



## A new Harlequin Toad from the Cordillera Oriental of the Colombian Andes (*Bufo*idae: *Atelopus*)

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**Abstract.** Both the Cordillera Central and Cordillera Oriental harbor much of Colombia's Harlequin Toad (*Atelopus*) diversity, with twelve species described from each of these mountain ranges. Most of them are poorly studied and several species are known from a few localities or a single locality only. No Harlequin Toads have been documented in about 200 km in the southern portion of the Cordillera Oriental. We examined historic material from Parque Nacional Natural Cueva de los Guácharos, department of Huila, that has not been considered previously and cannot be assigned to any available name. Although only a single specimen is known, we here describe this *Atelopus* from the southern Cordillera Oriental as a species new to science, as it is readily distinguished from all congeners by a combination of morphological characters (e.g., size, snout profile, webbing, supratympanic crests, skin texture and coloration). Our work provides yet another example of forensic taxonomy and underlines the need for further examination of the Harlequin Toads from the Andes of Colombia in an integrative taxonomic framework.

Key words. Amphibia, Anura, *Atelopus guacharo* sp. n., morphology, osteology, systematics, taxonomy.

**Resumen.** La Cordillera Central y la Cordillera Oriental albergan gran parte de la diversidad de sapos arlequines (*Atelopus*) de Colombia, con doce especies descritas en cada una de las dos. Sin embargo, no se ha documentado ningún sapo arlequín en 200 km de la parte sur de la Cordillera Oriental hasta su confluencia con la Cordillera Central. La mayoría de los sapos arlequines de la Cordillera Central y la Cordillera Oriental han sido poco estudiados y varias especies se conocen de unas pocas localidades o de una sola. Examinamos recientemente material histórico del Parque Nacional Natural Cueva de los Guácharos, departamento del Huila, que no había sido considerado previamente y no pudimos asignarlo a ninguno de las especies conocidas. Aunque sólo se dispone de un ejemplar, aquí describimos ese *Atelopus* del sur de la Cordillera Oriental como una especie nueva para la ciencia, ya que se distingue fácilmente de todos los congéneres por una combinación de caracteres morfológicos (ej. tamaño, perfil del hocico, membranas interdigitales, crestas supratimpánicas, textura de la piel y coloración). Nuestro trabajo proporciona otro ejemplo de taxonomía forense y subraya la necesidad de examinar más a fondo los sapos arlequines de los Andes de Colombia en un marco taxonómico integrador.

Palabras clave. Amphibia, Anura, *Atelopus guacharo* sp. n., morfología, osteología, sistemática, taxonomía.

### Introduction

With 103 species known, Neotropical Harlequin Toads of the genus *Atelopus* comprise the most species-rich bufonid genus. The diversity of this endemism-rich group peaks in the Andean cloud forests and paramos of Colombia and Ecuador (LÖTTERS 1996, RUEDA-ALMONACID et al. 2005,

LÖTTERS et al. 2023, 2025). Systematics of Harlequin Toads remain poorly understood (VELÁSQUEZ-TRUJILLO et al. 2024) and shedding light on *Atelopus* taxonomy is especially hampered by the unparalleled declines and extinctions that have hit the genus since the late 1980s. Most upland populations have been lost, with the persisting species being in urgent need of conservation action (LA MARCA et

al. 2005, LÖTTERS et al. 2023). As a result, several Harlequin Toads are only known from a few specimens and a single locality, partly resulting in an underestimation of *Atelopus* diversity (LÖTTERS et al. 2023, 2025).

The problem here is that undescribed species generally remain ‘invisible’ to practitioners and decision-makers (VELÁSQUEZ-TRUJILLO et al. 2024, LÖTTERS et al. 2025), which impedes urgent conservation action (DE MAGALHÃES et al. 2018). It is of critical importance to resolve the taxonomy of unstudied amphibians that may be close to extinction and are therefore hard to find, so that names can be coined for them where needed. The dilemma here is that taxonomic decisions are best being made in an integrative taxonomic approach, in anurans including information on larval stages and bioacoustics, combined with adult external and internal morphological as well as molecular phylogenetic data (cf. PADIAL et al. 2010). However, for many *Atelopus* such information is not available (LÖTTERS et al. 2025) and taxonomy is forensic rather than integrative (cf. MENDELSON & MULCAHY 2010, VELÁSQUEZ-TRUJILLO et al. 2024). As it remains a challenge to obtain molecular genetic information from old, fluid-preserved museum material (e.g. SCHERZ et al. 2020), forensic taxonomy is often left with external and internal morphology.

Twelve taxa are currently recognized from the central and northern parts of the Cordillera Oriental in Colombia (Fig. 1): *Atelopus minutulus* RUÍZ-CARRANZA, HERNÁNDEZ-CAMACHO & ARDILA ROBAYO, 1988 and *A. petriruizi* ARDILA-ROBAYO, 1999 from lower-elevation forests on the Amazonian versant; *A. farci* LYNCH, 1993, *A. mittermeieri* ACOSTA-GALVIS, RUEDA-ALMONACID, VELÁSQUEZ-ÁLVAREZ, SÁNCHEZ-PACHECO & PEÑA-PRIETO, 2006, *A. monohernandezii* ARDILA-ROBAYO, OSORNO-MUÑOZ & RUÍZ-CARRANZA, 2002 and *A. subornatus* WERNER, 1899 (with two junior synonyms, *A. echeverrii* RIVERO & SERNA, 1985 and *A. flaviventris* WERNER, 1899) from montane forests on the western versant; and *A. guitarraensis* OSORNO-MUÑOZ, ARDILA-ROBAYO & RUÍZ-CARRANZA, 2001, *A. lozanoi* OSORNO-MUÑOZ, ARDILA-ROBAYO & RUÍZ-CARRANZA, 2001, *A. mandingues* OSORNO-MUÑOZ, ARDILA-ROBAYO & RUÍZ-CARRANZA, 2001, *A. ebenoides marinkellei* COCHRAN & GOIN, 1970, *A. muisca* RUEDA-ALMONACID & HOYOS, 1992 and *A. pedimarmoratus* RIVERO, 1963 from subparamos and paramos. Further, close to its juncture with the southern part of the Cordillera Oriental, the Cordillera Central is home to montane forest and paramo *Atelopus*, including *A. angelito* ARDILA-ROBAYO & RUÍZ-CARRANZA, 1998, *A. e. ebenoides* RIVERO, 1963, *A. eusebianus* RIVERO & GRANADOS-DÍAZ, 1993 and *A. simulatus* RUÍZ-CARRANZA & OSORNO-MUÑOZ, 1994 in the departments of Cauca and Huila in Colombia and *A. ardila* COLOMA, DUELLMAN, ALMENDÁRIZ, RON, TERÁN-VALDEZ & GUAYASAMIN, 2010, *A. gigas* COLOMA, DUELLMAN, ALMENDÁRIZ, RON, TERÁN-VALDEZ & GUAYASAMIN, 2010, *A. pastuso* COLOMA, DUELLMAN, ALMENDÁRIZ, RON, TERÁN-VALDEZ & GUAYASAMIN, 2010, and *A. orcesi* COLOMA, DUELLMAN, ALMENDÁRIZ, RON, TERÁN-VALDEZ & GUAYASAMIN, 2010 on the eastern Andean highlands and slopes in Nariño and the

Nudo de Pasto massif, Colombia, and/or adjacent Ecuador (RUEDA-ALMONACID et al. 2005, LÖTTERS et al. 2023, 2025, FROST 2025).

In the course of revising specimens of Colombian *Atelopus*, we became aware of a single female *Atelopus*, collected in the 1970s in Parque Nacional Natural Cueva de Los Guácharos, department of Huila, Colombia. Extensive searches in national and international natural history collections did not yield any additional material attributable to the Huila *Atelopus*. Although the available data is limited, the specimen is well distinguished in both external and internal morphology from all recognized *Atelopus* species, and no name is available for it. We here describe it as a species new to science. By naming the new species we hope to stimulate further efforts to search for, to rediscover and help conserve the Harlequin Toads of Andean Colombia.

### Material and methods

Specimens examined are in FMNH (Field Museum of Natural History, Chicago), IAvH (Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva), ICN (Instituto de Ciencias Naturales, Universidad Nacional, Bogotá), KU (Museum of Natural History, University of Kansas, Lawrence), MHNG (Muséum d’Histoire Naturelle Geneva), NHMW (Naturhistorisches Museum Wien, Vienna), USNM (National Museum of Natural History, Washington D.C.), and ZFMK (Zoologisches Forschungsmuseum Alexander Koenig, Bonn). Material examined in addition to the new species is listed in Appendix 1.

Sex was determined as described in COLOMA et al. (2000). Measurements were taken to the nearest 0.1 mm with manual calipers and are given in mm as mean  $\pm$  one standard deviation. Abbreviations are as follows: SVL, snout–vent length; TIBL, tibia length; FOOT, foot length; HLSL, head length from the squamosal; IOD, interorbital distance; HDWD, head width; EYDM, eye diameter; EYNO, eye to nostril distance; ITNA, internarial distance; FAL, length of flexed forearm; HAND, hand length; THBL, thumb length; SW, sacrum width. FAL was measured according to BRAVO-VALENCIA & RIVERO-CORREA (2011), SW according to COLOMA (2002) and ITNA according to LÖTTERS et al. (2025). All other definitions of measurements follow GRAY & CANNATELLA (1985). The foot webbing formula was taken in the manner of SAVAGE & HEYER (1997). Finger nomenclature follows FABREZI & ALBERCH (1996) and COLOMA et al. (2010). We refer to the terms “coni” and “spiculae” as defined in COLOMA et al. (2010).

We obtained skeletal data from the holotype of the new species using a Diondo d2 micro-computed tomography system ( $\mu$ CT) at F. & G. Hachtel GmbH & Co. KG, Aalen. The specimen was rehydrated overnight in 1X PBS buffer and subsequently embedded in a 4% agarose gel in polypropylene tubes for scanning. It was imaged with a 300 kV microfocus X-ray tube and tungsten target with the voltage and current set to 160 kV and 310  $\mu$ A, respectively. We used an X-ray pre-filter of 1.0 mm Al to compensate for the

agarose gel and polypropylene tubes. The radiographs were reconstructed with Siemens Cera into a tomogram which can be loaded as a volume. The tomogram was imported into VGSTUDIO MAX 2024.1 (Hexagon) and the surface data of the skeletons was converted into STL files using the surface determination and mesh conversion tool.

Computed tomography (mesh) data have been deposited in MorphoSource (<https://www.morphosource.org>). Skull character terminology and descriptions follow MC-DIARMID (1971), COLOMA (2002) and COLOMA et al. (2010).

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature (ICZN). Hence, the new name given herein is available under the code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN (Life Science Identifier, LSID) under urn:lsid:zoobank.org:pub: 241B4BBB-69C3-4C63-9212-438C318DFCFC. The electronic edition of this work was published in a journal with an ISSN and has been archived and is available from the following digital repositories: [salamandra-journal.com](http://salamandra-journal.com), [zenodo.org](http://zenodo.org).

Along with previous authors (e.g. RUEDA-ALMONACID et al. 2005, LÖTTTERS et al. 2025), we do not use subspecific categories and tentatively consider *A. e. ebenoides* and *A. e. marinkellei* as distinct taxa (*A. ebenoides* and *A. marinkellei*) at the species level. We consider Colombian populations of *A. angelito*, *A. e. ebenoides* and *A. eusebianus* to comprise a species complex, herein referred to as *A. ebenoides* complex (while the status of Ecuadorian populations referred to *A. angelito* remains uncertain and we here consider them as *A. sp. carchi*; cf. LÖTTTERS et al. 2025).

## Results

### *Atelopus guacharo* sp. n.

Figs 2, 4, 5, 6

ZooBank LSID: urn:lsid:zoobank.org:act:294D5E20-53F1-4374-89B4-E837348F8F53

Holotype: IAvH-Am-544; Colombia: Departamento de Huila, Parque Nacional Natural Cueva de los Guácharos, trail to cabaña 2 (approximately 1.615 N, 76.101 W); rough-

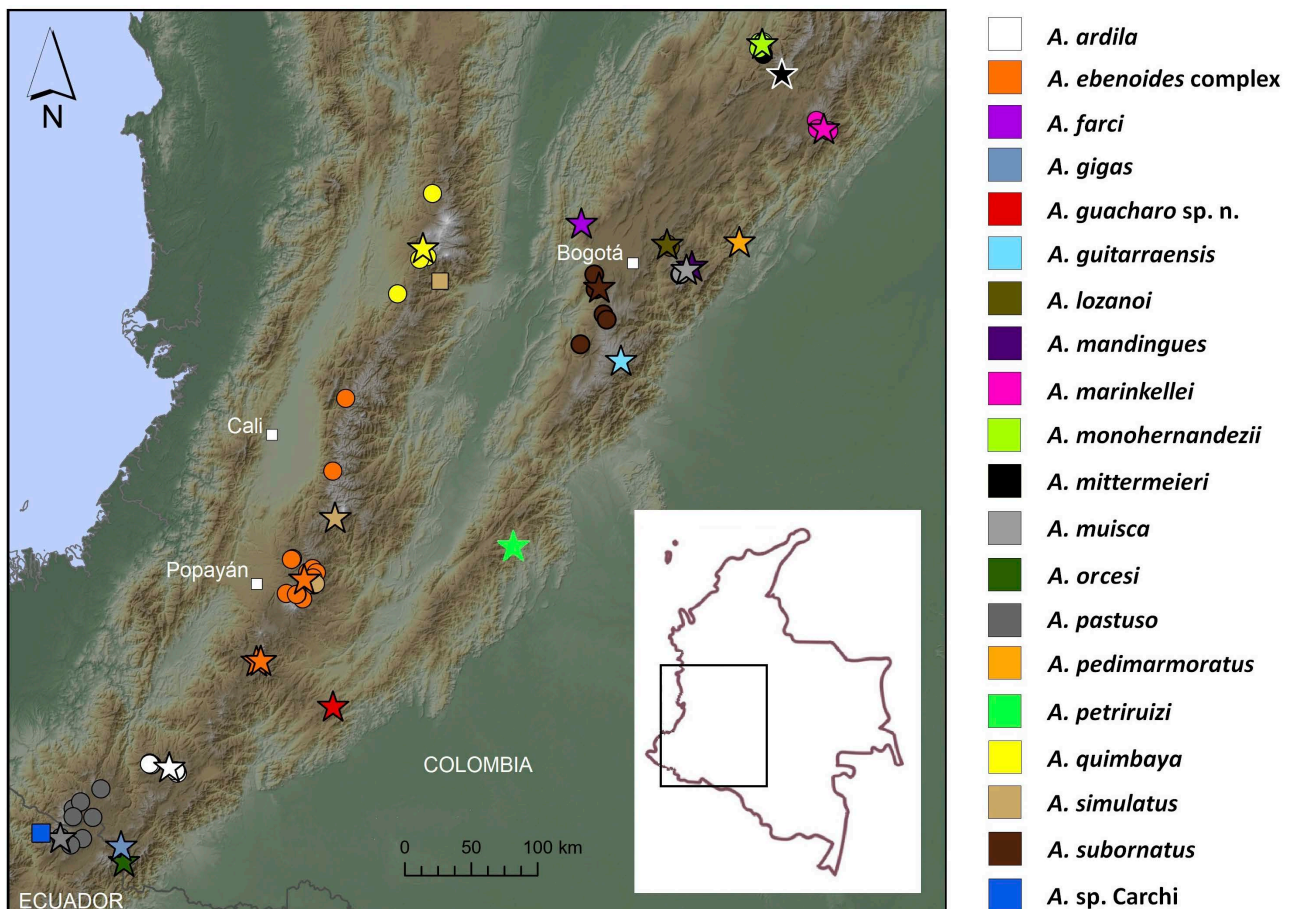


Figure 1. Distribution of *Atelopus* species from the southern Cordillera Central and Oriental of Andes of Colombia (inset) and adjacent Ecuador discussed in this paper. Type localities are indicated by stars, additional localities by dots in the same color and localities of uncertain taxonomic status by squares.

ly 1950 m a.s.l.; 03 August 1972; leg. unknown (however, extensive collections of birds and to a lesser extent herpetofauna deposited at IAVH have been made by CARLOS CHAPARRO-RODRÍGUEZ and CARLOS LEÓN-MARTÍNEZ in the study area in May and August 1972, rendering them potential collectors).

**Diagnosis:** The new species is placed in the genus *Atelopus* based on: snout pointed with head longer than wide; presence of supratympanic crest; absence of parotid gland and tympanic membrane; annulus tympanicus not visible or absent; presacrals I and II fused. The new species is defined by the combination of the following characters: (1) A medium-sized species with SVL of the only known adult female 34.0; (2) robust body (SW/SVL 0.33) with (3) relatively short legs for an *Atelopus* (TIBL/SVL 0.39) and (4) projected snout, protruding beyond apex of lower jaw, subacuminate in dorsal view, curved downwards towards tip in lateral view with apex at about the same height as lower corner of eye; (5) columella and tympanic membrane absent, annulus tympanicus not visible; (6) phalangeal formula of hand 2-2-3-3, hand webbing absent; (7) thumb (finger II) long (THBL/HAND 0.54); (8) phalangeal formula of foot 2-2-3-4-3, foot webbing formula 10-0II0-1III1-3IV3-½V; (9) dorsal and lateral skin on body and limbs densely covered with large, round and flat warts with some conical in the tympanic area; ventral surfaces smooth, areolate on upper arm and thigh; (10) vertebral column, neural processes, sacral diapophyses and urostyle not visible through the skin; (11) in preservative, dorsal surfaces of body and limbs dark brown with some warts being light brown, tip of snout, canthus rostralis, supratympanic crest and dorsal warts on brown head dark cream; tongue entirely cream; laterally light brown becoming darker towards venter, covered with dark brown warts, head light brown, conical tips of brown warts in tympanic area cream; ventrally brown, dark brown on limbs, towards flanks, on chest and distal parts of throat.

**Comparison:** *Atelopus guacharo* sp. n. (Fig. 2), at least adult females, can be readily distinguished from all other described species by the combination of relatively small size, absence of hand webbing, subacuminate snout projected, in lateral view protruding beyond apex of lower jaw, curved downwards towards tip in lateral view, skin of flanks and dorsum of body and limbs covered with large, round and flat warts with some in the tympanic area conical, and in preservative dark brown dorsum and limbs with some warts being light brown, tip of snout, canthus rostralis, supratympanic crest and dorsal warts on brown head dark cream; laterally light brown becoming darker towards venter, covered with dark brown warts, head light brown, conical warts in tympanic area with cream tips; ventrally brown, dark brown on limbs, towards flanks, on chest and distal parts of throat. The new species is most similar to *A. guitarransensis*. In addition, *A. guacharo* sp. n. resembles *A. ardila*, the *A. ebenoides* complex, *A. gigas*, *A. pastuso*, *A. quimbaya* and *A. simulatus* from the Cordillera Central,

*A. farci*, *A. lozanoi*, *A. mandingues*, *A. marinkellei*, *A. mittermeieri*, *A. monohernandezii*, *A. muisca*, *A. subornatus* (and its junior synonyms *A. echeverrii* and *A. flaviventris*) and *A. pedimarmoratus* from the Cordillera Oriental and *A. orcesi* from adjacent Andean Ecuador. No relevant Harlequin Toads are known from males only, allowing the new species to be readily distinguished. Comparative characters are presented in Table 1.

The new species differs from *A. guitarransensis* in having supratympanic crests directed towards mid-dorsum axis posteriorly in dorsal view (vs. supratympanic crests parallel, both by external and internal examination), in having toes only partially webbed without a lateral fringe on toe V (vs. complete foot webbing with all toes completely embedded and a lateral fringe on toe V), and in smaller adult female size (34.0, N = 1, vs.  $38.9 \pm 1.51$ , range 37.4–41.1, N = 4). In addition, *A. guacharo* sp. n. can be distinguished from *A. guitarransensis* by female coloration in preservative: dorsally, tip of snout, canthus rostralis, supratympanic crest and dorsal warts on brown head dark cream; ventrally, dark brown on limbs, towards flanks, on chest and distal parts of throat (vs. dorsally, entire head and supratympanic crests dark brown; ventrally, varying extent of cream on vent with irregular reddish brown blotches, reddish brown on limbs with cream hands and feet, reddish brown towards flanks, on chest and throat; Fig. 3).

*Atelopus guacharo* sp. n. differs from *A. ardila* in having prominent supratympanic crests directed towards mid-dorsum axis posteriorly in dorsal view (vs. supratympanic crests not prominent, parallel), projected snout, protruding beyond apex of lower jaw (vs. snout shorter, barely protruding beyond apex of lower jaw; Fig. 4), smaller adult female size (34.0, N = 1, vs.  $46.5 \pm 2.85$ , N = 48), absence of spiculae and coni except conical warts in tympanic area (vs. coni present on dorsum, limbs, flanks and in females spiculae and coni present in gular region), and absence of pale coloration in preservative except on head (vs. dorsum pale cream to black with gray to black spiculae, venter cream).

The new species can be distinguished from the *A. ebenoides* complex by having, in females, a projected snout, protruding beyond apex of lower jaw (vs. snout truncate; Fig. 4), smaller adult female size (34.0, N = 1, vs.  $44.0 \pm 5.39$ , N = 10), absence of spiculae (vs. spiculae present on flanks and limbs in most specimens), and by absence of pale coloration in preservative except on head (vs. dark brown to black dorsal surfaces with cream, yellowish, tan, reddish brown or greenish irregular markings, in some populations light pattern predominant with few diffuse dark brown to black markings only, laterally dark brown to black with some intrusions of light dorsal pattern and white to cream warts in some specimens; most specimens presenting a pale band between eye and upper lip, sometimes reduced to a pale spot on lower corner of eye; spiculae and conical tips of warts cream to gray; ventrally dark brown to black with whitish, yellowish or cream irregular marks or bands, palms and plants yellowish cream to cream brown with small dark irregular markings).

*Atelopus guacharo* sp. n. can be distinguished from *A. gigas* by having supratympanic crests directed towards mid-dorsum axis posteriorly in dorsal view (vs. supratympanic crests directed towards flanks posteriorly in dorsal view), having a projected snout, protruding beyond apex of lower jaw (vs. shorter, not protruding beyond apex of lower jaw), smaller adult female size ( $34.0$ ,  $N = 1$ , vs.  $53.8 \pm 4.32$ ,  $N = 9$ ), absence of spiculae (vs. spiculae present on flanks in females), and absence of pale coloration except on head in preservative (vs. unicolored yellowish cream to yellowish tan).

The new species can be distinguished from *A. pastuso* by having prominent supratympanic crests directed towards mid-dorsum axis posteriorly in dorsal view (vs. supratympanic crests not prominent, parallel), projected snout, protruding beyond apex of lower jaw (vs. snout rounded, slightly protruding beyond apex of lower jaw; Fig. 4), absence of spiculae and coni except conical warts in tympanic area (vs. prominent coni present on dorsum, limbs, flanks; single and clustered spiculae present on dorsal and lateral surfaces of limbs), presence of warts on head (vs. smooth), and absence of pale coloration in preservative ex-



Figure 2. Female holotype of *Atelopus guacharo* sp. n. (IAvH-Am-544) (A) in dorsal, ventral and lateral views, and (B) ventral surfaces of hand and foot. Scale bar 10 mm, (B) not to scale. Photographs by CHRISTOPHER HEINE.

Table 1. Differential characters in the species discussed. For additional details and differences in coloration, see Comparison section. Convex supratympanic crest indicates that both anterior and posterior part are directed towards mid-dorsum axis.

Species	Habitat	Female SVL	Snout	Supratympanic crest	Warts	Spiculae	Basal hand webbing	Foot webbing
<i>guacharo</i>	cloud forest in Cordillera Oriental	34.0, N=1	projected, in lateral view protruding beyond apex of lower jaw, curved downwards towards tip, in dorsal view round	posteriorly directed towards mid-dorsum axis	dorsal and lateral surfaces of limbs and body incl. head	absent	absent	partial
<i>ardila</i>	paramo on Nudo de Pasto	46.7±2.85, N=48	rounded, barely protruding beyond apex of lower jaw	parallel	coni on dorsal and lateral surfaces of limbs and body excl. head as well as on chest	present	absent	partial
<i>ebenooides</i> complex	paramo in Cordillera Central	44.0±5.39, N=10	truncate, barely protruding apex of lower jaw, in dorsal view round	convex to parallel	dorsal and lateral surfaces of limbs and body incl. head, most specimens with conical warts on limbs	present	present between fingers II and III	high intra-population variation
<i>farci</i>	cloud forest in Cordillera Oriental	36.1-36.4, N=2	strongly projected, elongate, almost straight in lateral view	posteriorly directed towards mid-dorsum axis	dorsal and lateral surfaces of limbs and body excl. head; dorsolateral row of enlarged warts	absent	present between fingers II and III	partial
<i>gigas</i>	unknown habitat on Nudo de Pasto	53.8±4.32, N=9	short, not protruding beyond apex of lower jaw	posteriorly directed towards flanks	coni on lateral surface of body excl. head, dorsal and lateral surfaces of limbs	present	absent	partial
<i>guitarraensis</i>	paramo in Cordillera Oriental	38.9±1.51, N=4	slightly projected, in lateral view protruding beyond apex of lower jaw, not curved downwards towards tip, in dorsal view round	parallel	dorsal and lateral surfaces of body incl. head and limbs	absent	absent	complete
<i>lozanoi</i>	paramo in Cordillera Oriental	38.4±1.70, N=12	projected, in lateral view protruding beyond apex of lower jaw, not curved downwards towards tip, in dorsal view round	posteriorly directed towards mid-dorsum axis	dorsal and lateral surfaces of limbs and body excl. head	present, partially clustered	present	variable, lateral fringe present on toe V
<i>mandingues</i>	subparamo in Cordillera Oriental	35.9±3.04, N=5	projected, in lateral view protruding beyond apex of lower jaw, not curved downwards towards tip, in dorsal view round	posteriorly directed towards mid-dorsum axis	dorsal and lateral surfaces of limbs and body excl. head	present, partially clustered	present	variable, lateral fringe present on toe V, complete in most specimens
<i>marinkellei</i>	paramo in Cordillera Oriental	43.5±1.95, N=5	slightly projected, in lateral view protruding beyond apex of lower jaw, in dorsal view round	slightly convex	dorsal and lateral surfaces of limbs and body incl. head, small warts on chest	present, partially clustered	absent	partial
<i>mittermeieri</i>	cloud forest in Cordillera Oriental	43.7±1.74, N=5	slightly projected, in lateral view protruding beyond apex of lower jaw, in dorsal view round	parallel to slightly convex	dorsal and lateral surfaces of limbs and body excl. head	present, partially clustered	absent	partial
<i>monohernandezii</i>	cloud forest in Cordillera Oriental	32.2±1.72	strongly projected, in lateral view protruding beyond apex of lower jaw, in dorsal view triangular	posteriorly directed towards flanks	dorsal and lateral surfaces of limbs and posterior third of body; dorsolateral row of enlarged warts	absent or few spiculae	present	partial
<i>muisca</i>	paramo in Cordillera Oriental	41.2±0.85, N=14	projected, in lateral view protruding beyond apex of lower jaw, in dorsal view round	convex to posteriorly directed towards mid-dorsum axis	dorsal and lateral surfaces of limbs and dorsolateral to lateral surfaces of body	present, partially clustered	present	complete

Table 1 continued

Species	Habitat	Female SVL	Snout	Supratympanic crest	Warts	Spiculae	Basal hand webbing	Foot webbing
<i>orcesi</i>	cloud forest on E slopes of Ecuadorian Andes	42.1, N=1	projected, in lateral view protruding beyond apex of lower jaw with snout almost straight, in dorsal view triangular	parallel	dorsal and lateral surfaces of limbs, dorsolateral row of small warts	minute spiculae on flanks and in tympanic area	absent	partial
<i>pastuso</i>	paramo on Nudo de Pasto	38.7±3.9, N=153	rounded, slightly protruding beyond apex of lower jaw	parallel	coni on dorsal and lateral surfaces of limbs and dorso-lateral to lateral surfaces of body	present, partially clustered	absent	partial
<i>quimbaya</i>	cloud forest in Cordillera Central	32.4±2.25	projected, in lateral view protruding beyond apex of lower jaw, curved downwards towards tip, in dorsal view triangular	parallel	dorsal and lateral surfaces of limbs and posterior third of body	present	present	complete, in few specimens partial
<i>simulatus</i>	cloud forest in Cordillera Central	33.7±1.45	projected, in lateral view protruding beyond apex of lower jaw, in dorsal view round	parallel	dorsal and lateral surfaces of limbs	present	present	complete
<i>subornatus</i>	cloud forest in Cordillera Oriental	38.0±0.91	projected, in lateral view protruding beyond apex of lower jaw, not curved downwards towards tip, in dorsal view round	parallel	dorsal and lateral surfaces of limbs and body excl. head	present, partially clustered	present	partial
<i>pedimarmoratus</i>	paramo in Cordillera Oriental	NA	projected, in lateral view protruding beyond apex of lower jaw, in dorsal view round	parallel	dorsal and lateral surfaces of limbs and body excl. head	present	present	partial

cept on head (vs. dorsum cream to black with gray to black spiculae, venter cream).

The new species differs from *A. quimbaya* in having supratympanic crests directed towards mid-dorsum axis posteriorly in dorsal view (vs. supratympanic crests parallel), snout curved downwards towards tip in lateral view with apex at about the same height as lower corner of eye (vs. snout almost straight in lateral view; Fig. 4), absence of hand webbing and foot being partially webbed (vs. presence of basal hand webbing and completely webbed toes), absence of spiculae and coni except conical warts in tympanic area (vs. several conical warts on flanks and limbs, flanks and upper arms covered in spiculae), and absence of light coloration except on head in preservative (vs. dark cream to brown dorsum with tan to brown markings, cream dorsolateral line in some specimens, light tan flanks with brown warts and whitish gray spiculae, cream venter, in some specimens with brown markings).

*Atelopus guacharo* sp. n. differs from *A. simulatus* in absence of hand webbing and having foot partly webbed (vs. presence of basal hand webbing, completely webbed toes), absence of spiculae and presence of warts on dorsum (vs. flanks and upper arms covered with spiculae, absence of dorsal warts), and absence of pattern and pale coloration except on head in preservative (vs. greenish pale to tan dorsum with reddish to dark brown markings, forming a sometimes fragmented X-shaped mark on head and

suprascapular region in some specimens, broad irregular cream lateral band, framed by reddish brown line, gray spiculae surrounded by brown lines, greenish to yellowish pale venter with reddish brown irregular markings, pale cream plantar and palmar surfaces and webbing).

The new species can be distinguished from *A. farci* by having the projected snout curved downwards towards tip in lateral view with apex at about the same height as lower corner of eye (vs. snout strongly projected, elongate, almost straight in lateral view), presence of warts on dorsal surface of head (vs. warts on head absent), absence of a dorsolateral row of enlarged warts (vs. dorsolateral wart row present) and dark ventral coloration in preservative (vs. venter olive brown to tan).

*Atelopus guacharo* sp. n. can be distinguished from *A. lozanoi* and *A. mandingues* by absence of hand webbing (vs. presence of basal hand webbing) and absence of lateral fringe on toe V (vs. lateral fringe present on toe V), spiculae (vs. presence of warts on flanks covered in partially clustered spiculae), presence of warts on dorsal surface of head (vs. warts on head absent; Fig. 4), and absence of pale coloration except on head in preservative (vs. brown dorsum with yellow, cream or whitish irregular markings).

*Atelopus guacharo* sp. n. can be distinguished from *A. marinkellei* by smaller adult female size (34.0, N = 1, vs. 43.3 ± 2.01, N = 5), absence of spiculae (vs. spiculae on

flanks, dorsal surface of thigh and posterior dorsum densely covered in spiculae), and absence of pale coloration except on head in preservative (vs. entire body black, dark brown or dark gray with white or light cream irregular markings, mostly dots; Fig. 4).

The new species differs from *A. mittermeieri* in smaller adult female size (34.0, N = 1, vs.  $43.7 \pm 1.74$ , N = 5), absence of spiculae (vs. warts on flanks bearing clustered spiculae as well as well-defined, single spiculae on dorsal surface of limbs; Fig. 4), and absence of pale coloration except on head in preservative (vs. presence of few small

whitish cream dots on limbs and flanks, venter and ventral surfaces of hands and feet cream with brown gular band).

*Atelopus guacharo* sp. n. can be distinguished from *A. monohernandezii* by absence of hand webbing (vs. presence of basal hand webbing between all fingers), snout round from nostrils to the tip of snout in dorsal view (vs. triangular, strongly projected; Fig. 4), dense presence of warts on dorsum and flanks (vs. absence of warts on body with the exception of a dorsolateral row of large warts and few warts on posterior third of dorsum), outer metatarsal

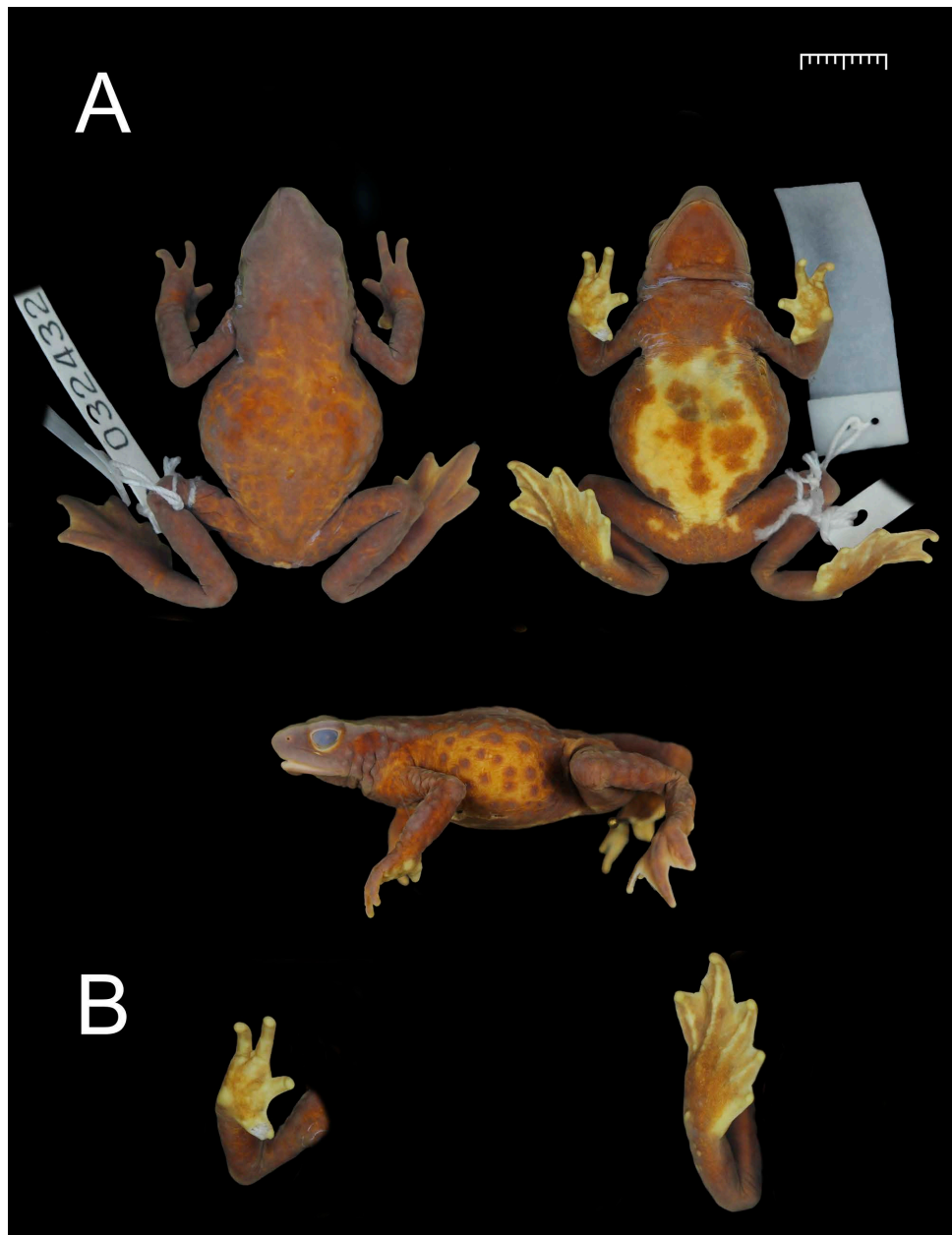


Figure 3. Female paratopotype of *Atelopus guitarraensis* (ICN 32432) (A) in dorsal, ventral and lateral views, and (B) ventral surfaces of hand and foot. Scale bar 10 mm, (B) not to scale. Photographs by PHILIPP BÖNING.

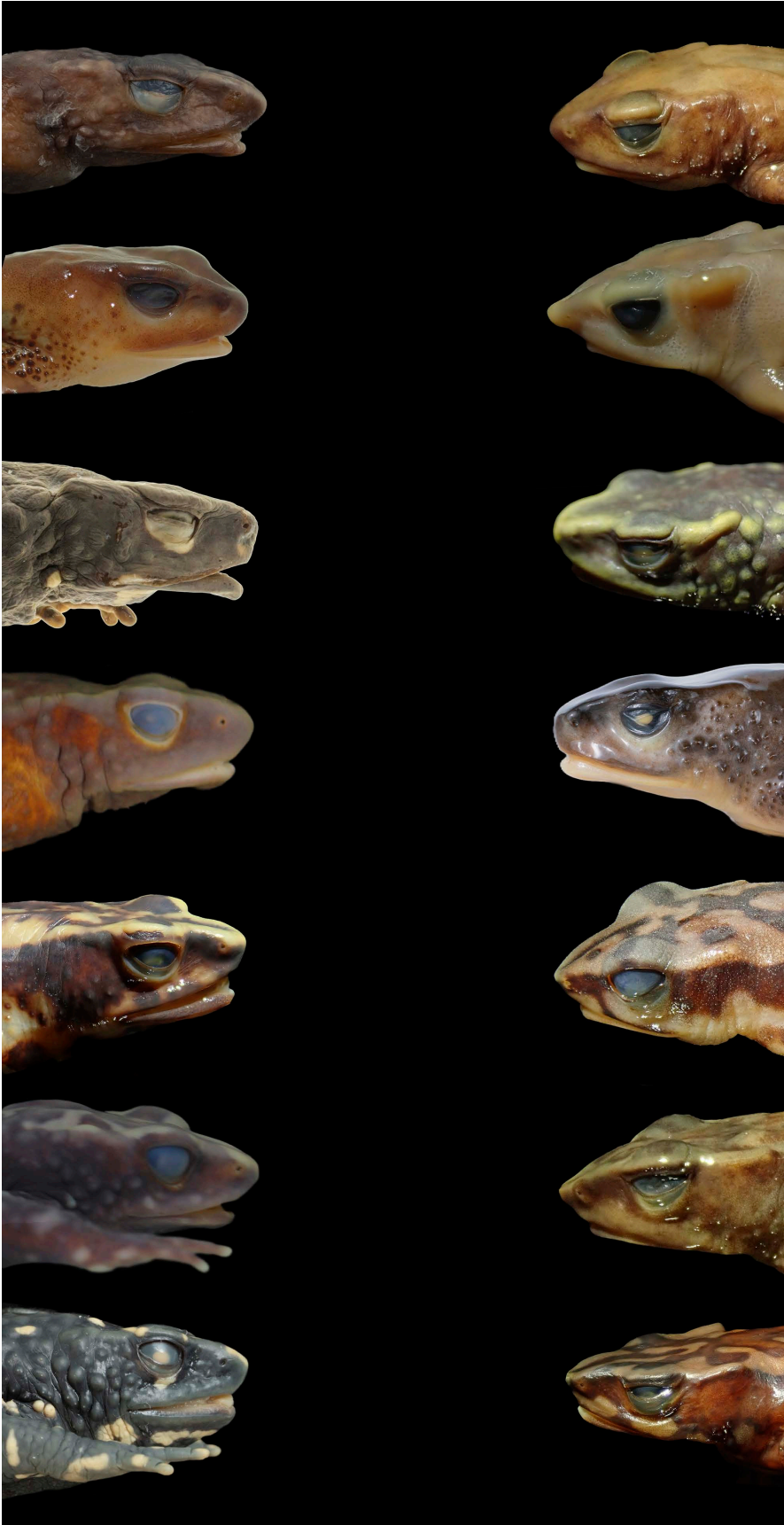


Figure 4. Dorsolateral and lateral views of head profiles in Harlequin Toads from the Cordillera Oriental and Central. Left column from above: *Atelopus guacharo* sp. n. (IAvH-Am-544, holotype), *A. ardila* (IAvH-Am-21), *A. ebenoides* (FMNH 69746, holotype), *A. guitarraensis* (ICN 32432, paratopotype), *A. lozanoi* (IAvH-Am-3105), *A. mandingues* (ICN 34286, paratype), *A. marin-kellei* (IAvH-Am-6046). Right column from above: *A. mittermeieri* (ICN 7372), *A. monoherandezii* (ICN 5527, holotype), *A. muisca* (IAvH-Am-5087, paratype), *A. pastuso* (NHMW 32174/2), *A. petriruizi* (IAvH-Am-6519, paratopotype), *A. quimbaya* (ICN 23339, holotype) and *A. simulatus* (IAvH-Am-4963, paratype). Not to scale. Photographs by PHILIPP BÖNING, CHRISTOPHER HEINE, RACHUNLIU KAMEI and AMADEUS PLEWNIA.

tubercle larger than poorly developed inner metatarsal tubercle (vs. inner metatarsal tubercle about twice the size of outer metatarsal tubercle), and absence of pale coloration except on head in preservative (vs. cream to whitish venter).

*Atelopus guacharo* sp. n. differs from *A. muisca* in absence of hand webbing and foot being partially webbed without a lateral fringe on toe V (vs. presence of basal hand webbing and completely webbed toes with a lateral fringe on toe V), smaller adult female size (34.0, N = 1, vs. 41.2 ± 0.85, N = 14), absence of spiculae (vs. warts on flanks covered in clustered spiculae), presence of warts on dorsal surface of head (vs. warts on head absent in females), and absence of pale coloration except on head in preservative (vs. greenish to yellowish cream to greenish tan with cream palmar and plantar surfaces and black markings on venter in some specimens; Fig. 4).

The new species differs from *A. subornatus* (and its junior synonyms *A. echeverrii* and *A. flaviventris*) in absence of hand webbing (vs. presence of basal hand webbing), snout curved downwards towards tip in lateral view with apex at about the same height as lower corner of eye (vs. snout almost straight in lateral view), absence of spiculae (vs. warts on flanks covered in clustered spiculae), presence of warts on dorsal surface of head (vs. warts on head absent); and, in females, a dark venter in preservative (vs. cream).

*Atelopus guacharo* sp. n. can be distinguished from *A. pedimarmoratus* by the presence of dorsal warts (vs. dorsal warts absent) and absence of pattern and pale coloration except on head in preservative (vs. dorsal surfaces light tan with reddish brown irregular markings).

The new species can be distinguished from *A. orcesi* by having supratympanic crests directed towards mid-dorsum axis posteriorly in dorsal view (vs. supratympanic crests parallel), by having the snout curved downwards towards tip in lateral view with apex at about the same height as lower corner of eye (vs. snout almost straight in lateral view), smaller adult female size (34.0, N = 1, vs. 42.1, N = 1), absence of spiculae (vs. presence of minute spiculae on flanks and in tympanic area), presence of dorsal warts on body (vs. dorsal warts absent on body), and absence of pattern and pale coloration except on head in preservative (vs. dorsum pale brown with a fragmented X-shaped mark on head and suprascapular region, flanks pale brown with irregular reddish brown band framed by dark brown line, venter and throat cream with a large brown mark extending to chest).

Description of holotype: Adult female. Body robust (SW/SVL 0.33); head longer than wide (HLSQ/HDWD 1.17); snout projected, protruding beyond apex of lower jaw, subacuminate in dorsal view, round from nostrils to the tip of snout, snout curved downwards towards tip in lateral view with apex about the same height as lower corner of eye; nostrils directed anterolaterally, protuberant, not visible in dorsal view, situated about two thirds from eye to tip of snout in lateral view, posterior corner situated above

apex of lower jaw; canthus rostralis well defined, straight in dorsal view; loreal region concave; lips not flared; choanae small, rounded; tongue not broadened, anterior half attached to floor of mouth; head plain between eyes in frontal view, concave between canthi; eyelid flared; tympanum absent, annulus tympanicus not visible; supratympanic crests prominent, directed towards mid-dorsum axis posteriorly in dorsal view, straight in lateral view, slightly longer than EYDM, no externally visible exostosis present; pretympnic crest poorly developed, shorter than EYDM; vertebral column, neural processes, sacral diapophyses and urostyle not visible through the skin.

Hind limbs short and slender (TIBL/SVL 0.39); relative length of toes I<II<III<V<IV, phalangeal formula of foot 2-2-3-4-3, webbing formula of toes I<sub>0</sub>-0II<sub>0</sub>-1III<sub>1</sub>-3IV<sub>3</sub>-½V; tarsal fold absent; foot about as long as tibia; outer metatarsal tubercle round, well defined, inner metatarsal tubercle oval, poorly developed; supernumerary plantar tubercles indistinct; subarticular tubercles on toes distinct, small, rounded; tips of toes rounded, not widened; toes and fingers lack lateral fringes; relative length of fingers II<III<V<IV; phalangeal formula of hand 2-2-3-3; webbing absent on hand; palmar tubercle round, large, well defined; thenar tubercle elongated, straight, well defined; supernumerary palmar tubercles well defined; subarticular tubercles of digits poorly defined; tips of fingers rounded, not widened.

Dorsal and lateral skin on body and limbs densely covered with large, round, and flat warts with some in the tympanic area conical; ventral surfaces smooth, areolate on upper arm and thigh.

Coloration in preservative: Dorsal surfaces of body and limbs dark brown with some warts being pale brown, tip of snout, canthus rostralis, supratympanic crest and dorsal warts on brown head dark cream; tongue cream; laterally pale brown becoming darker towards venter, covered with dark brown warts, head pale brown, brown conical warts in tympanic area with cream tips; ventrally brown, dark brown on limbs, towards flanks, on chest and distal parts of throat.

Coloration in life: Unknown.

Measurements: SVL 34.0, TIBL 13.3, FOOT 12.8, HLSQ 10.2, ITOR 3.7, HDWD 8.7, EYDM 2.9, EYNO 2.5, ITNA 3.0, HAND 7.5, THBL 4.0, SW 11.3, FAL 9.6, TIBL/SVL 0.39, SW/SVL 0.33, HLSQ/SVL 0.30, FAL/SVL 0.28, HLSQ/HDWD 1.17, THBL/HAND 0.54.

Osteology: General osteological features of the female holotype (IAvH-Am-544) are depicted in Figures 5–6. The skull of *A. guacharo* sp. n. is triangular in dorsal view and broadest at about height of anterior corner of squamosal. The skull length is 9.9, the skull width is 8.5. The skull roof is rugose. In anterior view, the septomaxilla is C-shaped with medial and lateral rami that extend posteriorly towards the vomer. The ossified sphenethmoid is slightly rugose and underlies the posterior and medial margins of the nasals, as well as the anterior margins of the frontoparietals. The posterior limit of the sphenethmoid

is about one-half the length of the margin of the orbit. The rugose prootics are fused to the posterolateral edge of the frontoparietals. The exoccipitals are fused to the frontoparietals, the prootics, and the parasphenoid. The otic capsule is well-ossified. Columellae are absent. The nasals are elliptic in dorsal view and bear a maxillary process with two acuminate projections that extend ventrolaterally toward the maxilla with the outer projection contacting (right) or nearly contacting (left) the pars facialis of the maxilla. The nasals are in contact medially in the anterior half with a small suture line evident and are anteriorly strongly curved downwards in lateral view. The frontoparietals are rectangular and broadly fused with incomplete medial articulation only in the anterior portion. Occipital grooves are present and completely covered with bone. Posteriorly, the frontoparietals are fused to the prootics and exoccipitals. The vomers are small, edentate, medially separated, crescent-shaped, and triradiate with an anterior ramus, prechoanal ramus and postchoanal ramus. The anterior ramus is directed anterolaterally, bearing an elongated tip. The prechoanal ramus is short. The postchoanal ramus is fused to the sphenethmoid. The neopalatine is narrow, elongate, slightly curved, and pointed towards the tips. It underlies and is fused to the sphenethmoid and extends towards but barely reaches the maxilla. The parasphenoid has an inverted T-shape. The cultriform process is fused with the sphenethmoid at about midpoint of orbit. The parasphenoid alae are di-

rected posterolateral to the cultriform process, becoming broader distally and are fused to the overlying bones. The parasphenoid presents a medial posterior process. The maxillary arcade is complete and edentate. The paired premaxillae each possess a dorsal alary process that is directed anterolaterally at about 60°. The tip of the alary process is rounded. Alary processes are directed dorso-laterally in frontal view. The rugose maxilla is posteriorly broadly articulated with the pterygoid but not in contact with the quadratojugal. The pars fascialis of the maxilla is directed medially and contacts the maxillary process of the nasal. The anterior end of the maxilla is broad with a subacuminate projection below which fuses with the premaxilla. The posterior end of the maxilla is pointed and is separated from the quadratojugal. The quadratojugal is small, L-shaped and fused with the overlying ventral arm of the squamosal and contacts the pterygoid. The squamosal possesses an otic ramus dorsally, a zygomatic ramus anteriorly, and a ventral ramus. The otic ramus is well ossified and strongly rugose, expanded dorsally with a pointed tip posteriorly and has a broad articulation with the otic capsule. The zygomatic ramus is small, flat, and directly medially. The angle between the dorsal surface of the squamosal and the anterior margin of the ventral ramus is about 80°. The ventral ramus is flat, broadened and truncate. The pterygoid is triradiate, bearing anterior, medial, and posterior rami. The anterior ramus articulates with the pars palatina of the maxilla. The medial ramus

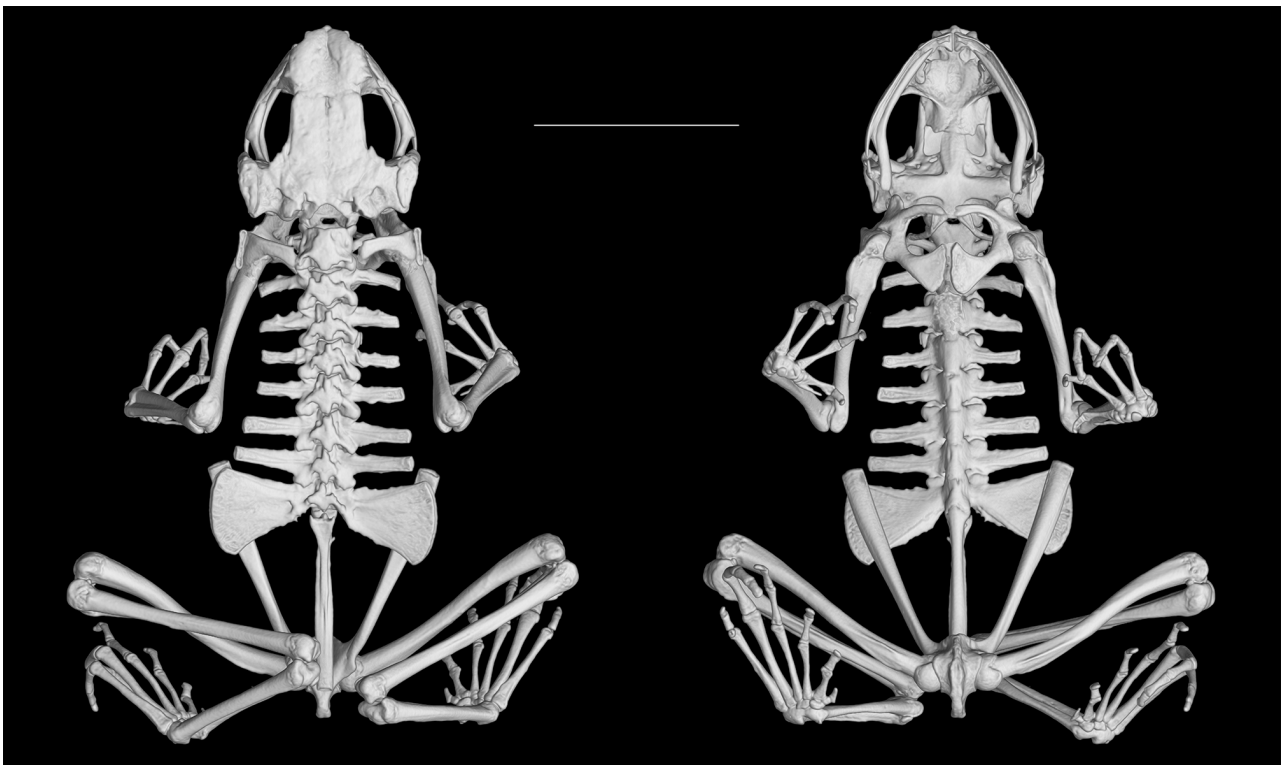


Figure 5. Skeletal features of the female holotype of *Atelopus guacharo* sp. n. (IAvH-Am-544) in dorsal and ventral views. Scale bar 10 mm. 3D renderings by KAMIL SZEPANSKI.

is distally widened with two rounded tips and nearly contacts the prootic. The posterior ramus is short, flat and rounded and contacts the quadratojugal. On the lower jaw, the mentomeckelian forms a cartilaginous symphysis at the midline of the jaws. Dorsally, the mentomeckelian is fused to the thin and edentate dentary, which overlays the anterior half of the angulosplenial.

Clavicles thin, curved. Coracoids flattened, large, strongly broadened medially resulting in an almost triangular shape. Scapula longer than the coracoid, acromion processes prominent. Cleithrum ossified, anterior margin almost straight, posterior margin concave, suprascapula cartilaginous (barely visible in scan). Sternum cartilaginous (barely visible in scan).

Seven presacral vertebrae distinct as presacrals I and II (atlas and axis) are fused, length of transverse processes  $1 < 4 < 3 < 5 < 2 < 6 < 7$ , transverse processes flattened, directed anterolaterally in presacral I, posterolaterally in II and

laterally in all others. The proximal end of the transverse processes is noticeably wider than the terminal end. Small processes are present at the anterior and posterior borders of transverse processes of presacrals, most noticeably in presacral IV.

Sacral diapophyses large, axe-shaped, laterally protruding beyond ilium and transverse processes of vertebrae in dorsal view. Urostyle shorter than presacral column, not fused with sacrum; lateral crests present on urostyle. Ilium V-shaped in dorsal view, broadened anteriorly. The distal end of ilium surpasses the anterior border of the sacral diapophysis.

Humerus with a distinct ventral crest, sulcus intermedius broad with flared outer edge, prepollex consists of a single, thin and elongated element in the CT dataset. However, additional cartilaginous elements as reported for other *Atelopus* (COLOMA et al. 2010) cannot be assessed from our dataset. Radiale, ulnare and centrale distinct, distal carpals

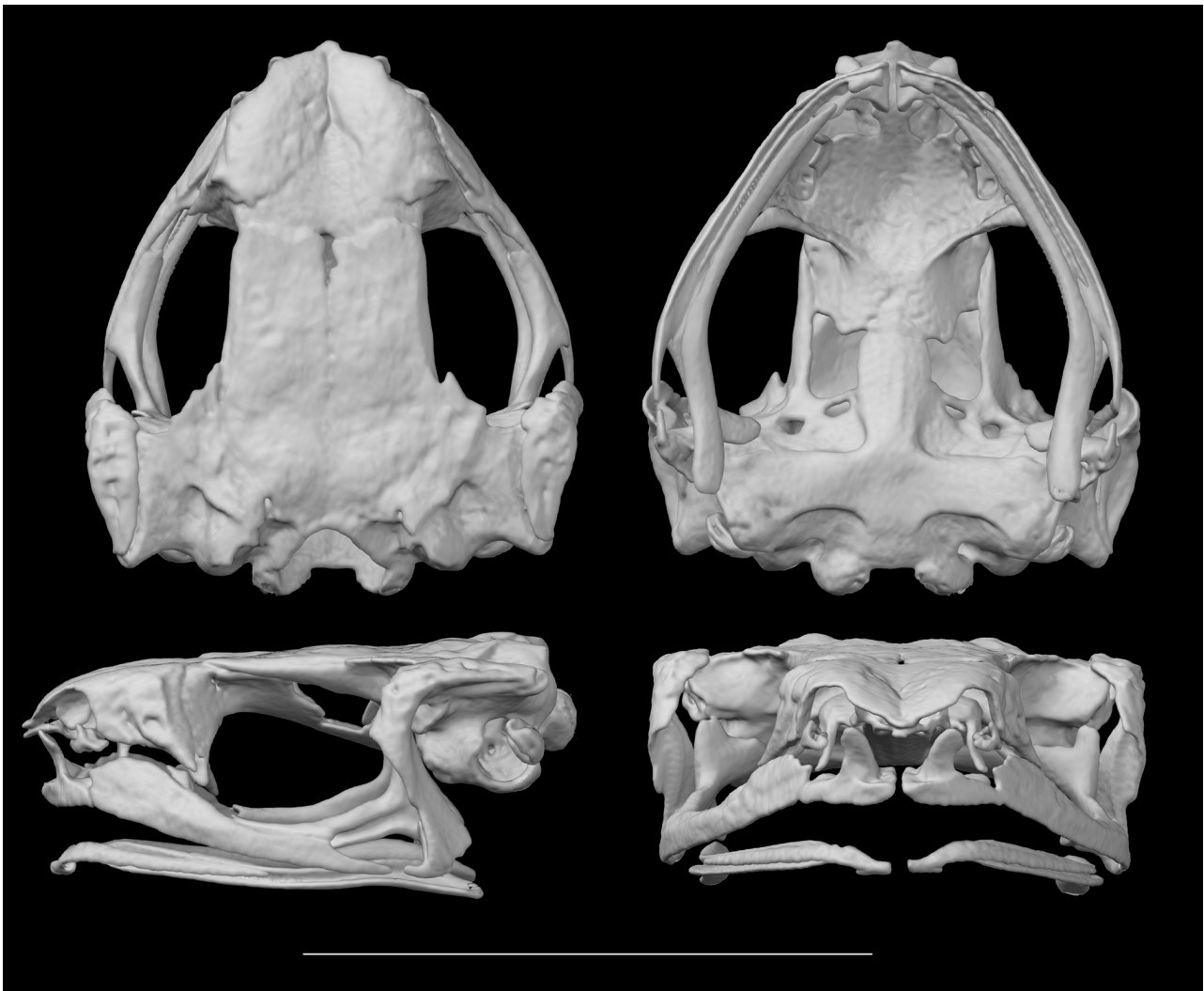


Figure 6. Skull of the female holotype of *Atelopus guacharo* sp. n. (IAvH-Am-544) (A) in dorsal, ventral, lateral and frontal views. Scale bar 10 mm. 3D renderings by KAMIL SZEPANSKI.

fused with a large, round and flat sesamoid below the distal carpals. Phalangeal formula of hand 2-2-3-3, terminal phalanges with broad, rounded tip.

Femur slightly sigmoid, about as long as tibiofibular, with distinct groves towards foramen; tibiofibula slightly convex, tibiae and fibulae fused proximally and distally, fibulae with distinct ridge ventrally. Prehallux consists of two ossified elements with the distal being pointed with a sharp proximal projection protruding laterally beyond the proximal element. Phalangeal formula of foot 2-2-3-4-3, terminal phalanges with broad, rounded tip.

*Atelopus guacharo* sp. n. differs from the most similar *A. guitarraensis* (based on examination of cleared and stained material and OSORNO-MUÑOZ et al. 2001) in having the nasals in contact in dorsal view (vs. separated), in the squamosal extending laterally beyond the maxilla (vs. not protruding) and in squamosal shape (outer edge sinusoidal, inner edge convex with a distinct appendix on anterior third vs. outer edge straight to convex with a projected appendix on anterior distal part, inner edge irregular). However, the discriminatory power of osteological features needs to be seen with some caution as intraspecific variation and taxonomic value remain poorly understood for Harlequin Toads (PLEWNIA et al. 2024, LÖTTTERS et al. 2025).

**Etymology:** The specific name *guacharo* is a noun in apposition that refers to the “guácharo”, also known as oilbird (*Steatornis caripensis*, Steatornithidae), whose famous breeding colonies in southern Huila led to the protection of the habitat of the new *Atelopus* through the establishment of Parque Nacional Natural Cueva de los Guácharos. As the English common name, we propose Guácharo Harlequin Toad.

**Distribution:** *Atelopus guacharo* sp. n. is known only from the type locality on the western versant of the southern Cordillera Oriental of Colombia at roughly 1950 m a.s.l. (Fig. 1). The holotype was collected in a cloud forest in Parque Nacional Natural Cueva de los Guácharos, department of Huila.

**Conservation status and threats:** We suggest listing *A. guacharo* sp. n. as Data Deficient under the criteria of the IUCN Red List of Threatened Species as it is known only from a single specimen collected in 1972. No recent information on population status and threats is available due to the general lack of herpetological inventories in the area. The type locality lies within a protected area, Parque Nacional Natural Cueva de los Guácharos, which is poorly studied and appears well forested based on satellite photos from 2024. However, particularly all Andean Harlequin Toads from montane forests have been proven highly susceptible to chytridiomycosis caused by *Batrachochytrium dendrobatidis* (*Bd*), the latter considered a main driver of extinctions in *Atelopus* (LIPS et al. 2008; SCHEELE et al. 2019; LÖTTTERS et al. 2023). So far, no surveys for the pathogen have been carried out in the general area. Further, the region appears suitable to *Bd* according to species distribution models and

the pathogen was detected as close as in adjacent Cauca in the juncture between the Cordillera Central and Cordillera Oriental (FLECHAS et al. 2017, OLSON et al. 2021). Climate change may become an additional threat to *Atelopus guacharo* sp. n. in the near future (cf. LÖTTTERS et al. 2023).

**Remarks:** *Atelopus guacharo* sp. n. fills the observed distributional gap of almost 200 km between the southernmost known *Atelopus* from the Cordillera Oriental (*A. petriruizi*) and various species from the southern Cordillera Central (Fig. 1). Nothing is known about the natural history of the new species. Vocalizations and larval stages of *A. guacharo* sp. n. remain unknown.

## Discussion

*Atelopus* taxonomy is challenging, as intraspecific character variation can be larger than interspecific variation in some species (LÖTTTERS et al. 2022). On the other hand, populations with conserved morphology can comprise well distinguished species, when studied in an integrative frame addressing external morphology, osteology, bioacoustics, larval features and molecular genetics (PLEWNIA et al. 2024). LÖTTTERS et al. (2025) conclude that both ‘splitting’ and ‘lumping’ might be warranted to advance *Atelopus* taxonomy. *Atelopus guacharo* sp. nov. is described on morphological and osteological features and its closest relative (based on phenetic similarity and geographic proximity) is likely the (also) poorly studied *A. guitarraensis*. The two, as far known, are separated by a distance of more than 300 km airline and occupy different habitats in distinct drainage systems of the Cordillera Oriental (Fig. 1) that are of different geological age (see MORENO-SÁNCHEZ et al. 2020). *Atelopus guacharo* sp. n. occurs in cloud forest at about 1950 m asl in the Río Magdalena catchment of the much older Garzón massif, while *A. guitarraensis* lives in paramo at about 3400 m a.s.l. in the Orinoco river catchment of the Quetame massif. Because highland *Atelopus*, especially in cloud forests, have rather limited distributions and elevational ranges are rather restricted to one habitat type (LÖTTTERS 1996, LÖTTTERS et al. 2023, 2025), we conclude that the specific distinctness of *A. guacharo* sp. n. is warranted.

Describing a species based on a single specimen inherently limits our understanding of intraspecific variation, sexual dimorphism, and ontogenetic changes. Nevertheless, in the case of highly threatened groups like *Atelopus*, naming distinct lineages from singletons can be crucial to facilitate conservation efforts. We encourage a redescription of *Atelopus guacharo* should additional material, especially males or tadpoles, become available in the future.

So far, phylogenetic relationships are poorly known for Colombia’s Andean *Atelopus*. One reason is that ancient DNA sequencing is particularly challenged due to the lack of comparative molecular data for any of the species from the Cordillera Oriental and adjacent Cordillera Central except non-topotypic material assigned to *A. lozanoi* and

*A. subornatus*, with most of the relevant congeners considered ‘possibly extinct’ (LÖTTERS et al. 2023, 2025). Currently, ancient DNA sequencing is an emerging yet costly approach that is capable of generating mitochondrial fragments based on target enrichment or high-throughput shotgun sequencing (e.g. SCHERZ et al. 2020, GRANT et al. 2025, PETZOLD et al. 2025). However, the lack of contemporary material for the relevant Harlequin Toads precludes phylogenetic reconstruction from ancient DNA sequencing due to ancient sequences being both short and ‘patchy’ in most cases. Nevertheless, with ever decreasing sequencing costs and further establishment of museomics, high-throughput might become increasingly feasible for generating entire ‘ancient phylogenies’ of Harlequin Toads in the future.

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- COLOMBIA: Cesar, Valledupar, Cuenca alta del Río Guatapurí, IAvH-Am-5641 (holotype), 5642, 5643 (paratopotypes); Parque Nacional Natural Sierra Nevada de Santa Marta, cumbre Hato del Medio, surroundings of Lago Curigua, IAvH-Am-5297 (paratype). *Atelopus ebenoides* complex: COLOMBIA: Huila, Páramo de las Papas, FMNH 69746 (holotype of *A. ebenoides*); La Plata, Río Bedón, cascada de San Nicolás, IAvH-Am-3920; 23 km E of Puracé, IAvH-Am-8; Cauca, Totoró, Malvasa, MCZ- Herp-A-117992 (field number HGD [= Humberto Granados-Díaz] 702), USNM 328737 (field number 722) (both paratopotypes of *A. eusebianus*); Totoró, ICN 7597-7608; Hacienda Alaska, ICN 33014; surroundings of Totoró, road from Totoró to Inzá, ICN 393-409; Parque Nacional Natural Puracé, San Rafael, IAvH-Am-526, 6284, 6285; Silvia, IAvH-Am-37, 7882; [near] Popayán, en páramo, IAvH-Am-9739-9741; San Sebastián, Parque Nacional Natural Puracé, Páramo de las Papas, km 5–6 on mule track from Valencia to Quinchana, IAvH-Am-6497, ICN 33407 (paratopotypes of *A. angelito*), 33408 (holotype of *A. angelito*), 33410–33415 (paratopotypes of *A. angelito*); Valle del Cauca, 7 km NE Tenerife, KU 169259. *Atelopus farci*: COLOMBIA: Cundinamarca, Albán, Granja de Padre Luna, ICN 14488 (holotype), ICN 14489–14533 (paratopotypes). *Atelopus guitarraensis*: COLOMBIA: Meta, Muzo de Sumapaz, Laguna La Guitarra, ICN 23348 (holotype), ICN 23349–23351, 32432, 32433 (cleared & stained), ICN 32530 (cleared & stained) (all paratopotypes). *Atelopus laetissimus*: COLOMBIA: Magdalena, Parque Nacional Natural Sierra Nevada de Santa Marta, San Lorenzo, IAvH-Am-3199, 3201, 3203, SW of the Estación Experimental San Lorenzo, ICN 410 (holotype), 415, 417, 418, 420, 1196, 1199, 33734–33737 (all paratopotypes). *Atelopus lozanoi*: COLOMBIA: Cundinamarca, La Calera, Parque Nacional Natural Chingaza, Páramo de Palacio, Quebrada Caliche, ICN 378–383, 384 (paratopotype), ICN 385, 386 (paratopotype), ICN 387, 388 (paratopotype), ICN 389 (paratopotype), ICN 390, 391, 392 (paratopotype), ICN 1125 (paratopotype), ICN 1126 (paratopotype), ICN 1127, 1128, 1254, 1255, 1296, 1297 (paratopotype), ICN 1299 (paratopotype), ICN 1300, 1301 (holotype), ICN 33376–33378 (paratopotypes); road from La Calera to Guasca, km 24–25 from Chuza, ICN 21147, 21148; Páramo de Palacio, IAvH-Am-3105, 3499; Parque Nacional Natural Chingaza, IAvH-Am-5904, 5905, 7167, 7168, 8635, 8636, 8667, 52, 6633, 14893, 14894, 14896, 14902, 9796, 9797, 9812. *Atelopus mandingues*: COLOMBIA: Cundinamarca, Junin, Reserva Biológica Carpanta, ICN 19569, 21155, 22351, 26102, 34286, 34716–34723 (paratopotypes), ICN 34959 (holotype), ICN 34286, 34287, 45149, 45150. *Atelopus marinkellei*: COLOMBIA: Boyacá, Páramo de Bijagual, between Tunja and Zetaquirá, approximately 2,660 m asl, USNM 150644 (holotype), USNM 150645–150646 (paratopotypes); Aquitania, Vadamondo, Alto Cusiana, IAvH-Am-51; Páramo de Toquilla, IAvH-Am-2324, 9657; KU 169141; Toquilla, Río Cusiana, IAvH-Am-3619, 3622, 3624–3626, 4356; Inspección de Policía de Toquilla, Páramo de Siscuní, IAvH-Am-6042–6055; unknown locality, ZFMK 85071, 85072. *Atelopus mittermeieri*: COLOMBIA: Santander, El Encino, Santuario de fauna y flora Guanentá, Alto Río Fonce, Quebrada Aguas Claras, ICN 52993 (holotype); Gambita, Bogotá, km 55–56 of Duitama-Charalá road, Río Guillermo, ICN 12752–12762, 12765–12769 (paratypes), ICN 7372, 7378, 7386, 7389, 7392, 7395, 7397, 7399. *Atelopus monohernandezii*: COLOMBIA: Santander, Virolín, Hacienda La Argentina, sitio Buena Vista, ICN 5366, 5386, 5388, 5425, 5426, 5496, 5497, 5526 (all paratopotypes), 5527 (holotype), 5680, 5709, 5991–5998, 6000, 6003, 6004 (all paratopotypes); trail from Zapatoca to San Vicente de Chucurí (Camino real de los Yariquíes), IAvH-Am-658–662; Velez, Quebrada La Lechera, tributary of Río Opón, USNM 144937–144940. *Atelopus muisca*: COLOMBIA: Cundinamarca, Junin, Reserva Biologi-

### Appendix 1

#### Material examined in addition to the new species

*Atelopus ardila*: COLOMBIA: Nariño, Pasto, Hacienda San Gerardo, ICN 450, 459, 469, 471, 473 (paratypes); Volcán Galeras, ICN 3406 (paratypes); La Laguna, San Fernando, ICN 3636–3638 (paratypes); 12 km E of Pasto, IAvH-Am-21. *Atelopus arsyecue*:

ca Carpanta, ICN 21158 (paratype), ICN 21159; Parque Nacional Natural Chingaza, surroundings of Laguna de Chingaza, IAvH-Am-16585-16591, 16619-16623; Parque Nacional Natural Chingaza, sector Chuza, IAvH-Am-5398-5407; Chuza reservoir, IAvH-Am-4630 (paratype), IAvH-Am 5045-5051 (paratypes); Chuza reservoir, Quebrada Babilonia, IAvH-Am-5091 (paratype); Chuza reservoir, Montaña del Cóndor, IAvH-Am-4648, 4649, 1650 (holotype), IAvH-Am 4652; km 6 from Chuza, sitio La Arboleda, IAvH-Am-4758 (paratype), 5030-5032; Parque Nacional Natural Chingaza, sector Río La Playa, IAvH-Am-5052-5059 (paratypes), 5080-5092 (paratypes). *Atelopus orcesi*: ECUADOR: Sucumbios, road from La Alegría to Sibundoy, MHNG 2684.75 (holotype), MHNG 2559.67 (paratopotype). *Atelopus pastuso*: COLOMBIA: Nariño, Cumbal: ICN 26570, 26574, 26580, 26585, 26586; ECUADOR: Carchi, Tulcán, MHNG 2258.64-2258.74, 2271.39, 2271.40. *Atelopus quimbaya*: COLOMBIA: Risaralda, Pereira, Parque Regional Ucumari, Cedral-Ceilan trail, ICN 23339 (holotype), ICN 23340-23347 (paratopotypes); Quindío, Salento, Reserva Forestal del Caño del Quindío, vereda Cocora or Río Arriba, Estación La Montaña, IAvH-Am-5191-5198, 7175, 7178. *Atelopus simulatus*: COLOMBIA: Cauca, road from Belalcázar to Cabaña La Termal of INDERENA, banks of Río Paez, ICN 6708-6710 (paratypes); km 41 on road from Belalcázar to Cabaña La Termal of INDERENA, ICN 7259-7260 (paratypes), 7261 (holotype), ICN 7262-7264 (paratopotypes), ICN 7265-7268; Vereda Río Sucio, km 66-67 and 55-56 on road from Popayan to Inzá, ICN 11331, 11332, 11346, 11347 (paratypes). *Atelopus subornatus*: COLOMBIA: Cundinamarca, Fusagasugá, ZFMK 28104 (lectotype), 28105 (paralectotype); Alto de Sibaté, ZFMK 28106 (paralectotype), 28107 (holotype of junior synonym *A. flaviventris*); km 7 on road from Bogotá to Sibaté, quebrada Agua Bonita, ICN 34275-34279.