

A new species of *Atelopus* (Anura: Bufonidae) from the Amazonian slopes of the Andes in south-eastern Peru

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Abstract. We describe a new species of *Atelopus* from the Amazonian slopes of the Cordillera Oriental in southern Peru. The new species is superficially similar to the northern Peruvian species *A. pulcher* and *A. spumarius*, but molecular markers place it in a different clade. In addition, it lacks a middle ear and has its dorsal skin covered with minute conical tubercles. The putative distribution of the new species includes the Andean piedmont in the departments of Cusco, Madre de Dios and Puno, encompassing an area of approximately 400 km in length and an altitudinal range of 400–1,000 m above sea level.

Key words. Amphibia, *Atelopus loettersi* sp. n., *A. pulcher*, *A. spumarius*, Peru, systematics.

Introduction

The Neotropical harlequin frogs (genus *Atelopus* DUMÉRIEUX & BIBRON, 1841) are known from humid environments from Costa Rica south to Bolivia and eastwards into the Amazon basin. They are one of the most threatened vertebrate groups of the World, with the majority of the more than 100 species having undergone severe declines, apparently related to the amphibian fungal disease chytridiomycosis (LA MARCA et al. 2005, STUART et al. 2008).

Not only because many species have become virtually absent from the wild and cannot be studied in detail, *Atelopus* taxonomy and phylogeny are complicated (e.g., COLOMA et al. 2000). When involving molecular markers, it has been demonstrated that the picture is highly contrasting to attempts purely based on morphology (e.g., NOONAN & GAUCHER 2005, GUAYASAMIN et al. 2010, LÖTTERS et al. 2011). Harlequin frogs are colourful and have remarkable patterns that actually should aid in species separation and identification (see PETERS 1973); however, convergence in colour and pattern combined with high intraspecific variation and low interspecific variation (i.e., cryptic species diversity), precludes easy taxonomic allocation for many species. Furthermore, species of remarkable likeness can even belong to different clades (LÖTTERS et al. 2010, 2011). This problem is well exemplified by harlequin frogs a priori referable to *A. spumarius* COPE, 1871 and *A. pulcher* (BOULENGER, 1882). Both belong to a complex of apparently different species from the upper Amazon basin of

northern Peru and adjacent Brazil, Colombia and Ecuador, whose external morphology conflicts with osteological and molecular data so that only an integrative taxonomic approach can help resolving the problems posed (LÖTTERS et al. 2002, 2011).

Until recently, the southernmost species of (i) *spumarius*–*pulcher*-like *Atelopus* and at the same time (ii) lowland species from altitudes below 1,000 m above sea level was *A. pulcher*, extending southward into the northern Cordillera Azul in Peru (department of San Martín) (LÖTTERS et al. 2002, S. LÖTTERS unpubl. data). Despite this, a photograph of a colourful *Atelopus* similar to *A. pulcher* or *A. spumarius* taken at the Río Távora, Peru, near the Bolivian border (department of Puno), was published by A. BAERTSCHI (see MACQUARRIE et al. 2001: 259). This finding was highly exciting for herpetologists involved in researching this region, suggesting that lowland harlequin frogs were present much more southwards than previously expected. The putative new species was later reported as “*Atelopus* sp., Río Távora” by LÖTTERS et al. (2005). In 2006, during fieldwork carried out in the region of Cusco, we collected *Atelopus* frogs similar to those from Río Távora. Our samples were loaned to colleagues involved in important and comprehensive research on Amazonian *Atelopus* to be examined in a phylogenetic context and readily identified as representatives of an undescribed species, neither closely related to *A. pulcher* nor *A. spumarius*. It was subsequently reported as “an apparently undescribed species from the Department of Cuzco” (LEHR et al. 2008), “*Atelopus* sp. Cusco”

(LÖTTERS et al. 2010) and “*Atelopus* sp. 2” (LÖTTERS et al. 2011), respectively, but has remained undescribed. In this paper, we formally describe this new species of *Atelopus* from south-eastern Peru.

Material and methods

Individuals of the new species were collected in the field, photographed alive, fixed in 10% formalin and preserved in 70% ethanol. A tissue sample was taken for molecular analyses (see LEHR et al. 2008, LÖTTERS et al. 2010, 2011). All material was deposited at the MHNC (Museo de Historia Natural de Cusco, Cusco, Peru) and MNCN (Museo Nacional de Ciencias Naturales, Madrid, Spain). The following comparative material was available from the ZFMK (Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany): *Atelopus pulcher*: ZFMK 48573, 76243–244, 85060–061, Tarapoto, San Martín, Peru; ZFMK 50680–685, 75796, between Tarapoto and Yurimaguas, San Martín, Peru.

External characters of specimens were examined under a stereomicroscope and measurements were taken with a digital calliper to the nearest 0.1 mm. Abbreviations used are: SVL, snout-vent length; HL, head length; HW, head width; TL, tibia length; FL, foot length; THBL, thumb length; HAND, hand length. The diagnosis, description and definition of measurements and characters follow LÖTTERS et al. (2002) and the references quoted therein.

Osteological skull characters were examined as described by GUIGAY et al. (2007) and VAN DER MEIJDEN et al. (2007) with X-ray synchrotron propagation phase contrast microtomography and holotomography at the ID19 beam-line of the European Synchrotron Radiation Facility (ESRF, Grenoble, France). The holotype of the new species and an unnumbered specimen of *A. pulcher* (from the vicinity of Tarapoto, department of San Martín, Peru, in the collection of S. LÖTTERS) were placed in a small polypropylene tube for imaging. We acquired tomographic data in phase contrast mode (energy: 35 Kev; propagation distance: 300 mm; voxel size: 8.06 μ m). Radiographic images with a size of 2,048 x 2,048 and 1,024 x 1,024 pixels were obtained by using a FReLoN CCD camera at different angles of 0–180 degrees. Dark current and reference images without sample were recorded to perform flat field corrections on the projections. Phase retrieval was performed using the mixed approach. After phase retrieval, tomographic reconstruction was performed using a 3D version of the filtered back projection algorithm to reconstruct the 3D refractive index distribution. From this, the 3D skull structure and soft tissue details were extracted. Three-dimensional renderings were obtained after semi-automatic segmentation of the skeleton, using Avizo 6.1 (Mercury Computer Systems, Chelmsford, MA, USA).

Atelopus loettersi sp. n.

(Figs. 1–2)

Atelopus sp. Río Távora – LÖTTERS et al. 2005: 345.

Atelopus sp. – LEHR et al. 2008: 377.

Atelopus sp. Cusco – LÖTTERS et al. 2010: 2130.

Atelopus sp. 2 – LÖTTERS et al. 2011: 45.

Holotype: MHNC 5412, adult male, from km 6.2 from Puente Fortaleza towards Quincemil (13°11'08.53" S, 70°34'58.79" W, 464 m above sea level), province Quispicanchis, department of Cusco, Peru, collected on 22 February 2006 by S. CASTROVIEJO-FISHER, J. C. CHAPARRO, I. DE LA RIVA and J. M. PADIAL.

Paratypes: MHNC 5410–11, juveniles, same data as holotype; MHNC 6020, adult female, and MHNC 6021, adult male, from Pozo Samanio (12°12'34.41" S, 72°56'39.33" W, 682 m above sea level), Río Saringabeni, province La Convención, department of Cusco, Peru, collected on 25 June 2006 by J. A. OCHOA; MHNC 7303–05, three adult males, from Chinguriato Alto, near Pongo de Mainique (12°15'10.44" S, 72°53'47.36" W, ca. 1,000 m above sea level), province La Convención, department of Cusco, Peru, collected on 9–10 July 2007 by J. A. DELGADO and O. TANAPARI.

Diagnosis: A medium-sized *Atelopus* (SVL of one adult female 35.2 mm, range of five males 24.7–26.7 mm) characterized, in addition to size, by the following combination of characters: (1) body slender, snout acuminate with the tip rounded; (2) neural spines not marked externally; (3) hind limbs long, tibiotarsal articulation reaching anterior corner of eye when leg is adpressed forward along body (average of males TL/SVL 0.46; $n = 5$); (4) foot shorter than tibia (average of males FL/TL 0.82; $n = 5$); (5) stapes, annulus tympanicus and tympanic membrane absent; (6) dorsal parts of body and limbs covered by minute coni (pointed spiculae), best visible under a stereomicroscope; (7) foot webbing formula Io–oII–oIII–3IV3–oV; (8) thumb short (average THBL/HAND 0.29; $n = 5$); (9) plantar and palmar surfaces mostly smooth with subarticular tubercles poorly defined; (10) in preservative, dorsum dark brown or tan with greyish-green irregular, well-defined markings; a similar pattern on limbs; throat, venter; ventral surfaces of thighs and palmar and plantar surfaces cream; some brown blotches may be present on the venter. In life, dorsal parts dark brown or tan with irregular pale green markings; ventral surfaces cream, white or yellow (mostly red in females); lower surface of thighs, and palmar and plantar surfaces red; (11) for a fragment of the 16S rRNA gene of the holotype see GenBank (accession number EU672980).

Colour and pattern readily distinguish *Atelopus loettersi* from all described *Atelopus* species, except the geographically close *A. pulcher* sensu stricto and *A. spumarius* sensu stricto (see LÖTTERS et al. 2002). Both differ from *A. loettersi* by their smooth dorsal skin. They lack the minute coni on the dorsal faces of body and limbs (present in the new species); while *A. pulcher* sensu stricto is entirely smooth, *A. spumarius* sensu stricto possesses small warts behind the eye. Moreover, the second mentioned species is considerably smaller than the new species [SVL of females of *A. spumarius* sensu stricto 25.2 ± 1.94 mm, $n = 6$ (LÖTTERS et al. 2002) versus 35.2 mm in the only female known of *A. loettersi*]. In addition, contrary to *A. loettersi*, *A. pulcher* sensu stricto possesses a middle ear (i.e. stapes, tympanic annulus, tympanum; Fig. 3); this status is unknown in *A. spumarius* sensu stricto.

Apart from this, DNA barcoding plus a tree-based taxonomic approach (using a fragment of the 16S rRNA gene)

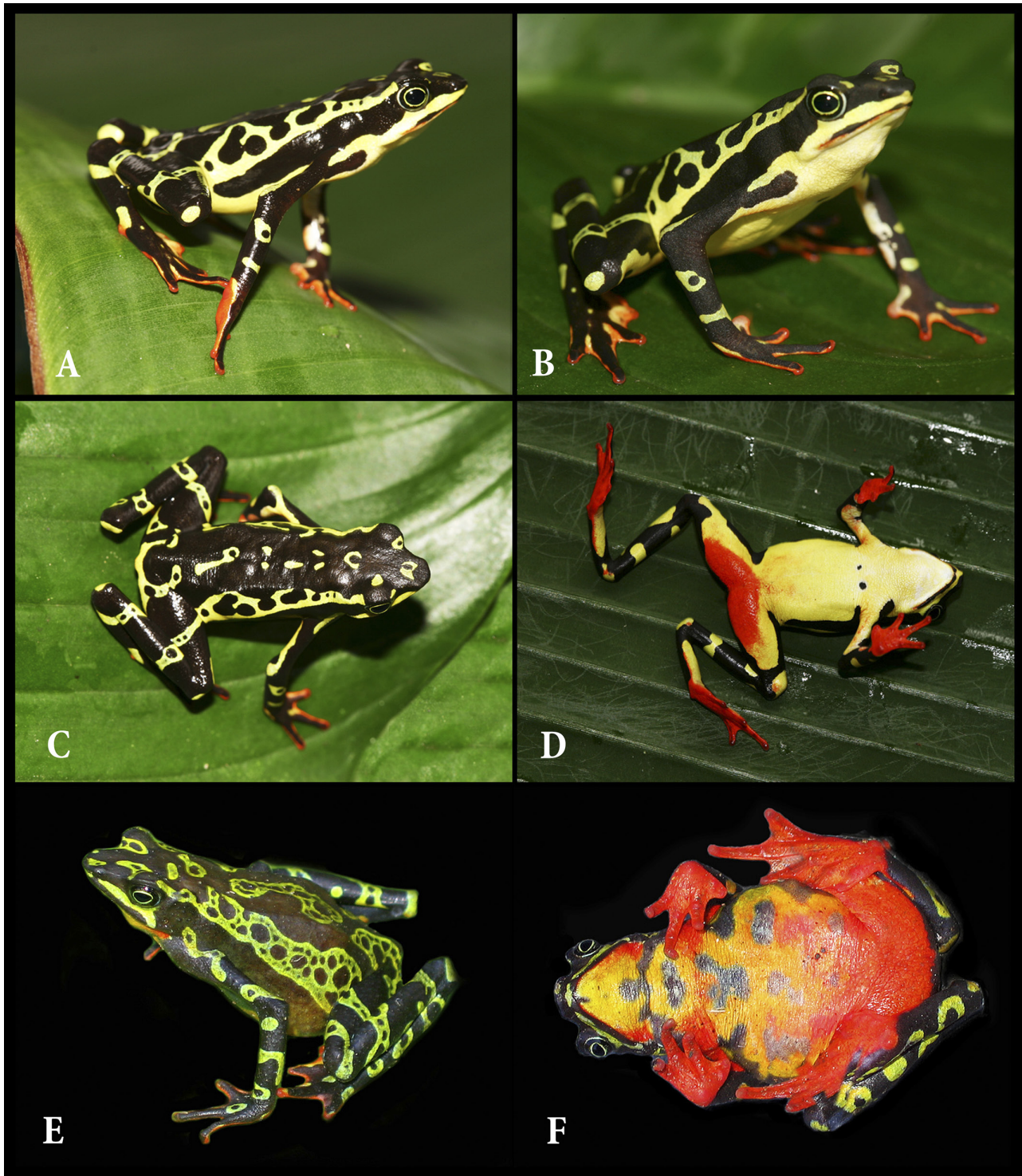


Figure 1. A–D – live male holotype of *Atelopus loettersi* sp. n. (MHNC 5412; SVL 26.7 mm) in lateral, dorsal and ventral views; E–F – female paratype (MHNC 6020; SVL 35.2 mm).

demonstrate that *A. loettersi* and *A. pulcher* sensu stricto belong to different major clades among Amazonian harlequin frogs (data for *A. spumarius* sensu stricto is lacking). *Atelopus loettersi* is nestled with other Peruvian-Bolivian species (i.e., not from northern Peru and adjacent areas), namely *A. tricolor* (BOULENGER, 1902) and *A. oxapampae* LEHR, LÖTTERS & LUNDBERG, 2008. They share with the

new species the absence of a middle ear and the absence of smooth skin. *A. tricolor* and *A. oxapampae* are dorsally covered with well-visible warts and both differ from *A. loettersi* in size, colouration, and genetic distance in a fragment of the 16S rRNA gene (LÖTTERS & DE LA RIVA 1998, LEHR et al. 2008, LÖTTERS et al. 2011, S. LÖTTERS unpubl. data). For details, see Discussion.



Figure 2. Dorsal and ventral views of the preserved holotype of *Atelopus loettersi* sp. n. (MHNC 5412; SVL 26.7 mm).

Description of the holotype: Body slender; neural spines not marked externally; head wider than long ($HW/HL = 1.14$); head length 25% of SVL; snout acuminate, with the tip rounded, dorsally depressed; upper jaw extending beyond lower; nostrils lateral, not visible from above; tongue twice longer than wide, its anterior half attached to floor of mouth; cantus rostralis straight from nostril to tip of snout, concave from eye to nostril; nostril closer to tip of snout than to eye; loreal area moderately concave; eye diameter slightly larger than distance from eye to nostril; stapes, tympanic annulus and tympanum absent. Tibia long, tibiotarsal articulation reaching anterior corner of eye when leg is adpressed forward along body ($TL/SVL = 0.50$); foot shorter than tibia ($FL/TL = 0.78$); relative length of toes $I < II < III < V < IV$; foot webbing formula $I_0 - oII - 3^{+}III_3 - 3 - IV_3 - oV$; outer metatarsal tubercle round, moderately prominent; inner metatarsal tubercle poorly defined, oval, flattened, larger than outer; subarticular tubercles poorly defined. Forelimb long, slender; relative length of fingers $I < II < IV < III$; hand webbing formula $I_0 - 2II - 3^{+}III_3 - 3 - IV$; outer palmar tubercle distinct, flattened, quadrangular, approximately the same size as oval inner; subarticular tubercles moderately marked, round (double on the base of second finger in the left hand); thumb moderately short, distance from tip to outer edge of inner palmar tubercle less than the length of this tubercle ($THBL/HAND = 0.29$); thumb covered by a pad of minute, keratinized, pale brown spiculae. Skin of dorsal faces of body and limbs seemingly smooth, but in fact covered with minute coni (pointed spiculae) when observed under a stereomicroscope; skin of ventral surfaces finely wrinkled.

In preservative, dorsal surfaces dark brown, almost black, with greyish –green, irregular, well-defined markings, especially in the dorsolateral regions; a similar pattern on limbs; throat, venter, ventral faces of thighs, and palmar and plantar faces cream; two small dark brown blotches on the chest.

In life (Fig. 1A–D), the dorsum was dark brown with irregular pale green markings; the upper lip was yellow; the

throat was cream and the chest and venter pale yellow; the lower faces of the thighs and the palmar and plantar faces were a vivid red; a faint red colouration entered the belly; also, an irregular red line was present on the margin of the lower jaw. The iris was black with a narrow, pale green ring surrounding the pupil. Besides the photographs presented herein, the holotype was illustrated in life by LÖTTERS et al. (2011: 47).

Variation: The paratypes in general correspond to the description given above. Contrary to males, the female paratype has the head longer than wide ($HW/HL = 0.93$) and the eye diameter is smaller than the eye–nostril distance; it has a paler dorsum and in life, it had more extensive red colouration on belly, throat and chest, and the venter was yellow with some irregular grey blotches (Fig. 1E–F).

Measurements [in mm; holotype followed by range of males (holotype plus four male paratypes), and single female paratype in parentheses]: snout–vent length, 26.7 (24.7–26.7, 35.2); head length, 6.8 (6.0–6.8, 9.3); head width, 7.8 (6.3–7.8, 8.7); internarial distance, 2.9 (2.4–2.9, 3.3); eye–nostril distance, 2.2 (2.0–2.4, 3.3); eye diameter, 2.4 (2.4–2.6, 2.6); tibia length, 13.4 (12.0–13.4, 16.7); foot length, 10.5 (9.5–10.5, 14.5); hand length, 7.1 (6.2–7.1, 8.9); thumb length, 2.1 (1.7–2.1, 2.6).

Skull osteology of holotype (Fig. 3): Skull not depressed, well ossified; sphenethmoid broadly exposed ventrally, moderately exposed dorsally, its anterior portion as broad as nasals, reaching their anterior border and the alary processes of premaxilla; prootic fused with exoccipital; frontoparietals fused posteriorly; frontoparietal fenestra reduced to a long and narrow suture; anterior border of frontoparietals reaching level of anterior border of orbits; nasals subrectangular, elongate, in broad contact with sphenethmoid; maxillary process of nasals slightly touching the preorbital process of pars facialis of maxilla; parasphenoid robust, cultriform process reaching level of

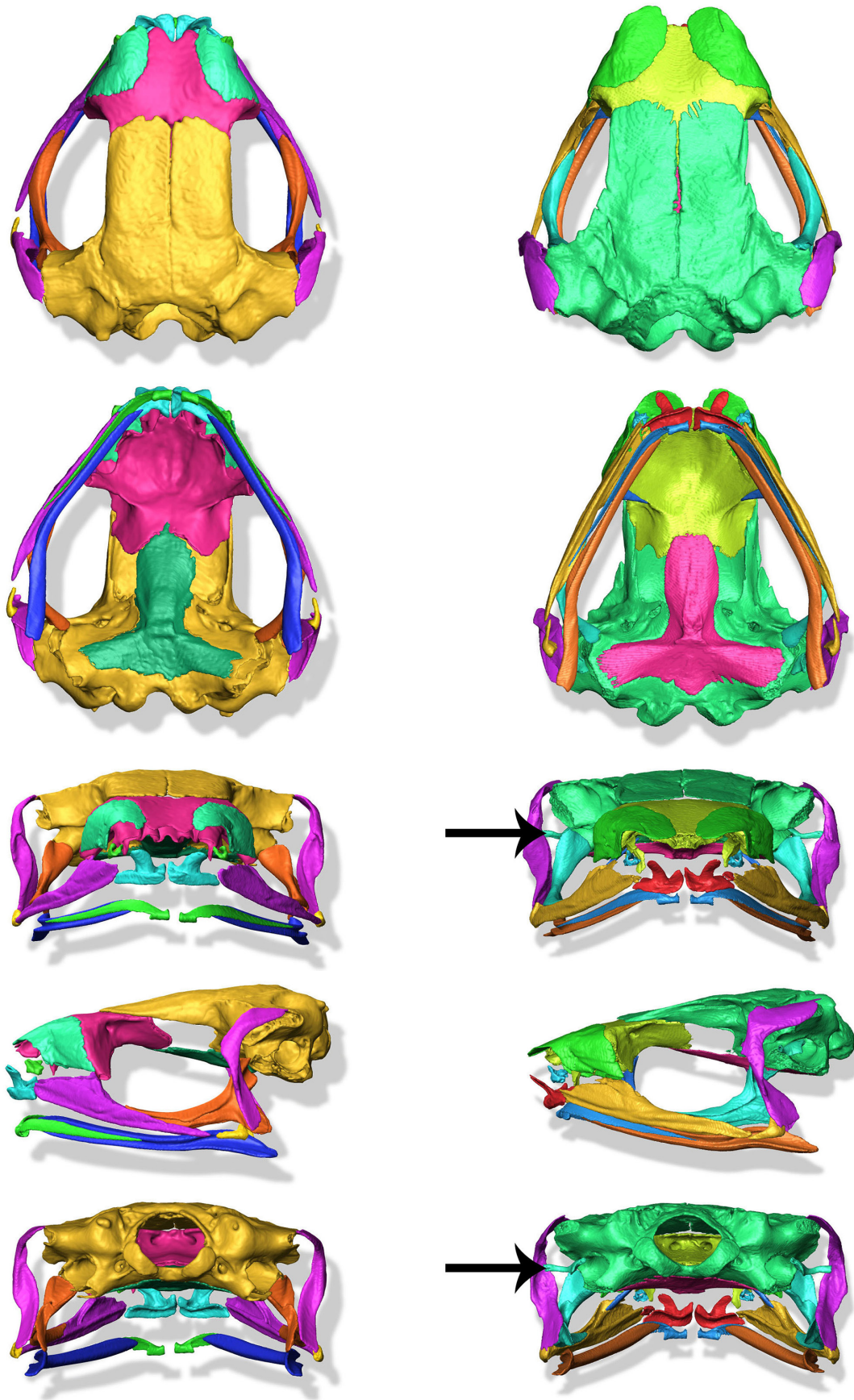


Figure 3. Comparative skull morphology of *Atelopus loettersi* sp. n. (holotype, left) and *A. pulcher* (unnumbered specimen in the collection of S. LÖTTERS, right). From top to bottom: dorsal, ventral, anterior, lateral and posterior views; note the presence of stapes in *A. pulcher* (arrows).

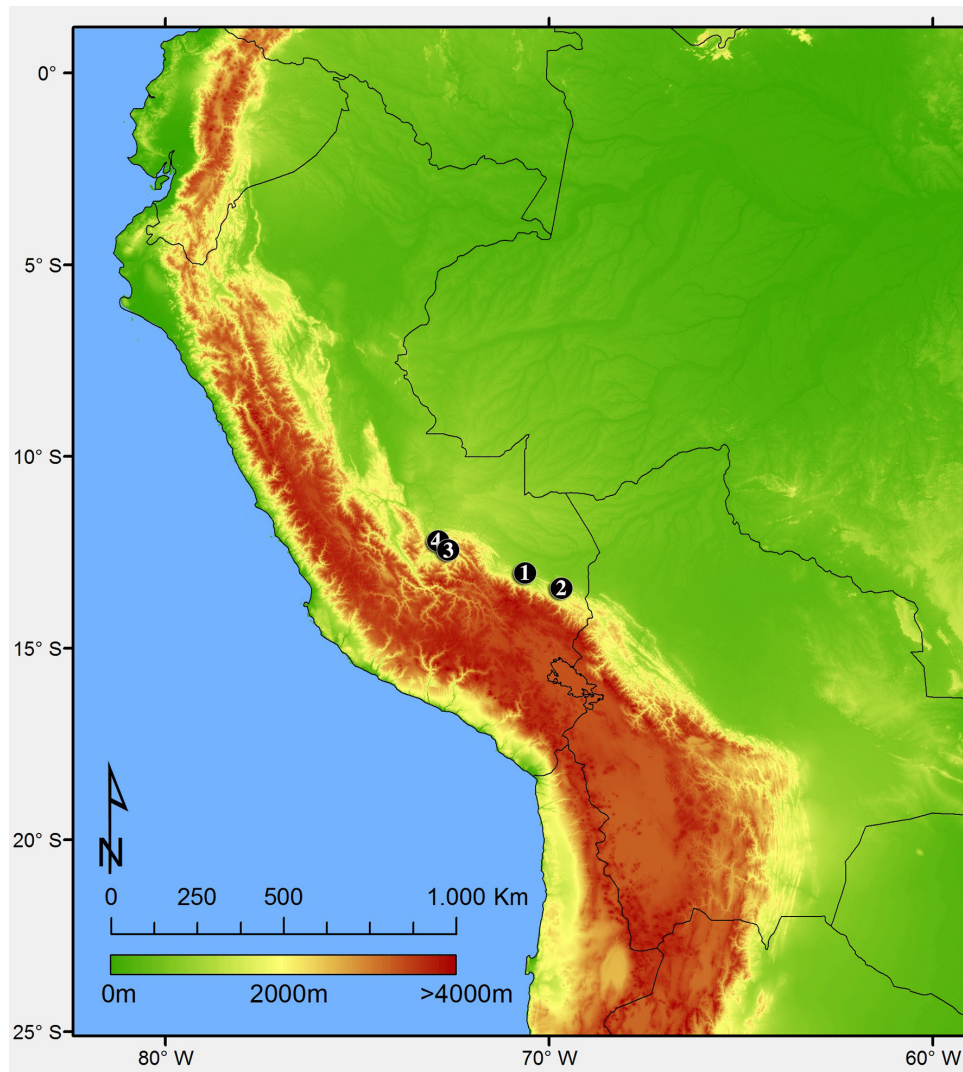


Figure 4. Map of the western part of central South America (Peru, Bolivia) showing the putative distribution of *Atelopus loettersi* sp. n. (see text): (1) km 6.2 from Puente Fortaleza to Quincemil (type locality); (2) Río Távora; (3) Chinguriato Alto; (4) Pozo Samario.

the middle of the orbits; alae of parasphenoid moderately large, forming an angle of approximately 120° with cultriform process; pterygoid well developed and robust, anterior and posterior rami forming a brace between maxilla and otic capsule; medial ramus of pterygoid long, contacting prootic; maxillary arch complete; alary process of premaxilla long, flat, not pointed; quadratojugal short, not contacting maxilla; otic ramus of squamosal long, robust, broadly contacting crista parotica; zygomatic ramus short, barely protruding from anterior margin of ventral ramus; plectral apparatus, stapes and annulus tympanicus absent.

Distribution and ecology: The type locality lies near the Nusinuscato River, a tributary of the Araza River in the headwaters of the Madre de Dios river basin drainage system; the general area is composed of lowland tropical rainforest. The creek where the holotype was found was about 3 m wide and held a rich fauna of invertebrates, clear water, and no apparent signs of human perturbation. The holotype was perching on a leaf near the water during night-

time, whereas the tiny juveniles were collected on the moss covering a large rock wall on the river bank. Neither additional adults or tadpoles were found, nor calls were heard that would have been allocable to *Atelopus loettersi*.

The localities of the paratypes are in the Lower Urubamba River region. One of them, Pozo Samario, is situated between two protected areas, the Reserva Comunal Machiguenga and the Santuario Nacional Megantoni; the other locality, Chinguriato Alto, lies within the Santuario Nacional Megantoni. Both localities are at an approximate distance of 270 km (airline) from the type locality. *Atelopus loettersi* is putatively also present in the extreme southeastern portion of Peru, near the Bolivian border, in the regions of Puno and Madre de Dios, as suggested by the specimen photographed at Río Távora (approximately at $13^\circ 30' S$, $69^\circ 40' W$), mentioned in the introduction, and tentatively allocated here to the new species (no voucher specimens available). This locality lies 376 km (airline) distant from Pozo Samario. Thus, the putative distribution of *A. loettersi* may include the piedmont of the Cordillera Oriental

of Peru in the departments of Cusco, Madre de Dios and Puno, encompassing an area of approximately 400 km in length and an altitudinal range of ca. 400–1,000 m above sea level (Fig. 4). The species has not yet been found in Bolivia, but its presence in the Madidi National Park is perhaps to be expected.

Etymology: We dedicate this species to our colleague and friend STEFAN LÖTTERS (Trier University, Germany) in recognition of his continuous contributions towards a better understanding of the taxonomy and systematics of harlequin frogs and their conservation.

Discussion

Genetic differences are usually low between sister species with great phenetic similarity, but there are cases of species markedly different in morphology having remarkably low genetic divergences. This is well exemplified by *Atelopus loettersi*, *A. pulcher* sensu stricto, and related harlequin frogs. LÖTTERS et al. (2011) found that not only *A. loettersi* (as “*Atelopus* sp. 2”) and *A. pulcher* belonged to different clades, but that their genetic divergence (i.e., uncorrected pairwise distance in a fragment of the 16S rRNA gene) was 9.9%, while it was only 6% between *A. loettersi* and the highly different Andean *A. tricolor*, and 5% between *A. loettersi* and the equally distinct *A. oxapampae*. These three species form a clade that is well supported and separated from the other Amazonian-Guianan *Atelopus* clade, whose members possess a middle ear (except *A. seminiferus*) (LÖTTERS et al. 2011). In DNA barcoding of anuran amphibians, the proposed “threshold” for the distinction of species in the 16S rRNA gene is about 3% and this has subsequently been discussed in the context of its applicability for taxonomic conclusions (e.g., VENCES et al. 2005, VIEITES et al. 2009). Of course, such a standard “threshold” needs to be carefully checked at a case-by-case basis as it varies across groups of organisms and even amongst closely related taxa (PADIAL et al. 2009). Genetic distances are useful as a first screening tool to obtain preliminary estimates of the actual species diversity within a certain group. Even within a phylogenetic context and when geographical sampling allows asserting that intraspecific divergences do not overlap with interspecific divergences of putative sister species, a combination with other lines of evidence should be applied to draw sound taxonomic conclusions. Although such an ideal scenario is often unavailable for most tropical species, genetic divergences between few allopatric specimens combined with phylogenetic information and distinct qualitative morphological characters can form the basis of robust inferences on divergent species (e.g., GLAW et al. 2010, PADIAL & DE LA RIVA 2010, PADIAL et al. 2010, VIEITES et al. 2009). Paraphyly in mitochondrial gene trees can be high due to different reasons (high variability of the gene at species level, incomplete lineage sorting, introgression etc.; see FUNK & OMLAND 2003). The presence of informative morphological characters supports the phylogenetic results based on genetic data, thus allowing an integrative approach in which taxonomic decisions are more soundly grounded. To us, the recognition of *A. loettersi* as a distinct species is clearly justified by large genetic diver-

gences, its phylogenetic position (not sister with the morphologically most similar species), qualitative differences in skin texture, and middle ear condition.

A gap of ca. 600 km in the distribution range of harlequin frogs seems to exist in the Amazonian Andean foothills of southern Peru, where no species have as yet been reported from between the southernmost known locality for *A. pulcher* sensu stricto (northern Cordillera Azul) and the northern populations of *A. loettersi* (S. LÖTTERS pers. comm.). Further surveys should determine whether this gap is “real” (provided that intermediate populations have not been driven into extinction). This absence of a geographic overlap between *A. loettersi* and *A. pulcher* sensu stricto raises the question of the amazingly convergent evolution of colour patterns in species belonging to different lineages, which perhaps cannot be explained by Müllerian mimicry (LÖTTERS et al. 2011).

Given the fact that most species of *Atelopus* are severely threatened, that *A. loettersi* does not seem to be an abundant species, and that the impact of human perturbations in the area (new roads, mining, illegal logging, etc.) is increasing, we suggest that this species be tentatively included in the IUCN’s category of ‘Endangered’, until more comprehensive data become available. Especially, it is advisable to study how chytridiomycosis might affect this species.

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References

- COLOMA, L. A., S. LÖTTERS & A. W. SALAS (2000): Taxonomy of the *Atelopus ignescens* complex (Anura: Bufonidae): designation of a neotype of *Atelopus ignescens* and recognition of *Atelopus exiguus*. – *Herpetologica*, **56**: 303–324.
- FUNK, D. J. & K. E. OMLAND (2003): Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. – *Annual Reviews in Ecology, Evolution and Systematics*, **34**: 397–423.
- GLAW, F., J. KÖHLER, I. DE LA RIVA, D. R. VIEITES, & M. VENCES (2010): Integrative taxonomy of Malagasy treefrogs: combination of molecular genetics, bioacoustics and comparative morphology reveals twelve additional species of *Boophis*. – *Zootaxa*, **2383**: 1–82.
- GUAYASAMIN, J. M., E. BONACCORSO, W. E. DUELLMAN & L. A. COLOMA (2010): Genetic differentiation in the nearly extinct harlequin frogs (Bufonidae: *Atelopus*), with emphasis on the Andean *Atelopus ignescens* and *A. bomolochos* species complexes. – *Zootaxa*, **2574**: 55–68.

- GUIGAY, J. P., M. LANGER, R. BOISTEL & P. CLOETENS (2007): Mixed transfer function and transport of intensity approach for phase retrieval in the Fresnel region. – *Optic Letters*, **32**: 1617–1619.
- LEHR, E., S. LÖTTTERS & M. LUNDBERG (2008): A new species of *Atelopus* (Anura: Bufonidae) from the Cordillera Oriental of central Peru. – *Herpetologica*, **64**: 368–378.
- LA MARCA, E., K. R. LIPS, S. LÖTTTERS, R. PUSCHENDORF, R. IBÁÑEZ, J. V. RUEDA-ALMONACID, R. SCHULTE, C. MARTY, F. CASTRO, J. MANZANILLA-PUPPO, J. E. GARCÍA-PÉREZ, F. BOLAÑOS, G. CHAVES, J. A. POUNDS, E. TORAL & B. E. YOUNG (2005): Catastrophic population declines and extinctions in Neotropical harlequin frogs (Bufonidae: *Atelopus*). – *Biotropica* **37**: 190–201.
- LÖTTTERS, S. & I. DE LA RIVA (1998): Redescription of *Atelopus tricolor* Boulenger from southeastern Peru and adjacent Bolivia, with comments on related forms. – *Journal of Herpetology*, **32**: 481–488.
- LÖTTTERS, S., W. HAAS, S. SCHICK & W. BÖHME (2002): On the systematics of the harlequin frogs (Amphibia: Bufonidae: *Atelopus*) from Amazonia. II. Redescription of *Atelopus pulcher* (Boulenger, 1882) from the eastern Andean versant in Peru. – *Salamandra*, **38**: 165–184.
- LÖTTTERS, S., R. SCHULTE, J. H. CÓRDOVA, & M. VEITH (2005): Conservation priorities for harlequin frogs (*Atelopus* spp.) of Peru. – *Oryx*, **39**: 343–346.
- LÖTTTERS, S., A. VAN DER MEIJDEN, D. RÖDDER, T. E. KÖSTER, T. KRAUS, E. LA MARCA, C. F. B. HADDAD & M. VEITH (2010): Reinforcing and expanding the predictions of the disturbance vicariance hypothesis in Amazonian harlequin frogs: a molecular phylogenetic and climate envelope modelling approach. – *Biodiversity and Conservation*, **19**: 2125–2146.
- LÖTTTERS, S., A. VAN DER MEIJDEN, L. A. COLOMA, R. BOISTEL, P. CLOETENS, R. ERNST, E. LEHR & M. VEITH (2011): Assessing the molecular phylogeny of a near extinct group of vertebrates: the Neotropical harlequin frogs (Bufonidae: *Atelopus*). – *Systematics & Biodiversity*, **9**: 45–57.
- MACQUARRIE, K., J. BLASSI & A. BAERTSCHI (2001): Where the Andes meet the Amazon. – Francis O. Patthey & Sons.
- NOONAN, B. P. & P. GAUCHER (2005): Phylogeography and demography of Guianan harlequin toads (*Atelopus*): diversification within a refuge. – *Molecular Ecology*, **14**: 3017–3031.
- PADIAL, J.M. & I. DE LA RIVA (2010): A response to recent proposals of integrative taxonomy. – *Biological Journal of the Linnean Society*, **101**: 747–756.
- PADIAL, J. M., S. CASTROVIEJO-FISHER, J. KÖHLER, C. VILÀ, J. C. CHAPARRO & I. DE LA RIVA (2009): Deciphering the products of evolution at the species level: the need for an integrative taxonomy. – *Zoologica Scripta*, **38**: 431–447.
- PADIAL, J. M., A. MIRALLES, I. DE LA RIVA & M. VENCES (2010): The integrative future of taxonomy. – *Frontiers in Zoology*, **7**: 16.
- PETERS, J. A. (1973): The frog genus *Atelopus* in Ecuador (Anura: Bufonidae). – *Smithsonian Contributions of Zoology*, **145**: 1–49.
- STUART, S. N., M. HOFFMAN, J. CHANSON, N. COX, R. BERRIDGE, P. RAMANI & B. YOUNG (eds.) (2008): Threatened amphibians of the world. – Lynx Editions, Barcelona, Spain; IUCN, Gland, Switzerland; Conservation International, Arlington, Virginia, U.S.A.
- VAN DER MEIJDEN, A., R. BOISTEL, J. GERLACH, A. ÖHLER, M. VENCES & A. MEYER (2007): Molecular phylogenetic evidence for paraphyly of the genus *Sooglossus*, with the description of a new genus of Seychellean frogs. – *Biological Journal of the Linnean Society*, **91**: 347–359.
- VENCES, M., M. THOMAS, A. VAN DER MEIJDEN, Y. CHIARI & D. R. VIEITES (2005): Comparative performance of the 16S rRNA gene in DNA barcoding of amphibians. – *Frontiers in Zoology*, **2**: 5.
- VIEITES, D. R., K. C. WOLLENBERG, F. ANDREONE, J. KÖHLER, F. GLAW & M. VENCES (2009): Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. – *Proceedings of the National Academy of Sciences of the USA*, **106**: 8267–8272.