castellana (6°08′2.32″N, 75°30′39.90″W, 2500 m), collected on 21 June 2003 by Lucas Barrientos. MHUA-A 4140 (male): same locality, collect-

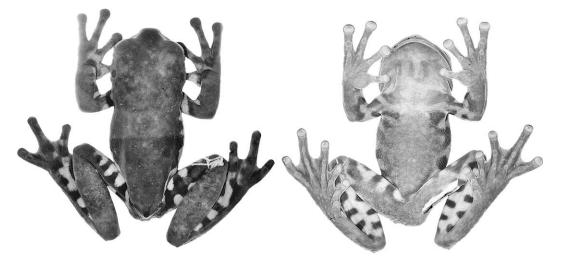


FIG. 4.—Dorsal and ventral view of the holotype of Hyloscirtus antioquia sp. nov., MHUA-A 7227; SVL 56.6 mm.

ed on 3 December 2005 by Mauricio Arias. MHUA-A 1707-08 (males) and MHUA-A 1709, 1716 (females): Colombia, Antioquia, Municipio de Santa Rosa de Osos, Llanos de Cuivá (6°36′7.75″N, 75°18′13.83″W; 2700 m), collected 13-16 October 2001 by Paul Gutiérrez. ICN 9399 (male): Colombia, Antioquia, Municipio de Sonsón, 12 km E Sonsón, 2560 m, collected on 10 July 1981 by John Lynch and José V. Rueda. MHUA-A 6138 (male): Colombia, Antioquia, Municipio de Sonsón, Vereda San Francisco, Páramo las Palomas trail, 2920 m, collected on 22 November 2008 by Juan Pablo Hurtado. MHUA-A 6012, 6014 (males): Colombia, Antioquia, Municipio de Yarumal, Corregimiento Llanos de Cuivá, Vereda San Antionio del Rio, finca Los Lagos (6°51'7.0"N, 75°29'28"W, 2660 m), collected on 19 July 2008 by Felipe Duarte.

Diagnosis.—Hyloscirtus antioquia can be distinguished from the other 13 species of the *H. larinopygion* group by the following characters: reddish-brown dorsum with a rough reticular pattern of orange markings that turn to yellow toward the black flanks and are delimited with blue or pale-gray outlines; thighs with yellow and black stripes; discs grayish-black dorsally and bluish-gray ventrally, and iris gray with burgundy reticulation; large nuptial pad with dark-brown epidermal projections; and broad elliptical prepollex that is not modified as a projecting spine.

Hyloscirtus antioquia has been previously confused with *H. larinopygion*, but differs from the latter in color pattern (dorsum light brown to dark brown, white-gravish or bluegrayish flanks with black stripes in *H. larinopygion*, see above for details), iris coloration (iris golden or silver with black reticulations in H. larinopygion), and morphology and color of the nuptial pad (creamy-white nuptial pad and a smaller distal component in *H. larino*pygion; see Fig. 6). Hyloscirtus lindae and H. pantostictus also have a gray iris but without reticulation (dull bluish-gray with minute black flecks in *H. lindae* and gray without flecks in *H. pantostictus*) and both species have orange digital discs; *H. pantostictus* also has orange spots all over the body (absent in *H. antioquia*). The broad elliptical prepollex, not modified as a projecting spine, distinguishes H. antioquia from H. tapichalaca (prepollex modified as a projecting spine). See Table 1 for a summary of some diagnostic characters of all species of the *Hyloscirtus larinopygion* group.

Description of holotype.—Adult male of 56.6 mm SVL (Fig. 4). Body robust. Head barely wider than long; head as wide as body; head width 37% of SVL; head length 35% of SVL. Snout rounded in dorsal view and truncate in profile (Fig. 5A,B); canthus

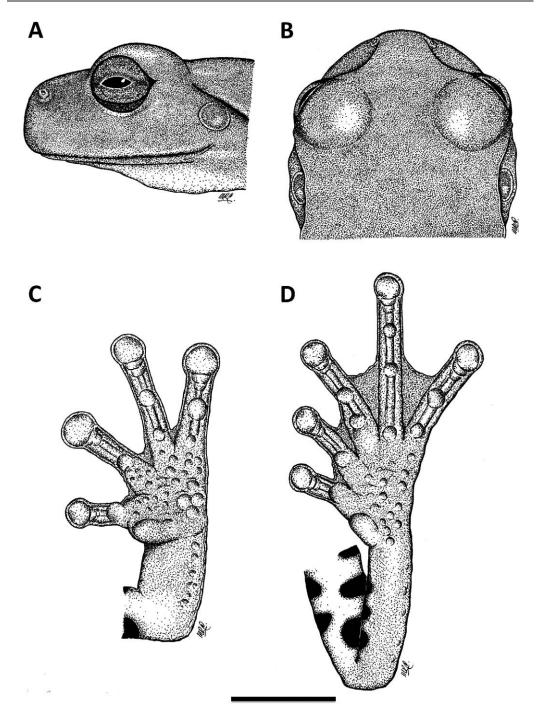


FIG. 5.—Holotype of *Hyloscirtus antioquia* sp. nov., MHUA-A 7227. (A) Head in lateral view (B) head in dorsal view; (C) left hand in ventral view; (D) left foot in ventral view. Scale bar = 10 mm.



FIG. 6.—Dorsal view of right nuptial pads in males of (A) *Hyloscirtus antioquia* (ICN 9390); (B) *H. larinopygion* (TG 2150). Scale bar = 5 mm. (A color version of this figure is available online.)

rostralis rounded, indistinct; loreal region concave; lips rounded, not flared; nostrils slightly protuberant, directed anterolaterally, slightly posterior to anterior margin of lower jaw. Internarial region and top of head flat. Interorbital distance slightly shorter than upper eyelid. Eye prominent; its diameter larger than eye-nostril distance. Tympanum and tympanic annulus visible, rounded, and inclined medially toward the longitudinal body axis, such that almost the complete tympanum is visible from above; its diameter equals 51% eye diameter. Supratympanic fold prominent, starting behind the eye and extending to the anterior margin of the insertion of the arm, slightly covering the dorsal margin of tympanum. Region between head and suprascapulae quite depressed. Vomerine teeth in two large, transverse series abutting medially, posterior to the choanae; each series is slightly S-shaped, and bears 15 teeth. Choanae small, ovoid, separated by a minimum distance larger than 3.5 times their maximum diameter. Tongue cordiform, attached overall (narrowly free around lateral and posterior margin). Vocal slits present, longitudinal, originating on the sides of the tongue and extending to the corner of the mouth. Vocal sac not evident externally, single, median, and subgular. Mental gland absent.

Forearm robust; axillary membrane absent; low ulnar tubercles present. Fingers short, thick, and bearing large, ovoid discs, with circumferential groove of each disc clearly defined by the size difference between the disc and the smaller pad; width of disc on Finger III is 13% greater than the tympanum diameter. Relative lengths of fingers: 1 < 2 < 4 < 3. Fingers with wide dermal fringes, webbed basally; webbing formula: I-II 2-3 III $2^{\frac{3}{4}}-2^{\frac{1}{2}}$ IV (Fig. 5C). Subarticular distal tubercles large, single, rounded, and conic; distal tubercles on Finger IV globular. Large supernumerary tubercle, high, and round at the base of the palm. Outer metacarpal tubercle poorly differentiated, bifid. Inner metacarpal tubercle large, thick, elliptical. Broad elliptical prepollex, not modified as a spine. Nuptial pad large, covering medial margin of prepollex and Metacarpal II; with a distal component that partially covers the dorsal surface of the finger; with dark-brown epidermal projections. Hind limbs robust;

TABLE 2.—Measurements (in mm) of the type series of Hyloscirtus antioquia sp. nov. See text for abbreviations.

Measurement	Males (n	= 20)	Females	(n = 6)
	Mean \pm SD	Range	Mean \pm SD	Range
SVL	55.7 ± 1.64	53.4-58.0	61.0 ± 2.30	58.6-63.4
HL	18.1 ± 0.66	17.0-19.8	19.2 ± 0.97	18.1 - 20.8
HW	19.4 ± 1.01	18.0-21.3	20.5 ± 0.97	18.9-22.3
ED	6.3 ± 0.56	5.3 - 7.4	6.2 ± 0.54	5.3 - 6.7
END	4.9 ± 0.52	4.2-6.3	5.1 ± 0.58	4.6 - 5.9
NSD	2.6 ± 0.17	2.2-2.9	2.7 ± 0.42	2.3 - 3.4
IND	4.7 ± 0.43	3.9-5.3	4.8 ± 0.43	4.2 - 5.2
AMD	10.7 ± 0.6	9.5-12.0	11.6 ± 0.40	10.5 - 12.3
TD	2.9 ± 0.3	2.2 - 3.5	3.2 ± 0.35	2.9 - 3.7
TL	28.2 ± 1.2	25.4 - 30.5	30.9 ± 1.17	29.5-33.0
FL	24.6 ± 1.10	22.4-26.3	27.6 ± 0.97	25.9-29.3
TFD	3.0 ± 0.36	2.5-3.7	3.5 ± 0.30	3.1 - 4.0
FTD	2.7 ± 0.32	2.3-3.2	2.9 ± 0.29	2.6-3.4

tibia length 53% of SVL; foot length 46% of SVL. Small pyramidal calcar tubercle present; tarsal fold absent; small tubercles along the outer margin of the tarsus, starting in the tibio-tarsal articulation and reaching the base of outer metatarsal tubercle. Inner metatarsal tubercle large, ovoid; outer metatarsal tubercle small, round. Toes short, with lateral fringes, bearing discs smaller than those on fingers. Relative length of toes: 1 < 2 < 3 = 5 < 4; toe webbing formula: I 2-2⁺ II 1^{1/3}-2^{1/3} III $1^{2/3}-2^{2/3}$ IV $2^{2/3}-1^{1/2}$ V (Fig. 5D). Subarticular tubercles large, round, and conical; single rows of smaller supernumerary tubercles along the axis of every toe. Cloacal opening directed posteroventrally, at midlevel of thighs; no supracloacal flap; margins of vent with numerous small folds; two large, swollen glandular areas at proximal posterior thighs; cloacal sheath short. Dorsal skin, gular region, and pectoral region smooth; flanks, belly, and proximal ventral region of thighs granular. Pectoral fold absent.

Color in life of the holotype.—Dorsal surfaces dull reddish-brown with a conspicuous reticular pattern of orange markings that become yellow toward the black flanks. Anterior and posterior surfaces of thighs and shanks black with yellow bars thinly outlined in blue. Dorsal surfaces of fingers and toes dirty-gray with some black horizontal bars; discs dark-gray dorsally and bluish-gray ventrally. Gular region brown. Ventral surfaces dirty gray in medial area; ventral surfaces of hands, feet, and webbing dirty gray. Pericloacal region grayish brown. Iris gray with burgundy reticulation.

Color in preservative of the holotype.— Dorsal surfaces brown with gray reticulated markings; flanks black with gray blotches. Anterior and posterior surfaces of thighs and shanks black with light-gray bars. Fingers and toes dirty gray with some black horizontal bars; discs dark gray dorsally. Gular region, belly, and ventral surfaces of hands, feet, webbing, and pericloacal region dirty gray.

Measurements of the holotype (in mm).— SVL 56.6; HL 19.8; HW 21.3; ED 6.7; END 4.5; NSD 2.6; IND 4.7; AMD 11.2; TD 2.8; TL 29.8; FL 26.3; TFD 3.7; FTD 3.2.

Variation and sexual dimorphism.—Measurements are given in Table 2. The number, size, and shape of lateral markings vary among individuals; hue varies as well, with some individuals almost orange. One specimen has irregular lichen-like orange markings on the dorsum (ICN 18597); whereas, some have orange vertical bars on the thighs (ICN 9384, 9390, 9392; MHUA-A 7228, 7230). Dark-gray or black markings occasionally occur on the belly (ICN 9390). Calcar tubercle more developed in some individuals (ICN 9387, 18597; MHUA-A 2647) than others. Vomerine teeth series in contact medially (ICN 9389, 9392) or with an obvious gap (ICN 9384, 9387, 9390). Number of vomerine teeth 14-18/12–20. In some individuals, the series are slightly S-shaped. The toe-webbing formula varies as follows: I $(2-2^+)-(2-2^+)$ II $(1^{1/2}-1^{1/3})$ $-(2^{1/2}-2^{1/3})$ III $(1^{1/2}-1^{2/3})-(2^{2/3}-3^{-})$ IV $(2^{2/3}-3)$ $-(\overline{1}^{1/2}-\overline{1}^{2/3})$ V. Females are larger than males (Table 2), the forearm is more slender, and secondary sexual characters (nuptial pad, vocal slits, vocal sac) are absent. The ovarian oocytes in a female (MHUA-A 5707) are unpigmented and have a diameter of 2.5–3.0 mm(n = 30).

Distribution and natural history.—The new species is known from eight localities north of the Cordillera Central of Departmento de Antioquia, Colombia (Fig. 2). Hyloscirtus antioquia inhabits cloud forests of high mountains and subpáramo, 2500-3200 m above sea level. It occurs in streams or small puddles formed by flowing water and seems to prefer small trees and Common Bamboo, *Chusquea* sp. Individuals have been observed perched <3 m high. Male acoustic activity begins at the beginning of the night and decreases toward early morning. The call consists of low-pitched notes that resemble the stridulation of crickets, and along the noise of the stream it is sometimes difficult to hear vocalizing males. Some individuals have been observed resting among bracts of Espeletia sp. and different species of terrestrial bromeliads in the forest, distant from streams. Amplexus and egg clutches remain unknown. Adults often release a bitter white secretion and strong smell; there is a change of color from reddish-brown to a gray during handling.

Remarks.—We assigned the new species to the genus *Hyloscirtus* on the basis of the wide

dermal fringes on fingers and toes (Faivovich et al., 2005), the sole adult morphological synapomorphy so far identified for the genus. There are no known morphological synapomorphies for the *Hyloscirtus larinopygion* species group, and we assign the new species tentatively to this group on the basis of its similarity with *H. larinopygion*.

Etymology.—The specific epithet is in allusion to the Departmento de Antioquia, Colombia, where this new species is distributed. Although the origin of the word *Antioquia* is unclear, it is considered by some historians to be an Amerindian word meaning "mountain of gold." This species is named after one of the most diverse regions of amphibians in the neotropics and in recognition of the Grupo Herpetológico de Antioquia for their contribution to the knowledge of the herpetofauna of the region. The name is used here as a noun in apposition.

DISCUSSION

The description of *H. antioquia* raises to 14 the number of known species in the *H. larinopygion* group. The colorful patterns of most of these frogs have historically biased the diagnoses of species toward coloration characters, and there has been little or no discussion about other morphological characters, such as nuptial pads, calcar tubercles, and swollen cloacal region.

Nuptial pads in the *H. larinopygion* group are known to occur in *H. sarampiona* (Ruiz-Carranza and Lynch, 1982), H. caucanus, H. larinopygion, H. lindae (Ardila-Robayo et al., 1993), H. staufferorum (Duellman and Coloma, 1993), H. tigrinus (Mueses-Cisneros and Anganoy-Criollo, 2008; Mueses-Cisneros and Perdomo-Castillo, 2011), H. princescharlesi (Coloma et al., 2012), H. pantostictus (MRC, personal observation), and *H. antioquia* sp. nov. (this paper). Nuptial pads have been reported to be absent in *H. pacha*, *H.* psarolaimus, H. ptychodactylus (Duellman and Hillis, 1990), H. criptico (Coloma et al., 2012), and H. tapichalaca (Kizirian et al., 2003).

A notable difference between the nuptial pads of *H. larinopygion* and *H. antioquia* is that, in the latter, the nuptial pad is covered with dark-brown epidermal projections; whereas, it is creamy white in *H. larinopygion* (Fig. 6). In both cases, the shape of the pad is similar: a medial component that expands distally and covers dorsally a portion of the digit, although the latter is notably broader in *H. antioquia* than in *H. larinopygion*. These differences are constant in 28 males of *H. antioquia* and 20 of *H. larinopygion*. Our study of five male specimens of *H. tigrinus* (including two paratypes) failed to find the nuptial pads reported by Mueses-Cisneros and Anganoy-Criollo (2008) and Mueses-Cisneros and Perdomo-Castillo (2011).

Hyloscirtus tigrinus was defined mainly based on the coloration and the presence of a well-developed, fleshy, calcar tubercle (Mueses-Cisneros and Anganoy-Criollo, 2008). This character state is present only in the holotype (adult female). The males of the type series and two additional specimens studied (including one living individual from Balsa de los Sapos, PUCE, Ecuador) have a fleshy calcar tubercle that is poorly developed (Fig. 7A). The calcar tubercle has been used in diagnoses of species in the H. larinopygion group; however, we found that this structure is polymorphic (Fig. 7B-E) and that its prominence is easily exacerbated in dehydrated individuals. Therefore, descriptions of size and shape of the calcar tubercle in species of the *H. larinopygion* group must be considered carefully.

The specific name *larinopygion* comes from the swollen cloacal region, unusual in other known neotropical hylids (Duellman, 1973). This swelling occurs because of a series of large, flat tubercles or bumps lateral and ventral to the cloacal opening. In spite of the putative uniqueness of the cloacal region in *H*. larinopygion (Duellman, 1973), and subsequent descriptions noticing the presence of glandular swellings of the cloaca, these swellings were not included in early characterizations of the *H. larinopygion* group (Duellman and Hillis, 1990; Duellman et al., 1997). This character should be properly defined, and its taxonomic distribution studied in the other species groups of *Hyloscirtus*. Interestingly, in *H. tapichalaca*, these tubercles are associated with a chevron-shaped white blotch that is conspicuous in a presumed antipredator posture (Kizirian et al.,

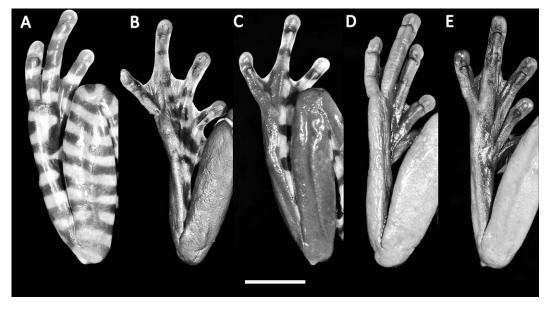


FIG. 7.—Dorsal view of left hindlimb of (A) *Hyloscirtus tigrinus* (ICN 53806); (B, C) *H. larinopygion* (TG 2150 and MRC 575); (D, E) *H. sarampiona* (JMR 2431 and JMR 2434). Note the poor development of calcar tubercle in *H. tigrinus* and variation in different individuals of *H. larinopygion* and *H. sarampiona*. Scale bar = 10 mm.

2003), which so far is unknown in other species of the group.

Mental Glands and Reproductive Biology of Hyloscirtus

Mental glands are cutaneous secretory structures apparently involved in reproductive activities such as courtship and mating, and have been previously reported in the Hyloscirtus bogotensis and H. armatus species groups (Duellman, 1972; Faivovich and De la Riva, 2006). Additionally, mental glands have been observed in other species of the tribe Cophomantini, such as the *Hypsiboas benitezi* species group (Faivovich et al., 2006), H. cinerascens and H. punctatus of the H. punctatus species group (Hoogmoed, 1979; Brunetti et al., 2012), H. heilprini (a species of the H. albopunctatus group; Trueb and Tyler, 1974), and more recently in Bokermannohyla (Faivovich et al., 2009). However, mental glands are not present in species of the Hyloscirtus larinopygion group, suggesting that this character state might have reversed in this clade. The reproductive biology of *Hyloscirtus* is largely unknown, and only a few observations are available for *H. platydactylus* (La Marca, 1985), which is part of the H.

bogotensis group. As more information becomes available, it may become possible to assess whether the absence of mental glands in the *H. larinopygion* group is related to changes in reproductive behavior in comparison with the other species groups of *Hyloscirtus*.

Wide Dermal Fringes or Thick Digits?

Faivovich et al. (2005) suggested that wide dermal fringes are a putative synapomorphy of Hyloscirtus. Coloma et al. (2012) stated that lateral fringes are absent on the fingers in H. criptico and H. princecharlesi. However, their figures 7B,C and 12B,C show the typical "thick" fingers and toes of species of Hyloscirtus, where the discs are barely wider than the digits. There seems to be little variation in Hyloscirtus in this regard (the two species of the H. armatus group being the exception; see Faivovich et al., 2005). However, for what we consider to be similar morphologies, different authors have referred to as dermal fringes (e.g., Duellman and Altig, 1978; Ruiz-Carranza and Lynch, 1982; Ardila-Robayo et al., 1993; Mueses-Cisneros and Anganoy-Criollo, 2008), explicitly mentioned their absence (Duellman and Coloma, 1993; Coloma et al., 2012), or

omitted any mention of them (Duellman, 1972, 1973; Duellman and Berger, 1982; Duellman and Hillis, 1990). Kizirian et al. (2003), for example, described the fingers of *H. tapichalaca* as lacking lateral fringes but being broad. We believe that these differences stem more from different perceptions on how fringes should be defined (see Grant et al., 2006, for extensive discussion), and different mechanical styles of descriptions, than from actual morphological differences.

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Appendix

Specimens Examined

Hyloscirtus caucanus: COLOMBIA, Cauca, Páez, Hacienda Montenegro, Km. 34.5 Belalcazar–Tacueyo, 2400 m., ICN 7071 (holotype), 7002, 7056, 7072–76, 7238, 7241–48, 7250–52, 7055, 7239, 7253.

Hyloscirtus criptico: ECUADOR, Imbabura, Cuellaje, Reserva Cotacachi–Cayapas, 2760–2885 m., QCAZ 43516–18, 43528 (paratypes).

Hyloscirtus larinopygion: COLOMBIA, Caldas, Villa Maria, Km. 7 Villa Maria–Mariquita, ICN 34433; Caldas, Pensilvania, Km. 24 Pensilvania–Arboleda, 2000 m., ICN 36518–19; Cauca, Popayan, Santa Teresa stream, 2200 m., KU 144127 (holotype); Huila, Belalcazar, Parque Nacional Natural Nevado del Huila, 2900 m., ICN 41880; Quindío, Salento, Hacienda La Caleria, 2300 m., ICN 15626–27; Risaralda, Pereira, Parque Regional Ucumarí, Las Delicias stream, 2340 m., ICN 36133–38, 34970–72; Tolima, Ibague, Juntas, El Silencio, 2600–2820 m., ICN 9380–82, 9670; Valle del Cauca, El Cairo, Las Amarillas, 2140–2200 m., ICN 28926, 28828–29, 42779; Valle del Cauca, Farallones de Cali, Campamento Corea, 2600 m., ICN 13595. ECUADOR, Carchi, Espejo, Morán, 2452 m., QCAZ 41826.

Hyloscirtus lindae: ECUADOR, Napo, Papallacta, 2.660 m., KU 164402 (holotype), 155476 (paratype); Pacto Sumaco, Parque Nacional Sumaco, Refugio La Laguna, 2476–2775 m., QCAZ 41232, 41294–98, 45345–47.

Hyloscirtus pacha: ECUADOR, Morona Santiago, Plan de Milagro, 2350 m., KU 202762 (holotype); Plan de Milagro, Km. 8 Plan de Milagro–Cuenca, 2150–2300 m., QCAZ 48237–41.

Hyloscirtus pantostictus: ECUADOR, Sucumbios, Km. 5 Santa Bárbara–La Bonita, 2650 m., KU 190000 (holotype); Santa Barbara, 2590–2800 m., QCAZ 10488,11660–67, 12171, 12174, 14084, 30529–31, 38421, 40331, 41393, 41412, 42350, 45434–38, 45443–44, 45446, 45450–53.

Hyloscirtus princecharlesi: ECUADOR, Imbabura, Cuellaje, Reserva Cotacachi–Cayapas, 2720–2794 m., QCAZ 43654, 44893 (paratypes).

Hyloscirtus psarolaimus: ECUADOR, Napo Papallacta, Km. 11 Papallacta–Baeza, 2660 m., KU 164313 (holotype), QCAZ 13252, 23070; Carchi, Tulcán–Santa Bárbara road, QCAZ 15366; Morona Santiago, San Vicente, Parque Nacional Sangay, 15 Km. to road Lagunas de Atillo, 2815 m., QCAZ 31671; Sucumbios, La Sofía, Campamento Río Verde, 2726 m., DHMECN 6493–94.

Hyloscirtus ptychodactylus: ECUADOR, Cotopaxi, Pilalo, 2320 m., KU 209780 (holotype).

Hyloscirtus sarampiona: COLOMBIA, Cauca, Parque Nacional Natural Munchique, Sopladero stream, 33 Km., 2190 m., ICN 7440 (holotype), 7441 (paratype).

Hyloscirtus staufferorum: ECUADOR, Napo, 27 Km. N Jondachi, 2040 m., KU 217695 (holotype); Pacto Sumaco, Lago Sumaco, 2500 m., QCAZ 3701–03; Pastaza, Santa Clara, Puyo–Tena road, Comunidad San Rafael– Chonta Yaku, 2250 m., QCAZ 45962–63, 45965–67.

Hyloscirtus tapichalaca: ECUADOR, Zamora Chinchipe, Reserva Tapichalaca, 2667 m., QCAZ 15083–85, 16704–06, 17776–77 (paratypes).

Hyloscirtus tigrinus: COLOMBIA, Nariño, Pasto, El Encano, Reserva Natural Privada Castelví, 3060 m., ICN 53804 (holotype), ICN 53805–06 (paratypes).