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A partial taxonomic revision of *Atelopus* (Anura: Bufonidae) from the central and eastern Andes of Colombia

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Abstract

A partial taxonomic revision of *Atelopus* (Anura: Bufonidae) from the central and eastern Andes of Colombia. Harlequin toads, genus *Atelopus,* are a species-rich group of Neotropical anurans. Unparalleled declines and extinctions have hampered a thorough understanding of *Atelopus* systematics with numerous species only known from few specimens and a single or few localities. Major knowledge gaps particularly remain in the Cordillera Central and Cordillera Oriental of the Colombian Andes. In the central Andes, the names *Atelopus angelito, A. ebenoides,* and *A. eusebianus* have caused taxonomic confusion because populations can show vast plasticity, and populations assigned to these names were thought to occur in sympatry and parapatry. The virtual disappearance of all populations has prevented an integrative taxonomic assessment and rendered molecular approaches highly challenging. Based on adult and larval morphology, we propose that these populations correspond to a single polymorphic taxon and establish *A. ebenoides* as the senior synonym. In contrast, a form from the northern Cordillera Oriental has been considered a subspecies of the latter, *A. ebenoides marinkellei.* These geographically highly distant populations differ in morphology, particularly in tadpole characters and do not appear to represent conspecifics. We therefore elevate the form *marinkellei* to species rank and provide detailed morphological redescriptions and tadpole accounts for both *A. ebenoides* and *A. marinkellei.*

Keywords: *Atelopus ebenoides, Atelopus marinkellei,* Conservation, Harlequin Toads, Morphology, Synonymy, Tadpoles.

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Resumen

Revisión taxonómica parcial de *Atelopus* (Anura: Bufonidae) de los Andes centrales y orientales de Colombia. Los sapos arlequines, del género *Atelopus*, conforman un grupo de anuros neotropicales rico en especies. Declives y extinciones sin precedentes han dificultado una comprensión profunda de la sistemática de *Atelopus*, ya que numerosas especies se conocen sólo de unos pocos especímenes y una o pocas localidades. En particular, persisten importantes vacíos de conocimiento sobre las especies de la Cordillera Central y la Cordillera Oriental de los Andes colombianos. En los Andes centrales de Colombia, los nombres *Atelopus angelito*, *A. ebenoides* y *A. eusebianus* han causado confusión taxonómica, ya que las poblaciones pueden mostrar una gran variabilidad, además de que se considera que ocurrían en simpatría y parapatría. La desaparición virtual de todas las poblaciones ha impedido hasta ahora una evaluación taxonómica integrativa, resultando en que implementar enfoques moleculares sea altamente desafiante. Utilizando la morfología de adultos y larvas, sugerimos que estas poblaciones corresponden a un único taxón polimórfico y establecemos a *A. ebenoides* como el sinónimo principal. En contraste, una forma del norte de la Cordillera Oriental ha sido previamente considerada como una subespecie de *A. ebenoides*, *A. ebenoides marinkellei*. Sin embargo, estas poblaciones geográficamente muy distantes difieren en morfología, particularmente en caracteres del renacuajo y no parecen ser el mismo taxón. Por tanto, elevamos la forma *A. e. marinkellei* al rango de especie y proporcionamos redescripciones morfológicas detalladas y descripciones de renacuajos tanto para *A. ebenoides* como para *A. marinkellei.*

Palabras clave: *Atelopus ebenoides*, *Atelopus marinkellei*, Conservación, Morfología, Renacuajos, Sapos arlquines, Sinonimia.

Resumo

Revisão taxonômica parcial de *Atelopus* (Anura: Bufonidae) dos Andes centrais e orientais da Colômbia. Sapos-arlequins, gênero *Atelopus*, constituem um grupo diverso de anuros neotropicais. Declínios populacionais sem precedentes e extinções dificultaram uma compreensão abrangente da sistemática do grupo, resultando em diversas espécies conhecidas apenas por poucos espécimes e localidades restritas. Lacunas significativas de conhecimento persistem especialmente na Cordilheira Central e na Cordilheira Oriental dos Andes colombianos. Nos Andes centrais, os nomes *Atelopus angelito*, *A. ebenoides* e *A. eusebianus* geraram confusão taxonômica, uma vez que as populações apresentam grande plasticidade, além de populações atribuídas a esses nomes terem sido consideradas como simpátricas ou parapátricas. O desaparecimento de todas essas populações têm impedido uma avaliação taxonômica integrativa e tornado abordagens moleculares altamente desafiadoras. Com base na morfologia de adultos e larvas, sugerimos que essas populações correspondem a um único táxon polimórfico, estabelecendo *A. ebenoides* como o sinônimo sênior. Em contraste, indivíduos da porção norte da Cordilheira Oriental têm sido considerados uma subespécie deste último, *A. ebenoides marinkellei*. No entanto, essas populações, geograficamente muito distantes, diferem em morfologia, especialmente em características dos girinos, e não parecem pertencer à mesma espécie. Assim, elevamos *marinkellei* ao status de espécie e fornecemos redescrições morfológicas detalhadas e descrições dos girinos para *A. ebenoides* e *A. marinkellei*.

Palavras-chave: *Atelopus ebenoides, Atelopus marinkellei,* Conservação, Girinos, Morfologia, Sapos-arlequins, Sinonímia.

Introduction

Harlequin toads, genus *Atelopus,* are a species-rich group of true toads (Bufonidae) and have radiated over large parts of Central and tropical South America. Harlequin toad diversity peaks in the Andean cloud forests and paramos of Colombia (Lötters 1996, Rueda-Almonacid *et al.* 2005, Lötters *et al.* 2023, 2025, Velásquez-Trujillo *et al.* 2024). In this region, however,

Atelopus taxonomy is particularly poorly resolved and further challenged by the virtual absence of most populations since the 1980s, when unparalleled declines hit the genus (La Marca *et al.* 2005, Lötters *et al.* 2023). As a result, several taxa are known only from a few specimens and a single locality, likely resulting in an underestimation of both within- and between-species diversity (Lötters *et al.* 2023, 2025, Plewnia *et al.* 2025). The problem here is that a limited and spatially restricted sampling favors oversplitting as natural variation along a geographic gradient remains underestimated (Herrera-Lopera *et al.* 2025). Overlooked synonymy could in turn result in an overestimation of the species under serious threat, misguiding conservation prioritization (Dufresnes *et al.* 2023, Mahony *et al.* 2024).

Four species of *Atelopus* have been described from a relatively small area of the Cordillera Central (Figure 1) in the Departments of Cauca and adjacent Huila, east of Popayán (Rivero 1963, Rivero and Granados-Díaz 1993, Ruíz-Carranza and Osorno-Muñoz 1994, Ardila-Robayo and Ruíz-Carranza 1998): (1) *Atelopus angelito* Ardila-Robayo and Ruíz-Carranza, 1998 from "San Sebastián, Inspección de policía Valencia, km 5–6 on mule track from Valencia to Quinchana (Páramo de las Papas)," based on a series of nine individuals; (2) *A. ebenoides* Rivero, 1963 from the "Páramo de las Papas," based on a single specimen; (3) *A. eusebianus*

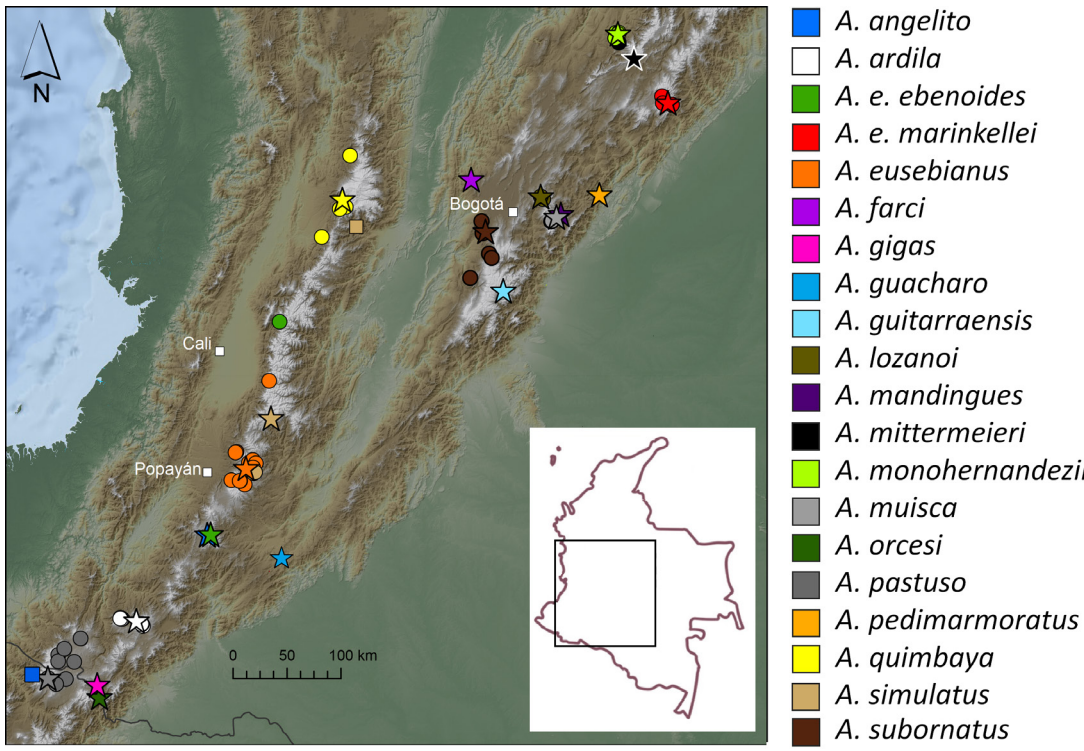

Figure 1. Distribution of species of *Atelopus* from the southern central and eastern Andes of Colombia (inset) and adjacent Ecuador discussed in this paper. Type localities are indicated by stars, additional localities by dots in the same color and localities of uncertain taxonomic status by squares in the color of the closest resembling taxon. Note that the symbols of the type localities of *A. angelito* and *A. ebenoides* partly overlap.

Rivero and Granados-Díaz, 1993 from "Municipio de Totoró, Malvasa," based on ca. 18 specimens (the exact number of specimens remains unclear because of errors with regard to the field number HGD 921, which appears twice under different collection sites and dates; Rivero and Granados-Díaz 1993: 12); (4) *A. simulatus* Ruíz-Carranza and Osorno-Muñoz, 1994 from "Municipio Belalcázar, km 11 on the road from Belalcázar to Tóez," based on a series of 30 specimens. While the latter is a humid montane forest species that is similar to *A. orcesi* Coloma, Duellman, Almendáriz, Ron, Terán-Valdez, and Guayasamin, 2010 and *A. quimbaya* Ruíz-Carranza and Osorno-Muñoz, 1994, the others are all known from paramo and subparamo habitats. They highly resemble each other, and in their original descriptions, taxonomic justifications are only briefly discussed and diagnoses barely consider other species.

For a form from the Páramo de Bijagual in the northern Cordillera Oriental, Department of Boyacá (Figure 1), subspecific status was suggested, *A. ebenoides marinkellei* Cochran and Goin, 1970. Several authors have commented on the taxonomic status either suggesting conspecificy or distinct species status, but without providing comparative evidence or taking formal taxonomic action (Kattan 1986, Rivero and Granados-Díaz 1993, Lötters 1996, Ruíz-Carranza *et al.* 1996, Coloma 1997, Rueda-Almonacid *et al.* 2005, Frost 2025).

The situation is complicated further because taxonomic decisions are best made using an integrative approach. In anuran amphibians, this approach includes external and internal larval and adult characters and bioacoustics, as well as molecular genetic data (cf. Padial *et al.* 2010). For many *Atelopus* that have virtually disappeared, it is highly challenging to obtain molecular genetics from old, formalin-fixed museum material. Particularly for Andean Colombian harlequin toads, (so far) barely any populations have been included in phylogenetic approaches, and topotypic sequences are yet missing for all species. Phylogenetic placement of particular populations is therefore insufficient to resolve taxonomic issues for the Colombian Andean forms (Lötters *et al.* 2025). As a result, forensic taxonomy is limited to external and internal morphology, which is best studied using 'next generation' approaches in anatomy such as synchrotron scanning of soft and hard tissues and electron microscopy of larval forms (cf. Boistel *et al.* 2011, 2013, Dias and Anganoy-Criollo 2024).

We reexamined adult and larval material related to *A. angelito, A. ebenoides ebenoides* Cochran and Goin, 1970, and *A. eusebianus* across their distributional ranges and suggest *A. ebenoides* as a senior synonym for them. In contrast, we elevate the subspecies *A. ebenoides marinkellei* from the Cordillera Oriental, Department of Boyacá, to species rank. We provide redescriptions and tadpole accounts for both *A. ebenoides* and *A. marinkellei.*

Materials 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), UIS (Universidad Industrial de Santander, Bucaramanga), USNM (National Museum of Natural History, Washington D.C.), and ZFMK (Zoologisches Forschungsmuseum Alexander Koenig, Bonn). Material examined in addition to the redescribed species is provided in Appendix I. We examined all type material of the species revised in this paper. However, for *A. eusebianus,* we could only trace and study two paratopotypes (MCZ-Herp-A-117992, USNM 328737). This is because in the original description, no museum vouchers but only field numbers were provided for all paratypes, rendering the destiny of

paratypes unclear. The holotype, given as ICN 20010 in the original description, could neither be traced during visits at ICN in 1995 (SL) nor in 2017 (JPR), 2022, and 2024 (AP, PB, CH, JPR, SL) and does not appear in the collection files. Actually, this collection number is not attributed to any specimen.

Sex was determined as described in Coloma *et al.* (2000) based on the presence of eggs in females and nuptial pads and vocal slits in males. Measurements were taken to the nearest 0.1 mm with manual calipers and are given in mm as mean ± one standard deviation. Abbreviations are as follows: SVL, snout–vent length; TIBL, tibia length; FOOT, foot length; HLSQ, 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 and SW were measured according to Bravo-Valencia and Rivera-Correa (2011) and ITNA according to Lötters *et al.* (2025). All other definitions of measurements of adults follow Gray and Cannatella (1985). Tadpole measurements follow the abbreviations for adults where applicable with the addition of LTRF, labial tooth row formula. The foot webbing formula was taken in the manner of Savage and Heyer (1997). Finger nomenclature follows Fabrezi and Alberch (1996) and Coloma *et al.* (2010). We refer to the terms coni and spiculae as defined in Coloma *et al.* (2010).

We further studied external morphology and anatomy of the buccopharyngeal cavity in tadpoles of *Atelopus ebenoides* (from topotypic populations of *A. angelito* and *A. eusebianus*), and *A. marinkellei.* For imaging of buccopharyngeal cavities, one individual per species was manually dissected following Wassersug (1976) and prepared and imaged with scanning electron microscopy (SEM) following Dias and Anganoy-Criollo (2024). Terminology of tadpole characters follows Wassersug (1976, 1980), Lötters *et al.* (2022), and Dias and Anganoy-Criollo (2024).

Results

Atelopus ebenoides Rivero, 1963
Ebony harlequin toad
(Figures 2–5, 6A, 7A–C, E, 8A–B)

Atelopus ebenoides Rivero, 1963: 120, Figures 6, 9, holotype FMNH 69746 from "Páramo de las Papas, 3,600 m [above sea level], [Departamento de] Huila, Colombia." Kattan 1986: 653, Rivero and Granados Díaz 1993: 17, Ruíz-Carranza, Ardila-Robayo and Lynch 1996: 366, Coloma 1997: Appendix IV, Acosta-Galvis 2000: 293, Rueda-Almonacid, *et al.* 2005: 70, Bernal and Lynch 2008: 22, Lötters *et al.* 2023: Appendix 1, Frost 2025, Lötters *et al.* 2025: Appendix 2.

Atelopus ebenoides ebenoides Cochran and Goin 1970: 122, Lynch 1993: 84, Lötters 1996: 24, Rueda-Almonacid, Lynch, and Amézquita 2004: 112.

Atelopus eusebianus Rivero and Granados-Díaz, 1993: 12, Figures 1–3, holotype ICN 20010 from "Malvasa, Municipio de Totoró, [Departamento de] Cauca, Colombia". Ruíz-Carranza and Osorno-Muñoz 1994: 165, Lötters 1996: 26, Ruíz-Carranza, Ardila-Robayo, and Lynch 1996: 366, Coloma 1997: Appendix IV, Ardila-Robayo and Ruíz-Carranza 1998: 283, Acosta-Galvis 2000: 293, Rueda-Almonacid, Lynch, and Amézquita 2004: 185, Rueda-Almonacid *et al.* 2005: 71, Bernal and Lynch 2008: 23, Hernández-Córdoba *et al.* 2014: 682, Lötters *et al.* 2023: Appendix 1, Frost 2025, Lötters *et al.* 2025: Appendix 2.

Atelopus angelito Ardila-Robayo and Ruíz-Carranza, 1998: 281, Figures 1–4, holotype ICN 33408 from "Colombia, Departamento de Cauca, Municipio San Sebastián, Inspección de policía Valencia, ca Km. 5–6 por camino de herradura de Valencia a Quinchana, 2900–3000 m" above sea level. Acosta-Galvis 2000: 293, Osorno-Muñoz, Ardila-Robayo, and Ruíz-Carranza 2001: 517, Rueda-Almonacid *et al.* 2005: 56, Bernal and Lynch 2008: 22, Coloma *et al.* 2010: 34, Lötters *et*

al. 2023: Appendix 1, Frost 2025, Lötters *et al*. 2025: Appendix 2.

Atelopus ebenoides complex—Plewnia *et al.* 2025: 269.

Holotype.—Colombia: Departamento de Huila, Páramo de las Papas (approximately 01.935° N, 76.608° W); approximately 3600 m a.s.l.; Oct. 1951; leg. Philip Hershkovitz; FMNH 69746, an adult female.

Additional material examined.—Colombia: Departamento de Huila, La Plata, Río Bedón, cascada de San Nicólas, IAvH-Am-3920; Departamento de Huila, La Plata, Río Bedón basin, IAvH-Am-6282; Departamento de Huila, 23 km E of Puracé, IAvH-Am-8; Departamento de Cauca, Totoró, Malvasa, MCZ-Herp-A-117992 (field number HGD [= Humberto Granados-Diaz] 702), USNM 328737 (field number 722) (both paratopotypes of *A. eusebianus*); Departamento de Cauca, Totoró, ICN 7597-7608; Departamento de Cauca, Portachuelo, Vereda Loma Alta, Hacienda Alaska, 1 km SW of Laguna de Calvache, ICN 32946–33012, 33128 (tadpoles); Departamento de Cauca, Hacienda Alaska, ICN 33014; Departamento de Cauca, surroundings of Totoró, road from Totoró to Inzá, ICN 393–409; Departamento de Cauca, km 3 on road from Totoró to Inzá, detour to Corrales, ICN 33015, 33126 (tadpoles); Departamento de Cauca, km 3 on road from Totoró to Inzá, vereda Betania, Quebrada Betania, ICN 33208 (tadpoles); Departamento de Cauca, km 7 on road from Totoró to Inzá, vereda La Pedrera, Quebrada Gallinazo, ICN 33207 (tadpoles, not used for morphological description); Departamento de Cauca, Parque Nacional Natural Puracé, San Rafael, IAvH-Am-526, 6284, 6285; Departamento de Cauca, km. 4.5 Northeast of Silvia, IAvH-Am-37, 7882; Departamento de Cauca, [near] Popayán, en páramo, IAvH-Am-9739–9741; Departamento de Cauca, San Sebastián, Parque Nacional Natural Puracé, creek near the headwaters of Rio Caquetá, ICN 33215 (tadpoles, not used for morphological description); Departamento de Cauca, 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*); Departamento de Valle del Cauca, 7 km NE Tenerife, KU 169259; Departamento de Cauca, Totoro, km 55–56 on the road from Popayán to Inzá, ICN 11303 and 11305 (tadpoles, not used for morphological description).

Definition.—*Atelopus ebenoides* is placed in the genus *Atelopus* based on: presence of supratympanic crest; absence of parotid gland, tympanic membrane; annulus tympanicus not visible or absent; presacrals I and II fused; gastromyzophorous tadpole with LTRF 2/3 (Coloma 1997). It is defined by the combination of the following characters: (1) A large species with SVL 35.0 ± 1.47, $N = 5$, in males and 44.0 ± 5.39, $N = 10$, in females; (2) robust body (SW/SVL 0.28 ± 0.016, $N = 5$, in males and 0.28 ± 0.027, $N = 10$, in females) with (3) relatively short legs (TIBL/SVL 0.37 ± 0.012, $N = 5$, in males and 0.35 ± 0.028, $N = 10$, in females) and (4) projected snout, moderately protruding beyond apex of lower jaw, acuminate in dorsal view in males; truncate snout, barely protruding beyond apex of lower jaw, round in dorsal view in females; (5) columella and tympanic membrane absent, annulus tympanicus not visible; (6) phalangeal formula of hand 2-2-3-3, basal, fleshy webbing present between first two fingers on hand; (7) first finger long (THBL/HAND 0.61 ± 0.030, $N = 5$, in males and 0.66 ± 0.029, $N = 10$, in females); (8) phalangeal formula of foot 2-2-3-4-3, foot webbing formula **I**0 to $^1/_2$—0 to 1**II**0 to 1—$^1/_2$ to 1**III**$^1/_2$ to $1^1/_2$—2 to 3**IV**2 to 3—0 to 2**V**; (9) dorsal and lateral skin on body and limbs densely covered with large, round warts with those on flanks, humerus, and femur bearing conical tips or spiculae in most specimens; ventral surfaces strongly areolate to granular, gular area granular; (10) vertebral

column, neural processes, sacral diapophyses, and urostyle not visible through the skin; (11) in preservative, dark brown to black dorsal surfaces with cream, yellowish, tan, reddish brown, or greenish irregular markings, in some populations light pattern predominant with little, diffuse dark brown to black pattern only, laterally dark brown to black with some intrusions of light dorsal pattern and white to cream warts in some specimens, most specimens present a light band between eye and upper lip, sometimes reduced to a light 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 soles yellowish cream to cream brown with small dark

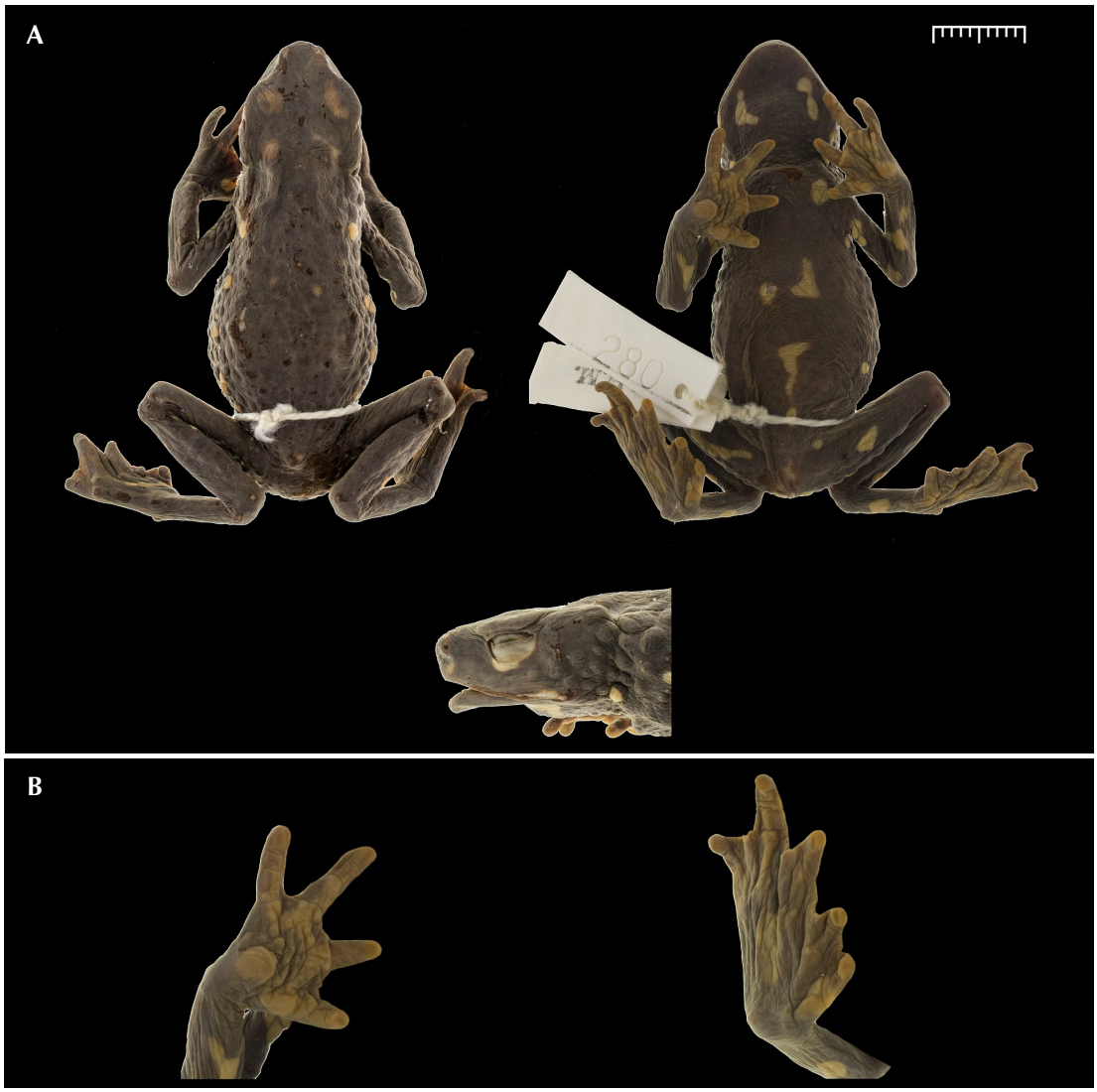

Figure 2. Female holotype of *Atelopus ebenoides* (FMNH 69746) (**A**) in dorsal, ventral and lateral views, scale 10 mm; (**B**) ventral surfaces of right hand and foot. Photographs by Rachunliu Kamei.

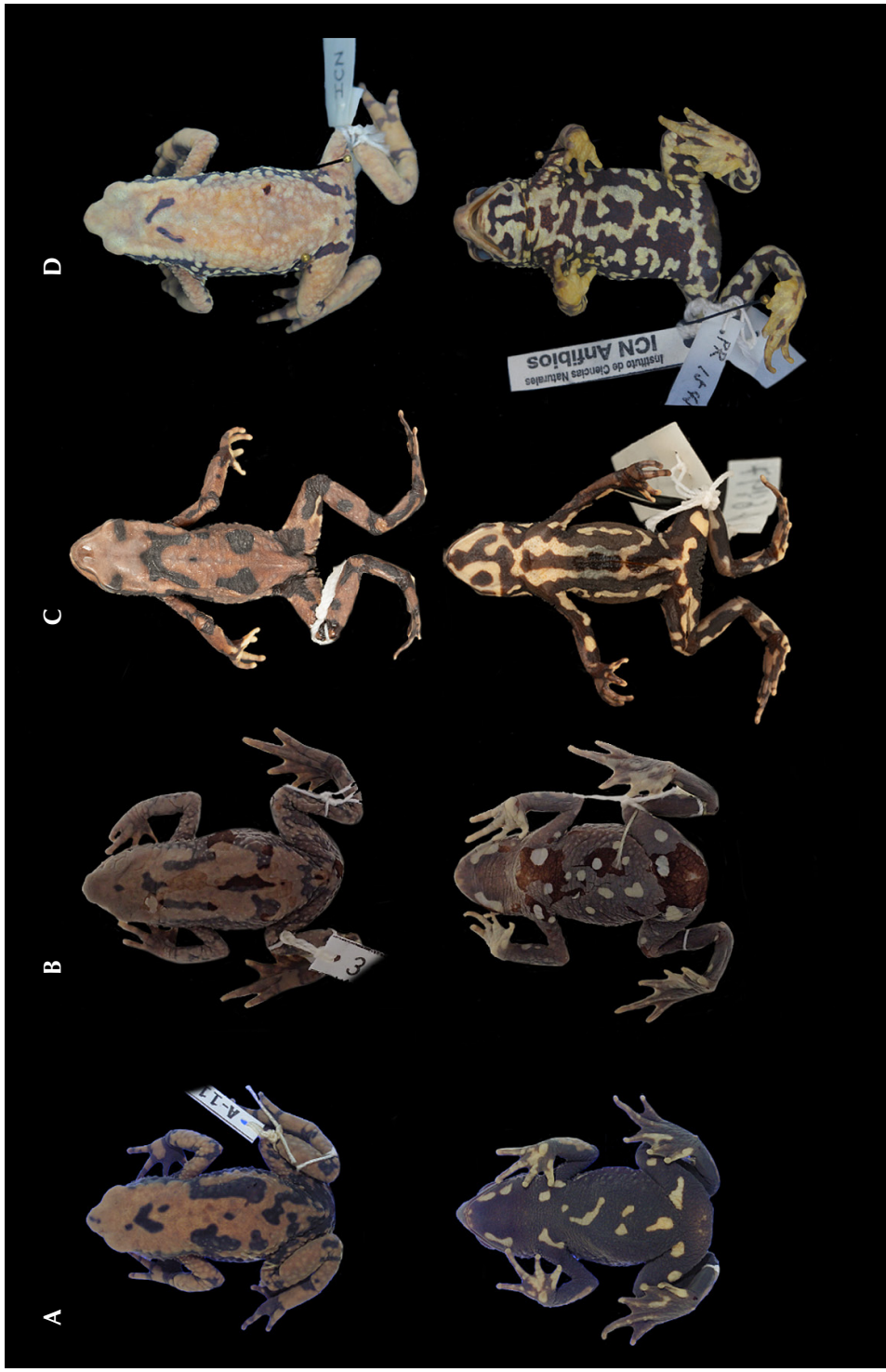

Figure 3. From left to right, female paratopotypes each in dorsal and ventral views of *Atelopus eusebianus:* (**A**) MCZ-Herp-A-117992, (**B**) USNM 328737*;* and *Atelopus angelito:* (**C**) IAvH-Am-6497, (**D**) ICN 33413. Not to scale. Photographs by MCZbase, Harvard University (2024), Addison Wynn, Amadeus Plewnia and Philipp Böning.

Figure 4. Variation of material in dorsal and ventral views attributed to *Atelopus ebenoides:* (**A**) IAvH-Am-3920; and *A. eusebianus:* (**B**) IAvH-Am-6285, (**C**) IAvH-Am-37, (**D**) IAvH-Am-6284, (**E**) ICN 395, (**F**) ICN 394. Not to scale. Photographs by Christopher Heine and Philipp Böning.

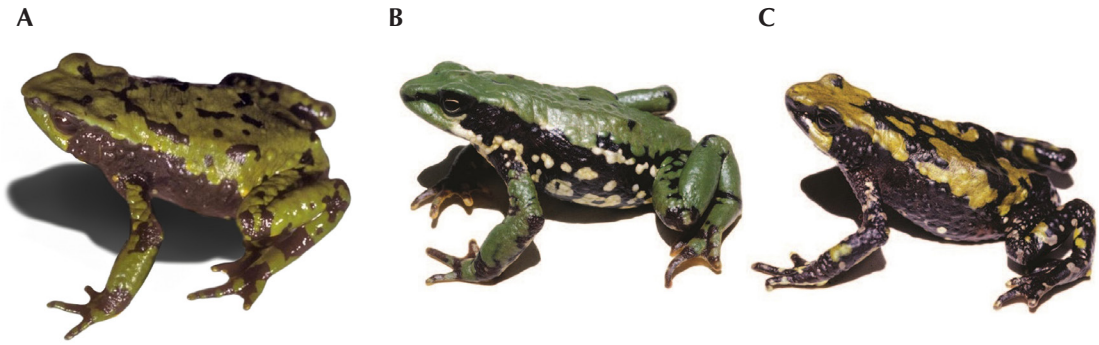

Figure 5. Variation of coloration in *Atelopus ebenoides:* (**A**) Páramo de las Hermosas, Departamento Valle del Cauca (KU 169259); (**B**) Páramo de las Papas, Departamento Cauca (holotype of *A. angelito,* ICN 33408); (**C**) Departamento Cauca (exact locality unknown). Not to scale. Photographs by (A) William E. Duellman, KU Herpetology Digital Archive (KUDA), and (B, C) reproduced from Rueda-Almonacid *et al.* (2005: 56, 74).

irregular markings; tongue whitish to cream; (12) in life, dark pattern black, light dorsal pattern yellow to green; lateral warts white in some specimens; light ventral pattern whitish to yellow; (13) tadpoles in preservative with light markings (some larger than tadpole EYDM) on brownish dorsum.

Diagnosis.—Atelopus ebenoides (Figures 2–5, 6A, 7A–C, E, 8A–B, Table 1) can be readily distinguished from all other described species by the combination of relatively large size, presence of poorly developed fleshy webbing between first and second fingers, truncate, round snout in females; moderately projected, acuminate snout in males, skin covered with large, round warts on dorsum, limbs, and flanks with most specimens having spiculae present on flanks and limbs, and in preservative dark brown to black dorsal surfaces with cream, yellowish, tan, reddish brown, or greenish irregular markings, in some populations light pattern predominant with little diffuse dark brown to black pattern only, laterally dark brown to black with some intrusions of light dorsal pattern and white to cream warts in some specimens, most specimens present a light band between eye and upper lip, sometimes reduced to a light 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 soles yellowish cream to cream brown with small dark irregular markings.

Atelopus ebenoides is phenotypically most similar to *A. ardila* Coloma, Duellman, Almendáriz, Ron, Terán-Valdez, and Guayasamin, 2010, *A. gigas* Coloma, Duellman, Almendáriz, Ron, Terán-Valdez, and Guayasamin, 2010, *A. ignescens* Cornalia, 1849 (including its junior synonyms *Phryniscus laevis* Günther, 1858 and *A. carinatus* Andersson, 1945), *A. pastuso* Coloma, Duellman, Almendáriz, Ron, Terán-Valdez, and Guayasamin, 2010, *A. quimbaya* and *A. simulatus* from the Cordillera Central of Colombia and Ecuador, as well as *A. guacharo* Plewnia, Venegas-Valencia, Szepanski, Heine, Böning, Ramírez, and Lötters, 2025, and *A. marinkellei* from the Cordillera Oriental of Colombia.

It differs from *A. ardila* in lacking spiculae and coni in gular region (*vs.* present in females), in having large round warts on dorsum (*vs.* dorsum smooth, bearing minute stippling and posteriorly small coni), strongly areolate to granular ventral skin (*vs.* smooth) and light pattern on dark brown, black, or greenish tan dorsum and a dark venter with light markings in preservative (*vs.* uniform pale cream to black dorsum and uniform cream or yellowish venter).

Figure 6. The gastromyzophorous tadpoles of (**A**) *Atelopus ebenoides* (ICN 33126) and (**B**) *A. marinkellei* (ICN 33205) in preservative. Not to scale. Photographs by Philipp Böning.

Atelopus ebenoides is distinguished from *A. gigas* in having large round warts on dorsum (*vs.* dorsum mostly smooth, bearing few warts in some specimens), strongly areolate to granular ventral skin (*vs.* smooth) and light pattern on dark brown, black, or greenish tan dorsum and a dark venter with light markings in preservative (*vs.* uniform yellowish dorsum and uniform cream venter).

It can be distinguished from *A. ignescens* by the absence of spiculae and coni in gular and pectoral region (*vs.* spiculae and coni present in females and some males) and by having light dorsal pattern and a dark venter with light markings in preservative (*vs.* uniform black to dark brown dorsum and uniform cream, yellow, or light brown venter).

It differs from *A. pastuso* in having large round warts on dorsum (*vs.* dorsum mostly smooth, posteriorly bearing few warts in some specimens), strongly areolate to granular venter (*vs.* venter smooth to slightly areolate, but throat areolate) and in the presence of dark pattern on venter (*vs.* venter uniform cream).

Atelopus ebenoides differs from *A. quimbaya* and *A. simulatus* in having, in lateral view, a truncate snout barely protruding apex of lower jaw in females (*vs.* projected snout, protruding beyond apex of lower jaw), large round warts on dorsal surfaces and flanks (*vs.* dorsum smooth, toward flanks bearing small coni and spiculae, flanks bearing conical warts and spiculae, dorsal surfaces of limbs with round warts; some male specimens with warts on dorsum and a dorsolateral row of warts in *A. quimbaya*), ventral skin strongly areolate to granular (*vs.* venter smooth, but gular area areolate), basal fleshy webbing poorly developed between first and second fingers only (*vs.* extensive webbing between first and second fingers and often between third and fourth). In addition, it further differs from *A. quimbaya* in having dark pattern

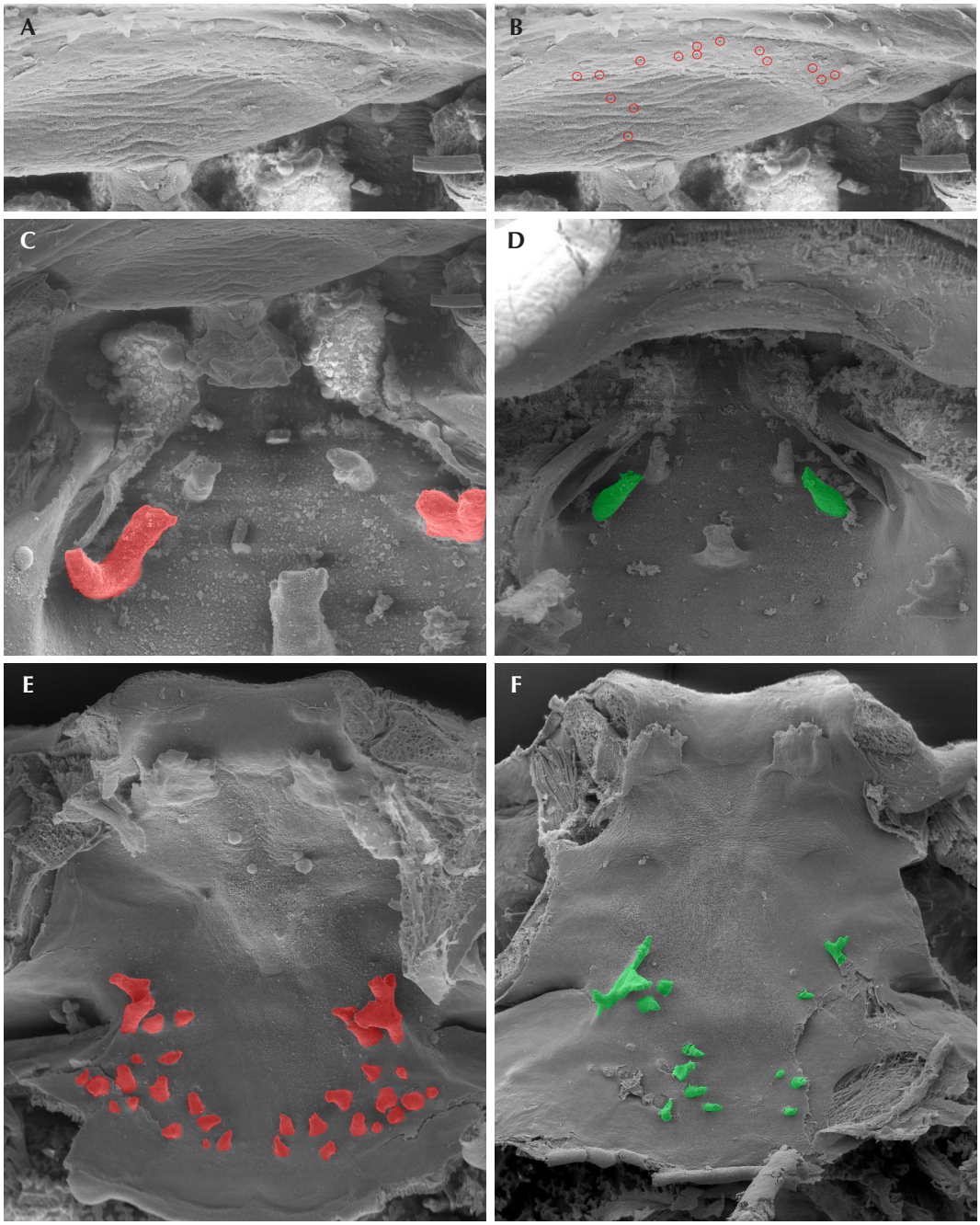

Figure 7. Comparative buccopharyngeal morphology of (**A–C**, **E**) *Atelopus ebenoides* (ICN 33126) and (**D**, **F**) *A. marinkellei* (ICN 34215): (**A**, highlighted in **B**) presence of secretory pits in the anterior region of the buccal roof of *A. ebenoides,* which are absent in *A. marinkellei* (not shown); the shape of postnarial papillae, (**C**) bifurcate in *A. ebenoides* and (**D**) simple in *A. marinkellei;* and the number of buccal floor papillae, (**E**) larger in *A. ebenoides* than in (**F**) *A. marinkellei.*

on venter (*vs.* venter uniform cream, with few small brown spots on throat in some male specimens).

It differs from *A. guacharo* in having a truncate snout, barely protruding apex of lower jaw in females (*vs.* snout projected, protruding beyond apex of lower jaw), adult female size (44.0 ± 5.39, *N* = 10 *vs.* 34.0, *N* = 1 in *A. guacharo*), spiculae present on flanks and limbs in most specimens (*vs.* absent), and by having cream, yellowish, tan, reddish brown, or greenish irregular markings in preservative (*vs.* body entirely dark except on head).

Atelopus ebenoides differs from *A. marinkellei* in coloration and pattern in life (light pattern extended over large part of dorsum in most populations, light pattern yellow to green *vs.* light spots scarce, mostly white, sometimes yellow in *A. marinkellei*), having extensive foot webbing (*vs.* feet only partially webbed; however, considerable within-population variation occurs in *A. ebenoides*) and spiculae restricted to flanks and dorsal surfaces of humerus and femur (*vs.* additionally present on dorsum in most specimens). The two species differ in osteology (sacrum and coccyx fused, posterolateral process of hyoid and scattered pits on dorsal surface of presacrals present *vs.* not fused, absent in *A. marinkellei;* Coloma 1997). The two species differ in larval pattern and coloration (in preservative, presence of light markings on brownish dorsum, always some markings larger than tadpole EYDM *vs.* uniformly dark or with minute light dots, smaller than tadpole EYDM in *A. marinkellei;* Figure 6); and in spiracle shape (conical *vs.* cylindrical in *A. marinkellei*). Further, *A. ebenoides* can be distinguished by having the vent tube distally free (*vs.* completely fused in *A. marinkellei*), the presence of secretory pits situated immediately posterior to the upper jaw sheaths (*vs.* absent in *A. marinkellei*), the presence of bifurcate postnarial papillae (not bifurcate in *A. marinkellei*), and the larger number of buccal roof papillae (16–17 *vs.* 7–8 in *A. marinkellei;* Figure 7).

Redescription of holotype.—Adult female (Figure 2). Body robust (SW/SVL 0.28); head robust, as long as wide (HLSQ/HDWD 0.99); snout truncate, slightly protruding beyond apex of lower jaw, rounded in dorsal view; nostrils directed laterally, protuberant, not visible in dorsal view, situated about four-fifths distance from eye to tip of snout in lateral view, situated above apex of lower jaw; canthus rostralis prominent, concave in dorsal view; loreal region concave; lips slightly flared; choanae large, rounded; tongue long, slightly broadened posteriorly, 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 well defined, slightly convex in dorsal view, straight in lateral view, longer than EYDM, no externally visible exostosis present, pretympanic crest well defined, about the size of EYDM; vertebral column, neural processes, sacral diapophyses, and urostyle not visible through the skin.

Limbs short (TIBL/SVL 0.36); relative length of toes I < II < III < V < IV, phalangeal formula of foot 2-2-3-4-3, webbing formula of toes **I**0-0**II**0-$^{1}/_{2}$**III**$^{1}/_{2}$-3**IV**3-$^{1}/_{2}$**V**; tarsal fold absent; foot about as long as tibia; outer metatarsal tubercle round, well defined, inner metatarsal tubercle oval, flat; supernumerary plantar tubercles indistinct; subarticular tubercles on toes distinct, rounded; tips of toes rounded, digital pads distinct; toes and fingers lack lateral fringes; relative length of fingers I < II < IV < III; phalangeal formula of hand 2-2-3-3; basal fleshy webbing poorly developed between first two fingers on hand only; palmar tubercle round, large, well defined; thenar tubercle oval, well defined; supernumerary palmar tubercles present; subarticular tubercles of digits poorly defined, evident on third finger only; tips of fingers rounded, not widened.

Dorsal and lateral skin on body and limbs densely covered with large, round warts, coni and spiculae absent; ventral surfaces, palms and soles strongly areolate, granular in gular area, chest and femur.

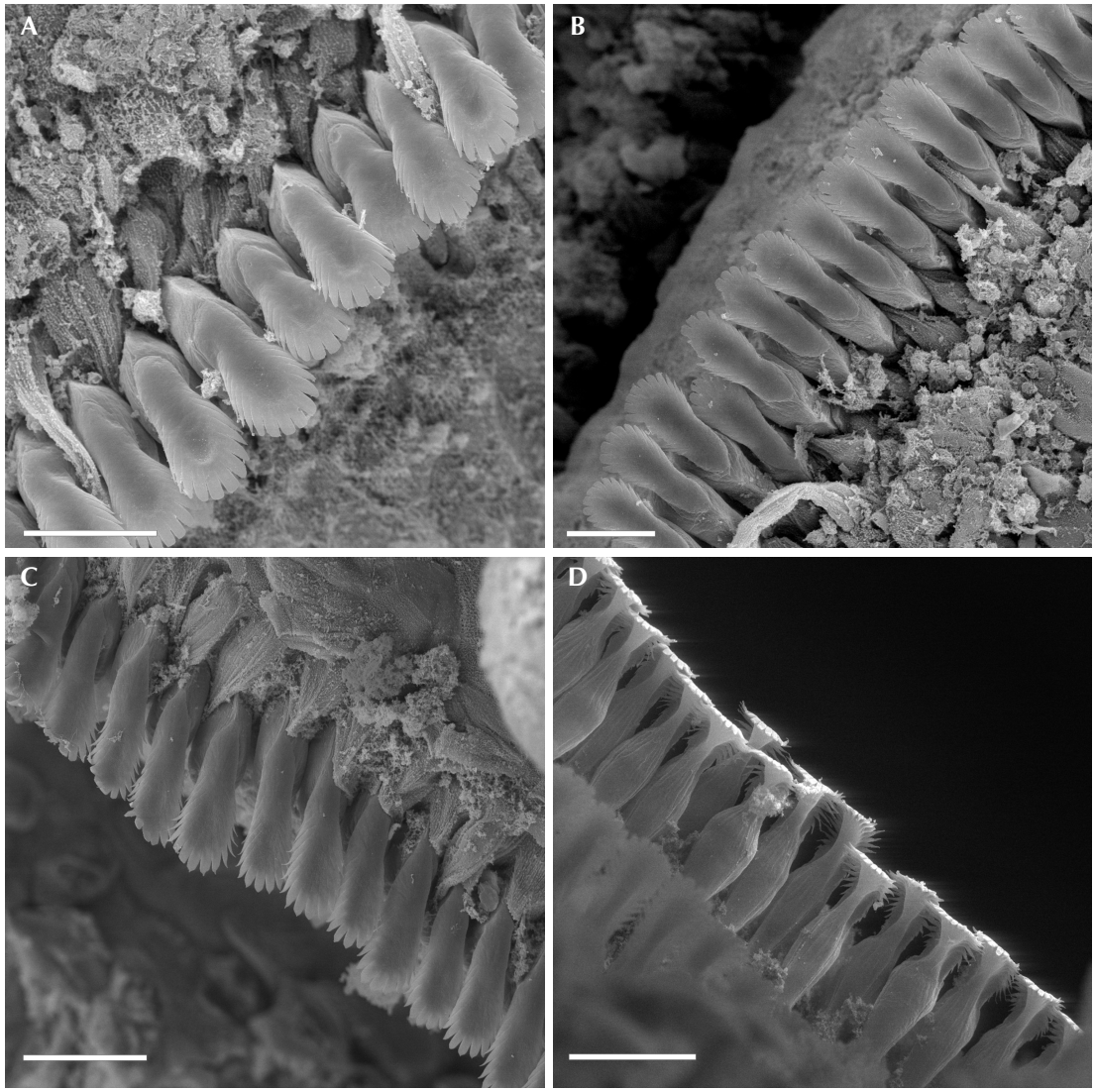

Figure 8. Scanning electron microscope images of the labial teeth (= keratodonts) in (**A**, **B**) dorsal view in *Atelopus ebenoides* (ICN 33126) and in (**C**) dorsal and (**D**) ventral view in *A. marinkellei* (ICN 34215). Scale 20 µm.

Coloration in preservative.—Surfaces of body and limbs brownish black with irregular brownish to yellowish cream spots on dorsum and flanks, cream irregular marks on ventral surfaces of body, limbs and throat; palms and soles brownish cream; tongue cream.

Coloration in life.—Unknown.

Measurements (in mm).—SVL 49.7, TIBL 17.8, FOOT 17.1, HLSQ 13.5, ITOR 4.6, HDWD 13.6, EYDM 5.1, EYNO 3.8, ITNA 9.2, HAND 11.5, THBL 7.7, SW 13.8, FAL 13.4, TIBL/SVL 0.36, SW/SVL 0.28, HLSQ/SVL 0.27, FAL/SVL 0.27, HLSQ/HDWD 0.99, THBL/HAND 0.67.

Variation.—Meristic variation is provided in

Table 1. Specimens from numerous localities in the Puracé area (including the type material of *A. angelito* and *A. eusebianus*) generally correspond to the description above. Sexual dimorphism is apparent with males being smaller than females (Table 1), having keratinized nuptial pads in the dorsal surface of the first and to a lesser extent second fingers and having a projected snout, which protrudes beyond apex of lower jaw, acuminate in dorsal view (*vs.* truncate snout, barely protruding beyond apex of lower jaw, round in dorsal view in females). Considerable variation occurs in foot webbing between specimens (**I**0 to $^{1}/_{2}$-0 to 1**II**0 to 1-$^{1}/_{2}$ to 1**III**$^{1}/_{2}$ to 1$^{1}/_{2}$-2 to 3**IV**2 to 3-0 to 2**V**), which does not follow a geographic signal but can be observed within localities. The large round warts on dorsum are densely distributed in most specimens (with e.g., IAvH-Am-6284 from San Rafael, Parque Nacional Natural Puracé, completely covered in warts) but less dense in some of the specimens from San Sebastián, Parque Nacional Natural Puracé, Páramo de las Papas, km 5–6 on mule track from Valencia to Quinchana, which could be related to a preservation artifact to some extent. Coni and spiculae are present on most specimens but vary in their extent from covering flanks, humerus and femur (e.g., IAvH-Am-37 and 7882 from Silvia) to being restricted to the tympanic area (e.g., ICN 396, 397 from the surroundings of Totoró, road from Totoró to Inzá) or being absent (FMNH 69746, holotype of *A. ebenoides,* IAvH-Am-6284 from San Rafael, Parque Nacional Natural Puracé).

In preservative (Figures 2–4), the dark pattern can vary from almost completely extending over the body (FMNH 69746, holotype of *A. ebenoides,* IAvH-Am-3920 from La Plata, Río Bedón, Cascada de San Nicólas) to being restricted to few small patches only (ICN 33407, paratopotype of *A. angelito,* 33408 holotype of *A. angelito,* 33410–33415 paratopotypes of *A. angelito*); similarly, there is variation in the extent of light markings in ventral coloration; lateral warts black in most specimens but whitish in material from San Sebastián, Páramo de las Papas, km 5–6 on mule track from Valencia to Quinchana (e.g., IAvH-Am-6497, ICN 33407, paratopotypes of *A. angelito,* ICN 33408, holotype of *A. angelito*).

In life (Figure 5), light dorsal markings range from yellow to green.

Tadpoles.—We studied larval series of *A. ebenoides* collected from Portachuelo and the Totoró to Inzá road, Department of Cauca, partially topotypic to its junior synonym *A. eusebianus* (ICN 33126 [used for SEM], 33128, 33208). We further studied a series from San Sebastián, Department of Cauca, topotypic to its junior synonym *A. angelito* (ICN 34211 [used for SEM]). They belong to the gastromyzophorous ecomorphological guild of anuran larvae (*sensu* Altig and Johnston 1989).

External morphology (Figure 6A): in dorsal view, body oval, widest between eye and spiracle; snout rounded. In profile, body depressed (height 2/3 body width), flattened ventrally. Eyes dorsolateral, relatively large (diameter about half of tadpole IOD). Nares large, dorsolateral, elongate, with a weak rim, tadpole ITNA slightly smaller than IOD. Spiracle sinistral, lateral, conical, directed posteroventrally, closer to the vent tube than to the snout, free from the body wall, positioned below midline of body. Digestive tract coiled; switchback point laterally dislocated from the center of abdominal region. Abdominal sucker sub-circular and occupying about three quarters of body length. Vent tube short, medial, cylindrical, distally free from the tail. Tail musculature poorly developed; tail muscle does not reach tail tip. Tail fins about equal in height; dorsal fin originating at the body–tail junction. Tail tip rounded. Oral disc enlarged, positioned and directed ventrally, not emarginate, with a single, continuous, lateral row of rounded, marginal papillae; large gap in papillae present in the lower lip; few submarginal papillae present in both lips. LTRF 2/3 A1 = A2, P1 = P2 = P3. Jaw sheaths present, weakly serrate, keratinized; upper jaw sheath arch-shaped; lower jaw sheath V-shaped. Body and

head of each labial tooth (= keratodont) marked by a constriction; teeth distally enlarged, spatulated, multicuspidate (Figure 8A–B).

According to Marcillo-Lara *et al.* (2020), coloration, especially presence vs. absence of light markings on different parts of the body or tail represent useful characters to distinguish species. All tadpoles of *A. ebenoides* examined possess in preservative numerous irregular light markings (always some markings larger than tadpole EYDM) on a brownish dorsum. The caudal musculature is brown with light dots in some specimens (smaller or equal to tadpole EYDM) and rarely forms a distinct tail band. Tail fins are translucent with thin brown vessels (Figure 6A). In life, coloration was black with cream or white spots or blotches (field notes of P. M. Ruíz-Carranza at ICN on ICN 33207, 33208, 33215, 33126). A more detailed description is available for tadpole lots ICN 11303 and 11305 (field notes of P. M. Ruíz-Carranza at ICN): "Black body with a few white dots, anterior ca. two–thirds of tail black, posterior third transparent (= tail fin) and cream (= musculature). Leg-bearing specimens having cream soles; body dark brown laterally with sagittal region brown, anterior two-thirds of tail metallic dark brown; transparent with abundant black melanophores on the posterior third; the dark-brown musculature continues to the apex."

Buccopharyngeal morphology: buccal roof (Figures 7A–C) triangular. Prenarial arena semi-elliptical, with a pendulum-like papilla and several secretory pits. Internal nares elliptical, transversally oriented; posterior valve free, lacking marginal projection. Vacuities present, circumscribed by margins of inner nares, presenting ciliated cells. Postnarial arena diamond-shaped, two conical, tall postnarial papillae; first pair shorter than second pair; second pair bifurcate. Lateral ridge papillae short, triangular, bifurcated. Median ridge tall, conical, papilla-like. Buccal roof arena poorly defined, completely lacking papillae or pustulation. Dorsal velum medially discontinued, devoid of papillae or projections, arch-shaped. Buccal floor (Figure 7E) triangular. Single pair of flat, wide, infralabial papillae; tip crenulated. Lingual bud poorly defined; lingual papillae absent. Buccal floor arena bell-shaped; 16–17 buccal floor arena papillae present. Buccal floor arena lacking pustulations. Prepocket papillae and pustulation absent. Buccal pockets deep, wide, oblique slit-shaped. Ventral velum present; spicular support inconspicuous; medial notch absent; marginal projections present; secretory pits poorly developed; secretory ridges present. Branchial basket triangular, short, poorly developed, wider than long. Three filter cavities, well-defined, partially covered by ventral velum.

Distribution.—Atelopus ebenoides is known from several localities on the summits of the southern Cordillera Central at approximately 2500–4700 m a.s.l. (Figure 1), where the species inhabits paramo and subparamo environments. The range reaches from Páramo de las Papas northwards to the town of Silvia in the Departamentos de Huila and Cauca (cf. Rivero 1963, Rivero and Granados-Díaz 1993, Ardila-Robayo and Ruíz-Carranza 1998, Rueda-Almonacid *et al.* 2004, Rueda-Almonacid *et al.* 2005), with additional records from Páramo de las Tinajas (Hernández-Córdoba *et al.* 2014) and the Páramo de Las Hermosas (KU 169259; Figure 5A), both in the Departamento de Valle del Cauca as well as a single record from Departamento del Tolima (UIS-A 5510). The entire geographic range from north to south encompasses about 200 km (Figure 1) and it remains to be studied if the species is continuously distributed.

Conservation status and threats.—Atelopus ebenoides as well as its junior synonyms, *A. angelito* and *A. eusebianus,* are currently listed as Critically Endangered (Possibly Extinct) under criterion D of the IUCN Red List of Threatened Species (IUCN SSC Amphibian Specialist Group 2017, 2019, 2021). Despite numerous visits to historic localities, the species has not been seen in any of its localities since 2007 (Lötters *et al.* 2023,

Table 1. Meristic variation in *Atelopus ebenoides* including type and additional material of the species and its junior synonyms *A. angelito* and *A. eusebianus*: mean ± standard deviation followed by the range in parentheses. Measurements are based on males ICN 33408 (holotype of *A. angelito*), 33410-33411 (paratopotypes of *A. angelito*), IAvH-Am-6284, 9740 and females MCZ 117992 (paratopotype of *A. eusebianus*), ICN 33413 (paratopotype of *A. angelito*), IAvH-Am-37, 526, 3920, 6282, 6285, 6497 (paratopotype of *A. angelito*), 7882, 9739. For individual measurements see Appendix II.

	Males (*N* = 5)	**Females (*N* = 10)**
SVL	35.0 ± 1.47 (32.8-36.4)	44.0 ± 5.39 (33.4-55.2)
TIBL	12.9 ± 0.45 (12.3-13.5)	15.4 ± 1.55 (11.5-17.2)
FOOT	14.6 ± 0.75 (13.7-15.3)	16.3 ± 1.99 (12.5-19.3)
HLSQ	10.5 ± 0.97 (8.8-11.1)	12.2 ± 1.15 (10.1-13.7)
IOD	3.7 ± 0.36 (3.3-4.1)	4.5 ± 0.44 (3.8-5.1)
HDWD	10.2 ± 0.58 (9.5-11.0)	11.6 ± 0.88 (9.5-12.6)
EYDM	3.2 ± 0.26 (2.9-3.5)	3.6 ± 0.26 (3.2-4.1)
EYNO	2.7 ± 0.25 (2.3-3.0)	3.3 ± 0.35 (2.8-3.8)
ITNA	3.8 ± 0.16 (3.6-4.0)	4.0 ± 0.37 (3.5-4.4)
FAL	10.2 ± 0.24 (10.0-10.5)	11.7 ± 1.09 (9.4-12.8)
HAND	8.6 ± 0.51 (8.1-9.3)	10.2 ± 1.34 (7.7-11.8)
THBL	5.3 ± 0.51 (4.6-5.8)	6.7 ± 0.75 (5.4-8.0)
SW	9.8 ± 0.21 (9.5-10.0)	12.0 ± 1.56 (9.1-14.0)
TIBL/SVL	0.37 ± 0.012 (0.36-0.39)	0.35 ± 0.028 (0.28-0.38)
SW/SVL	0.28 ± 0.016 (0.26-0.30)	0.28 ± 0.027 (0.22-0.30)
HLSQ/SVL	0.30 ± 0.034 (0.25-0.34)	0.28 ± 0.029 (0.21-0.30)
FAL/SVL	0.29 ± 0.012 (0.27-0.31)	0.27 ± 0.022 (0.22-0.29)
HLSQ/HDWD	1.03 ± 0.085 (0.93-1.12)	1.06 ± 0.059 (0.92-1.11)
THBL/HAND	0.61 ± 0.031 (0.57-0.63)	0.66 ± 0.029 (0.61-0.71)

AP unpublished data 2019, Gustavo Pisso Florez and Jesse Erens, pers. comm. 2024). The majority of the range of this species lies within the well-protected Parque Nacional Natural Puracé. Nearly all Andean harlequin toads from high Andean ecosystems have been proven highly susceptible to chytridiomycosis caused by *Batrachochytrium dendrobatidis* Longcore, Pessier, and Nichols, 1999 (*Bd*), considered a main driver of extinctions in *Atelopus* (e.g., La Marca *et al.* 2005, Lips *et al.* 2008, Flechas *et al.* 2017, Olson *et al.* 2021, Lötters *et al.* 2023). Although *Bd* has not been detected directly from *A. ebenoides,* at least in the year 2021 *Bd* was confirmed on syntopic species in its geographic range (Laura Victoria Rivera Jaimes, pers. comm. 2022) and has likely led to its decline. Climate change may become an additional threat to *Atelopus ebenoides* in the near future (Lötters *et al.* 2023).

Etymology.—Rivero (1963) did not provide a *derivatio nominis.* The epithet *ebenoides* (Greek adjective) means ebony-like or resembling ebony and apparently refers to the almost entirely black coloration of the holotype, resembling ebony wood.

Remarks.—Coloma (1997) studied osteological characters of some species of *Atelopus,* including *A. eusebianus* (syn. ad *A. ebenoides*). The author confirmed fusion of presacrals I and II, absence of a columella, and phalangeal formulae of hand and foot being 2-2-3-3 and 2-2-3-4-3, respectively.

The central and northern Andean paramos and subparamos of Colombia, Ecuador, and Peru are inhabited by species of *Atelopus* with a toad-like appearance. Using molecular genetics and morphology, they are phylogenetically related and can be referred to as an *A. ignescens* clade with various subclades (Guayasamin *et al.* 2010, Lötters *et al.* 2025). However, we lack molecular genetic data for most Colombian Andean harlequin toads.

The coordinates of the type localities for the names *A. angelito* and *A. eusebianus* are likely in error in the original descriptions. In *A. angelito,* the coordinates (01.850° N, 76.783° W) correspond to a site northwest of the town of San Sebastián. Instead, the type locality on the Valencia–Quinchana mule trail is located at the approximate corrected coordinates of 01.9152° N, 76,6248° W. The coordinates for the type locality of *A. eusebianus* (02.05° N, 76.4° W) that were given in the original description correspond to a site in the Departamento del Huila, 51.3 km south of the type locality Totoró. However, this locality is likely incorrect, with the correct type locality of the species being 02.50° N, 76.4° W, close to the village of Totoró.

Coloma *et al.* (2010), Coloma (2002), and Coloma and Duellman (2025) assigned material from Ecuador, Carchi province, Reserva Ecológica El Ángel, Comunidad de Morán, Río La Plata (KU 178417) to *A. angelito* (i.e., syn. ad *A. ebenoides*) based on an examination of the type series. The record lies more than 180 km airline southwest of the type locality of *A. angelito,* separated by the distributional ranges of *A. ardila* and *A. pastuso.* Besides allocation to this species, the authors noted subtle differences in webbing, size, and coloration. We were unable to examine the KU specimens and additional material from the same general area reported as *Atelopus* sp. 14 by Rueda-Almonacid *et al.* (2005). Additional examination is required to confirm its potential conspecificy with *A. ebenoides.*

Atelopus marinkellei Cochran and Goin, 1970
Marinkelle's harlequin toad
(Figures 6B, 7D, F, 8C–D, 9–10)

Atelopus ebenoides marinkellei Cochran and Goin, 1970: 123, plate 18G–H, holotype USNM 150644 from "Páramo [de] Vijagual [= Páramo de Bijagual], [Departamento de] Boyacá, Colombia." Lynch 1993: 84, Lötters 1996: 24, Ruíz-Carranza, Ardila-Robayo, and Lynch 1996: 366, Acosta-Galvis 2000: 293, Rueda-Almonacid, Lynch, and Amézquita 2004: 112, Acosta-Galvis *et al.* 2006: 282, Galvis-Cordoba and Carvajalino-Fernández 2025: 852.

Atelopus ebenoides (non Rivero)—Péfaur and Duellman 1980: 52, Coloma 1997: Appendix IV, Lynch and Mayorga 2011: 239.

Atelopus marinkellei—Rivero and Granados Díaz 1993: 17, Rueda-Almonacid *et al.* 2005: 71, Lötters *et al.* 2023: Appendix 1, Frost 2025, Lötters *et al.* 2025: Appendix 2, Plewnia *et al.* 2025: 269.

Holotype.—Colombia: Departamento de Boyacá, Páramo de Bijagual, between Tunja and Zetaquirá (approximately 05.36° N, 73.28° W); approximately 2660 m a.s.l.; unknown date; leg. Hno. Nicéforo María; USNM 150644, an adult female.

Additional material examined.—Colombia: Departamento de Boyacá, Páramo de Bijagual, USNM 150645–150646 (paratopotypes); NHMW 32716/1; Departamento de Boyacá, Aquitania, Vadamondo [= Vadohondo], Alto Cusiana, IAvH-Am-51; Departamento de Boyacá, Vadohondo, Páramo de Toquilla, IAvH-Am-2324, 9657; KU 169141; Departamento de Boyacá, Páramo de Toquilla, ICN 34215 (tadpoles); Departamento de Boyacá, Toquilla,

Río Cusiana, IAvH-Am-3619, 3622, 3624–3626, 4356; Departamento de Boyacá, Aquitania, Alto Río Cusiana, Páramo de Toquillo, km 53–57 on road from Sogamoso, ICN 33205 (tadpoles); Departamento de Boyacá, Inspección de Policía de Toquilla, Páramo de Siscunsí, IAvH-Am-6042–6055; Departamento de Boyacá, unknown locality, ZFMK 85071, 85072.

Definition.—Atelopus marinkellei is placed in the genus *Atelopus* based on: presence of supratympanic crest; absence of parotid gland and tympanic membrane; annulus tympanicus not visible or absent; presacrals I and II fused; gastromyzophorous tadpole with LTRF 2/3 (Coloma 1997). It is defined by the combination of the following characters: (1) A large species with SVL 32.7 ± 1.10, $N = 5$, in males and 43.5 ± 1.95, $N = 5$, in females; (2) robust body (SW/SVL 0.26 ± 0.007, $N = 5$, in males; 0.28 ± 0.013, $N = 5$, in females) with (3) relatively short legs (TIBL/SVL 0.37 ± 0.0106, $N = 5$, in males; 0.33 ± 0.014, $N = 5$, in females) and (4) projected acuminate snout, protruding beyond apex of lower jaw (most prominent in males); (5) columella and tympanic membrane absent, annulus tympanicus not visible; (6) phalangeal formula of hand 2-2-3-3, basal, fleshy webbing present between first two fingers on hand; (7) first finger long (THBL/HAND 0.61 ± 0.053, $N = 5$, in males; 0.64 ± 0.044, $N = 5$, in females); (8) phalangeal formula of foot 2-2-3-4-3, foot webbing formula **I**0 to $^{1}/_{2}$-$^{1}/_{2}$ to 1**II**0 to 1-1 to 2**III**$^{1}/_{2}$ to 1$^{1}/_{2}$-2 to 3**IV**2 to 3-0 to 1**V**; (9) dorsal and lateral skin on body and limbs densely covered with large, round warts extending to varying extent on dorsum, additionally covered to a variable extent with large spiculae that are often clustered on lateral warts; ventral surfaces areolate with minute coni on venter, chest, and throat in some specimens; (10) vertebral column, neural processes, sacral diapophyses, and urostyle not visible through skin; (11) in preservative, overall brown to black, dorsally with whitish to yellowish cream dots (smaller than eye diameter) and occasionally irregular markings on dorsal surfaces (markings can be absent on extremities), with always a whitish mark immediately below eye; ventrally with whitish to yellowish cream blotches (up to about the size of eye diameter), sometimes including ventral surfaces of extremities; throat sometimes almost entirely whitish cream; sole and palm with whitish cream or yellowish tan marks, metatarsal and metacarpal tubercles always whitish cream or yellowish tan, other tubercles and tips of toes and fingers sometimes whitish cream or yellowish tan; tongue cream; (12) in life, black with white and/or yellowish spot pattern as described; (13) in preservative, tadpoles uniformly dark or with few minute light dots on dorsum (smaller than tadpole EYDM) with cream band on proximal half of tail.

Diagnosis.—Atelopus marinkellei (Figures 6B, 7D, F, 8C–D, 9–10, Table 2) can be readily distinguished from all other described species by the combination of relatively large size, presence of poorly developed fleshy webbing between first and second fingers, truncate, acuminate snout projected (most prominent in males), dorsal and lateral skin on body and limbs densely covered with large, round warts extending to varying extent on dorsum, additionally covered at variable extent with large spiculae that are often clustered on lateral warts; ventral surfaces areolate with minute coni on venter, chest, and throat in some specimens, and in preservative entirely brown to black coloration with whitish to yellowish cream or dots (smaller than eye diameter) and occasionally irregular markings on dorsal surfaces, with always a whitish mark immediately below the eye, and whitish to yellowish cream blotches (up to about the size of eye diameter) on venter.

Atelopus marinkellei is phenotypically most similar to *A. ebenoides, A. guacharo, A. guitarraensis* Osorno-Muñoz, Ardila-Robayo, and Ruíz-Carranza, 2001, and *A. mittermeieri* Acosta-Galvis, Rueda-Almonacid, Velásquez-Álvarez, *et al*., 2006 from the Colombian Andes and *A. arsyecue* Rueda-Almonacid, 1994 from

Figure 9. Female holotype of *Atelopus marinkellei* (USNM 150644) in dorsal (left) and ventral views; scale 10 mm. Photographs by Stefan Lötters.

the Sierra Nevada de Santa Marta, Colombia.

Atelopus marinkellei differs from *A. ebenoides* (including its junior synonyms *A. angelito* and *A. eusebianus*) in coloration and pattern (light spots scarce, mostly white, sometimes yellow *vs.* light pattern extended over large part of dorsum in most populations, light pattern yellow to green in life in *A. ebenoides*) and presence of spiculae on dorsum in most specimens (*vs.* restricted to flanks and dorsal surfaces of humerus and femur). The two species can be distinguished by aspects of osteology (sacrum and coccyx not fused, posterolateral process of hyoid and scattered pits on dorsal surface of presacrals absent *vs.* fused, present in *A. ebenoides;* Coloma 1997).

The two species differ in larval features, i.e., coloration in preservative, uniformly dark or with minute light dots (smaller than tadpole EYDM) *vs.* presence of light markings (always some markings larger than tadpole EYDM) on dorsum in *A. ebenoides* (Figure 6B); and in spiracle shape (cylindrical *vs.* conical in *A. ebenoides*). Further, *A. marinkellei* can be distinguished by having the vent tube completely fused (*vs.* distally free in *A. ebenoides*), absence

of secretory pits situated immediately posterior to the upper jaw sheaths (*vs.* present in *A. ebenoides*), by the postnarial papillae not being bifurcate (bifurcate in *A. ebenoides*), and by the smaller number of buccal roof papillae (7–8 *vs.* 16–17 in *A. ebenoides;* Figure 7).

Atelopus marinkellei can be distinguished from *A. guitarraensis* by having feet only partially webbed (*vs.* fully webbed), dense presence of spiculae in most specimens (*vs.* absent) and, in preservative, presence of light dorsal pattern and light dots on venter up to EYDM size (*vs.* dorsally dark brown to black without pattern, venter in most female specimens yellow with little dark markings, throat, chest, and limbs dark brown).

It differs from *A. guacharo* in adult female size (43.5 ± 1.95, $N = 5$ *vs.* 34.0, $N = 1$ in *A. guacharo*), presence of spiculae in most specimens (*vs.* absent) and, in preservative, presence of light dorsal pattern and light dots on venter (*vs.* body entirely dark except on head).

It differs from *A. mittermeieri* in absence of red ventral coloration in life (*vs.* venter uniformly red with few small cream spots and a brown band on chest) and tadpole coloration [uniformly dark or with few minute light dots (smaller than tadpole EYDM) on dorsum *vs.* presence of light markings (larger than tadpole EYDM) in *A. mittermeieri;* Acosta-Galvis *et al.* 2006].

Atelopus marinkellei differs from *A. arsyecue* by smaller adult size (males ≤ 34.0 *vs.* ≥ 45.2, females ≤ 46.0 *vs.* ≥ 53.0), whitish or yellowish dorsal dots being larger (smaller than *vs.* equal to or larger than eye diameter), and by the presence of a whitish dot immediately below the eye (*vs.* absent).

Redescription of holotype.—Adult female (Figure 9). Body robust (SW/SVL 0.29); head robust, longer than wide (HLSQ/HDWD 1.09); snout acuminate, rounded in dorsal view, moderately protruding beyond apex of lower jaw; nostrils directed laterally, protuberant, not visible in dorsal view, situated about four–fifths distance from eye to tip of snout in lateral view, situated before apex of lower jaw; canthus rostralis prominent, straight in dorsal view; loreal region concave; lips slightly flared; choanae large, rounded; tongue long, slightly broadened posteriorly, 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 well defined, slightly convex in dorsal view, straight in lateral view, about as long as EYDM, no externally visible exostosis present, pretympanic crest indistinct; vertebral column, neural processes, sacral diapophyses, and urostyle not visible through the skin.

Limbs short (TIBL/SVL 0.34); relative length of toes I < II < III < V < IV, phalangeal formula of foot 2-2-3-4-3, webbing formula of toes **I**0-$^1/_2$**II**0-1**III**$^1/_2$-2**IV**2-0**V**; tarsal fold absent; foot slightly longer than tibia; outer metatarsal tubercle round, well defined, inner metatarsal tubercle oval, well defined; supernumerary plantar tubercles indistinct; subarticular tubercles on toes ill-defined, rounded; tips of toes rounded, digital pads distinct; toes and fingers lack lateral fringes; relative length of fingers I < II < IV < III; phalangeal formula of hand 2-2-3-3; basal fleshy webbing poorly developed between first two fingers on hand only; palmar tubercle round, large, well defined; thenar tubercle oval, well defined; supernumerary palmar tubercles and subarticular tubercles of digits poorly defined; tips of fingers rounded, not widened.

Dorsal skin covered with large spiculae (absent toward head and on arm, and most dense on posterior dorsum and femur); dorsolaterally and on flanks as well as dorsal surfaces of limbs covered with large, flat, and round warts with those on flanks and femur bearing one to many, often clustered, spiculae; ventral surfaces areolate with small coni on venter, chest, and posterior throat.

Coloration in preservative.—Overall brown with dorsally whitish cream dots (smaller than eye diameter) and occasionally irregular markings

Figure 10. *Atelopus marinkellei* in life from Vadohondo (Departamento Boyacá, Colombia, KU 169141). Photograph by William E. Duellman, KU Herpetology Digital Archive (KUDA).

on head, with a whitish mark immediately below the eye, spiculae gray; ventrally with whitish cream dots (most up to about the size of eye diameter) from throat to femur; sole and palm with whitish cream marks, metatarsal and metacarpal tubercles whitish cream, tips of toes and fingers tan.

Coloration in life.—Unknown.

Measurements (in mm).— SVL 43.4, TIBL 15.0, FOOT 17.2, HLSQ 12.9, ITOR 3.8, HDWD 11.8, EYDM 5.1, EYNO 3.1, ITNA 3.2, HAND 9.4, THBL 6.8, SW 12.7, FAL 11.7, TIBL/SVL 0.34, SW/SVL 0.29, HLSQ/SVL 0.30, FAL/SVL 0.27, HLSQ/HDWD 1.09, THBL/HAND 0.72.

Variation.—Meristic variation is provided in Table 2. Considerable variation in skin texture occurs with spiculae almost absent in some specimens (e.g., NHMW 32716), warts almost absent to predominant on dorsum, and ventral coni absent in most specimens with some having flat warts on the lateral parts of the venter (e.g., IAvH-Am-9657). Sexual dimorphism is apparent with males smaller than females, having keratinized nuptial pads in the dorsal surface of the first and to a lesser extent second finger, and having a more projected snout in lateral view.

Color and pattern in preservative show little variation with some specimens bearing irregular markings on dorsal surfaces and light circles instead of dots ventrally (e.g., IAvH-Am-6048). Dark color varies from brown to black.

In life (Figure 10), *A. marinkellei* is black with the light dots on dorsum white to yellow and those on flanks and venter white.

Tadpoles.—We examined larval series of this species from Department of Boyacá, Páramo de Toquilla (ICN 33205, ICN 34215). They belong to the gastromyzophorous ecomorphological guild of anuran larvae (*sensu* Altig and Johnston 1989).

External morphology (Figure 6B): in dorsal view, body oval, widest between eye and spiracle; snout rounded. In profile, body depressed (height 2/3 body width), flattened ventrally. Eyes dorsolateral, relatively large (diameter about half of tadpole IOD). Nares large, dorsolateral, elongate, with a weak rim, tadpole ITNA slightly smaller than IOD. Spiracle sinistral, lateral, cylindrical, directed posteroventrally, closer to the vent tube than to the snout, free from the body wall, positioned below midline of body. Digestive tract coiled; switchback point laterally dislocated from the center of abdominal region. Abdominal sucker sub-circular and occupying about three quarters of body length. Vent tube short, medial, cylindrical, completely fused to tail. Tail musculature poorly developed; tail muscle does not reach tail tip. Tail fins about equal in height; dorsal fin originating at body–tail junction. Tail tip rounded. Oral disc enlarged, positioned and directed ventrally, not emarginate, with a single, continuous, lateral row of rounded, marginal papillae; large gap in papillae present in lower lip; few submarginal papillae present in both lips. LTRF 2/3 A1 = A2, P1 = P2 = P3. Jaw sheaths present, weakly serrate, keratinized; upper jaw sheath arch-shaped; lower jaw sheath V-shaped. Body and head of each labial tooth (= keratodont) marked by a constriction; teeth distally enlarged, spatulated, multicuspidate (Figure 8C–D).

According to Marcillo-Lara *et al.* (2020),

Table 2. Meristic variation in *Atelopus marinkellei:* mean ± standard deviation followed by the range in parentheses. Measurements are based on males IAvH-Am 2324, 4356, 6047, 9657, NHMW 32716 and females IAvH 6045, 6046, 6050, 6055, USNM 150644 (holotype). For individual measurements see Appendix II.

	Males (*N* = 5)	**Females (*N* = 5)**
SVL	32.7 ± 1.10 (31.4–34.0)	43.5 ± 1.95 (41.0–46.0)
TIBL	12.2 ± 0.26 (11.8–12.5)	14.5 ± 0.37 (14.0–15.0)
FOOT	13.1 ± 0.28 (12.8–13.4)	16.2 ± 0.69 (15.3–17.2)
HLSQ	10.4 ± 0.29 (10.0–10.7)	12.6 ± 0.65 (11.5–13.2)
IOD	3.6 ± 0.29 (3.4–4.0)	3.8 ± 0.23 (3.5–4.0)
HDWD	9.4 ± 0.26 (9.0–9.7)	10.9 ± 0.54 (10.4–11.5)
EYDM	3.3 ± 0.28 (3.1–3.8)	3.9 ± 0.70 (3.4–5.1)
EYNO	2.6 ± 0.25 (2.4–3.0)	3.2 ± 0.27 (2.8–3.4)
ITNA	3.2 ± 0.17 (3.0–3.4)	3.7 ± 0.34 (3.2–4.0)
FAL	9.7 ± 0.42 (9.0–10.0)	11.6 ± 0.44 (11.0–12.0)
HAND	8.1 ± 0.44 (7.7–7.8)	10.1 ± 0.50 (9.4–10.6)
THBL	4.9 ± 0.19 (4.6–5.1)	6.5 ± 0.32 (6.0–6.8)
SW	8.5 ± 0.23 (8.3–8.8)	11.9 ± 0.64 (11.0–12.7)
TIBL/SVL	0.37 ± 0.011 (0.36–0.39)	0.33 ± 0.014 (0.32–0.35)
SW/SVL	0.26 ± 0.007 (0.25–0.27)	0.28 ± 0.013 (0.26–0.29)
HLSQ/SVL	0.32 ± 0.011 (0.30–0.33)	0.29 ± 0.008 (0.28–0.30)
FAL/SVL	0.30 ± 0.01 (0.28–0.31)	0.27 ± 0.013 (0.25–0.28)
HLSQ/HDWD	1.11 ± 0.040 (1.08–1.18)	1.16 ± 0.058 (1.09–1.23)
THBL/HAND	0.61 ± 0.053 (0.53–0.66)	0.64 ± 0.044 (0.62–0.72)

coloration, especially presence *vs.* absence of light markings on different parts of the body or tail do represent useful characters to distinguish species. All tadpoles of *A. marinkellei* studied are in preservative uniformly dark or show few minute light dots (always smaller than EYDM). The blackish brown caudal musculature has a complete or partially interrupted cream band on proximal half of tail. Tail fins are blackish brown on proximal half and translucent with blackish vessels on distal half (Figure 6B). In life, they were black with a white band on the proximal half of the tail (field notes of ICN 33205, J. D. Lynch at ICN).

Buccopharyngeal morphology: buccal roof triangular (Figure 7D). Prenarial arena semi-elliptical, with short, pendulum-like papilla; secretory pits absent. Internal nares elliptical, transversally oriented; posterior valve free, lacking marginal projection. Vacuities present, circumscribed by margins of inner nares, presenting ciliated cells. Postnarial arena diamond-shaped, two conical, tall postnarial papillae, subequal in size. Lateral ridge papillae short, triangular, bifurcated. Median ridge tall, conical, papilla-like. Buccal roof arena poorly defined, completely lacking papillae or pustulation. Dorsal velum medially discontinued,

devoid of papillae or projections, arch-shaped. Buccal floor triangular (Figure 7F). Single pair of flat, wide, infralabial papillae; tip crenulated. Lingual bud poorly defined; lingual papillae absent. Buccal floor arena bell-shaped; 7–8 buccal floor arena papillae present. Buccal floor arena lacking pustulations. Prepocket papillae and pustulation absent. Buccal pockets deep, wide, oblique slit-shaped. Ventral velum present; spicular support inconspicuous; medial notch absent; marginal projections present; secretory pits poorly developed; secretory ridges present. Branchial basket triangular, short, poorly developed, wider than long. Three filter cavities, well-defined, partially covered by ventral velum.

Distribution.—Atelopus marinkellei is known from several localities on the eastern versant of the Cordillera Oriental (Department of Boyacá) in the paramo complex comprising the Páramo de Siscunsí, Páramo de Pisba, Páramo de Toquilla, and Páramo de Bijagual, 2600–3650 m a.s.l. (cf. Rueda-Almonacid *et al.* 2004, 2005, Galvis-Cordoba and Carvajalino-Fernández 2025; Figure 1).

Conservation status and threats.—Atelopus marinkellei is currently listed as Critically Endangered under criterion D of the IUCN Red List of Threatened Species (IUCN SSC Amphibian Specialist Group 2024). Despite numerous visits to historic localities in the last 20 years (Lötters *et al.* 2023, AP unpublished data 2024, 2025), the species has only been seen three times in the area of the regional Natural Park of Paramo de Siscunsí-Ocetá at sites above 3,000 m a.s.l.: one individual was discovered each in May and October 2006 and most recently in April 2025 (Galvis-Cordoba and Carvajalino-Fernández 2025). The majority of the range of the species lies outside of protected areas with only Parque Nacional Natural Pisba covering the northernmost range (IUCN SSC Amphibian Specialist Group 2024). All Andean harlequin toads from high Andean ecosystems have been proven highly susceptible to chytridiomycosis caused by *Batrachochytrium dendrobatidis* (*Bd*), which is considered a main driver of extinctions in *Atelopus* (e.g., La Marca *et al.* 2005, Lips *et al.* 2008, Lötters *et al.* 2023). Although *Bd* has not been detected in *A. marinkellei* or syntopic species, wave-like mortality events that were likely induced by the pathogen have been reported (IUCN SSC Amphibian Specialist Group 2024). The species is affected by habitat modification, and invasive trout are widespread in its range (Lötters *et al.* 2023, Galvis-Cordoba and Carvajalino-Fernández 2025, AP unpublished data 2024, 2025). Climate change may become an additional threat to *Atelopus marinkellei* in the near future (Lötters *et al.* 2023).

Etymology.—Cochran and Goin (1970) named this form in honor of Cornelis Johannes Marinkelle (1925–2012), a Dutch-born biologist at the Universidad de Los Andes, Bogotá.

Discussion

Previously, *Atelopus eusebianus* was distinguished from *A. ebenoides sensu stricto* only by coloration in life, i.e., dorsally dark green, bluish green, or yellowish green with bluish markings and ventrally bluish with yellow markings *vs.* uniformly black (Rivero and Granados Díaz 1993). As shown in Figure 2, the only type specimen of *A. ebenoides* (FMNH 69746) is not uniformly black but bears small light markings (cf. Rivero 1963, Cochran and Goin 1970). *Atelopus angelito* was not compared to *A. ebenoides sensu stricto* in its original description, but to *A. eusebianus.* In the original description, it differs in having a slightly larger adult size despite broad overlap between measurements (female 41.0, $N = 1$; males 33.8 ± 0.95, range 33.0–34.8, $N = 6$ *vs.* in *A. eusebianus:* females 39.8 ± 5.24, range 33.0–45.0, $N = 12$; males 34.2 ± 1.4, range 32.5–36.1, $N = 6$ [cf. Rivero and Granado- Díaz 1993]), a slightly more webbed foot, coloration in life (ventrally white with irregular black markings *vs.* ventrally bluish with yellow markings) and lateral warts (large whitish *vs.* small black) (Ardila-Robayo and

Ruíz-Carranza 1998). Based on our comparative reexamination of type material and additional specimens from the general area, we conclude that adult size, webbing, skin texture, and coloration show high intrapopulation variation. We consider differences in these traits as given in the original description as within-species variation and place the names *A. angelito* and *A. eusebianus* in the synonymy of *A. ebenoides,* the oldest available name.

Lötters (1996) mentioned the possible species status of the form originally described as *A. ebenoides marinkellei* based on P. M. Ruíz (pers. comm.). Ruíz-Carranza *et al.* (1996) commented on the taxonomic status ("No hay evidencia que sea una subespecie de *A. ebenoides*" [There is no evidence that it is a subspecies of *A. ebenoides*]) but it is unclear if their intention was to suggest synonymy or to reject conspecificy. Coloma (1997) instead considered *A. ebenoides marinkellei* to be a possible junior synonym of *A. ebenoides,* while other authors gave full species status to it as *A. marinkellei* (e.g., Kattan 1986, Rivero and Granados-Díaz 1993, Rueda-Almonacid *et al.* 2005, Frost 2025). None of these authors provided any arguments based on comparative studies, but Vélez-Rodríguez and Ruíz-Carranza (1997) stated that tadpoles of *A. eusebianus* (syn. ad *A. ebenoides sensu stricto*) can be distinguished from those of *A. ebenoides marinkellei* by coloration. Our reexamination of tadpoles confirmed distinctive coloration and provided additional evidence. Unlike adult coloration, larval pattern and coloration have been considered species-specific discriminatory characters (e.g., Marcillo-Lara *et al.* 2020). Moreover, external larval traits as well as buccopharyngeal morphology clearly differentiate *A. ebenoides* from *A. marinkellei,* both in the presence/absence and number of traits, demonstrating, again, the value of larval morphology for bufonid taxonomy (Dias *et al.* 2024).

Particularly in the Cordillera Oriental, additional taxonomic revisions may become necessary in the future (Plewnia *et al.* 2025). Here, 13 taxa are currently recognized (Figure 1): *Atelopus minutulus* Ruíz-Carranza, Hernández-Camacho, and Ardila Robayo, 1988 and *A. petriruizi* Ardila-Robayo, 1999 from lower elevation forests on the Amazonian versant; *A. farci* Lynch, 1993, *A. guacharo, A. mittermeieri, A. monohernandezii* Ardila-Robayo, Osorno-Muñoz, and Ruíz-Carranza, 2002, and *A. subornatus* Werner, 1899 (with two junior synonyms, *A. echeverrii* Rivero and Serna, 1985 and *A. flaviventris* Werner, 1899) from montane forests on the western versant; and *A. guitarraensis, A. lozanoi* Osorno-Muñoz, Ardila-Robayo, and Ruíz-Carranza, 2001, *A. mandingues* Osorno-Muñoz, Ardila-Robayo, and Ruíz-Carranza, 2001, *A. marinkellei, A. muisca* Rueda-Almonacid and Hoyos, 1992, and *A. pedimarmoratus* Rivero, 1963 from subparamos and paramos (Rueda-Almonacid *et al.* 2005, Lötters *et al.* 2023, 2025, Frost 2025). While most of these species can be distinguished by external morphology, several names were coined for sympatric or parapatric populations from the Bogotá region (cf. Rueda-Almonacid *et al.* 2005), that only differ in adult coloration and pattern, although integrative data are lacking: *A. lozanoi, A. mandingues, A. muisca, A. pedimarmoratus,* and *A. subornatus.* Taxonomic decisions are challenging and best being made using high-throughput sequencing approaches for ancient DNA (e.g., Scherz *et al.* 2020, Grant *et al.* 2025). These types of studies may shed light on the central highland populations from the Cordillera Oriental as a next step in *Atelopus* systematics.

Conclusions

While recent taxonomic work has led to a steady increase of recognized harlequin toad species in some clades, poor morphologic descriptions and the disappearance of most populations have hampered a thorough understanding of alpha taxonomic relationships in Andean species of Colombia. Overlooked synonymy may misdirect conservation priorities. By synonymizing the polymorphic *Atelopus angelito* and *A. eusebianus* with *A. ebenoides sensu stricto* and elevating *A. marinkellei* to species level based on in-depth examination of adult and larval characters, we provide

redescriptions and take taxonomic action as a first step toward resolving the systematics of Andean harlequin toads of Colombia. Additional work, particularly ancient DNA sequencing, osteological examination, and larval morphology, will be required to resolve the remaining taxonomic challenges in the group.

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Appendix I. *Comparative specimens examined.*

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: Colombia: Cesar, Valledupar, Cuenca alta del Río Guatapurí, IAvH-Am-5641 (holotype), 5642, 5643 (paratopoypes); Parque Nacional Natural Sierra Nevada de Santa Marta, cumbre Hato del Medio, surroundings of Lago Curigua, IAvH-Am-5297 (paratype).

Atelopus farci: Colombia, Cundinamarca, Albán, Granja de Padre Luna, ICN 14488 (holotype), ICN 14489–14533 (paratopotypes).

Atelopus guacharo: Colombia, Huila, Parque Nacional Natural Cueva de los Guácharos, trail to cabaña 2, IAvH-Am-544 (holotype).

Atelopus guitarraensis: Colombia, Meta, Macizo 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 Biologica Carpanta, ICN 19569, 21155, 22351, 26102, 34286, 34716–34723 (paratopotypes), ICN 34959 (holotype), ICN 34286, 34287, 45149, 45150.

Appendix I. *Continued.*

Atelopus mittermeieri: Colombia: Santander, El Encino, Santuario de fauna y flora Guanentá, Alto Río Fonce, Quebrada Aguas Claras, ICN 52993 (holotype); Gambita, Bogotacito, km 55–56 of Duitama-Charala road, Río Guillermo, ICN 12752–12762, 12765–12769 (paratypes).

Atelopus muisca: Colombia: Cundinamarca, Junin, Reserva Biologica 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, Sucumbíos, road from La Alegría to Sibundoy, MHNG 2684.75 (holotype), MHNG 2559.67 (paratopotype).

Atelopus pastuso: 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); Quindio, Salento, Reserva Forestal del Caño del Quindio, 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 61–67 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.

Appendix II. *Individual measurements (in mm) of specimens of* Atelopus *included in Tables 1 and 2. For measurements of holotypes, see the redescriptions.*

Specimen	Species	Type status	Sex	SVL	TIBL	FOOT	HLSQ	IOD	HDWD	EYDM	EYNO	ITNA	FAL	HAND	THBL	SW
MCZ 117992	*A. ebenoides*	paratype (*eusebianus*)	female	43.6	15.4	16.1	12.5	4.2	11.7	3.2	2.9	3.8	10.9	11.1	7.3	12.9
ICN33413	*A. ebenoides*	paratype (*angelito*)	female	43.7	16.6	14.4	10.9	4.7	11.8	3.4	2.9	4.3	11.2	8.9	6	11.9
IAvH 6497	*A. ebenoides*	paratype (*angelito*)	female	33.4	11.5	12.5	10.1	4.1	9.5	3.4	2.8	3.5	9.4	7.7	5.4	9.1
IAvH 6282	*A. ebenoides*	N	female	55.2	15.4	16.1	11.5	3.8	11.7	3.6	3.1	4.2	12	10.5	7	11.9
IAvH 3920	*A. ebenoides*	N	female	46.6	17.2	19.3	13.6	4	12.5	4.1	3.6	4.4	12.7	11.8	8	14
IAvH 37	*A. ebenoides*	N	female	40.7	14.8	15.5	12.1	4.8	10.9	3.8	3.2	3.8	11.3	8.5	6	10.4
IAvH 7882	*A. ebenoides*	N	female	42.6	15.3	18	12	4.4	11.4	3.6	3.3	3.6	11.6	11	6.7	10.8
IAvH 526	*A. ebenoides*	N	female	46	16	16	13.7	4.6	12.6	3.7	3.4	4.4	12.8	10.2	6.7	13.8
IAvH 6285	*A. ebenoides*	N	female	44	15.8	18.4	13	5.1	11.7	3.9	3.8	3.5	12.8	11.2	7.1	12.7
IAvH 9739	*A. ebenoides*	N	female	43.8	16.3	17.1	12.8	5	12	3.7	3.7	4.2	12.6	10.8	7.1	12.9
IAvH 6284	*A. ebenoides*	N	male	36.1	13.2	15	11	4.1	10.5	3.5	3	4	10.5	8.7	5.5	9.8
IAvH 9740	*A. ebenoides*	N	male	32.8	12.8	13.8	11	4	10	3.3	2.6	3.6	10	8.1	4.6	9.8
ICN 33408	*A. ebenoides*	holotype (*angelito*)	male	34.3	12.3	15.3	11.1	3.8	9.9	2.9	2.7	3.9	NA	NA	NA	NA
ICN 33411	*A. ebenoides*	paratype (*angelito*)	male	36.4	13.5	15	10.6	3.3	11	3.2	2.7	3.7	10	9.3	5.8	9.5
ICN 33410	*A. ebenoides*	paratype (*angelito*)	male	35.4	12.9	13.7	8.8	3.4	9.5	2.9	2.3	3.9	10.2	8.4	5.3	10

Appendix II. *Continued.*

Specimen	Species	Type status	Sex	SVL	TIBL	FOOT	HLSQ	IOD	HDWD	EYDM	EYNO	ITNA	FAL	HAND	THBL	SW
IAvH-Am-6045	*A. marinkellei*	N	female	42.5	14.7	16	12.7	4	10.7	3.4	3.4	3.6	12	10.4	6.4	11.9
IAvH-Am-6046	*A. marinkellei*	N	female	44.8	14.4	16.4	12.8	3.6	11	3.6	3.4	4	12	10.2	6.6	11.7
IAvH-Am-6050	*A. marinkellei*	N	female	41	14	15.3	11.5	3.5	10.4	3.5	2.8	3.5	11	9.7	6	11
IAvH-Am-6055	*A. marinkellei*	N	female	46	14.6	16.2	13.2	4	10.7	3.7	3.4	4	11.3	10.6	6.7	12.2
IAvH-Am-2324	*A. marinkellei*	N	male	31.4	12.2	12.8	10	3.4	9.3	3.1	2.7	3.2	9.8	7.7	5.1	8.6
IAvH-Am-4356	*A. marinkellei*	N	male	32.7	12.3	13.3	10.7	3.5	9.5	3.2	2.5	3.4	10	8.7	4.6	8.3
IAvH-Am-6047	*A. marinkellei*	N	male	34	12.5	13	10.3	3.4	9.4	3.2	2.4	3.4	9.5	7.8	5	8.8
IAvH-Am-9657	*A. marinkellei*	N	male	33.6	12.1	13.4	10.6	4	9.7	3.8	2.4	3.2	10	8.4	5	8.7
NHMW 32716	*A. marinkellei*	N	male	31.9	11.8	12.8	10.6	13.6	9	3.4	3	3	9	7.8	5	8.3