A new red-eyed of stream treefrog of *Hyloscirtus* (Anura: Hylidae) from Peru, with comments on the taxonomy of the genus

MAURICIO RIVERA-CORREA\textsuperscript{1,4,5}, KARLA GARCÍA-BURNEO\textsuperscript{2} & TARAN GRANT\textsuperscript{3}

\textsuperscript{1}Laboratório de Sistemática de Vertebrados, Faculdade de Biociências, Pontifícia Universidade Católica do Rio Grande do Sul, Av. Ipiranga 6681, 90619-900, Porto Alegre, RS, Brazil

\textsuperscript{2}División de Herpetología, Centro de Ornitología y Biodiversidad (CORBIDI), Santa Rita 117, Huertos de San Antonio, Surco, Lima, Peru

\textsuperscript{3}Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, 05508-090 São Paulo, SP, Brazil

\textsuperscript{4}Current address: Grupo Herpetológico de Antioquia, Instituto de Biología, Universidad de Antioquia, Medellín, Colombia

\textsuperscript{5}Corresponding author. E-mail: mauriciorivera79@gmail.com

Abstract

We describe a remarkable new species of monophyletic genus *Hyloscirtus* from northeastern Peru. The presence of an enlarged, curved, and protruding prepollical spine; hypertrophied forelimbs; large, thick supracloacal flap and supratympanic fold; large size; nuptial pad absent and iris dark red diagnose this species. We hypothesize that the new species is closely related to *H. condor* and *H. tapichalaca* of southern Ecuador due to the apparently synapomorphic occurrence in these species of an enlarged, curved prepollical spine, and small, conical vomerine odontophore processes with 3–6 prominent teeth each without contact between these. Additional research explicitly incorporating *H. diabolus* new species in a phylogenetic analysis is required to further test our hypothesis and provide a better understanding of the evolution of morphological attributes described herein. Finally we discuss some aspects concerning the taxonomy of the genus *Hyloscirtus*.

Key words: Andes Mountains, Hylidae, *Hyloscirtus larinopygion* species group, morphology, systematics, taxonomy

Introduction

Recent contributions (Faivovich \textit{et al.} 2005; Coloma \textit{et al.} 2012; Rivera-Correa and Faivovich 2013; Almendáriz \textit{et al.} 2014; Guayasamin \textit{et al.} 2015) significant increased knowledge of the diversity, taxonomy, and phylogeny of the Neotropical genus *Hyloscirtus* Peters 1882, a monophyletic group with remarkable morphological variation and whose species are confined strictly to Andean creeks and streams (Faivovich \textit{et al.} 2005; Coloma \textit{et al.} 2012; Guayasamin \textit{et al.} 2015). Among species of *Hyloscirtus*, the occurrence of an enlarged, curved prepollical spine is extremely rare. Until not long ago, *H. tapichalaca* (Kizirian \textit{et al.} 2003) was the only species of the genus to exhibit this morphology. Recently, Almendáriz \textit{et al.} (2014) also reported this morphology in *H. condor* Almendáriz \textit{et al.} 2014, and to date these are the only two species known to possess it. Another striking attribute shared by these two species and the species of the *H. armatus* species group are conspicuously hypertrophied forelimbs in adult males (see Duellman \textit{et al.} 1997). In this paper we describe the third species of the *H. larinopygion* species group with a prepollical spine and hypertrophied forelimbs from remote localities in northeastern Peru. We also discuss some aspects of the morphology of these species and its systematic implications for the *H. larinopygion* species group and some aspects concerning the taxonomy of the genus *Hyloscirtus*.

Materials and methods

Specimens were fixed in 10% formalin and stored in 70% ethanol. All measurements were taken with digital calipers with the aid of a dissecting microscope and rounded to the nearest 0.1 mm. Measurements are those established by Duellman (1970) and Heyer \textit{et al.} (1990) and modified by Rivera-Correa and Faivovich (2013).
Abbreviations are SVL (snout–vent length), HL (head length), HW (head width), ED (eye diameter), END (nostril–eye distance), NSD (nostril–tip-of-snout distance), IND (inter–nostril distance), AMD (distance between the anterior margins of eyes), TD (tympanum diameter), FAL (forearm length), FAB (forearm breadth), HAL (hand length), THL (thigh length), TL (tibia length), TAL (tarsus length), FL (foot length), TFD (considering the diameter of the disc of Finger III), and FTD (considering the diameter of the disc of Toe IV). Webbing formulae follow the terminology of Savage and Heyer (1967), as modified by Myers and Duellman (1982). Sex was determined by examination of secondary sexual characters (prepollical spine, vocal slits, expanded vocal sac). Color pattern in life was described from color photos. Illustrations were made using a Zeiss stereomicroscope with a drawing tube. Information on other species was obtained from preserved specimens (listed in Appendix I), field notes, photographs of living specimens, and the literature. Institutional abbreviations used throughout this paper are CORBIDI (División de Herpetología, Centro de Ornitología y Biodiversidad), MUSA (Museo de Historia Natural de la Universidad Nacional de San Agustín, Arequipa, Perú), 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 diabolus** sp. nov. (Figs. 1–3)

**Holotype.** CORBIDI 12885, adult male, Peru, Departamento de Amazonas, Provincia de Chachapoyas, Distrito La Jalca, km 10 from La Colpa–Rodríguez de Mendoza (-6.398944, -77.226278, 2300 m a.s.l.) Collected 14 November 2012 by Karla García-Burneo.

**Paratype.** MUSA 3864, adult male, Peru, Departamento de Amazonas, Provincia de Pedro Ruiz Gallo, Comunidad Shipasbama (-5.845833, -78.071944, 2180 m a.s.l.). Collected on 18 September 2011 by Roy Santa Cruz Farfán.

**Diagnosis.** *Hyloscirtus diabolus* (Fig. 1) can be diagnosed by the following characters: large size (SVL 82.3–89.2 mm, n = 2); vertical keel in the snout and upper lip cleft in the region of the premaxilla; vomerine odontophores with a conical-shape and a gap medially, each process with two or three prominent teeth; large, thick, supracloacal flap and supratympanic fold present; finger webbing formula: I 2½–2½ II 12/3–22/3 III 2½–2 IV, toe webbing formula: I 1½–2 II 1–2 III 1½–2½ IV 2½–1 V; nuptial pad absent; hypertrophied forelimbs and enlarged, curved and protruding spine prepollex present; fleshy calcar tubercle present; dorsum, thighs, shanks, finger, toes and discs brown with abundant tiny yellow marks; iris dark red without reticulation.

**Comparison.** The only species of the *H. larinopygion* species group with hypertrophied forelimbs in adult males and broad elliptical prepollex, modified as a projective spine, are *H. tapichalaca* (Kizirian et al. 2003), *H. condor* Almendáriz et al. 2014, and *H. diabolus*. The remaining species of the group lack the hypertrophied forelimbs and their prepollex is trapezoidal (Kizirian et al. 2003; Rivera-Correa and Faivovich 2013; Table 1). *Hyloscirtus diabolus* differs from *H. condor* by having a strongly well developed, fleshy, heel tubercle (absent in *H. condor*), dark red iris (iris golden with fine tan reticulations in *H. condor*), gular region and belly dark reddish gray with pink marks in preservation (belly olive without marks and chest is light gray in *H. condor*), vertical keel in the snout and upper lip cleft in the region of the premaxilla (absent in *H. condor*) and greater adult male SVL (*H. condor*: 64.8–73.8 mm, n = 7 in). The new species differs from *H. tapichalaca* in dorsal and lateral color pattern: dorsum gray or brown, flanks gray brown, bearing pink-orange marks more conspicuous in axillary and inguinal regions, lateral and lower margin of cloaca, knee, elbow, and outer margin of forearm white in *H. tapichalaca*; and ventral color pattern: gular region and belly dark reddish gray with pink marks in preservation to *H. diabolus* (belly gray-blue and chest is light gray in *H. diabolus*), vertical keel in the snout and upper lip cleft in the region of the premaxilla (absent in *H. condor*) and greater adult male SVL (*H. condor*: 64.8–73.8 mm, n = 7 in). The new species differs from *H. tapichalaca* in dorsal and lateral color pattern: dorsum gray or brown, flanks gray brown, bearing pink-orange marks more conspicuous in axillary and inguinal regions, lateral and lower margin of cloaca, knee, elbow, and outer margin of forearm white in *H. tapichalaca*; and ventral color pattern: gular region and belly dark reddish gray with pink marks in preservation to *H. diabolus* (belly gray-blue and chest is light gray in *H. tapichalaca*), digital discs brown (digital discs white in *H. tapichalaca*), iris dark red (iris yellow-gold with fine black reticulations in *H. tapichalaca*), upper lip cleft in the region of the premaxilla (absent in *H. tapichalaca*) and greater adult male SVL (*H. tapichalaca*: 59.1–63.8 mm, n = 8). For a summary of others diagnostic characters of the *H. larinopygion* species group, see Table 1.
TABLE 1. Comparison of some diagnostic characters in species of the *Hyloscirtus larinopygion* group. Sources: (1) Almendáriz et al. 2014; (2) Ardila-Robayo et al. (1993); (3) Coloma et al. (2012); (4) Duellman (1973); (5) Duellman and Altig (1978); (6) Duellman and Berger (1982); (7) Duellman and Hillis (1990); (8) Duellman and Coloma (1993); (9) Kizirian et al. (2003); (10) Mueses-Cisneros and Anganoy-Criollo (2008); (11) Mueses-Cisneros and Perdomo-Castillo (2011); (12) Ruiz-Carranza and Lynch (1982); (*) this study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Dorsal pattern</th>
<th>Forelimbs</th>
<th>Iris color</th>
<th>Vomerine teeth</th>
<th>Nuptial pad</th>
<th>Prepollex</th>
<th>Calcar tubercle</th>
<th>Source</th>
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<tbody>
<tr>
<td><em>H. antioquia</em></td>
<td>Reddish brown; with or without scattered orange blotches</td>
<td>No hypertrophied</td>
<td>Gray with burgundy reticulations</td>
<td>In contact or not, 12–20 teeth/each</td>
<td>Medial and distal component; dark brown epidermal projections</td>
<td>Trapezoidal</td>
<td>Present</td>
<td>* (2)</td>
</tr>
<tr>
<td><em>H. caucanus</em></td>
<td>Brown or reddish brown with dark brown scattered blotches; with or without middorsal stripe</td>
<td>No hypertrophied</td>
<td>Pale yellow with brown reticulations</td>
<td>In contact, 10–14 teeth/each</td>
<td>Distal component only; creamy white</td>
<td>Trapezoidal</td>
<td>Present or Absent</td>
<td>* (2)</td>
</tr>
<tr>
<td><em>H. condor</em></td>
<td>Light brown with abundant yellow marks</td>
<td>Hypertrophied</td>
<td>Golden with minute reticulations</td>
<td>No contact, 3–4 teeth/each</td>
<td>Absent</td>
<td>Spine</td>
<td>Absent</td>
<td>(1)</td>
</tr>
<tr>
<td><em>H. criptico</em></td>
<td>Grayish brown, densely stippled with minute cream flecks and bright orange blotches</td>
<td>No hypertrophied</td>
<td>Dark gray</td>
<td>In contact or not, 8–15 teeth/each</td>
<td>Absent</td>
<td>Trapezoidal</td>
<td>Present</td>
<td>* (3)</td>
</tr>
<tr>
<td><em>H. diabolus</em></td>
<td>Brown with abundant yellow marks</td>
<td>Hypertrophied</td>
<td>Dark red, without reticulations</td>
<td>No contact, 2–3 teeth/each</td>
<td>Absent</td>
<td>Spine</td>
<td>Present</td>
<td>*</td>
</tr>
<tr>
<td><em>H. larinopygion</em></td>
<td>Light brown to dark brown; with or without dark brown reticulation</td>
<td>No hypertrophied</td>
<td>Golden or silver with black reticulations</td>
<td>In contact or not, 8–15 teeth/each</td>
<td>Medial and distal component; creamy white</td>
<td>Trapezoidal</td>
<td>Present or Absent</td>
<td>* (4)</td>
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<tr>
<td><em>H. lindae</em></td>
<td>Dark metallic brown</td>
<td>No hypertrophied</td>
<td>Dull bluish gray with minute black flecks</td>
<td>In contact, 11–13 teeth/each</td>
<td>Distal component; creamy white</td>
<td>Trapezoidal</td>
<td>Present</td>
<td>* (3, 5)</td>
</tr>
<tr>
<td><em>H. pacha</em></td>
<td>Dark brown with metallic orange flecks</td>
<td>No hypertrophied</td>
<td>Olive brown</td>
<td>In contact, 11–15 teeth/each</td>
<td>Absent</td>
<td>Trapezoidal</td>
<td>Present</td>
<td>* (3, 7)</td>
</tr>
<tr>
<td><em>H. pantostictus</em></td>
<td>Olive-brown with small orange spots</td>
<td>No hypertrophied</td>
<td>Dark gray</td>
<td>In contact or not, 10–14 teeth/each</td>
<td>Medial and distal component, light brown epidermal projections</td>
<td>Trapezoidal</td>
<td>Present or Absent</td>
<td>* (3, 5)</td>
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<tr>
<td><em>H. princecharlesi</em></td>
<td>Black with many round-oval orange blotches</td>
<td>No hypertrophied</td>
<td>Dark gray</td>
<td>In contact or not, 11–15 teeth/each</td>
<td>Medial and distal component; creamy white</td>
<td>Absent</td>
<td>*</td>
<td>(3)</td>
</tr>
<tr>
<td><em>H. psarolaimus</em></td>
<td>Grayish brown with dark brown and minute cream flecks; with or without middorsal stripe</td>
<td>No hypertrophied</td>
<td>Dull bronze with black reticulation</td>
<td>In contact, 10–18 teeth/each</td>
<td>Absent</td>
<td>Trapezoidal</td>
<td>Present *</td>
<td>(3, 7)</td>
</tr>
<tr>
<td><em>H. ptychodactylus</em></td>
<td>Orange-tan to reddish brown with minute orange-tan flecks enclosed in black markings; with or without middorsal stripe</td>
<td>No hypertrophied</td>
<td>Pale blue</td>
<td>In contact, 11–15 teeth/each</td>
<td>Absent</td>
<td>Trapezoidal</td>
<td>Present *</td>
<td>(3, 7)</td>
</tr>
<tr>
<td><em>H. sarampiona</em></td>
<td>Pale olive with orange spots</td>
<td>No hypertrophied</td>
<td>Gold with thin black reticulation</td>
<td>In contact or not, 8–16 teeth/each</td>
<td>Medial and distal component; dark brown epidermal projections</td>
<td>Trapezoidal</td>
<td>Present or Absent</td>
<td>(12)</td>
</tr>
<tr>
<td><em>H. staufferorum</em></td>
<td>Uniform dark brown</td>
<td>No hypertrophied</td>
<td>Metallic brown</td>
<td>In contact, 16–25 teeth/each</td>
<td>Creamy white</td>
<td>Present</td>
<td>*</td>
<td>(3, 8)</td>
</tr>
<tr>
<td><em>H. tapichalaca</em></td>
<td>Gray or dark brown</td>
<td>Hypertrophied</td>
<td>Yellow-gold with black reticulation</td>
<td>No contact, 4–6 teeth/each</td>
<td>Absent</td>
<td>Spine</td>
<td>Present *</td>
<td>(9)</td>
</tr>
<tr>
<td><em>H. tigrinus</em></td>
<td>Yellow-green or yellowish brown with transverse black stripes; sometimes reticulated; with or without middorsal stripe</td>
<td>No hypertrophied</td>
<td>Light gray or yellow with black reticulation</td>
<td>In contact, 10–15 teeth/each</td>
<td>Absent</td>
<td>Trapezoidal</td>
<td>Present *</td>
<td>(10, 11)</td>
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Description of holotype. Adult male, 82.3 mm SVL (Fig. 2). Body robust. Head 13% wider than long; head as wide as body; head width 35% of SVL; head length 27% of SVL. Snout rounded in dorsal view, truncate in profile (Fig. 3A–B); canthus rostralis rounded, distinct; loreal region weakly concave, nearly vertical; lips rounded, faintly flared; nostrils slightly protuberant, directed anterolaterally, located at level of anterior margin of lower jaw. Vertical keel on snout and upper lip cleft in region of premaxilla. Dorsal surface of internarial region concave. Interorbital distance slightly greater than upper eyelid width. Eye prominent, diameter greater than eye–nostril distance. Tympanum barely visible, round, positioned vertically such that is not visible from above; diameter 51% of eye diameter; tympanic annulus inconspicuous. Supratympanic fold prominent, extending from posterior to eye to posterior margin of arm insertion, slightly covering dorsal edge of tympanic membrane. Region between head and suprascapula depressed. Vomerine odontophores conical, separated by gap medially, positioned posterior to choanae; each process with 2–3 prominent teeth. Choanae small, ovoid, separated by a minimum distance greater than 3.5 times their maximum diameter. Tongue cordiform, barely free around lateral and posterior margin. Vocal slits longitudinal, originating on lateral to tongue and extending extending to the corner of the mouth. Vocal sac evident externally, large, single, median, subgular. Mental gland absent.

Upper arms and forearms hypertrophied; axillary membrane absent; ulnar fold and tubercles absent. Fingers short, thick, bearing large, ovoid discs, circumferential groove of each disc clearly defined; width of disc on Finger
III 46% greater than tympanum diameter. Relative lengths of fingers I < II < IV < III.; webbing formula: I – II 1²⁄₃ – 2²⁄₃ III 2²⁄₃ – 2 IV (Fig. 3C). Distal and proximal subarticular tubercles large, single, rounded, conical; distal tubercles on Finger IV globular. Palmar surfaces with deep folds. Large supernumerary tubercles, high and round, distributed over base of fingers. Outer metacarpal tubercle diffuse. Inner metacarpal tubercle large, its shape contouring underlying distal prepollex that is modified into an enlarged, protruding spine. Nuptial pad absent. Hind limbs robust; tibia length 50% of SVL; foot length 47% of SVL. Calcar tubercle large, fleshy; tarsal fold or tubercles absent; metatarsal fold thick. Inner metatarsal tubercle large, ovoid; outer metatarsal tubercle small, round. Toes short, lateral fringes absent, discs smaller than those of fingers, slightly wider than digit. Relative length of toes: I < II < V < III < IV; toe webbing formula: I 1¹⁄₂ – 2 II 1 – 2 III 1¹⁄₂ – 2³⁄₄ IV 2¹⁄₂ – 1 V (Fig. 3D). Subarticular tubercles large, round, conical; single row of smaller supernumerary tubercles along axis of each toe. Cloacal opening directed posteriorly at upper level of thighs; supracloacal flap large, thick; margins of vent with numerous small folds; cloacal sheath short. Dorsal skin, gular region, pectoral region and flanks smooth; belly and proximal ventral region of thighs granular.

**FIGURE 2.** Dorsal and ventral views (in preservative) of the holotype of *Hyloscirtus diabolus* sp. nov. (CORBIDI 12885; adult male, 82.3 mm SVL).

**Color of holotype in life.** Dorsum, flanks, anterior and posterior surfaces of thighs and shanks, calcar tubercle, dorsal surfaces of fingers and toes brown with an abundant tiny yellow marks; discs dark bluish gray ventrally. Gular region and ventral surfaces dirty gray with an abundant small yellow flecks and spots; ventral surfaces of hands, feet, and webbing dirty gray. Pericloacal region light gray. Iris solid dark red, without reticulations.

**Color of holotype in preservative.** Dorsum, flanks, anterior and posterior surfaces of thighs and shanks, dorsal surfaces of fingers and toes dark gray with an abundant light gray marks. Gular region and belly, ventral surfaces of thighs and shanks dark reddish gray with pink flecks and spots; hands, feet, webbing, and pericloacal region dirty gray.

**Measurements of holotype (in mm).** SVL 82.3; HL 22.4; HW 28.5; ED 9.0; END 5.7; NSD 3.7; IND 5.8; AMD 12.1; TD 2.7; FAL 14.3; FAB 12.0; HAL 29.7; THL 39.8; TL 41.0; TAL 22.0; FL 38.7; TFD 5.0; FTD 3.8.

**Variation.** The paratype MUSA 3864 (SVL = 89.2 mm) is remarkably larger than the holotype, possesses fewer yellow flecks and spots on the dorsum but more conspicuous on the loreal region, digits, flanks, thighs (Fig. 4), and belly in life. Foot webbing is more extensive: I 2 – 2³⁄₄ II 1²⁄₃ – 2³⁄₄ III 2 – 2 IV and I 1 – 1 ¹⁄₂ II 1 – 2 III 1¹⁄₃ – 2 IV 2 – 1 V. Other measurements of the paratype are: HL 23.9; HW 28.7; ED 8.8; END 6.0; NSD 3.9; IND 5.8; AMD 12.8; TD 2.7; FAL 14.3; FAB 11.8; HAL 30.5; THL 40.7; TL 44.0; TAL 25.6; FL 42.4; TFD 5.9; FTD 4.8.

**Distribution and natural history.** *Hyloscirtus diabolus* is currently known only from two localities approximately 100 km straight-line distance apart in the highlands on the eastern flank of the Cordillera Central,
northern Peruvian Andes (Fig. 5). The two known individuals were found in dense cloud forest adjacent to very rocky streams with strong flow and 30–35° slope. The specimens were collected while calling at night, perched on tree branches ca. 1.80 m above the ground and ca. 2 m from the edge of the stream. When handled, they clung tightly to the substrate, acquired a position with the head directed toward the belly and limbs pressed to the abdomen, and secreted a white, viscous, sticky, liquid over the entire body. Advertisement calls, reproductive biology, and tadpoles are unknown. No other anuran species was found syntopically with *H. diabolus*.

**Etymology.** The specific epithet *diabolus* is Latin for devil and is used as a noun in apposition. The devil according to Christianity is the spirit of evil and enemy of God, often represented as the ruler of hell and depicted as a human figure with horns, cloven hoofs, fire-red eyes, trident, and tail. The species name is in allusion to the hypertrophied forelimbs, enlarged prepollex with a projecting spine, trident vomers, and dark red iris in life.

**FIGURE 3.** *Hyloscirtus diabolus* sp. nov. (CORBIDI 12885, holotype). (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.
FIGURE 4. *Hyloscirtus diabolus* sp. nov. in life (MUSA 3864, paratype, adult male, 89.2 mm SVL). Note the dark marks (scars) in the anterior region of dorsum, which are consistent with the occurrence of male combat (see text). Photo: R. Santa Cruz.

FIGURE 5. Geographic distribution of *Hyloscirtus diabolus* sp. nov. (holotype locality, star; paratype locality, dot), *H. condor* (triangle), and *H. tapichalaca* (square).
FIGURE 6. Ventral view of left hands in males of some species of the *Hyloscirtus larinopygion* species group, showing morphological diversity in the group. (A) *H. princecharlesi* (QCAZ 44893); (B) *H. lindae* (QCAZ 41298); (C) *H. tapichalaca* (QCAZ 17776); (D) *H. diabolus* (CORBIDI 12885). Scale bar = 5 mm. Photos: M. Rivera-Correa.

Discussion

A noteworthy difference between the new species, *H. condor*, and *H. tapichalaca* and all other species of the *H. larinopygion* species group is the morphology of the prepollex. Most species of the *H. larinopygion* species group possess an enlarged, broad, elliptical prepollex (Duellman and Hillis, 1990; Faivovich *et al.* 2005; Figs. 6A–B), whereas in these three species it is modified into an enlarged protruding spine (Kizirian *et al.* 2003; Almendáriz *et
Although in most anurs the prepollical spine has not been associated with any behavior, in some treefrogs—particularly large species such as Hypsiboas faber, H. pardalis, and H. rosenbergi (Lutz 1960; Lutz 1973; Kluge 1981; Martins and Haddad 1988; Martins et al. 1998)—it is related to territoriality and combat whereby the prepollical spine is used to slash opponents during prolonged wrestling bouts (Wells 2007), sometimes resulting in fatal injuries (Kluge 1981). Two specimens of H. tapichalaca (both paratypes), have scars that might have resulted from combat (Kizirian et al. 2003). One of the two known males of H. diabolus also possesses scars in the dorsum (MUSA 3864); although they differ from the scars observed in H. tapichalaca, they might also owe to male-male combat. Nevertheless, additional field observations are needed to understand the functional and behavioral significance of this morphological structure in H. diabolus.

Although H. diabolus has yet to be included in a phylogenetic analysis, several lines of evidence lead us to hypothesize a close relationship with H. condor and H. tapichalaca. These three species share some character states, absent in the other species of the H. larinopygion species group: curved prepollical spine, markedly hypertrophied forelimbs (also present in the H. armatus species group) and small, conical vomerine odontophore processes with 3–6 prominent teeth each and never in contact between them (Kizirian et al. 2003; Almendáriz et al. 2014; this study). Additional research explicitly incorporating H. diabolus in a phylogenetic analysis is required to further test our hypothesis and provide a better understanding of the evolution of these morphological characters.

On the taxonomy of Hyloscirtus. In their monumental study of the systematics of Hylidae, Faivovich et al. (2005) resurrected Hyloscirtus from synonymy with Hyla, where it had been placed 35 years earlier by Duellman (1970). Subsequent studies have consistently corroborated the monophyly of the genus and have contributed additional molecular and morphological evidence for its recognition (Sánchez, 2010; Wiens et al., 2010; Pyron and Wiens, 2011; Faivovich et al. 2013; Guayasamin et al. 2015). With the description of H. diabolus, Hyloscirtus now comprises 36 species divided among the H. armatus (3 species), H. bogotensis (17 species), and H. larinopygion (16 species, including H. diabolus) species groups, with additional known species awaiting formal description.

Given the size of the clade and its morphological diversity and widespread geographic distribution, it might seem that the time has come to formally recognize the three groups as either full genera or subgenera. However, the apparently strong support for the recognition of these species groups reported in molecular studies is illusory due to limited taxon sampling. This is especially true of the H. bogotensis group, of which only seven named species were included in the most recent and largest molecular phylogenetic analysis of the genus (Guayasamin et al., 2015). Faivovich et al. (2005) referred species that lacked molecular data to the group on the basis of the synapomorphic occurrence of a mental gland in adult males (Duellman, 1972); however, it was recently shown that the mental gland arose in the common ancestor of the more inclusive clade Cophomantini (Brunetti et al. 2015; see also Faivovich and De la Riva, 2006). Consequently, the occurrence of a mental gland in adult males of Hyloscirtus is symplesiomorphic and there is no evidential basis to refer the 10 species (60% of the group) that lack molecular data to the H. bogotensis group. Similarly, although molecular data are available for a greater proportion of species of the H. larinopygion group (12 of the 16 named species), no morphological synapomorphies have been identified to assign the remaining species. As such, formal recognition of the existing species groups would entail a large number of species being either excluded from the newly recognized genera and treated as incertae sedis or included on the basis of something other than synapomorphy (e.g., symplesiomorphy, character-states of unknown polarity, impressions of overall similarity, geographic distribution), either of which would be a major step backwards in hylid taxonomy. Given that Hyloscirtus monophyly is not in question, we believe understanding of these frogs is better advanced by focusing efforts on gathering new evidence of relationships than by rushing new names to press in the absence of synapomorphy.

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Hyloscirtus antioquia: COLOMBIA, Antioquia, Bello, San Félix, Serranía Las Baldías, Corregimiento de San Félix, Vereda Las Huertas, Quebrada El Hato, 2660 m, Km 5 San Félix road—Truchera San Félix, MUHA-A 7227 (holotype), 7228–29 (paratypes)

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 condor: ECUADOR, Zamora Chinchipe, Cantón Nangaritza, Parroquia Nuevo Paraíso, Reserva Biológica Cerro Plateado, 2317 m, EPN 14758 (holotype), EPN 14754, 14755, 14756, 14757, 14759, 14760 (paratypes).

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

Hyloscirtus larinopygion: COLOMBIA, Caldas, Villamaría, Km 7 Villamaría–Mariquita, ICN 34433; Caldas, Pensilvania, Km 24 Pensilvania–Arboleda, 2000 m, ICN 36518–19; Cauca, Popayán, Santa Teresa stream, 2200 m, KU 144127 (holotype); Huila, Belalcazar, Parque Nacional Natural Nevado del Huila, 2900 m, ICN 41880; Quindío, Salento, Hacienda La Galería, 2300 m, ICN 15626–27; Risaralda, Pereira, Parque Regional Ucumarí, Las Delicias stream, 2340 m, ICN 41826.

Hyloscirtus lindae: ECUADOR, Napo, Papallacta, 2660 m, KU 164402 (holotype), 155476 (paratype); Pacto Sumaco, Parque Regional Ucumarí, Las Delicias stream, 2340 m, KU 144127 (holotype), 7002, 7056, 7072–76, 7238, 7241–48, 7250–52, 7055, 7239, 7253.

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; Sucumbíos, La Sofía, Campamento Río Verde, 2726 m., DHMENC 6493–94.

Hyloscirtus psychodactus: ECUADOR, Cotopaxi, Pilaló, 2320 m., KU 209780 (holotype).

Hyloscirtus sarampona: 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).