



A new species of harlequin toad (Bufonidae: *Atelopus*) from Amazonian Ecuador

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Abstract. For nearly four decades, harlequin toads, genus *Atelopus*, have suffered unparalleled population declines. While this also results in limited understanding of alpha-taxonomic relationships, these toads face an urgent need for advances in systematics to inform conservation efforts. However, high intraspecific variation and cryptic diversity have hindered a comprehensive understanding of *Atelopus* diversity. This is particularly exemplified among Amazonian populations related to *A. spumarius*, where decades of taxonomic work have not been able yet to unravel relationships between the many forms, while the names coined so far have led to taxonomic confusion leaving numerous lineages unnamed. A recent comprehensive phylogenetic study has revealed new insights into the systematics of harlequin toads with an emphasis on Amazonian forms, identifying several unnamed lineages. We here describe one of these evolutionary lineages as a new species, restricted to the Ecuadorian Amazon basin, in an integrative taxonomic approach using molecular, morphological, bioacoustic and larval information. With this, we contribute to a better understanding of *Atelopus* diversity as the baseline of conservation action.

Key words. Amphibia, Anura, amphibian crisis, bioacoustics, cryptic diversity, Neotropics, osteology, integrative taxonomy.

Resumen. Durante casi cuatro décadas, los sapos arlequín, del género *Atelopus*, han sufrido descensos poblacionales sin precedentes. Aunque esto también resulta en una comprensión limitada de las relaciones alfa-taxónicas, estos sapos enfrentan una necesidad urgente de avances en sistemática para orientar los esfuerzos de conservación. Sin embargo, la alta variación intraespecífica y la diversidad críptica han dificultado una comprensión integral de la diversidad de *Atelopus*. Esto se ejemplifica particularmente entre las formas amazónicas relacionado con *A. spumarius*, donde décadas de trabajo taxonómico aún no han podido esclarecer las relaciones entre las muchas formas, mientras que los nombres asignados hasta ahora han llevado a una confusión taxonómica que deja numerosos linajes sin nombre. Un reciente estudio filogenético integral ha revelado nuevos conocimientos sobre la sistemática de los sapos arlequín con énfasis en las formas amazónicas, identificando varios linajes sin nombre. Aquí describimos uno de estos como una nueva especie restringida a la cuenca amazónica ecuatoriana en un enfoque taxonómico integrativo utilizando información molecular, morfológica, bioacústica y larval. Con esto, contribuimos a una mejor comprensión de la diversidad de *Atelopus* como base para las acciones de conservación.

Palabras clave: Amphibia, Anura, bioacústica, crisis de anfibios, diversidad críptica, Neotrópicos, osteología, taxonomía integrativa.

Introduction

Unparalleled declines and possible extinctions have affected harlequin toads, *Atelopus* DUMÉRIL & BIBRON, 1841, over the last four decades with their conservation status not having improved since (LA MARCA et al. 2005, LÖTTTERS et al. 2023). As a result, harlequin toads are often considered the poster-child of the precipitous global amphibian declines commonly framed as the amphibian crisis (LÖTTTERS et al. 2023, LUEDTKE et al. 2023). With this, we see an urgent need for advancing *Atelopus* systematics in the context of conservation (cf. DE MAGALHÃES et al. 2018, VELASQUEZ-TRUJILLO et al. 2024).

With more than 100 species, many of which remain undescribed, harlequin toads are considered the most species-rich bufonid genus (RUEDA-ALMONACID et al. 2005, LÖTTTERS et al. 2023). High intraspecific plasticity coupled with cryptic diversity has yet prevented a comprehensive understanding of harlequin toad systematics, particularly regarding forms from the Amazon basin (NOONAN & GAUCHER 2005, LÖTTTERS et al. 2010, 2011, 2022).

Since the descriptions of *A. spumarius* by COPE (1871) from lowlands of western Amazonia and *A. pulcher* by BOULENGER (1882) from the Andean foothills of Amazonia, both names have been applied to many populations in both the western and eastern basin, with additional names coined for some of those as subspecies (reviewed by LÖTTTERS et al. 2002a, 2022).

In contrast to the earlier view, taxonomists have since agreed that most western and eastern Amazonian populations related to *A. spumarius* or *A. pulcher* represent distinct taxa (e.g. LÖTTTERS & DE LA RIVA 1998, LÖTTTERS et al. 2002a,b, 2022, RUEDA-ALMONACID et al. 2005, JORGE et al. 2020). However, it has remained difficult to draw taxonomic conclusions, particularly because (1) access to fresh material of *A. spumarius* sensu stricto for molecular studies was hampered, (2) *Atelopus* remain overall poorly sampled in Amazonia, and (3) at least for some nominal species, repeated contact during Pleistocene cold phases makes molecular delimitation challenging (LÖTTTERS et al. 2002a, NOONAN & GAUCHER 2005). Action is further complicated by the relatively low number of species included in molecular phylogenetic approaches (e.g. LÖTTTERS et al. 2011, RAMÍREZ et al. 2020).

A recent study (LÖTTTERS et al. in press) presents a broadly updated phylogenetic reconstruction of harlequin toads with vast taxonomic implications as a 'roadmap' for future systematic work. The sampling is best for Amazonian harlequin toads, revealing several formerly unnamed lineages in western Amazonia, which are often separated by riverine barriers. Moreover, the rediscovery of *A. spumarius* sensu stricto by the authors close to its type locality finally allows to thoroughly discriminate species from the available names (LÖTTTERS et al. in press). The purpose of this paper is to describe one of the new species-level lineages identified by LÖTTTERS et al. (in press) as a new species.

Material and methods

Nomenclatural acts

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 act it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Science Identifier) for this publication is: urn:lsid:zoobank.org:pub:1E6EC724-DC8C-4941-90B6-C50F12105FEE. 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, zenodo.org.

Material examined

Specimens examined are housed in AMNH (American Museum of Natural History, New York), BMNH (British Museum, London), ANSP (Academy of Natural Sciences, Philadelphia), CBF (Colección Boliviana de Fauna, La Paz), CJ (Centro Jambatu de Investigación y Conservación de Anfibios, San Rafael), DHMECN-INABIO (Instituto Nacional de Biodiversidad, Quito), FMNH (Field Museum, Chicago), GOV (field number, Gustavo Orcés, at USNM), IAVH-Am (Instituto Alexander von Humboldt – Colección de Anfibios, Villa de Leyva), ICN (Instituto de Ciencias Naturales, Bogotá), KU (Natural History Museum, The University of Kansas, Lawrence), LG (field number, Jean Lescure, at MNHNP), MCZ (Museum of Comparative Zoology, Harvard University, Cambridge), MHNC (Museo de Historia Natural del Cusco, Cusco), MHNG (Muséum d'histoire naturelle, Genève), MNCN (Museo Nacional de Ciencias Naturales, Madrid), MNHNP (Muséum National d'Histoire Naturelle, Paris), MTD (Museum für Tierkunde, Dresden), MUBI (Museo de Biodiversidad del Perú, Cusco), MUSM (Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima), NHMW (Naturhistorisches Museum Wien, Vienna), NHRM (Naturhistoriska Riksmuseet, Stockholm), QCAZ (Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito), USNM (National Museum of Natural History, Washington), UTA (University of Texas at Arlington, Arlington), and ZFMK (Zoologisches Forschungsmuseum Alexander Koenig, Bonn).

Morphology

Terminology and methods for the description of external morphology and morphometrics follow LÖTTTERS et al. (in press) and references therein. 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. Measurements are provided in mm.

Osteology

We obtained skeletal data using a GE v|tome|x M 240 micro-computed tomography system (microCT) at the University of Florida's Nanoscale Research Facility in Gainesville, Florida. Specimens were scanned with a 180kV X-ray tube and diamond-tungsten target with the voltage and current set to 100kV and 200µA, respectively. The raw X-ray data were processed using the GE datos|x software to produce tomogram and volume files. The volume files were imported into VG StudioMax (Volume Graphics, version 2023.4), and the skull and skeletons were isolated using VG StudioMax's suite of segmentation tools. Computed tomography data have been deposited in MorphoSource (<https://www.morphosource.org>). Osteological descriptions follow LÖTTERS et al. (in press) and references therein.

Bioacoustics

A recording of 60512 ms duration was available for analysis. Calls were analysed using Audacity 3.0.0. at a sampling rate of 44.1 kHz and 16-bit resolution. Frequency information was obtained using Fast Fourier Transformation (FFT width 1024 at Hann window function). Terminology, description and visualization follow LÖTTERS et al. (in press) and references therein. The analyzed call recording was deposited in full length in the Fonoteca Zoológica (www.fonozoo.com) of the Museo Nacional de Ciencias Naturales (CSIC), Madrid, and CJ sound archive. Calls were recorded by AP from the life holotype in the laboratory on 26 September 2021, ca. 06:00 pm, with a Sennheiser ME66 directional microphone attached to an Olympus DM-901 digital recorder. Distance to recorder was 0.6 m and ambient temperature was ca. 23 °C.

Tadpoles

Description format for larvae follows LÖTTERS et al. (2022). Developmental stages are those of GOSNER (1960). In this paper, we redescribe the tadpole of the new species based on a single specimen from Río Puyo (Ecuador), formerly described under the name *Atelopus spumarius spumarius* by DUELLMAN & LYNCH (1969), and on photos of laboratory-reared larvae in life.

Distribution and natural history

We compiled information on species distribution based on specimens from museum collections and field observations.

Conservation status

We suggest a category based on the IUCN Red List Categories and Criteria Version 3.1, Second edition (IUCN 2012). We calculated the Extent of Occurrence (EOO) for the species as the area contained by a minimum convex polygon over all known localities and the Area of Occupancy (AOO) as the area of inhabited grid cells when applying a grid cell size of 2 km by 2 km, centered around the coordinate in ESRI ArcGIS Pro 3.1.0. (IUCN 2012). Additional threats are discussed in this section.

Results

Based on the molecular results of LÖTTERS et al. (in press) as well as comparative evidence from external and internal morphological, bioacoustic and larval characters, we here describe one of the undescribed species-level lineages, occurring in the Ecuadorian Amazon basin, indentified by LÖTTERS et al. (in press) as a species new to science.

Atelopus colomai sp. n.

Figs 1–2, S1

ZooBank LSID: urn:lsid:zoobank.org:act:D11E9F1C-2826-419F-8112-659DF4E4E052

Atelopus spumarius non COPE. – RUEDA-ALMONACID et al. 2005: 126, RON et al. 2009: 58, CARRILLO-BILBAO & MARTIN-SOLANO 2013: 48, TARVIN et al. 2014: 291.

Atelopus spumarius spumarius non COPE. – DUELLMAN & LYNCH 1969: 232, LÖTTERS 1996: 47.

Atelopus pulcher non BOULENGER. – RIVERO 1963: 113, GASCON 1989: 235, PATZELT 1989: 270 (color illustration of paratype ZFMK 44976), LÖTTERS et al. 2002b: 104.

Atelopus pulcher pulcher non BOULENGER. – PETERS 1973: 42.

Atelopus aff. *spumarius*. – CULEBRAS et al. 2023: 180.

Atelopus sp. (aff. *A. pulcher*). – LÖTTERS et al. 2002a: 184.

Atelopus sp. 1 (*spumarius* complex). – WOMACK et al. 2018: 2.

A. sp. (*spumarius* complex from Puyo, Ecuador). – MARCILLLO-LARA et al. 2020: 11.

A. sp. Otoyacu (*spumarius* complex). – JAYNES et al. 2022: 6.

A. sp. cf. *spumarius* Centro Oriente. – LÖTTERS et al. 2023: Supplementary Table 1.

Holotype: Ecuador: Provincia Pastaza: Río Pucayacu, N of Diez de Agosto (1°22'43" S, 77°51'53" W, 951 m a.s.l.), CJ 12198 (Figs 1–2), adult male, leg. 23 September 2021 by JAIME CULEBRAS, AMANDA B. QUEZADA RIERA, DANILO MEDINA and AMADEUS PLEWNIA.

Paratopotypes: CJ 12200, 12405–12406, 12408–12409, 12425 (Fig. S1), adult females, same data as holotype.

Paratypes: Ecuador: Provincia Pastaza: NW of El Triunfo (1°23'43" S, 77°47'50" W, 1020 m a.s.l.), CJ 12196–12197, 12199, adult males, leg. 22 September 2021 by JAIME CULEBRAS, AMANDA B. QUEZADA RIERA, DANILO MEDINA, ZANE LIBKE and AMADEUS PLEWNIJA; Reserva Otoyacu (1°22'27" S, 77°51'07" W, 920 m a.s.l.), CJ 12341, 12431, adult males, and CJ 8188, 12430, adult females, leg. unknown; Finca la Argentina, N of Puyo (1°27'38.31" S, 77°58'58" W, 960 m a.s.l.), DHMECN-INABIO 18995, adult female, leg. 17 August 2023 by JUAN P. REYES PUIG, JOSÉ IGNACIO SEGOVIA LARREA, PAULET BENAVIDEZ, NANTA KUJA and PATRICIO VINUEZA; Río Cononaco, ZFMK 44976, subadult female, leg. April 1986 by ERWIN PATZELT; Río Villano, near Villano, BMNH 1970.117–1970.118 (375 m a.s.l.), adult females, leg. (date unknown) by RAMÓN OLALLA.

Referred material: Ecuador: Provincia Orellana: Yasuní National Park, road from Pompeya Sur to Iro on km 38, QCAZ 32664; Yasuní National Park, road from Pompeya Sur to Iro on km 66, QCAZ 5006, 5234, 7015, 11126, 77404; Provincia Pastaza: Reserva Otoyacu, CJ 8187, 9883,

12429, 12431, 12826–12828, 12835; Río Pucayacu, CJ 12407, CJ 12697; 2.5 km SE of Puyo, USNM 193476, 194838, JAP 1937–1938; Río Puyo, 3 km S Puyo, KU 121385; trail from Unión Base to Rosario Yacu, SE of Puyo, MCZ Herp A-95683–95688, A-95692–95696; Veracruz, ca. 10 km E of Puyo, USNM 193477, KU 120480–120485; Río Oglán, GOV S939; km 6 on road from San Ramón to El Triunfo, Río Pucayacu, QCAZ 30617, 30896, 31325–31326, 33304, 36956, 37270–37271, 37275, 37372, 37405–37406, 37663–37664, 3766–3768, 37710–37717, 37721–37722, 39545, 40489, 40512, 46483–46486, 46491–46493, 46850, 50579; Finca de la Cooperativa Mariscal Sucre, Río Pucayacu, QCAZ 50291; Parroquia Teniente Hugo Ortiz, QCAZ 17780; Cononaco, UTA WWL 3669; Canelos, MCZ Herp A-17927–17928; Baños and Canelos, AMNH 16713–16715; Río Villano: BMNH 1970.68–69; Puyo, FMNH 28078; historic province Santiago-Zamora (now provinces Zamora Chinchipe and Morona Santiago), NHRM RRB/1937.809.3262 (2 specimens).

Definition: *Atelopus colomai* sp. n. is placed in the genus *Atelopus* based on having presacrals I and II fused, the presence of a gastromyzophorous tadpole with a ventral belly sucker and its mitochondrial and nuclear markers be-



Figure 1. Preserved male holotype of *Atelopus colomai* sp. n. in dorsal, ventral and lateral views (CJ 12198). Scale bar 10 mm. Photos by JAIME CULEBRAS.

ing nested within *Atelopus* (LÖTTERS et al. in press). The species is distinguished from all other species by the combination of the following characters: (1) A small-sized species with mean SVL of adult males 23.2 ± 1.46 mm, $N = 6$, and adult females 29.8 ± 2.05 mm, $N = 10$; (2) slender body (SW/SVL = 0.261 ± 0.020 in 6 males, 0.260 ± 0.016 in 10 females) with (3) long legs (TIBL/SVL = 0.433 ± 0.028 in 6 males, 0.443 ± 0.021 in 10 females); (4) acuminate snout in dorsal view, protruding beyond apex of lower jaw; (5) tympanic membrane absent, tympanic annulus not visible, columella present, ostia pharyngea present; (6) phalangeal formula of hand 1-2-3-3; webbing absent on hand; (7) first finger short (THBL/HAND = 0.448 ± 0.024 in 6 males, 0.425 ± 0.066 in 10 females), first finger in males with keratinized dark brown spiculae forming the nuptial pad; (8) phalangeal formula of foot 2-2-3-4-3, webbing formula of toes I0-0 to III0 to 0.5-III0.5 to 1-2.25 to 3IV2.5 to 3-0.5V; (9) skin smooth, dorsally and laterally covered with dense well-defined minute spiculae, resulting in a velvety appearance of the skin on respective surfaces; skin ventrally smooth to areolate; (10) vertebral column conspicuous, neural processes absent; (11) in life, dorsum black with few yellow-green asymmetric circles, dots or lines; dorsolaterally yellow-green foam-like reticulation forming a band from above eye to groin with numerous black rounded irregular spots (smaller than EYDM); laterally a black band present from tip of snout almost to groin, rarely interrupted by yellow-green lines; limbs and dorsal surfaces of hand and foot with yellow-green foam-like reticulation with black spots (smaller or larger than EYDM), thumb and sometimes tips of fingers and toes dorsally orange to vermilion red; in males, throat and venter cream, posteriorly becoming yellowish, sometimes with few tiny black dots (smaller than or equal to diameter of finger III) on throat and black dots (smaller than EYDM) on lateral and posterior vent; in females, throat and venter yellow with numerous black dots (smaller or larger than EYDM); in both sexes, palms, plants and an oval-shaped blotch on ventral surface of cloaca and adjacent areas of thighs vermilion red, the latter being surrounded by black dots (smaller than EYDM); iris black with a golden yellow ring surrounding horizontally oriented pupil; (12) in preservative: above dark brown background color with cream pattern, below whitish cream with brown dots; vermilion red life markings faded to pale orange, yellow or cream; (13) pulsed calls long for an *Atelopus* (2049 ± 220 ms) with dominant frequency 2848 ± 14 Hz.

Diagnosis: *Atelopus colomai* sp. n. (Figs 1-2, S1) can be readily distinguished from all other *Atelopus* species (as far known) by molecular genetics (monophyly in a concatenated (12S, 16S, CytB) mitochondrial phylogeny, support by molecular species delimitation and lack of haplotype sharing in POMC, LÖTTERS et al. in press). It can be morphologically distinguished from all congeners by the combination of small size, dorsal and lateral skin covered with dense well-defined minute spiculae, ventral skin smooth to slightly areolate, presence of a columella and dorsal pat-

tern, except from *A. spumarius* COPE, 1871 sensu stricto and *A. manauensis* JORGE, FERRÃO & LIMA, 2020. From these species, it differs by longer call duration (2049 ± 220 ms vs. 922 ± 24 ms in *A. spumarius* sensu stricto, LÖTTERS et al. in press; 744 ± 84 ms in *A. manauensis*, JORGE et al. 2020), in female ventral coloration and pattern in life (yellow with equally distributed black rounded dots on vent smaller or larger than EYDM vs. throat and chest orange or yellow, venter anteriorly cream yellow, posteriorly orange or yellow, anteriorly with numerous brown or black dots smaller than or equal to EYDM, sometimes forming a continuous band on chest in *A. spumarius* sensu stricto, LÖTTERS et al. in press; venter white or whitish cream with spots in *A. manauensis*, JORGE et al. 2020) and in having an oval vermilion red blotch surrounded by small black dots on ventral surface of cloaca and onto adjacent thighs in life (vs. ventral surface of cloaca and thighs bright orange in *A. spumarius* sensu stricto, and bright red in *A. manauensis*, all lacking black dots). Further, *A. colomai* sp. n. differs from both taxa in having a more pointed, acuminate snout in lateral view in females (vs. subacuminate to truncate and less protruding in *A. spumarius* sensu stricto; blunt in *A. manauensis*). Moreover, from *A. manauensis*, the new species differs in having a longer head (males HLSQ/HDWD 1.144 ± 0.067 , $N = 6$, vs. 1.054 in *A. manauensis*, $N = 11$, JORGE et al. 2020). The tadpole of the new species differs from that of *A. manauensis* by having the lower beak about twice as long as the upper one (vs. upper beak only slightly shorter than lower, GASCON 1989 under the name *A. pulcher*).

Atelopus colomai sp. n. is morphologically similar to its congeners of the *flavescens-spumarius* clade sensu LÖTTERS et al. (in press), as well as *A. andinus* RIVERO, 1968, *A. loettersi* DE LA RIVA, CASTROVIEJO-FISHER, CHAPARRO, BOISTEL & PADIAL, 2011, and the *A. tricolor* BOULENGER, 1902 complex (including the junior synonyms *A. rugulosus* NOBLE, 1921 and *A. willimani* DONOSO-BARROS, 1969) from the eastern Andean versant of Peru and Bolivia, and to *A. palmatus* ANDERSON, 1945 and *A. planispina* JIMÉNEZ DE LA ESPADA, 1875 from the eastern Andean versant of Ecuador. With respect to these superficially similar species, the new species differs as follows: from the nominal *A. barbotini* LESCURE, 1981, *A. flavescens* DUMÉRIL & BIBRON, 1841 (including its junior synonym *A. vermiculatus* MCDIARMID, 1973), *A. franciscus* LESCURE, 1974 and the *A. hoogmoedi* LESCURE, 1974 complex (including the available name *A. hoogmoedi nassau* OUBOTER & JAIRAM, 2012) in pattern and coloration in life (dorsally black with few yellow-green asymmetric circles, dots or lines; dorsolaterally yellow-green foam-like reticulation forming a band from above eye to groin with numerous black rounded irregular spots; males below cream, posteriorly becoming yellowish, sometimes with few tiny black dots and a vermilion red shaped blotch on ventral surface of cloaca and adjacent areas of thighs, females ventrally yellow with numerous black dots and a vermilion red shaped blotch on ventral surface of cloaca and adjacent areas of thighs vs. dorsally black with red to pink markings, ventrally reddish

pink in *A. barbotini*; dorsally unicolored reddish, brownish or yellow or brown and with olive, brownish reddish and copper-like vermiculation, ventrally reddish pink in males, pink in females in *A. flavescens*; dorsally olive to blackish brown, ventrally reddish in *A. franciscus*; dorsally dark brown or black with yellow, pink, bluish, white, greenish or orange irregular spots and reticulated dorso-lateral bands or solid bars, ventrally yellow, pink, bluish, white, greenish or orange, in some specimens with dark spots or blotches in the *A. hoogmoedi* complex). All these forms, except some populations of the *A. hoogmoedi* complex, lack red palmar and plantar surfaces in life (vs. present in *A. colomai* sp. n.). All Guianan harlequin toads have shorter call durations (2049 ± 220 ms vs. 1490 ± 140 ms in *A. barbotini*; 1530 ± 220 ms in *A. flavescens*; 1490 ± 150 ms in *A. franciscus*; 1190 ± 10 ms in the *A. hoogmoedi* complex from French Guiana; 1160 ± 390 ms in the *A. hoogmoedi* complex from Amapá, Brazil; $1060\text{--}1240$ ms in the *A. hoogmoedi* complex from Pará, Brazil; LESQUIRE 1981, COCROFT et al. 1990, COSTA-CAMPOS & CARVALHO 2018). Tadpoles of the new species differ from those of *A. flavescens*, *A. franciscus* and the *A. hoogmoedi* complex in having the lower beak about twice as long as the upper (vs. upper beak only slightly shorter than lower; BOISTEL et al. 2005, LÖTTERS et al. 2022) and in coloration in life (black to dark brown with dense irregular pale brown to golden markings that consist of aggregated minute dots vs. black with symmetrical golden spots anterior and posterior eye, at the base of the tail and on tail fin in *A. flavescens* and *A. franciscus*; ventrally entirely translucent with few whitish cream dots in the *A. hoogmoedi* complex (BOISTEL et al. 2005, LÖTTERS et al. 2022)). The new species can be distinguished from *A. pulcher* BOULENGER, 1882 by smaller male SVL (23.2 ± 1.46 mm, $N = 6$, vs. 27.27 ± 1.07 mm, $N = 13$, in *A. pulcher*; LÖTTERS et al. 2002a), female ventral coloration in life (yellow with numerous black dots and a vermillion red shaped blotch on ventral surface of cloaca and adjacent areas of thighs vs. vermillion red with irregular dark spots in *A. pulcher*, LÖTTERS et al. 2002a) and longer calls ($2,049 \pm 220$ ms vs. $1,200 \pm 100$ ms in *A. pulcher*, LÖTTERS et al. 2002a). Tadpoles of *A. colomai* sp. n. differ from those of *A. pulcher* in having the lower beak about twice as long as the upper (vs. one third to one fourth as long) and the nostrils positioned at about height of eye (vs. below height of eye; LÖTTERS et al. 2002a). *Atelopus colomai* sp. n. differs from *A. seminiferus* COPE, 1874 in smaller female SVL (29.8 ± 2.05 mm, $N = 10$, vs. 40.0 mm, $N = 1$), absence of lateral warts (present in *A. seminiferus*) and dorsal coloration in preservative (dorsally black with few yellowish cream asymmetric circles, dots or lines; dorsolaterally yellowish cream foam-like reticulation forming a band from above eye to groin with numerous black rounded irregular spots vs. dark brown without pattern in *A. seminiferus*). From *A. andinus*, *A. loettersi* and the *A. tricolor* complex, *A. colomai* sp. n. is distinguished by the presence of a columella (vs. absence; LÖTTERS et al. 2011, R. BOISTEL unpubl. data). From *A. loettersi*, it can be distinguished by female ventral coloration and pattern in life (yellow with numer-

ous black dots and a vermillion red shaped blotch on ventral surface of cloaca and adjacent areas of thighs vs. mostly red, in some specimens with irregular brown blotches in *A. loettersi*; DE LA RIVA et al. 2011). The new species can be distinguished from *A. andinus* and the *A. tricolor* complex by the absence of warts (vs. presence) and by presence of dorsolateral reticulation (vs. absence). Tadpoles of the new species differ from those of the *A. tricolor* complex in having the upper beak shorter than the lower (vs. longer; LAVILLA et al. 1997). *Atelopus colomai* sp. n. can be distinguished from *A. palmatus* and *A. planispina* by coloration and pattern in life (dorsally black with few yellow-green asymmetric circles, dots or lines; dorsolaterally yellow-green foam-like reticulation forming a band from above eye to groin with numerous black rounded irregular spots; males below cream, posteriorly becoming yellowish, sometimes with few tiny black dots and a vermillion red oval-shaped blotch on ventral surface of cloaca and adjacent areas of thighs, females below yellow with numerous black dots and a vermillion red oval-shaped blotch on ventral surface of cloaca and adjacent areas of thighs vs. green blotches on reddish brown dorsum, absence of reticulation; ventrally unicolored orange in females of *A. palmatus* and whitish to reddish in *A. planispina*; PETERS 1973) and skin texture (smooth, covered in minute spiculae vs. presence of small spiculae on flanks, upper arm and from eye fading towards groin; PETERS 1973). Tadpoles of *A. colomai* sp. n. differ from those of *A. palmatus* in exhibiting a golden tail pattern in life (vs. absence; MARCILLO-LARA et al. 2020) and in having the upper beak shorter than the lower (vs. longer; MARCILLO-LARA et al. 2020).

Description of holotype: Adult male. Body slender (SW/SVL 0.265); head slightly longer than wide (HLSQ/HDWD 1.103); in profile, snout protruding beyond apex of lower jaw, acuminate in dorsal view, forming a triangle from nostrils to tip of snout; nostrils directed laterally, moderately protuberant, not visible in dorsal view, about two thirds from eye to tip of snout in lateral view, situated anterior to apex of lower jaw; canthus rostralis well defined, concave in dorsal view between eye and nostril; loreal region concave; lips not flared; top of snout depressed; head plain in lateral view; eyelid flared, densely covered in minute spiculae; tympanic membrane absent, tympanic annulus not visible; supratympanic crest poorly developed; choanae small, rounded; ostia pharyngea present; tongue about twice as long as wide, broadest at its tip (situated posteriorly); vocal slits present; limbs long and slender (TIBL/SVL 0.446); webbing absent on hand; fingers and toes lack lateral fringes; palmar tubercle rounded, poorly developed; supernumerary palmar and plantar tubercles absent; thenar and subarticular tubercles indistinct; tips of digits rounded; phalangeal formula of hand 1-2-3-3; first finger short (THBL/HAND 0.431), dorsally covered with keratinized dark brown spiculae forming the nuptial pad; inner metatarsal tubercle indistinct, outer metatarsal tubercle rounded, poorly developed; relative length of toes I<II<III<V<IV; phalangeal formula of foot 2-2-3-4-3,

webbing formula of toes I0-0II0-1III0.5-3IV3-0.5V; tarsal fold absent; foot roughly three quarters of tibia; skin smooth on entire body, dorsally and laterally covered with dense, well-defined minute spiculae, resulting in a velvety appearance of the skin; skin smooth to slightly areolate on ventral surfaces of cloaca and adjacent areas of thighs, venter and throat; cloacal opening in an inconspicuous tube, directed posteriorly; vertebral column visible through the skin, neural processes absent.

In life (Fig. 2), dorsum black with few yellow-green asymmetric circles, dots or lines; dorsolaterally yellow-green foam-like reticulation, forming a band from above eye to groin bearing numerous black rounded markings (smaller than EYDM); lips bordered by thin black line; laterally a black band from tip of snout almost to groin; ventrolaterally transition from yellow-green reticulation with numerous black dots to unicolored cream throat and venter; throat and venter cream with few minute dark dots in

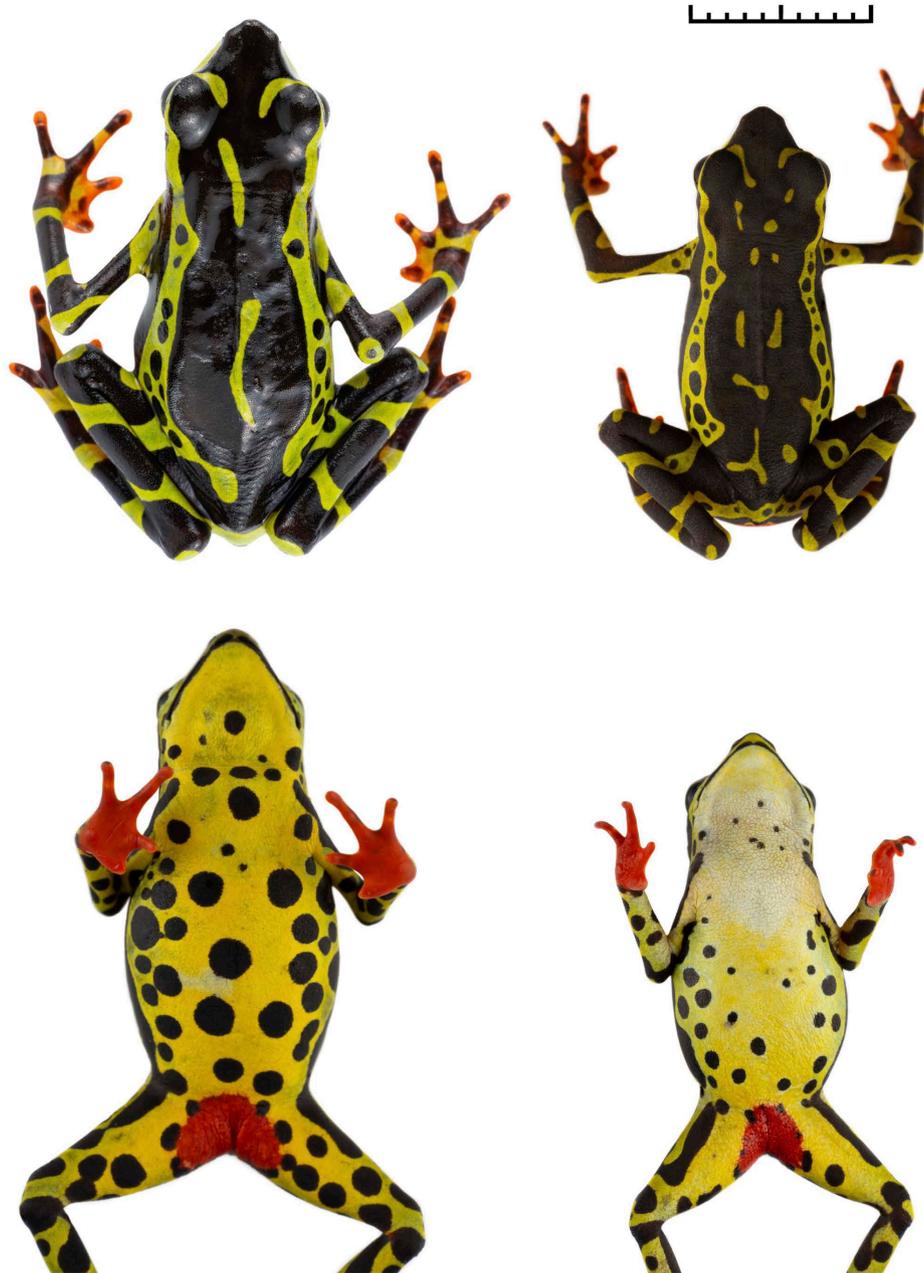


Figure 2. Life aspects of *Atelopus colomai* sp. n. from the type locality. Left column: dorsal (CJ 12406; top) and ventral (CJ 12409; bottom) views of adult female paratopotypes. Right column: dorsal and ventral views of adult male holotype (CJ 12198). Scale bar 10 mm. Photos by JAIME CULEBRAS.

gular region (smaller than or equal to diameter of finger III), venter posteriorly becoming yellowish with few black dots (smaller than EYDM); limbs dorsally black, covered in yellow-green bands, ventrally cream to yellow bearing black dots or bars; thumb and tips of fingers and toes dorsally orange to vermillion red; palms, plants and an oval-shaped blotch on ventral surface of cloaca and adjacent areas of thighs vermillion red, the latter being surrounded by black dots; iris black with a golden yellow ring surrounding horizontally oriented pupil.

In preservative, above blackish brown with yellowish cream pattern; below whitish cream with blackish brown dots; vermillion red life markings faded to pale cream with pale reddish remnants. Proximal (anterior) half of tongue has black pigmentation.

Measurements: SVL 22.3, TIBL 9.9, FOOT 7.5, HLSQ 7.4, IOD 2.3, HDWD 6.7, EYDM 2.7, EYNO 1.9, ITNA 2.0, FAL 7.7, HAND 5.1, THBL 2.2, SW 5.9.

Variation: For meristic variation of characters see Table 1. Paratypes (Fig. 2, S1) correspond to the description above. However, specimens from Reserva Otayacu and Río Villano are slightly larger than topotypic individuals and specimens from NW El Triunfo. Among the paratypes is one malformed specimen (CJ 12197) with partial anophthalmia, in which the right eye is not fully developed and almost completely covered with skin.

Sexual dimorphism is apparent in *A. colomai* sp. n. with females being larger than males (SVL 29.8 ± 2.05 mm, N = 10, vs. 23.2 ± 1.46 mm, N = 6). In addition, females lack nuptial pads and vocal slits, differ in coloration by having a yellow venter with equally distributed rounded black dots (smaller or larger than EYDM) in the gular region, on chest and venter (Fig. 2).

Cranial osteology: General osteological features of a male (CJ 8187; MorphoSource Media ID 000077646) and a female (CJ 8188, paratype; MorphoSource Media ID 000077646) are depicted in Figure 3. The skull of *A. colomai* sp. n. is triangular in dorsal view. The skull length is 8.5 mm, the skull width is 8.1 mm, and the skull height is 5.4 mm in CJ 8187; the skull length is 8.8 mm, the skull width is 7.8 mm, and the skull height is 5.2 mm in CJ 8188. The skull roof is smooth. In anterior view, the septomaxilla is U-shaped with medial and lateral rami that extend posteriorly towards the vomer. The lateral ramus is much broader than the medial ramus and bears a nasal process. The ossified sphenethmoid is smooth and underlies the posterior and medial margins of nasals, as well as the anterior and anterolateral margins of the frontoparietals. The posterior limit of the sphenethmoid is about one-third the length of the margin of the orbit. The prootics are fused to the posterolateral edge of the frontoparietals. The exoccipitals encircle the foramen magnum and are fused to the frontoparietals dorsally, the prootics laterally, and the parasphenoid anteroventrally. The otic capsule is well-ossified. Columellae are present, cylindrical in shape. The pars media of the columella is slender and slightly bowed, and the pars

Table 1. Measurements (in mm) and proportions of the type series of *Atelopus colomai* sp. n.; mean \pm SD (range), excluding subadult paratype ZFMK 44976. For abbreviations see Method section.

| | Males (N = 6) | Females (N = 10) |
|-----------|------------------------------------|------------------------------------|
| SVL | 23.2 \pm 1.46 (21.2–25.6) | 29.8 \pm 2.05 (26.4–33.7) |
| TIBL | 10.0 \pm 0.16 (9.9–10.3) | 12.9 \pm 0.47 (12.3–13.7) |
| FOOT | 7.5 \pm 0.37 (6.9–8.0) | 10.6 \pm 1.09 (8.8–12.0) |
| HLSQ | 7.6 \pm 0.33 (7.2–8.1) | 9.0 \pm 0.46 (8.4–9.9) |
| IOD | 2.5 \pm 0.37 (2.1–3.0) | 3.2 \pm 0.37 (2.7–3.9) |
| HDWD | 6.6 \pm 0.20 (6.3–6.8) | 8.0 \pm 0.27 (7.6–8.4) |
| EYDM | 2.8 \pm 0.09 (2.7–2.9) | 3.1 \pm 0.44 (2.4–3.9) |
| EYNO | 1.9 \pm 0.18 (1.6–2.0) | 2.6 \pm 0.27 (2.2–3.1) |
| ITNA | 2.1 \pm 0.08 (2.0–2.2) | 2.6 \pm 0.20 (2.3–3.0) |
| FAL | 7.4 \pm 0.34 (7.1–7.9) | 9.4 \pm 0.73 (8.1–10.6) |
| HAND | 5.1 \pm 0.05 (5.1–5.2) | 7.0 \pm 0.47 (6.4–7.9) |
| THBL | 2.3 \pm 0.13 (2.2–2.5) | 3.0 \pm 0.51 (1.8–3.6) |
| SW | 6.0 \pm 0.46 (5.5–6.8) | 7.7 \pm 0.48 (6.9–8.7) |
| TIBL/SVL | 0.433 \pm 0.028 (0.387–0.472) | 0.443 \pm 0.021 (0.407–0.466) |
| SW/SVL | 0.261 \pm 0.020 (0.230–0.289) | 0.260 \pm 0.016 (0.225–0.288) |
| HLSQ/SVL | 0.328 \pm 0.025 (0.289–0.350) | 0.303 \pm 0.010 (0.281–0.318) |
| FAL/SVL | 0.318 \pm 0.015 (0.301–0.338) | 0.315 \pm 0.026 (0.261–0.345) |
| HLSQ/HDWD | 1.144 \pm 0.067 (1.059–1.238) | 1.136 \pm 0.052 (1.036–1.238) |
| THBL/HAND | 0.448 \pm 0.024 (0.431–0.490) | 0.425 \pm 0.066 (0.281–0.507) |

interna is not ossified. The operculum in the fenestra ovalis is mineralized and visible. The nasals are triangular and bear an acuminate maxillary process that extends ventrolaterally toward the maxilla and contacts the pars facialis of the maxilla in CJ 8187 and nearly contacts the pars facialis of the maxilla in CJ 8188. The nasals are moderately separated medially. The frontoparietals are rectangular and the orbital edges are straight. Medial articulation is complete in both specimens. A suture line is visible only in CJ 8188. A supraorbital flange is absent. Occipital grooves, which are canals for the carotid artery, are present and partially roofed with bone. In both specimens, the grooves are cov-

ered along the midpoint but open at the anterior and posterior tips. 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, pointed at the anterior tip, and is roughly the same size as the pre- and postchoanal ramus. The pre- and postchoanal rami form the anteromedial margin of the choana. The prechoanal ramus is directed towards the maxilla, and the postchoanal ramus is directed posterolaterally. The postchoanal ramus is fused to the overlying sphenethmoid. The neopalatine is elongate and triangular. It underlies, and is partially fused to, the sphenethmoid and extends towards the maxilla, nearly making contact with the preorbital process in CJ 8188 and making contact in CJ 8187. The neopalatine is narrow and pointed at its medial tip, widens as it approaches the maxilla, and is cylindrical and pointed at its anterior border. The parasphenoid has an inverted T-shape and the cultriform process underlies the sphenethmoid in CJ 8188 (but does not in CJ 8187). The cultriform process extends beyond the midpoint of the orbit. The terminal end of the cultriform process is rounded in shape. The parasphenoid alae are directed posterolateral to the cultriform process and are fused to the overlying otic capsule. The posterior margin of the parasphenoid and a medial posterior process are difficult to discern. The maxillary arcade is complete and edentate. The paired premaxillae each possess a dorsal

alary process that is directed anterolaterally. The lower half of the alary process is the same width as the upper half. The pars palatina is biradiate with medial and lateral processes. The lateral process is more than twice as long as the medial process. The medial process is well developed and triangular. A concave border is present where the lateral and medial processes of the pars palatina come together. The posterior tip of the pars dentalis is pointed and articulates with the maxilla. The external surface of the maxillae is smooth. The pars palatina, which extend along the lingual margin of the maxilla, is narrow, and the posterior half of this shelf articulates with the anterior ramus of the pterygoid. The pars fascialis of the maxilla is directed; its dorsomedial margin variably contacts, or nearly contacts, the neopalatine, sphenethmoid, and maxillary process of the nasal. The anterior end of the maxilla is truncate and contacts the premaxilla. The posterior end of the maxilla is pointed and slightly overlaps the quadratojugal. The quadratojugal is a small, slender, L-shaped bone that underlies the ventral arm of the squamosal and contacts the posterior process of the maxilla at its anterior margin. The paired squamosals possess an otic ramus posterodorsally and a ventral ramus. An anterodorsal zygomatic ramus is not evident. The otic ramus is expanded dorsally and has a broad articulation with the crista parotica of the otic capsule, leaving only the posterior end of the prootic free. The angle between the dorsal surface of the squamosal and the anterior margin of the ventral ramus is nearly perpendicu-

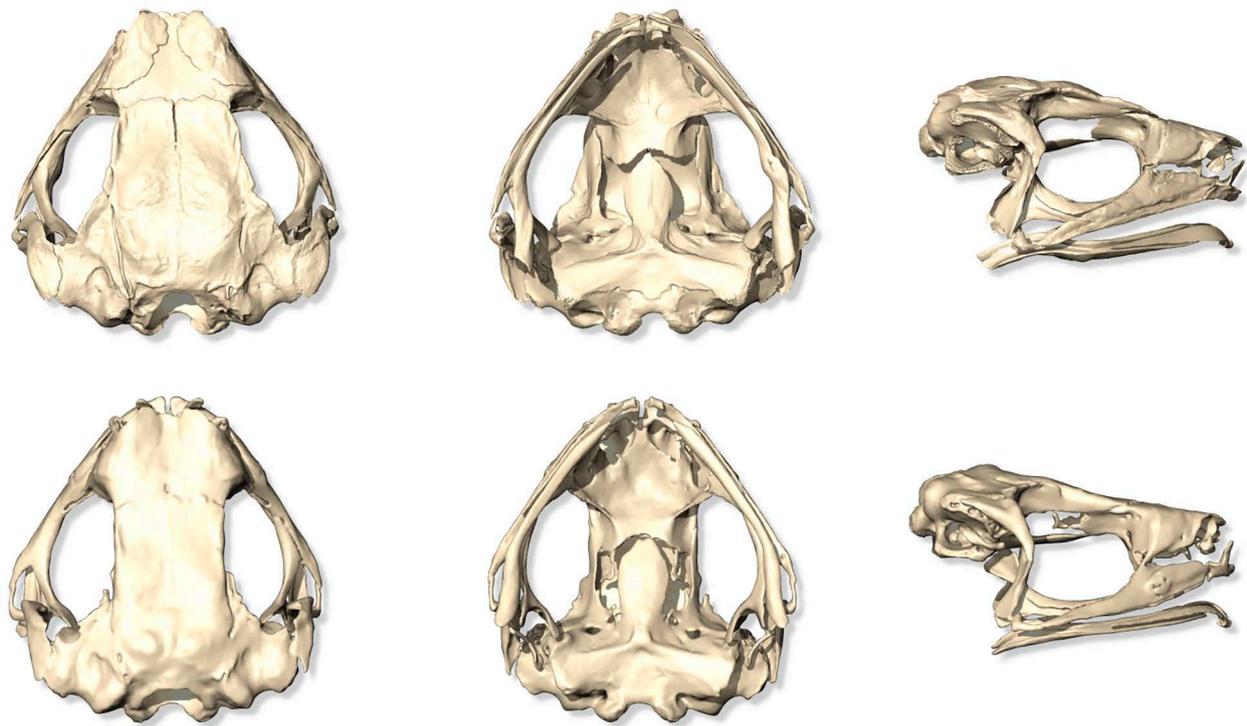


Figure 3. Comparative skull osteology of western Amazonian *Atelopus* in dorsal, ventral and lateral views. Top row: *A. spumarius* sensu stricto (female neotype, MNHNP 1979/8382, for details on scanning see LÖTTERS et al. in press). Bottom row: *A. colomai* (male CJ 8187 from Ecuador, Pastaza, Reserva Otoyacu). Not to scale.

lar. The ventral ramus is flat and blade-like. A small squamosal keel is present at the junction between the otic ramus and the upper half of the ventral arm. The pterygoid is triradiate, bearing anterior, medial, and posterior rami. The anterior ramus articulates with the pars palatina of the maxilla. The medial and posterior rami are of equal length but the medial ramus is much broader. The medial ramus nearly contacts the prootic. The posterior ramus is flat and blade-like. The palatoquadrate is cartilaginous and therefore not visible in the microCT dataset. The lower jaw is composed of three ossified elements and Meckel's cartilage, which is not visible in the microCT dataset. The mentomeckelian is the most anterior element that forms a cartilaginous symphysis at the midline of the jaws. Posterodorsally, the mentomeckelian is fused to the dentary. The dentary is slender, thin, and edentate; this element overlays the anterior half of the angulosplenic. The angulosplenic is the largest mandible element and forms the lingual surface of the lower jaws. The lower jaw length is 7.1 mm in CJ 8187 and 7.3 mm in CJ 8188, slightly shorter than the length as the skull from the occipital condyle to the premaxilla.

Atelopus colomai sp. n. can be distinguished from *A. spumarius* sensu stricto by its smooth skull roof (vs. rugose; Fig. 3), having the frontoparietals completely fused (vs. fused only over two posterior thirds of their total length; Fig. 3), the posterior end of the maxilla not being free (vs. free), the pars glenoidalis and the pars jugularis of the quadratojugal being subrectangular and elongated, respec-

tively (vs. pars glenoidalis thickened, pars jugularis short), and a less straight orbital margin of the maxilla. However, variation in these characters exists between the two populations of *A. spumarius* sensu stricto, which might be attributed to imaging conditions or natural variation (LÖTTERS et al. in press).

The discriminatory power of osteological features needs to be seen with some caution as intraspecific variation, sexual dimorphism and taxonomic value remain poorly understood for harlequin toads and other anuran genera (see e.g. KÖHLER et al. 2024). For a comparative discussion of osteological features in harlequin toads related to *A. spumarius* sensu stricto see Lötters et al. (in press).

Vocalization: The call recording (CJ ec.cj.aud.19; FonoZoo Sound Code 14651; Fig. 4) contains 11 pulsed calls with duration 2049 ± 220 ms (1747–2488 ms). Intervals between calls last 3601 ± 1791 ms (1791–6928 ms). Dominant frequency is 2848 ± 14 Hz (2821–2877 Hz). Amplitude is generally ascending over the course of the call being interrupted by 2–4 temporal decreases until it reaches its maximum followed by a subsequent decrease over the last 3–10 pulses (Fig. 4). Call energy is also present in the frequency components related to the pulse rate, which shows weak modulation and a minimal increase toward the end of the call. Each call consists of 52 ± 6 pulses (42–60), that show a length of 7 ± 2 ms (3–4 ms) each. Pulses slightly increase in length over the course of each call and are not modulated in frequency.

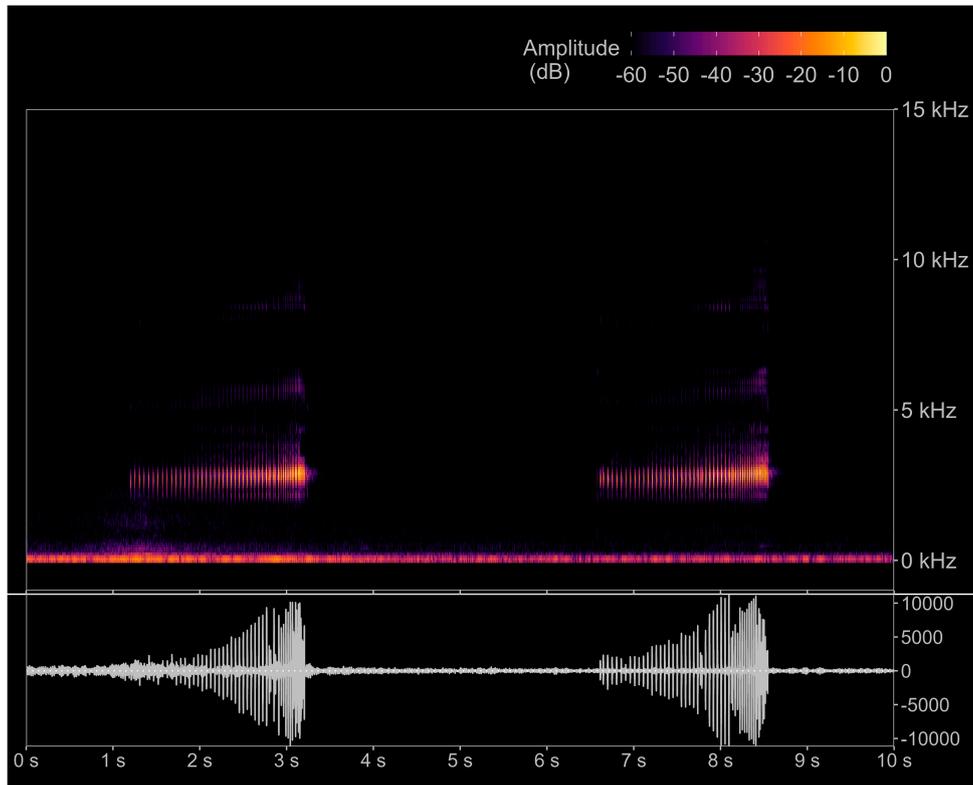


Figure 4. Oscillogram and corresponding spectrogram of two pulsed calls recorded from the holotype of *Atelopus colomai* sp. n.

Tadpole: DUELLMAN & LYNCH (1969) described a single gastromyzophorous tadpole from Río Puyo in Provincia Pastaza, Ecuador, under the name *A. spumarius spumarius*. We assign their specimen (KU 121385; Fig. 5) to *A. colomai* sp. n., based on the resemblance of living tadpoles (Fig. 6) reared from topotypic adults of *A. colomai* sp. n. under laboratory conditions and based on being the only harlequin toad known from the general area. Our examination of the tadpole in Stage 37 corroborates most characters given by DUELLMAN & LYNCH (1969). However, the illustration provided with the description needs rectification as the nostrils are actually located at the level of the eye, and not below the eye. In addition, the upper beak appears longer than the lower on the drawing, which is in error and conflicts the description. Our examination of the larva also suggests the presence of a submarginal papilla on each side at the end of the lowest row of labial teeth of the lower labium (P₃), although this requires further corroboration due to the poor status of preservation of the individual.

Based on this specimen and additional live specimens, the tadpole of *A. colomai* sp. n. is characterised by: body depressed in lateral view, flattened ventrally, longer than wide, widest between eye and spiracle, snout rounded in dorsal view; eyes large, directed laterally to anterolaterally and positioned dorsolaterally, not visible in ventral view; nares ovoid, directed anterodorsally, situated closer to eye than to

anterior margin of snout, situated at the height of the lower corner of eye; abdominal sucker circular to ovoid, anteriorly bordering the oral disc, posteriorly extended to height of the opening of spiracle; spiracle sinistral, cylindrical, short tube not attached to body wall, positioned ventrolaterally and oriented posteriorly; anal tube medial, tubular; caudal musculature massive, decreasing rapidly in distal half of rounded tail; caudal fins low, dorsal fin slightly rounded, highest in distal half of tail, not extending onto body; margin of ventral fin straight; oral disc ventral, almost as wide as body, anteriorly and laterally bordered by one row of short rounded papillae, submarginal papilla present on each side of lower labium (P₃). Labial tooth row formula 2/3, tooth rows all about equal in length; upper beak of jaw sheaths narrow, almost transverse; lower beak broadly V-shaped, about twice as long as upper beak.

In life, back, flanks and caudal muscle black to dark brown with dense irregular pale brown to golden markings that consist of aggregated minute dots, extending marginally on transparent tail fin; below, proximal half of body whitish translucent with black dots, dots most dense below suctorial disc, golden dots towards flanks, distal half of body black with scattered golden dots towards flanks and tail, tail cream with black and golden dots; pupil black surrounded by cupreous to golden ring; towards metamorphosis, the pattern and coloration remain stable with a decrease of golden markings at late stages; limbs turn orange in Stage 42 (Fig. 6). In preservative, the single specimen used for the tadpole description by DUELLMAN & LYNCH (1969) is entirely faded (Fig. 5).

There is limited variation in external morphology of *Atelopus* tadpoles. The upper beak being shorter than the lower is a larval character only known from the *flavescens-spumarius* clade (cf. MARCILLO-LARA et al. 2020, PÉREZ-GONZALEZ et al. 2020, LÖTTTERS et al. 2022). Tadpoles of five species from this clade have been described, *A. flavescens*, *A. franciscus*, the *A. hoogmoedi* complex, *A. manauensis* and *A. pulcher*. *Atelopus colomai* sp. n. can be distinguished from them in having the lower beak about twice as long as the upper. The upper beak is only slightly shorter than the lower in the other species except *A. pulcher* (GASCON 1989, BOISTEL et al. 2005, LÖTTTERS et al. 2022). It is only one third to one fourth the length of the lower beak in *A. pulcher* (LÖTTTERS et al. 2002a). From *A. pulcher*, the new species is distinguished further by having the position of the nostrils at about height of eye (vs. below height of eye; LÖTTTERS et al. 2002a). In aspects of life coloration, larvae of *A. colomai* sp. n. differ from those of *A. flavescens*, *A. franciscus* and the *A. hoogmoedi* complex by being black to dark brown with dense irregular pale brown to golden markings that consist of aggregated minute dots (black with symmetrical golden spots anterior and posterior eye, at the base of the tail and on tail fin in *A. flavescens* and *A. franciscus*; below entirely translucent with few whitish cream dots in the *A. hoogmoedi* complex; BOISTEL et al. 2005, LÖTTTERS et al. 2022). The coloration of *A. manauensis* is barely described (GASCON 1989 under the name *A. pulcher*) so that comparison with the new species remains uncertain.



Figure 5. Preserved tadpole of *Atelopus colomai* sp. n. (KU 121385, GOSNER Stage 37) in ventral, dorsal and lateral views (from top to bottom). Scale bar 5 mm. Photos: KUDA 14472–14474, KU Digital Archive.

Atelopus palmatus is the sole species with a described tadpole which is not assigned to any of the defined clades in LÖTTERS et al. (in press). Tadpoles of *A. colomai* sp. n. can be distinguished from those of *A. palmatus* (cf. MARCILLO-LARA et al. 2020) in having the upper beak shorter than the lower (vs. longer), and in having golden tail pattern in life (vs. lacking).

Distribution: *Atelopus colomai* sp. n. is known from the Amazonian lowlands of Ecuador, ranging from ca. 240–1020 m a.s.l. Historically, *A. colomai* sp. n. was reported from less than 30 localities in Orellana and Pastaza provinces, all situated between the Río Napo and the Río Pastaza (Fig. 7). However, specimens collected by ROLF BLOMBERG in 1937 (NHRM RRB/1937.809.3262) originate from



Figure 6. Ontogenetic change in an individual of *Atelopus colomai* sp. n. from tadpole to subadult, reared under laboratory conditions at CJ from parental stock collected at the type locality (specimens not preserved). Upper left: CJ (sc 10997), Stage 25, lateral, dorsal and ventral views, total length = 8.3 mm; upper right: Stage 41, total length = 14.5 mm; Stage 42, total length = 14.1 mm; Stage 46, 71 days after Stage 25, 6.8 mm SVL; bottom: subadult 244 days after Stage 46, 18 mm SVL. Scale bar 10 mm. Photos by STEVEN GUEVARA SALVADOR, CJ.

“Zamora”, which, by that time, was the name for large parts of the southern Ecuadorian and adjacent Peruvian Amazonian lowlands. Thus, the distributional limits south- and eastward remain uncertain. Throughout the last 20 years and despite intensive efforts to locate the species, *A. colomai* sp. n. was confirmed only in few localities in Pastaza province, NE and SE of Puyo.

Natural history: The species inhabits terra firme lowland rain forest and can be found in close proximity to slow-moving clear water streams and rivers (Fig. 8). Adult males were heard calling throughout the day with an activity peak after rainfalls, in the morning and late afternoon as observed in August and September. Reproductive males defend territories along the streams where entering males

are approached by the resident and pursued, accompanied by intense calling, observed in the same months. Territorial behavior was also observed by TARVIN et al. (2014). Males were found perching on elevated positions such as branches, fallen trees and rocks in the lower understory up to 1.5 m above ground during the day. At night, males were inactive, resting on leaves up to 2 m above ground. Females were found at night only, sleeping on leaves or in bromeliad axils 1–5 m above ground. At the type locality, amplexant pairs were observed in March, April, July–October and December (TARVIN et al. 2014; authors’ observations). Tadpoles were collected in July (DUELLMAN & LYNCH 1969) and metamorphs were observed in September suggesting that reproduction may take place year-round.

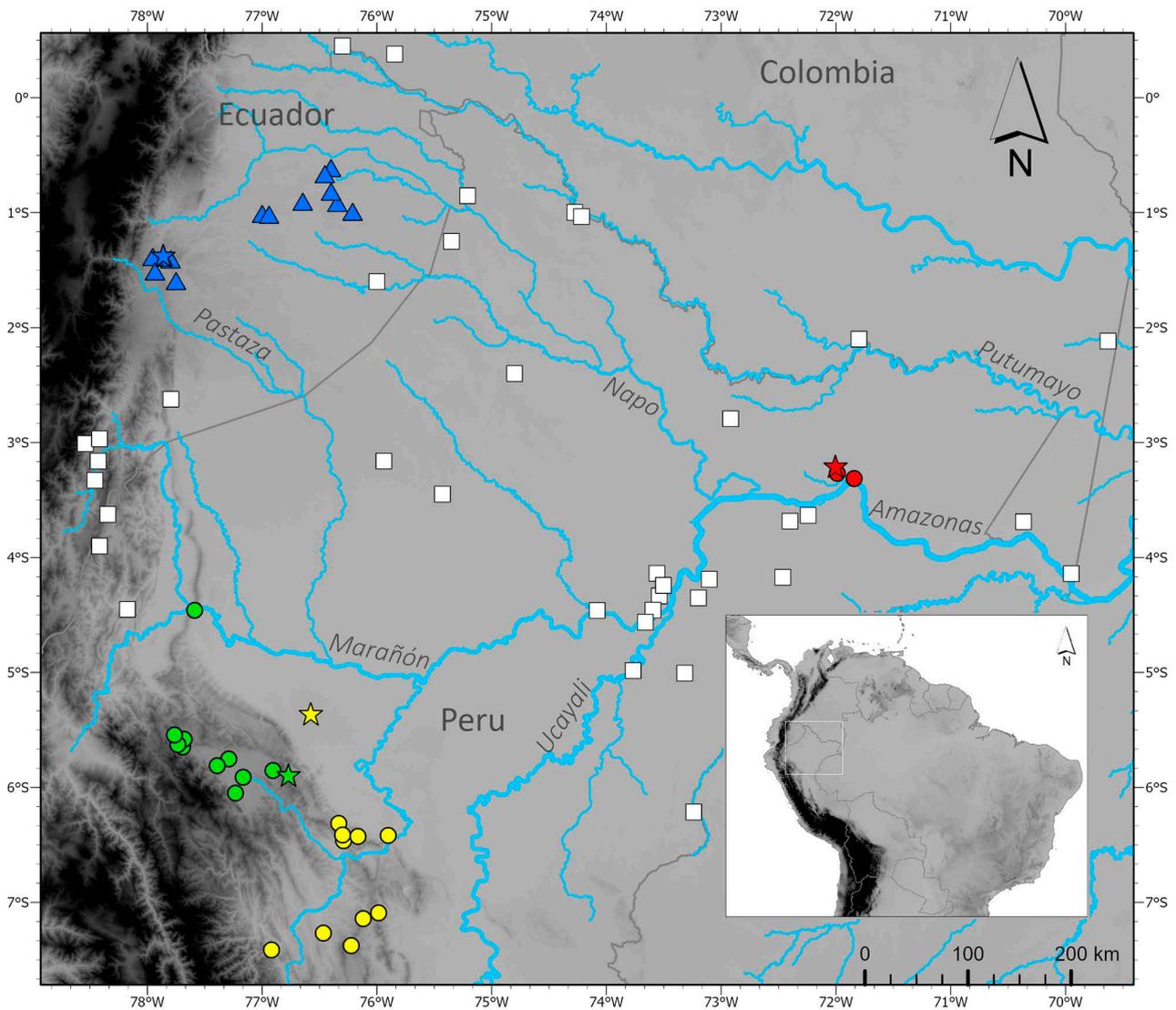


Figure 7. Map of the central upper Amazon basin showing the known distributions of western Amazonian *Atelopus* related to *A. spumarius*. Red dots correspond to *A. spumarius* sensu stricto, yellow dots to *A. pulcher*, green dots to *A. seminiferus*, blue triangles to *A. colomai* sp. n.; stars in the respective colors indicate type localities. White squares correspond to populations of unsolved taxonomic status. Basemap shows major Amazonian river systems and relief.

Atelopus colomai sp. n. can be locally abundant with up to 21 individuals per person*hour found in nocturnal visual encounter surveys at the type locality in September 2022. Northwest of El Triunfo, where some of the paratypes were collected, the species is less common with 5 individuals found in approx. 20 person*hours in 2021. TARVIN et al. (2014) observed 356 individually identified specimens through the course of a two-year capture-recapture study in a population along Río Pucayacu, close to the type locality. For information on syntopic anurans at the type locality see CULEBRAS et al. (2023). Monitoring studies conducted between 1994 and 2012 in Yasuní National Park (READ 2018) identified this species as rare. Only five individuals were discovered at two locations within the park.

When disturbed, specimens of *A. colomai* sp. n. present their colorful palms and soles while slowly walking away (PLEWNIA et al. 2024: Supplementary Video), simi-



Figure 8. Habitat of *Atelopus colomai* sp. n. at the type locality, with deforestation in the foreground (August 2022). Adults were found in the lower vegetation. Photo by AMADEUS PLEWNIA.



Figure 9. Deforestation in the habitat of *Atelopus colomai* sp. n. at the type locality with plantations of cassava on the right (August 2023). Photo by AMANDA B. QUEZADA RIERA.

lar to congeners from eastern Amazonia as described by RÖSSLER et al. (2019).

Conservation status: We suggest listing *Atelopus colomai* sp. n. as Endangered under criteria B1 and B2a,b of the IUCN Red List of Threatened Species as (1) it is known to persist only at six threat defined localities, (2) all of which are severely fragmented and (3) all of which are threatened by ongoing deforestation, agriculture, road construction and pollution (observed September 2021; August–September 2022, June–August 2023). Including historic localities, the EOO of the new species is roughly 7470 km² and AOO 64 km² while it is 172 km² and 24 km² for proven extant localities only.

At the type locality, an almost complete deforestation of remaining habitats occurred in late 2022 (Fig. 9). Fieldwork in August 2023 revealed the presence of few individuals in a remaining 10 m wide fragment of forest along one side of the stream. Deforestation has also been concluded as the reason for declines in another population of the new species by TARVIN et al. (2014). In the remaining four sites, there is a constant reduction in the extent and quality of remaining habitat. The species is known from one private protected area, Reserva Otoyacu, and was formerly found in Parque Nacional Yasuní from where it has not been confirmed for more than 20 years.

Batrachochytrium dendrobatidis (*Bd*), considered a main driver of extinctions in *Atelopus* (e.g. LA MARCA et al. 2005, LIPS et al. 2008, LÖTTTERS et al. 2023), has been repeatedly detected in *A. colomai* sp. n. (LÖTTTERS et al. 2023). However, no declines related to *Bd* were noticed, similar to other lowland *Atelopus* species (FLECHAS et al. 2012, 2015, BALLESTAS et al. 2021). TARVIN et al. (2014) conducted a comprehensive *Bd* sampling, documenting the pathogens' absence in *Atelopus* but its presence in syntopic anurans in their study site.

Atelopus colomai sp. n. is further likely to be threatened by climate change in the near future, which might both impact the species habitat as well as interfere and exacerbate existing threats such as disease (LÖTTTERS et al. 2023). The species from the western Amazon are among the harlequin toads likely to be most affected by climate change (LÖTTTERS et al. 2023).

Atelopus colomai sp. n. is currently kept in a laboratory survival-assurance colony in CJ, where it has already been bred successfully in F1 generation. A backup colony is held at Centro de Conservación de Anfibios, Bioparque Amaru, Cuenca.

Etymology: We dedicate this species to our friend and colleague LUIS A. COLOMA, who has continuously contributed to the study and protection of harlequin toads for decades. The specific name *colomai* is an eponym (i.e. a noun in genitive case). As English common name, we propose 'Coloma's harlequin toad'.

Remarks: Paratypes CJ 12406, 12409, 12425 (Fig. S1) remain alive (and were measured in life) to build up a laboratory survival-assurance colony.

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Material examined

Atelopus andinus: Peru: San Martín: upper Río Biabo valley, AMNH A 42657 (paratype), A 43200 (holotype); Loreto: Río Pisqui, AMNH A 43545 (paratype); border area of San Martín and Loreto: Río Cachiyacu (Tocachi), AMNH A 42914, A 43296, A 43297 (paratypes).

Atelopus barbotini: French Guiana: Saül vicinities, MNHNP 1979/1505 (holotype), 1979/1507–1979/1508, 1979/1510, 1979/1511, 1979/1514 (paratypes).

Atelopus flavescens: French Guiana: Cayenne area, MNHNP 256a (paralectotype), 803 (lectotype), LG 186–188, 191, 291, ZFMK 40682; Lac des Américains, ICN 05016–05017; Kaw area, MHNG 1225.11, 1225.21, 1225.26, ZFMK 39440, 39441.

Atelopus franciscus: French Guiana: Crique Grégoire (Kereroch), MNHNP 1979/1502 (holotype), 1975/1503–1975/1508 (paratypes).

Atelopus hoogmoedi complex: French Guiana: Haut Maroni: Monts Atachi-Bacca, MNHNP A522 (holotype), A515, A518–A521 (paratypes); Haut Oyapock, ICN 05018, 05019; Guyana: Karisparu, BM 1970.602–1970.613; Potaro District, Echerak, BM 1976.1999–1976.2001; Upper Patavo River, BM 1905.11.1.16; no exact locality, BM 1.3.46–1.3.49; Iwokrama, MTD 47888; Mabura Hill, MTD 47776; Suriname: Brownsberg, AMNH 7749, KU 206405, 206406; Kabo, MTD 47749; Nassau Mountains Plateau, MTD 49583 (referable to *A. hoogmoedi nassaui*). Brazil: Amapá: Serra do Navio, ZFMK 54384, 54385; Pará: Sudam Floral Reserve, 74 km south-east of Santarém, KU 129954–129960; no exact locality, BM 1874.7.16.1–1874.7.16.4, NHMW 3887/1, 13332/1.

Atelopus loettersi: Peru: Cusco: km 6.2 from Puente Fortaleza to Quincemil, MHNC 5412 (holotype), 5410–5411 (paratypes); Madre de Dios: Tambopata, MUSM 7635.

Atelopus manauensis: Brazil: Amazonas: N of Manaus, NHMW 33650/1, 33679/1–2.

Atelopus minutulus: Colombia: Meta: km 13–15 on road from Guayabetal to Manzanaraes, ICN 13709 (holotype), 4851–4853, 5028, 7085–7093, 12898 (paratypes), IAVH-Am 9913.

Atelopus palmatus: Ecuador: Pastaza: San Francisco on Río Pastaza, NHRM NNN/1937.418.4908 (5 syntypes); Río Negro, SC11443.

Atelopus planispina: Ecuador: Napo: Mount Sumaco, near San José Nuevo, MNCN 1390–1417 (syntypes); San Rafael, ICN 19151.

Atelopus pulcher: Peru: San Martín: vicinities of Tarapoto, KU 211676–211683, 212530, MUSM 1249, 1250, 6019–6023, ZFMK 48573, 50680–50685, 76243, 76244; Loreto: Chayahuitas (“Chyahvetas”), BM 1947.2.14.80 (lectotype), 1947.2.14.82–1947.2.14.83 (paralectotypes).

Atelopus seminiferus: Peru: from between Balsapuerto and Moyobamba, ANSP 11383 (holotype).

Atelopus spumarius sensu stricto: Peru: Loreto: Colonia (= Colonia Ancón on the right shore of Río Zumún close to the junction with the Río Yaguasyacu, a tributary to the Río Ampiyacu), MNHNP 1979/8382 (neotype); 3 km NE Pebas, AMNH A 103030–103035, MUBI 18222–18224.

Atelopus tricolor complex: Bolivia: La Paz: 17 km from Carasco, Serranía de Bellavista, CBF 285–288; Río Ñeques, km 10, Charazani-Apolo road, Yungas de La Paz, CBF 2502; Pilon-La-

jas, CBF 2487; Cochabamba: Río Ronco, Chapare, CBF 892; “old” road from Villa Tunari to Cochabamba, Chapare, ZFMK 69919–69920; Peru: Cuzco: Marcapata valley, BM 1947.2.14.57–1947.2.14.5759 (paralectotypes), MNHNP 03199 (paralectotype?), ZFMK 28103 (lectotype); 4 km south-west of Santa Isabel, Río Cosñipata, KU 162988; Puno: vicinity of Juliaca, AMNH 6097 (holotype of *A. rugulosus*).

Supplementary data

The following data are available online:

Supplementary Figure S1. Lateral, dorsal and ventral aspects of living paratopotypes kept at CJ (in columns from left to right CJ 12425, 12406, 12409). Photos by STEVEN GUEVARA SALVADOR (CJ).