



Misjudged for long: a new toad of the *Rhinella veraguensis* species group (Anura: Bufonidae) from the Yungas forests of Bolivia

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Abstract. We re-evaluate the taxonomic status of specimens of *Rhinella* collected from rainforests on the eastern Andean slopes and foothills of central Bolivia. The respective populations have been allocated to different nominal taxa, namely *Rhinella fissipes* and *R. leptoscelis*, in the past. By detailed morphological comparisons, including the type specimens of crucial taxa, as well as a phylogenetic analysis based on the mitochondrial 16S rRNA gene, we here demonstrate that the focal populations represent a divergent lineage within the *Rhinella veraguensis* species group, being apparently closely related to *R. rumbolli* from northern Argentina, but only distantly related to *R. leptoscelis*, with which they share several morphological character states. Also, the specimens of the focal lineage differ by a unique combination of morphological character states from all known nominal species currently assigned to the *R. veraguensis* group. Consequently, we describe this lineage as a new species. We discuss the history of its changing taxonomic allocations and demonstrate that former conclusions were barely justified and wrong. We also provide a description of the osteology of this species using computer tomography (micro-CT). Furthermore, we discuss the status of the nominal taxon *Bufo pleuropterus* SCHMIDT, 1857, currently considered to represent a junior synonym of *Rhinella margaritifera* (LAURENTI, 1768), and provide arguments for the specific distinctness of these two taxa. Consequently, we regard *Rhinella pleuroptera* (SCHMIDT, 1857) a valid species. Based on its external morphology, which is rather similar to that of *R. inca*, we speculate that *R. pleuroptera* is possibly related to species in the *R. veraguensis* group, although this remains in need of further research.

Key words. Amphibia, *Bufo pleuropterus*, computer tomography (micro-CT), molecular genetics, morphology, osteology, Peru, taxonomy, systematics.

Resumen. Revaluamos la situación taxonómica de especímenes de *Rhinella* colectados en las laderas orientales del centro de Bolivia (bosques de Yungas). Las poblaciones en cuestión fueron anteriormente consideradas como parte de *Rhinella fissipes* o *R. leptoscelis*. Sin embargo, el estudio detallado de la morfología, que incluye los ejemplares tipo de las especies clave, así como los análisis filogenéticos del gen 16S rRNA, apoyan que se trata de un linaje filogenético divergente, hermano a *R. rumbolli* del norte de Argentina, y más distante de *R. leptoscelis*, con los que comparte varios caracteres morfológicos. Los especímenes del linaje descubierto muestran una combinación única de caracteres anatómicos que la diferencian del resto de especies del grupo *R. veraguensis*. Describimos este linaje como una nueva especie y discutimos hipótesis alternativas sobre la taxonomía de estas poblaciones para mostrar que no estaban justificadas. Además, describimos la osteología de la nueva especie a partir de tomografías computerizadas (micro-CT). Por otro lado, discutimos el estado del taxón nominal *Bufo pleuropterus* SCHMIDT, 1857, actualmente un sinónimo de *Rhinella margaritifera* (LAURENTI, 1768), y argumentamos que ambos nombres representan especies distintas. Consideramos *Rhinella pleuroptera* (SCHMIDT, 1857) una especie válida en base a sus caracteres morfológicos, similar a *R. inca*, y especulamos sobre sus relaciones. Probablemente se trate de una especie del grupo *R. veraguensis*, pero para determinar la validez de esta afirmación precisamos estudios adicionales.

Palabras clave. Amphibia, *Bufo pleuropterus*, genética molecular, morfología, osteología, Peru, sistemática, taxonomía, tomografía computerizada (micro-CT).

Introduction

Among Neotropical toads placed in the genus *Rhinella* (sensu CHAPARRO et al. 2007, PEREYRA et al. 2021), various species groups and relationships have been proposed in the past, primarily based on phenetic similarities (e.g., GALLARDO 1961, MARTIN 1972, DUELLMAN & SCHULTE 1992). Among them is the *R. veraguensis* species group, erected by DUELLMAN & SCHULTE (1992), which was later demonstrated to be polyphyletic (PRAMUK 2006, CHAPARRO et al. 2007, PYRON & WIENS 2011). In a recent comprehensive study, PEREYRA et al. (2021) provided a new phylogeny of *Rhinella* based on a broad taxon and character sampling, revealing strongly supported major clades within the genus. As a result, existing species groups were newly defined, new species groups proposed and numerous species reallocated to species groups. The redefined *R. veraguensis* group of PEREYRA et al. (2021) contains nine nominal species plus a candidate species (their *Rhinella* sp. 2 from central Peru). All these species inhabit humid forests of the eastern Andean slopes of Argentina, Bolivia and Peru, with the exception of the tentatively included and possibly extinct species *R. chrysoptera* from Honduras (PRAMUK & LEHR 2005, PEREYRA et al. 2021).

During fieldwork in Bolivia in the late 1990s, we collected toads from a population in montane rainforests of the Chapare region in the Departamento Cochabamba, which at the time of collection were considered to represent a candidate species. However, these toads shared several phenetic characters with other species at that time placed in the *Rhinella veraguensis* group and comparison with type specimens, despite some discrepancies in character states, led KÖHLER (2000) to allocate this Chapare population to *R. fissipes*, a species described from Santo Domingo, Carabaya, southern Peru (BOULENGER 1903). Later, in revising toads collected in southern Peru, PADIAL et al. (2009) resurrected *R. leptoscelis* from the synonymy of *R. veraguensis* and considered the Bolivian toads suggested to represent *R. fissipes* by KÖHLER (2000) to be conspecific with *R. leptoscelis*. Both of these decisions, the initial suggestion by KÖHLER (2000) and the subsequent change by PADIAL et al. (2009), were barely accompanied by a convincing rationale. This led us to reinvestigate the status of these Bolivian toads and, most importantly, generate DNA sequences from tissue samples hidden for more than two decades in a freezer. Our results provide evidence that these toads neither represent *R. fissipes*, nor *R. leptoscelis*, but an unnamed species that we describe and name herein.

Materials and methods

Fieldwork and voucher specimens

Fieldwork was conducted in Bolivian montane forests during the rainy seasons between November 1997 and Febru-

ary 1999, among other regions covering different localities in the Departamentos Cochabamba and Santa Cruz (see KÖHLER 2000). Specimens were observed and collected during opportunistic searching at day and night using torches and headlamps. Geographic position was recorded using a handheld Magellan 3000 XL GPS receiver set to WGS84 datum.

Collected specimens were euthanized using an overdose of chlorobutanol solution. Tissue samples were taken prior to fixation and stored in 99% ethanol, while specimens were fixed using 96% ethanol and subsequently stored in 70% ethanol. Specimens were sexed by examination of gonads, and deposited at the herpetological collection of the Zoologisches Forschungsmuseum Alexander Koenig Bonn (ZFMK), Germany, and Hessisches Landesmuseum Darmstadt (HLMD), Germany. JKSL refers to JÖRN KÖHLER and STEFAN LÖTTERS field numbers. CBG refers to Centro de Biodiversidad y Genética, Cochabamba, Bolivia. Other museum abbreviations mentioned follow those listed by FROST (2023).

Morphology

Morphometric measurements (in millimetres) were taken by JK with a digital caliper to the nearest 0.1 mm. Abbreviations used throughout the text are: SVL, snout–vent length; HW, head width (at level of angle of jaws); HL, head length (from angle of jaw to tip of snout diagonally); ED, horizontal eye diameter; TD, horizontal tympanum diameter; IOD, interorbital distance; IND, internarial distance; E–N, eye–nostril distance (straight line distance between anterior corner of orbit and posterior margin of external nares); NSD, nostril–snout distance; SL, snout length (between anterior corner of eye and tip of snout); FL, forearm length (between flexed elbow and proximal edge of palmar tubercle); HNDL, hand length (between proximal edge of palmar tubercle and tip of finger III); FEML, femur length (between vent and knee); TL, tibia length; FOOTL, foot length (distance from proximal margin of inner metatarsal tubercle to tip of toe IV); PL, parotoid gland length (horizontal).

Fingers and toes are numbered preaxially to postaxially from I–IV and I–V, respectively. We determined comparative lengths of toes III and V by addressing both toes against toe IV; lengths of fingers I and II were determined by addressing the fingers against each other. We consider the tympanum being absent if there is no externally visible tympanic membrane, following the terminology of LYNCH & DUELLMAN (1997) and the definitions of PEREYRA et al. (2016). Cranial crest definitions follow TRUEB (1971) and PRAMUK (2006), using the term occipital crests instead of parietal crests. Webbing formulae follow SAVAGE & HEYER (1997). Description scheme and diagnosis follow CASTILLO-URBINA et al. (2021). Colouration in life is described based on colour slides taken of living individuals.

Osteology

To obtain high-resolution computer tomography (micro-CT) data of osteological features of the new species, one adult female (ZFMK 72569) of the focal specimens was scanned on a Phoenix V|tome|x M microfocus CT (Waygate Technologies, Hürth, Germany) by F. & G. Hachtel GmbH & Co. KG (Aalen, Germany). The specimen was placed with polystyrene and a wooden frame in a plastic bag with a small amount of ethanol to avoid desiccation. Scans were performed at a tube voltage of 190 kV and current of 300 μ A at resolution 0.0557 μ m. The scan resulted in 1,523 TIFF files, processed in 3D Slicer (version 5.2.2) and visualized in MeshLab version (2022.02). Osteological nomenclature follows DUELLMAN & TRUEB (1986), PRAMUK (2006) and PEREYRA et al. (2021), and for skeletal elements of the hand FABREZI & ALBERCH (1996).

Taxon sampling

Genetic analysis aimed at identifying lineage divergence among focal lineages of *Rhinella*. For representative taxon sampling, we largely followed the approach of CASTILLO-URBINA et al. (2021). First, we used BLAST searches (ALTSCHUL et al. 1990) of newly generated 16S rRNA sequences of *Rhinella* against the GenBank nucleotide archive for a preliminary check of plausibility, and to identify and download comparative sequences of greatest similarity to be included in downstream analysis. Next, we manually searched for sequences of species that bear morphological similarities to the target species (namely species in the *R. veraguensis* group, as well as representatives of species assigned to the *R. festae*, *R. margaritifera*, *R. marina* and *R. granulosa* species groups (sensu PEREYRA et al. 2021), plus *R. spinulosa*. For the *R. veraguensis* species group, we added six new samples collected by us at different localities in Bolivia. A sequence of *Bufo bufo* was used to root the tree. Information on used samples is provided in the Supplementary Table S1.

We follow PEREYRA et al. (2021) in recognizing the sequence with GenBank accession number DQ158478 as representing *R. tacana*, sequence KF992151 as representing *R. iserni*, and sequence DQ283386 as representing *R. quechua*. GenBank sequence KF992144 was renamed by us as *R. teotoniensis* given the respective revision of FERRO et al. (2022). Furthermore, we correct the locality and voucher number information for *R. dapsilis* (GenBank accession number DQ158448), erroneously given as La Perla, Pichincha, Ecuador by PRAMUK (2006), as in this case the field number of the sampled specimen has been confused with the museum collection number (see Appendix and Supplementary Table S1). The sequence MW003478 referred to as *R. fissipes* by PEREYRA et al. (2021) actually corresponds to an unnamed taxon (see below).

Molecular analysis

As in previous studies (e.g., CASTILLO-URBINA et al. 2021), we sequenced a DNA fragment of the mitochondrial 16S rRNA gene from tissue samples of newly collected specimens using standard protocols. We extracted genomic DNA following a standard salt extraction protocol and subsequently used polymerase chain reaction (PCR) with primers 16SAr-L (5'-CGCCTGTTTATCAAAAACAT-3') and 16SBr-H (5'-CCGGTCTGAACCTCAGATCACGT-3') (PALUMBI et al. 1991). The PCR products were directly sequenced on automated DNA sequencers by LGC Genomics (Berlin, Germany), validated and poor-quality stretches trimmed using CodonCode Aligner (CodonCode Corp.). All new DNA sequences were submitted to GenBank (accession numbers OR428682–OR428687). Reference sequences of other *Rhinella* spp. were downloaded from GenBank as flatfiles, converted to tabular format using DNAconvert, a tool part of the iTaxoTools suite (VENCES et al. 2021), and combined with own sequences in a curated spreadsheet with the appropriate metadata. Sequences were then converted into a fasta format, and exploratory analyses carried out as well as the most appropriate substitution model (GTR+G) determined using the Bayesian Information Criterion in MEGA7 (KUMAR et al. 2016). Sequences were then aligned using MAFFT (KATO et al. 2019) in Concatenator (part of iTaxoTools), and a Maximum Likelihood tree inferred in RaxML (STAMATAKIS 2014) using raxmlGUI v. 2.0 (EDLER et al. 2020), with node support assessed by 1000 thorough bootstrap replicates. To quantify genetic divergences, we calculated uncorrected pairwise distances among the sequences (p-distances) in MEGA7, after removal of several sequences that were substantially shorter than the overall alignment (in order to avoid biases by over-representation of highly variable regions in such short sequences). Diagnostic positions were calculated in MolD (FEDOSOV et al. 2022), as implemented in iTaxoTools, relative to the full 16S rRNA sequence of *Rhinella marina* (GenBank accession number MZ675575).

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new name contained herein is available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Science Identifier) for this publication is: urn:lsid:zoobank.org:pub: E769D9BE-57E4-4CDB-BCDD-E27E903134D4. 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: zenodo.org, salamandra-journal.com.

Results

Molecular relationships

Although the short fragment of the 16S gene used for phylogenetic analysis (alignment length 580 bp) is insufficient to establish reliable hypotheses on phylogenetic relationships within the genus *Rhinella* especially at deep nodes (see CHAN et al. 2022), our Maximum Likelihood tree (Fig. 1) generally is in agreement with recent more comprehensive phylogenies (PEREYRA et al. 2021). Proposed species groups within *Rhinella* are recovered monophyletic with high bootstrap support, and with the *R. veraguensis* species group being sister to a clade containing the *R. margaritifera* and *R. festae* species groups as revealed by PEREYRA et al. (2021). The focal sample of the Bolivian *Rhinella* is placed as a member of the *R. veraguensis* species group and clusters with a sequence assigned to *R. fissipes* (GenBank accession number MW003478) originating from the Isiboro Séure National Park at the border of the Departamentos Beni and Cochabamba in Bolivia. Given this result, we consider both samples representing the same species-level lineage, but as discussed below, they do not represent *R. fissipes* sensu BOULENGER (1903) given morphological differences to the holotype of that taxon. This lineage is recovered sister to *R. rumbolli* from northern Argentina, although this relationship did not receive significant support (bootstrap value 41%). The clade containing *R. rumbolli* and the focal lineage is sister to a clade containing *R. justinianoi*, *R. quechua* and *R. veraguensis*. This major clade within the species group is sister to another major clade containing *R. inca*, *R. leptoscelis* and an apparently unnamed taxon here referred to as *R. cf. leptoscelis* (see also CUSI et al. 2017, CASTILLO-URBINA et al. 2021; i.e., *Rhinella* sp. 2 of PEREYRA et al. 2021).

Our focal lineage had uncorrected pairwise distances in the studied 16S gene fragment of 4.9–5.3% to its possible sister lineage *R. rumbolli*, 4.4–4.9% to *R. veraguensis*, 4.1–4.2% to *R. quechua*, 5.7% to *R. justinianoi*, 7.6% to *R. inca* and 7.8% to *R. leptoscelis*, with the last value representing the greatest uncorrected p-distance among our samples of the *R. veraguensis* group. Our analysis revealed the lowest uncorrected p-distances within the species group between *R. quechua* and *R. veraguensis* (1.1–1.2%), *R. inca* and *R. leptoscelis* (1.8%), and *R. quechua* and *R. justinianoi* (3.0–3.2%).

Morphology

Our morphological re-examination of specimens of the focal *Rhinella* lineage from central Bolivia revealed substantial qualitative differences when compared to other nominal species in the *R. veraguensis* species group (see below). This comparison included the examination of type specimens of crucial taxa (see Appendix). The observed morphological differences are beyond those usually considered to represent intra-specific variation and in addition to the molecular differentiation provide further evidence for the presence of an unnamed taxon that we describe and name herein.

Taxonomy

Rhinella kuka sp. n.

Figs 2, 3, 6–9

ZooBank LSID: urn:lsid:zoobank.org:act:
F4CBAEAF-A3DA-43D0-9DD8-6BAA90613AE0

Remarks: This species has formerly been referred to as *Bufo fissipes* by KÖHLER (2000), *Rhinella fissipes* by PEREYRA et al. (2021) and PORTIK et al. (2023), and *Rhinella leptoscelis* (partim) by PADIAL et al. (2009).

Holotype: ZFMK 72668 (JKSL 730), adult female, from a point on the 'old Chapare road' connecting Villa Tunari and Cochabamba, 17°06' S, 65°34' W, 1450 m above sea level, in Carrasco National Park, Provincia Chapare, Departamento Cochabamba, Bolivia, collected on 3 January 1999 by J. KÖHLER and G. SUAREZ.

Paratypes: ZFMK 72669 (JKSL 731), ZFMK 72670 (JKSL 732), adult females, same data as holotype; HLMD-RA-3238 (JKSL 448), adult female, from a point on the 'old Chapare road', 17°07' S, 65°34' W, 1300 m a.s.l., in Carrasco National Park, Provincia Chapare, Departamento Cochabamba, Bolivia, collected on 6 February 1998 by J. KÖHLER and S. LÖTTERS; ZFMK 80036 (JKSL 692), adult female, ZFMK 72671 (JKSL 693), juvenile, from a point on the 'old Chapare road', 17°06'50" S, 65°34'19" W, 1250 m a.s.l., in Carrasco National Park, Provincia Chapare, Departamento Cochabamba, Bolivia, collected on 18 December 1998 by J. KÖHLER and S. LÖTTERS; ZFMK 80035 (JKSL 722), adult male, from a point on the 'old Chapare road', 17°07' S, 65°35' W, 1650 m a.s.l., in Carrasco National Park, Provincia Chapare, Departamento Cochabamba, Bolivia, collected on 3 January 1999 by J. KÖHLER and G. SUAREZ.

Referred specimen: CBG 599, from Santo Domingo, Territorio Indígena, Isiboro Séure National Park, 800 m a.s.l., at the border of Departamentos Beni and Cochabamba, Bolivia, collected in 2014 by I. DE LA RIVA. This specimen could not be examined, but corresponds to the tissue sample MNCN-ADN 6310 and GenBank accession number MW003478 (I. DE LA RIVA, pers. comm.; see Fig. 1).

Definition: A large-sized species in the *Rhinella veraguensis* species group, based on morphological similarities and phylogenetic relationships. The new species is characterized by (1) large size, SVL 62.8 mm in adult male ($n = 1$), SVL 66.0–72.1 mm in adult females ($n = 5$); (2) eight presacral vertebrae, presacrals I and II (atlas and axis) fused; skull hyperossified; (3) snout short, acuminate in dorsal view, rounded in lateral profile; (4) canthal, preorbital, supraorbital, and postorbital crests distinct and continuous; pretymppanic crest present; supratympanic crest distinct, short; occipital crests prominent, elevated; (5) tympanic membrane and tympanic annulus distinct; tympanum slightly higher than wide, its diameter slightly more than half the eye diameter; (6) mandibular angle slightly

A new toad of the *Rhinella veraguensis* species group

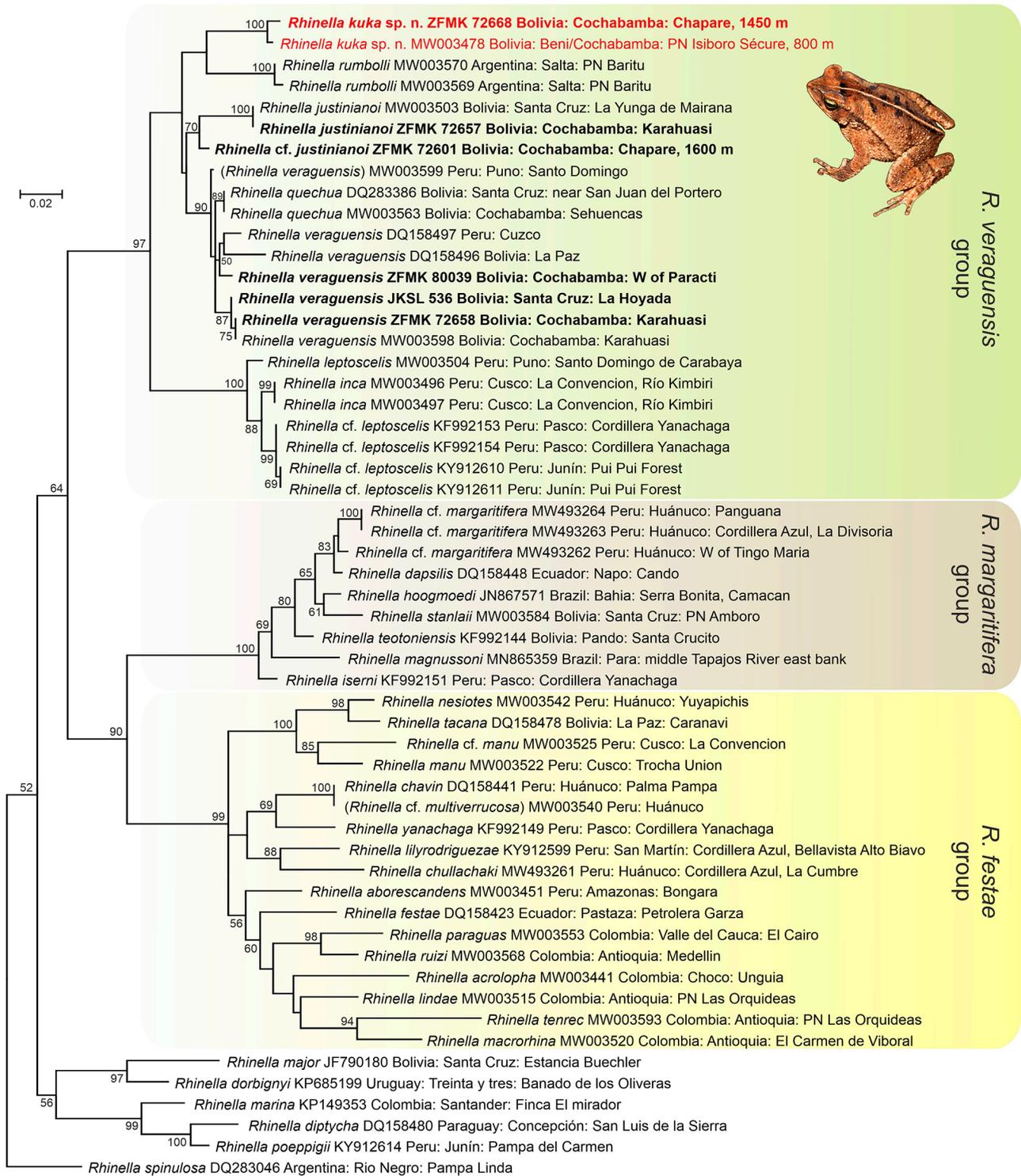


Figure 1. Maximum Likelihood phylogenetic tree of *Rhinella* species inferred from a 580 bp alignment of the mitochondrial 16S mRNA gene. The tree was rooted with *Bufo bufo* (not shown for better graphical presentation). Values at nodes are bootstrap proportions in percent (not shown if < 50%). Newly obtained sequences obtained for this study are in bold font. The taxon name is followed by the GenBank accession number or voucher number (for newly obtained sequences) and the locality. Species names in parentheses refer to samples with unverified species identification. The inset photo depicts the paratype specimen ZFMK 80036 of *R. kuka* sp. n. in life.



Figure 2. Dorsolateral views (left column) and ventral views (right column) of paratypes of *Rhinella kuka* sp. n. in life: (A, B) female ZFMK 72670; (C, D) female ZFMK 80036; and (E, F) male ZFMK 80035.

protruding in dorsal view; (7) parotoid glands moderately large, roughly subtriangular in outline; (8) continuous dorsolateral row of enlarged conical tubercles extending from parotoid gland to groin; (9) skin on dorsum tuberculate with a mix of relatively flat rounded tubercles and conical tubercles with keratinized tips; skin on flanks covered with keratinized conical tubercles; skin on throat, chest and venter granular; (10) hands with long and slender fingers; finger I longer than finger II; fingers only with a trace of fleshy webbing basally; (11) toes long and slender, moderately webbed; toe V shorter than toe III; (12) fingers and toes bearing serrated lateral fringes; (13) subarticular tubercles distinct, prominent, round to ovoid; (14) supernumerary tubercles present, ovoid and well developed; (15) cloacal sheath absent; cloacal opening protuberant, located at

upper level of thighs; (16) in life, dorsum reddish to orange brown, with different extents of dark brown to black markings, flecks and spots; dark brown interorbital flecks; narrow cream vertebral stripe, almost extending to tip of snout; upper surfaces of limbs brown, with dark brown transversal bars; ventral surfaces cream to orange cream, with dense dark brown mottling and flecking on throat, chest and anterior venter; more or less distinct Y-shaped cream marking on chest and anterior venter; palmar and plantar surfaces brown with reddish or orange coloured tubercles; iris greenish bronze, with black reticulation.

Diagnosis: The new species differs from other species in the *Rhinella veraguensis* species group as follows: The possible sister taxon *R. rumbolli* mainly differs from *R. kuka* by a bluntly rounded snout in lateral profile (vs. rounded), round to ovoid parotoid glands (vs. subtriangular), relative smaller tympanum with its diameter about half the eye diameter (vs. more than half the eye diameter), dark venter (vs. cream with scattered dark blotches and flecks), and a less distinct discontinuous dorsolateral row of enlarged tubercles (vs. distinct and continuous) (Figs 4, 5). *Rhinella justinianoi* mainly differs by the absence of a tympanum (vs. presence), relatively shorter fleshy fingers (vs. relatively long and slender fingers), relative shorter legs with TL ca. 32% of SVL (vs. 47–50%), skin on venter covered by spinous conical tubercles (vs. granular), parotoid glands ovoid (vs. subtriangular), head rounded in dorsal view (vs. acuminate), and absence of distinct serrated fringes on fingers and toes (vs. presence). *Rhinella quechua* mainly differs by dorsum and flanks bearing enlarged red warts in life (vs. absent), a cream coloured throat (vs. throat densely mottled with dark brown), discontinuous dorsolateral row of enlarged tubercles (vs. continuous), toes almost fully webbed (vs. toes moderately webbed), relative shorter legs with TL ca. 40% of SVL (vs. 47–50%), and smaller adult female size with a maximum of ca. 55 mm SVL (vs. ca. 66–72 mm SVL). *Rhinella veraguensis* mainly differs by having the first finger shorter than the second (vs. first finger longer than second); venter with dark pattern posteriorly reaching vent (vs. posterior venter cream coloured), parotoid glands round to ovoid (vs. subtriangular), relative smaller tympanum with its length ca. 20–30% of eye diameter (vs. 46–58%), fingers lacking serrated lateral fringes (vs. present), and a moderately ossified skull (vs. hyperossified). *Rhinella inca* mainly differs by skin on ventral surfaces homogeneously covered with rounded to conical tubercles (vs. granular), lack of dorsolateral row of enlarged tubercles (vs. distinct, continuous), snout protruding in lateral profile (vs. rounded), and major tubercles on palmar and plantar surfaces dark brown (vs. cream, contrasting with dark palmar and plantar surfaces). Morphologically, the new species shares character states with *R. leptoscelis*, namely subtriangular parotoid glands, long and slender fingers with serrated lateral fringes, first finger longer than second, distinct tympanum with its diameter more than half the eye diameter, and overall proportions. However, *R. leptoscelis* differs by the presence of distinctly enlarged and

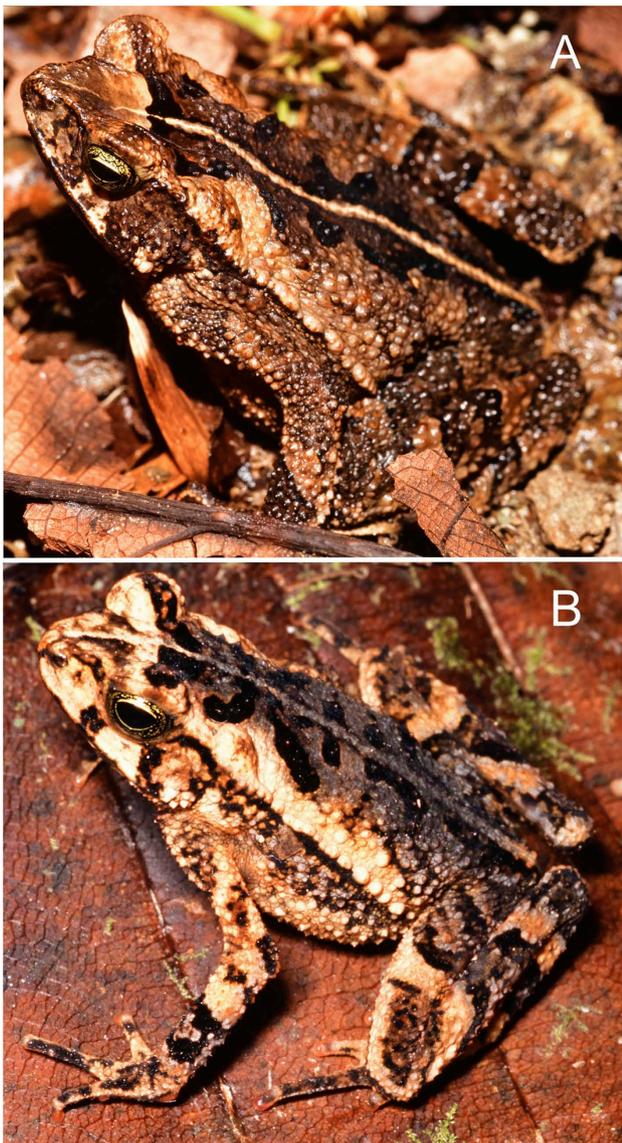


Figure 3. Dorsolateral views of paratypes of *Rhinella kuka* sp. n. in life: (A) HLMD-RA-3238, adult female; (B) ZFMK 72671, juvenile.

keratinized pointed conical tubercles (vs. a mix of rounded and conical tubercles, all less pointed in comparison), and ventral surfaces densely and homogeneously covered with small conical tubercles (vs. granular). Furthermore, from all the species mentioned so far, *R. kuka* differs by substantial differentiation in the 16S rRNA gene, with uncorrected pairwise distances ranging from 4.1–7.8%, and differences in numerous nucleotide positions. MolD identified an ‘A’ in the site 1130, ‘T’ in the site 1406, and ‘A’ in the site 1418 as diagnostic for *R. kuka* compared to the other taxa in our analysis (positions given relative to the *R. marina* full 16S sequence).

Rhinella fissipes, a species that has been associated with the *R. veraguensis* species group (GALLARDO 1961, DUELLMAN & SCHULTE 1992, PEREYRA et al. 2021), mainly differs from the new species by first and second finger being

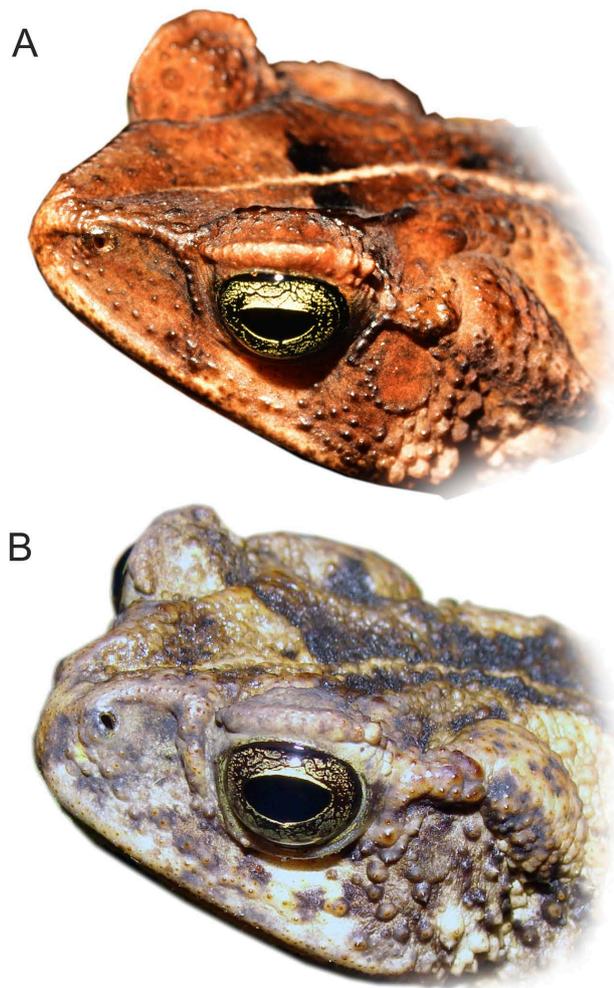


Figure 4. Comparative dorsolateral views of heads of living (A) *Rhinella kuka* sp. n. (ZFMK 80036, paratype) and (B) *R. rumibolli* from PN Baritu, Salta, Argentina (courtesy of J. FAIVOVICH). Note differences in lateral snout profile, visibility of tympanum, shape of parotoid glands and thickness of cranial crests. Not to scale.

equal in length (vs. first finger distinctly longer than second), toes with a trace of basal webbing (vs. toes moderately webbed), tympanum absent (vs. present), snout slightly protruding in lateral profile (vs. rounded), relative shorter legs with TL ca. 30% of SVL (vs. 47–50%), and orbital and occipital crests indistinct or absent (vs. present, distinct). *Rhinella gnustae* from Argentina is another species that has been tentatively associated with the species group (PEREYRA et al. 2021), but its actual relationships remain unclear (see LAVILLA et al. 2002). At least, it differs from *R. kuka* by lacking a dorsolateral row of enlarged tubercles and lacking serrated fringes on fingers and toes. Another species tentatively allocated to the *R. veraguensis* species group is *R. chrysophora* from Honduras (PRAMUK & LEHR 2005, PEREYRA et al. 2021). It differs from the new species at least by first finger being shorter than second (vs. first finger longer than second), absence of tympanum (vs. presence), presence of a tarsal fold (vs. absence), and smaller body size, with adult male SVL of 33.6–37.4 mm (vs. 62.8 mm). A potentially available name for species in the *R. veraguensis* group is *Bufo pleuropterus* SCHMIDT, 1857 (see Discussion). The holotype of this taxon differs from the new species by having the first and second finger about equal in length (vs. first finger longer than second), skin on ventral surfaces homogeneously covered with rounded to conical tubercles (vs. granular), lack of a dorsolateral row of enlarged tubercles (vs. distinct, continuous), and snout protruding in lateral profile (vs. rounded).

Description of the holotype: Adult female (Fig. 6); body robust; SVL 67.9 mm; head triangular in dorsal view; head wider than long (HW 1.15 times HL), head width 36% of SVL; head length 31% of SVL; head narrower than body; snout subacuminate in dorsal view, not bulbous at tip; distance from the nostril to the tip of the snout (2.4 mm) is distinctly less than the distance from the nostril to the eye (6.0 mm); snout short, not protuberant, rounded in profile; canthus rostralis bearing an elevated ridge, sharp and angular in cross-section, slightly convex in dorsal view; loreal region concave; nostrils medium-sized, rounded, slightly protuberant, directed laterally, at level of anterior margin of lower jaw; dorsal internarial area concave; eye diameter slightly less than interorbital distance (ED/IOD = 0.86), ED slightly greater than E–N; canthal crests distinct, elevated, posteriorly swollen at anterodorsal corner of orbit; preorbital crest present, slightly thickened; supraorbital and postorbital crests distinct, continuous; suborbital crests absent; occipital crests distinct, elevated, reaching from posterior orbit beyond anterior level of parotoid glands; pretympanic crest present, short; supratympanic crest distinct, short, barely extending to posterior margin of tympanum; tympanic annulus present, weakly developed, covered by thick skin posteriorly; tympanic membrane distinct, rounded, slightly higher than long; mandibular angle protruding in dorsal view, bearing some enlarged subconical tubercles laterally; parotoid glands evident, subrectangular in dorsal and lateral view, their length about twice the eye diameter, roughly round-

ed corners in outline; skin on the upper eyelids strongly granular, protruding and distinctly thickened laterally above the eye, bearing numerous low tubercles; forearms long, slender; forearm length 24% of SVL; dorsal surface of forelimbs spiculate, bearing densely scattered subconical tubercles; hand length 27% of SVL; hands with long and slender fingers (Fig. 7B); finger I longer than finger II; relative lengths of fingers II < I < IV < III (fourth finger of right hand cut for tissue sample); finger tips rounded,

their width those of fingers; fingers with a slight trace of basal, fleshy webbing; all fingers bear well-defined, serrated lateral fringes; palmar tubercle prominent, elevated, ellipsoid, larger than spade-like thenar tubercle; subarticular tubercles prominent, round to slightly triangular in outline; supernumerary tubercles evident, round (Fig. 7); hindlimbs moderately long, slender; tibia length 47% of SVL; tibia slightly longer than foot; FOOTL 44% of SVL; dorsal surfaces of hindlimbs spiculate, bearing numerous



Figure 5. Comparative photographic plate showing members of the *Rhinella veraguensis* species group in life (dorsolateral views): (A) female *R. leptoscelis* from Santo Domingo de Carabaya, Puno, Peru (MHNC 5975); (B) *R. inca* from Río Kimbiri, Cuzco, Peru; (C) adult female *R. quechua* from Incachaca, Cochabamba, Bolivia (ZFMK 66939); *R. veraguensis* from 'old Chapare road', Cochabamba, Bolivia (ZFMK 66986); (E) *R. justinianoi* from Karahuasi, Cochabamba, Bolivia (ZFMK 72657); (F) *R. rumbolli* from PN Baritu, Salta, Argentina (courtesy of J. FAIVOVICH). Small inset photos, if present, show ventral views of respective individuals. Not to scale.

conical tubercles; toes long and slender (Fig. 7A); relative lengths of toes $I < II < V < III < IV$; toe tips rounded, their width equaling toes widths; toes moderately webbed, webbing membranous, with the following formula: $I \ 0^{+1} \ II \ 0.5-2 \ III \ 1-2.5 \ IV \ 3-1 \ V$; free portions of all toes bear well-defined serrated lateral fringes; tarsal fold absent, but elevated and serrated tarsal ridge on inner tarsus; inner metatarsal tubercle medium-sized, oval, slightly protuberant; outer metatarsal tubercle ovoid, approximately half the size of inner metatarsal tubercle; subarticular tubercles distinct, ovoid; supernumerary tubercles present, small,

ovoid (Fig. 7A); skin on dorsal surface of head smooth, with few scattered flat tubercles; skin on dorsum tuberculate, bearing unevenly distributed rounded, flat tubercles, as well as more prominent conical tubercles with a keratinized tip; continuous dorsolateral row of enlarged conical tubercles extending from posterior margin of parotoid gland to groin; flanks with densely scattered keratinized conical tubercles; skin of belly, throat, chest granular; cloacal opening protruding, directed posteriorly at the upper level of the thighs; tongue narrow, about four times as long as wide, notched anteriorly, posterior three fourths free;

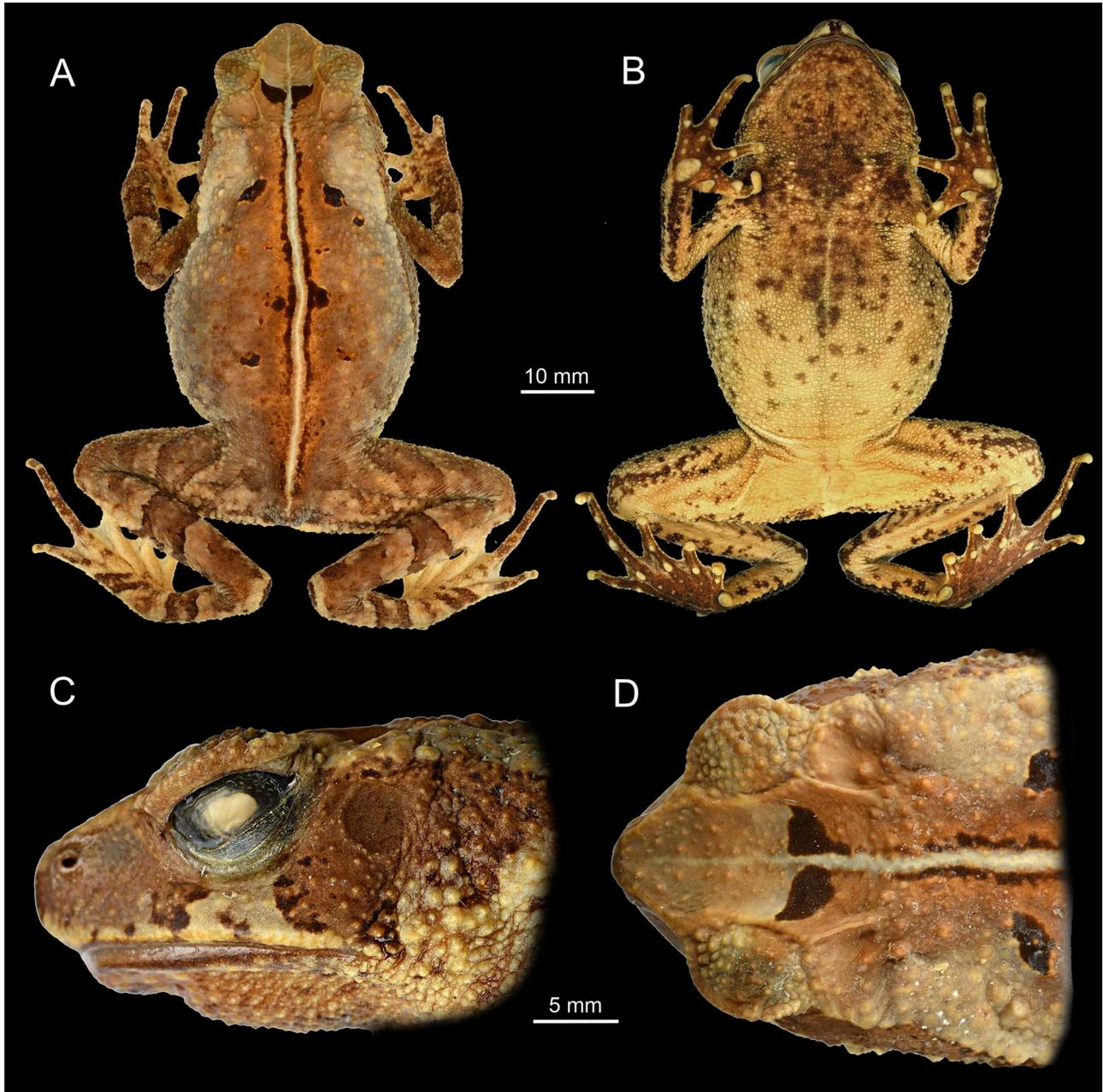


Figure 6. Preserved female holotype of *Rhinella kuka* sp. n. (ZFMK 72668) in (A) dorsal, (B) ventral views; (C) lateral and (D) dorsal views of head.

Table 1. Measurements and proportions of specimens of the type series of *Rhinella kuka* sp. n. For abbreviations used see Materials and methods.

	ZFMK 72668 female holotype	ZFMK 72669 female paratype	ZFMK 72670 female paratype	ZFMK 80036 female paratype	HLMD-RA-3238 female paratype	ZFMK 80035 male paratype	ZFMK 72671 juvenile paratype
SVL	67.9	66.0	66.3	72.1	69.3	62.8	28.7
HW	24.6	24.0	23.7	23.4	24.0	21.1	9.8
HL	21.3	21.1	21.1	21.3	21.5	19.8	9.5
ED	6.2	6.2	6.2	6.3	6.4	5.7	3.4
TD	3.6	3.6	3.3	3.3	3.2	2.6	1.8
IOD	7.2	7.2	7.3	7.7	6.7	6.7	3.1
IND	4.6	4.4	4.6	5.1	4.8	4.1	2.4
E-N	6.0	5.6	5.7	5.8	5.6	4.8	2.6
NSD	2.4	2.7	2.8	3.0	3.1	2.4	2.0
SL	9.7	8.7	8.6	9.3	9.6	8.5	3.9
FL	16.4	16.3	16.3	17.2	17.3	16.0	7.5
HNDL	18.5	18.8	19.9	18.3	20.0	18.9	8.6
TL	32.1	32.8	32.7	32.8	33.8	30.6	13.4
FOOTL	30.0	29.6	30.9	30.1	30.6	26.9	13.9
FEML	30.3	31.5	30.4	32.1	32.9	29.5	12.8
PL	12.4	12.0	13.1	12.6	13.1	11.6	4.9
TL/SVL	0.47	0.49	0.49	0.46	0.49	0.49	0.47
HW/HL	1.15	1.14	1.12	1.10	1.12	1.07	1.03
HNDL/FL	1.13	1.15	1.22	1.06	1.16	1.18	1.15
FOOTL/TL	0.93	0.90	0.94	0.92	0.91	0.88	1.04
ED/PL	0.50	0.52	0.47	0.50	0.49	0.49	0.69
TD/ED	0.58	0.58	0.53	0.58	0.50	0.46	0.52

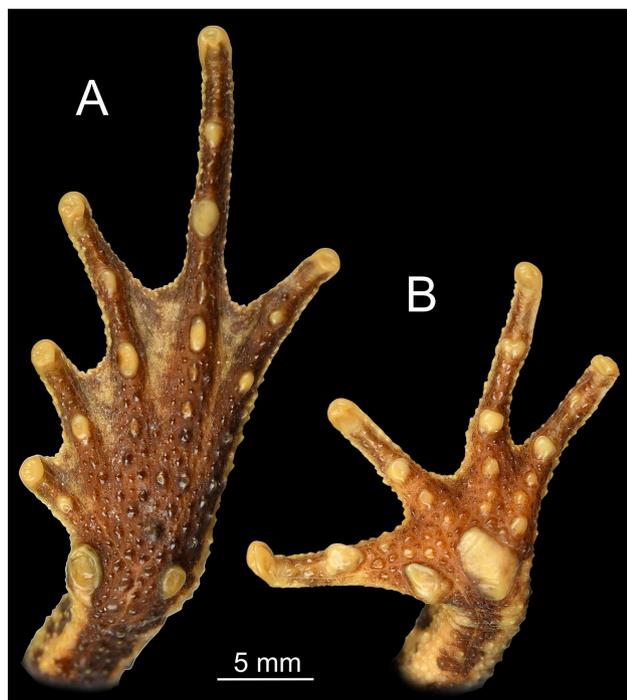


Figure 7. (A) Plantar and (B) palmar surfaces of left foot and left hand of the preserved female holotype of *Rhinella kuka* sp. n. (ZFMK 72668). Note that fingers may appear shorter in the photograph as they are slightly crooked.

choanae large, round, widely separated and partially concealed by palatal shelf of maxilla; maxillary, premaxillary and vomerine teeth absent. Measurements of the holotype are provided in Table 1.

After 24 years in preservative (Fig. 6), dorsal colouration light brown, with few dark brown, almost symmetrical markings, irregular flecks and blotches; interorbital area with dark brown flecks; pale narrow vertebral stripe, extending almost to tip of snout anteriorly and to cloaca posteriorly, bordered with dark brown lines from scapular region to sacral region; parotoid glands tan; dorsal surfaces of arms and legs tan with brown transversal bars; tympanic region brown; loreal region light brown; upper lip cream with some irregular dark brown flecking; flanks tan, with densely scattered dark brown spots and flecks, and a narrow dark brown stripe ventrally bordering the dorsolateral row of enlarged tubercles; throat light brown with dark brown mottling and irregular spots; chest and anterior venter densely mottled with dark brown spots, with exception of cream coloured areas forming a faint symmetric Y-shaped marking; venter yellowish-cream, with some dense dark brown spotting anteriorly and few scattered dark brown spots and flecks posteriorly; ventral surfaces of thighs yellowish-cream with few scattered brown spots; palmar and plantar surfaces brown, with major tubercles contrasting in cream; posterior surfaces of thighs brown with dark brown marbling. Colour in life not documented.

Variation: Variation among specimens of the type series is more or less limited to differences in colour pattern (see Figs 6, 8). The female ZFMK 80036 is rather similar in dorsal and ventral pattern to the holotype, with only few dark markings on dorsum, whereas the females HLMD-RA-3238, ZFMK 72669 and 72670 show a more contrasting and complex pattern of cream, brown, dark brown and almost black areas, flecks, blotches or spots on dorsum. Also, the dark transversal bars on upper surfaces of arms and legs are more distinct and contrasting in the latter specimens. Dark brown mottling and blotches on throat, chest and anterior venter are most conspicuous and contrasting in HLMD-RA-3238 and gradually less so in the females ZFMK 72669, 72670 and 80036 (Fig. 8). The male ZFMK 80035 differs in colour pattern from all female paratypes in exhibiting an almost uniformly brown dorsum, lacking darker flecks and blotches (with the exception of some dark flecking narrowly surrounding the parotoid glands), with the brown dorsum bordered with cream dorsolaterally. Its ventral colour pattern is the most contrasting of all available specimens (Fig. 8). In all specimens, the narrow cream vertebral stipe is bordered with brown lines, but these lines are rather faint in ZFMK 80036. The juvenile ZFMK 72671 generally shows a very similar colour pattern when compared to the adults, but colour borders on dorsum appear somewhat more contrasting and sharper outlined. All specimens, including the juvenile, exhibit the Y-shaped cream marking on chest and anterior venter, although this marking might be more or less distinctly expressed.

Colour in life was generally the same as in preservative, with the only differences referring to a more reddish to orange brown dorsal ground colouration, as well as ventral

surfaces exhibiting an orange, rusty brown or pinkish tint (see Figs 2, 3).

Variation in measurements and proportions among the adult type specimens are provided in Table 1. Morphologically, the continuous dorsolateral row of enlarged tubercles is more prominently expressed in the female paratypes, when compared to the holotype. Female HLMD-RA-3238 has a slightly more protruding snout in lateral profile when compared to the holotype and the left tympanum partly concealed by thick skin. The male ZFMK 80035 exhibits a slightly swollen cream nuptial pad on the first finger, but lacks vocal slits and a vocal sac.

Osteology: Osteological characters were inferred based on a micro-CT scan of the female paratype ZFMK 72569 (Fig. 9): Skull wider than long, triangular in dorsal view, broadest at bowing of quadratojugal, hyperossified, showing irregular exostosis on squamosals as well as on lateral and posterior parts of frontoparietals. Nasals anteriorly shaped acuminate, in contact with each other in a straight line medially, posteriorly forming an articulation along most of their margin with the frontoparietals. Nasals overlap the anterior margin of the ossified sphenethmoid and possess a ventrolaterally pointed maxillary process extending towards maxilla. Maxillae broadly in contact with anterior parts of pterygoid. Teeth absent. Premaxillae bear alary processes angled anteriorly to the anterior margin of the premaxillae, alary processes lie posterior to margins of nasals and are not in contact with the latter. Septomaxilla with anteriorly directed process present. Septomaxilla upward sinuous from posterior ramus to anterior ramus to lateral ramus to medial ramus. Prechoanal vomer well developed, not in contact with maxillae. Postchoanal vomer

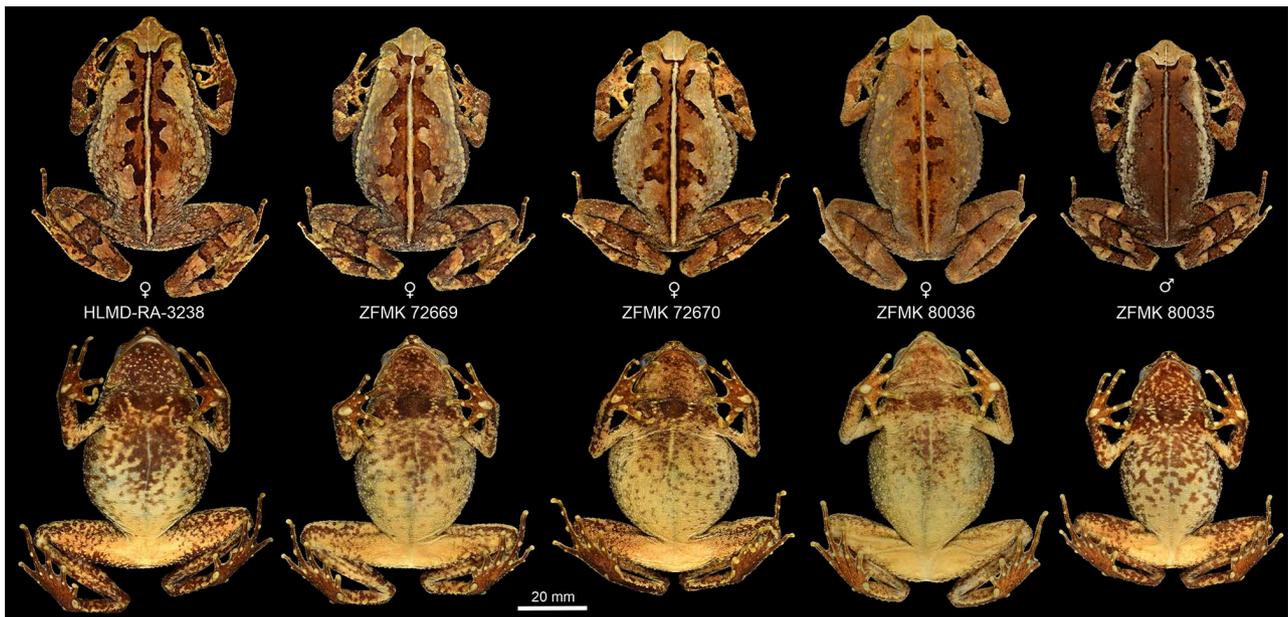


Figure 8. Preserved adult paratype specimens of *Rhinella kuka* sp. n. in dorsal (upper row) and ventral (bottom row) views, showing variation of colour pattern.

overlapping neopalatine, vomerine teeth absent. Frontoparietals medially articulated in a straight line. Pre-, supra- and postorbital as well as tympanic crest hyperossified, all visible from above. Pterygoid broad and triradiate, with anterior, medial and posterior rami; medial ramus of about same length as posterior ramus; posterior ramus not in contact with quadratojugal. Anterior ramus of pterygoid articulates along maxilla reaching palatine. Cultriform process of the parasphenoid broadly rounded anteriorly. Columella strongly ossified, not reaching beyond distal corner of squamosal, becoming thinner distally, columella footplate broad and concave. Processes of quadratojugal indistinct from bordering maxillae and squamosal, proximally possessing a rounded process.

Mandible edentate. Mentomeckelian small, not in contact with each other, dorsolaterally fused with dentary. Dentary thin, overlapping angulosplenic for half its

length. Angulosplenic broadening posteriorly, laterally possessing a channel running along its entire length being covered partially by dentary.

Pectoral girdle arciferal. Clavicles longer than coracoids, almost straight. Coracoids flattened, strongly flared laterally and medially. Scapula longer than the coracoid, acromion processes prominent. Cleithrum fused with ossified portion of the suprascapula. Posterior end of sternum broadly rounded, cartilaginous (not depicted in Fig. 9).

Eight presacral vertebrae present, presacrals I and II (atlas and axis) fused, length of transverse processes $1 < 7 < 6 < 5 < 2 < 4 < 3$, transverse processes broadened distally in presacrals II and III, of equal width over its entire length in presacral IV and becoming narrower towards distal edge in presacrals V–VIII. Processes directed anteriorly in presacral II, posteriorly in all others. Sacral vertebra with broadly expanded diapophyses, being about three times as wide on

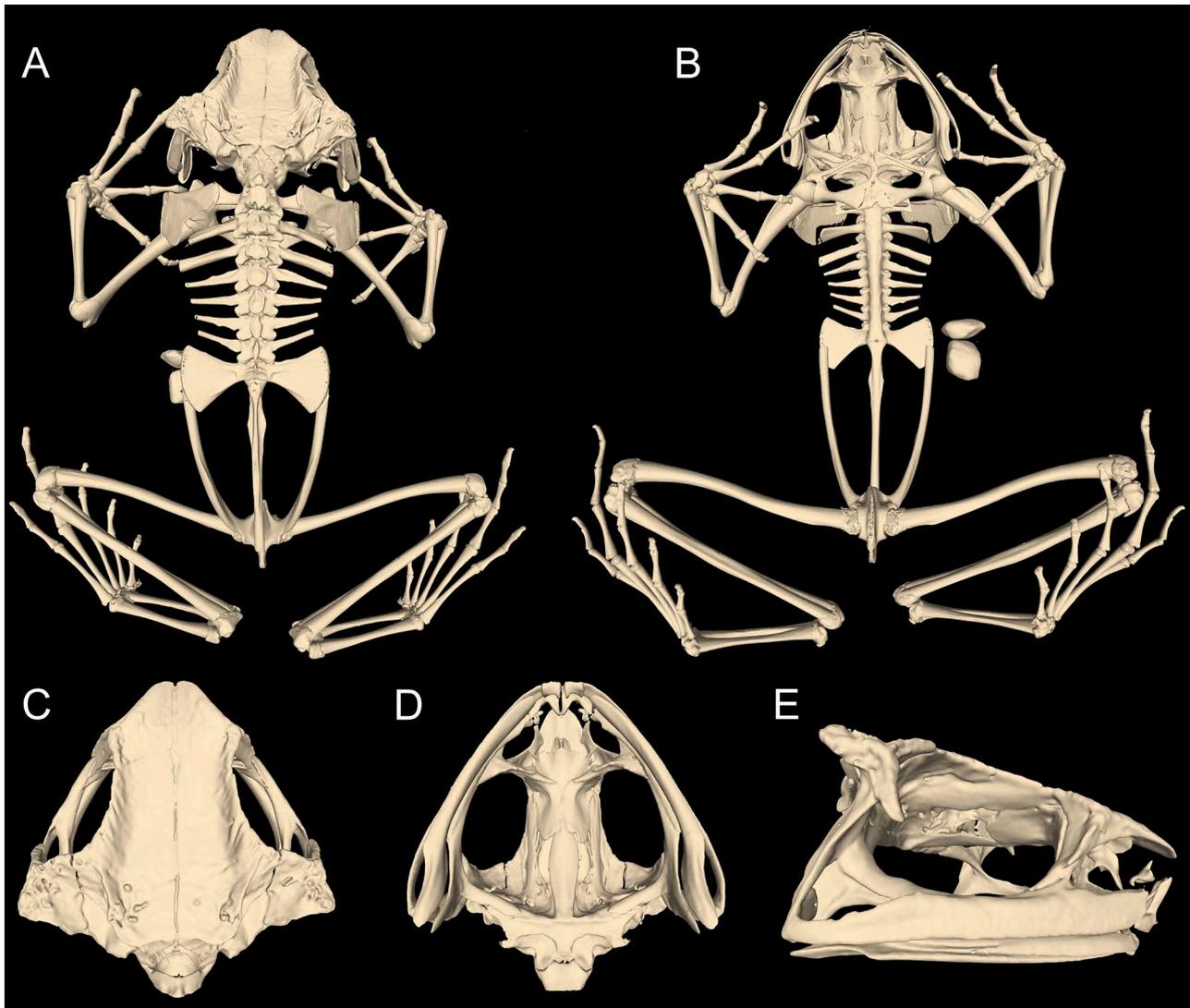


Figure 9. Micro-CT images of the preserved female paratype ZFMK 72669 of *Rhinella kuka* sp. n.: total (A) dorsal, (B) ventral views (the two visible solid objects are apparently referable to swallowed pebble stones); skull in (C) dorsal, (D) ventral and (E) lateral views.

its distal end than on its base. Sacral diapophyses articulate with ilia. Urostyle about as long as presacral column; lateral crests present on urostyle, widest at about one fourth of its length from anterior margin; dorsal crest present on urostyle, decreasing in height posteriorly, bluntly broadened at its anterior margin. Ilium V-shaped in dorsal view.

Humerus with a distinct ventral crest, radioulna with distinct sulcus intermedius on distal edge, prepollex consists of two elements, becoming narrower towards the tip. Radiale, ulnare, centrale and a large sesamoid present. Phalangeal formula of hand 2-2-3-3, terminal phalanges with broad, rounded tip.

Femur slightly sigmoid, slightly shorter than tibiofibula; tibiofibula straight, sulcus intermedius distinct; tibiale and fibulare fused proximally and distally. Tarsale 1 distinct, tarsale 2 and 3 fused, centrale distinct, prehallux short. Phalangeal formula of foot 2-2-3-4-3, terminal phalanges with broad, rounded tip.

Natural history: The habitat at the type locality and surroundings in the Carrasco National Park are part of the Yungas ecoregion (Level II, 18.3; GRIFFITH et al. 1998) consisting of perhumid lower montane rainforest along the Río San Mateo valley, characterized by steep slopes (Fig. 10A), with slope inclination frequently ranging between 40° and 85° (IBISCH 1996). The area is among those in Bolivia with the highest amounts of rainfall, possibly amounting up to 8000 mm/year in some parts of the Carrasco National Park (KESSLER 1999). Individuals of the new species were observed being active at night on the ground during rainfall. Most individuals were found on the road itself and along roadside ditches (Fig. 10B). The area is free of stagnant water bodies and is characterized by many small rivulets. The reproductive mode and larvae remain unknown, but all adult females collected in the months December, January and February contained eggs (with a dark pole) in their ovaries, arguing for a prolonged reproduction period during the rainy season. Other bufonids that occurred in sympatry with the new species in the Chapare region were *Ateolopus tricolor*, *Rhinella* cf. *justinianoi*, *R. stanlaidi*, and *R. veraiguensis* (see KÖHLER 2000 and KÖHLER & PADIAL 2016 for more details and other anuran species from that area).

Distribution: The new species is known from the Carrasco National Park, Provincia Chapare, Departamento Cochabamba, Bolivia, along the so-called ‘old Chapare road’ at elevations between 1250 and 1650 m a.s.l. Another genetically verified record (CBG 599) further north refers to the Isiboro Sécure National Park at the border of the Bolivian Departamentos Beni and Cochabamba at 800 m a.s.l. The species is apparently more widespread in the Bolivian Yungas, ranging westward into the Yungas de La Paz. A record from Caranavi, Departamento La Paz, mentioned by PADIAL et al. (2009; as *R. leptoscelis*) is in need of confirmation, but a photographic record from Suapi (ca. 1550 m a.s.l.), northwest of Coroico, Departamento La Paz, is referable to *R. kuka* (https://calphotos.berkeley.edu/cgi/img_query?seq_num=967229&one=T; Fig. 11).

Etymology: The specific epithet *kuka* is the Quechuan word for the coca plant (*Erythroxylum coca*). It refers to the fact that the known distribution of the new species is largely equivalent to the major range of coca plantations in the Bolivian Yungas. The name is treated as a noun in apposition.

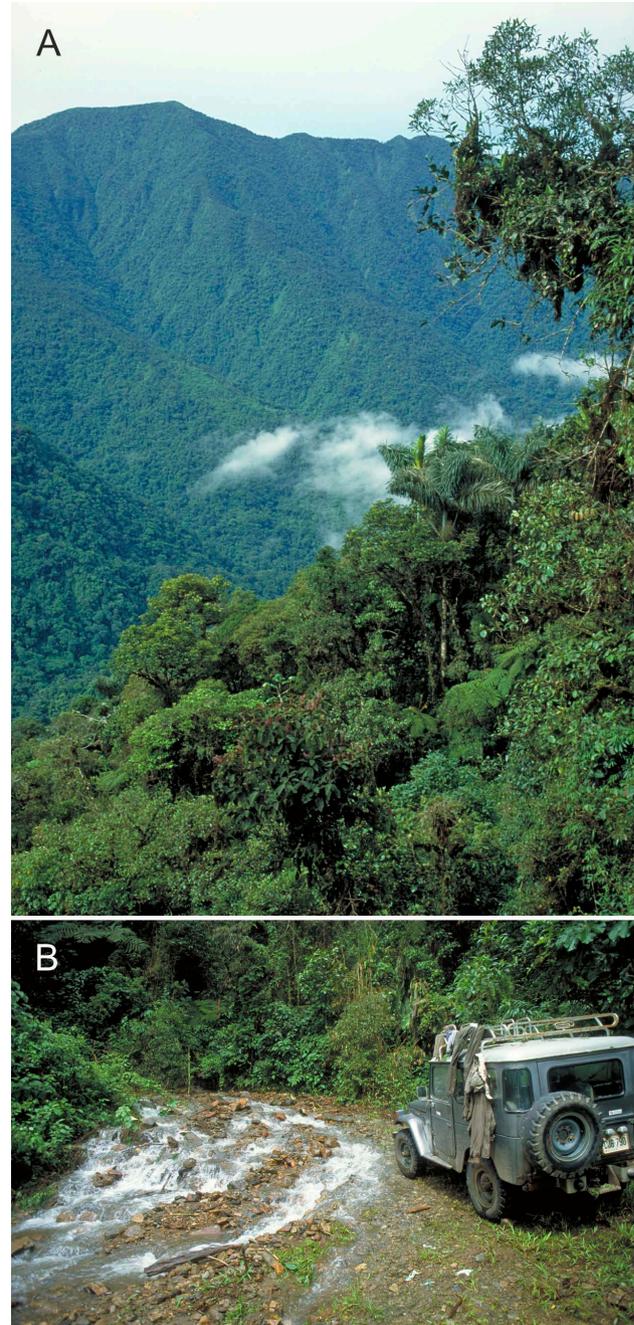


Figure 10. (A) Landscape view of the steep slopes and montane rainforest vegetation of the Río San Mateo valley in Carrasco National Park, Provincia Chapare, Departamento Cochabamba, Bolivia, close to the type locality of *Rhinella kuka* sp. n.; (B) detail of flooded ‘old Chapare road’ after heavy rainfall on 4 February 1998, showing rocky soil and road side vegetation, the habitat where individuals of the new species were found.

Discussion

After more than two decades, with the aid of molecular genetics and more detailed examination of morphological traits, we have only now been able to clarify the status of toads collected in the Yungas forest of central Bolivia, which have been misjudged and wrongly allocated to different available names before. Although not identified with certainty at first, KÖHLER (2000) allocated the collected specimens to *Bufo fissipes*, interpreting obvious morphological differences to the *B. fissipes* holotype (BMNH 1947.2.20.64; Fig. 12) as possible intra-specific variation. After examination of more specimens of members of the *Rhinella veraguensis* species group, it became clear that KÖHLER'S (2000) interpretation and judgement was wrong. The morphological differences between the focal specimens in question and the type specimen of *Bufo fissipes* are far beyond those observed at an intra-specific level among species in the *Rhinella veraguensis* group. The first finger being equal in length with the second, toes with only a trace of basal webbing, lack of a tympanum, rela-

tive shorter legs, and orbital and occipital crests indistinct or absent, readily distinguish *R. fissipes* from the Bolivian Yungas specimens (see also PADIAL et al. 2009). The *R. fissipes* sample used by PEREYRA et al. (2021) originates from specimen CBG 599 (Isiboro Sécura National Park, Bolivia) and was only tentatively identified as *R. fissipes* by the collector given the published information by KÖHLER (2000), which actually referred to the morphologically different Bolivian specimens (I. DE LA RIVA, pers. comm.). As a consequence, *R. fissipes* so far is absent from Bolivia and known only from southeastern Peru. We are not aware of any recent records of this species, and various colleagues were unable to find it during fieldwork at its type locality (Santo Domingo de Carabaya, Departamento Puno, Peru) or elsewhere in southeastern Peru (J. C. CHAPARRO, pers. comm.). We therefore conclude that *R. fissipes* so far is only known from its holotype, without any DNA sequence data available. Based on morphology, *R. fissipes* has been associated with species in the *R. veraguensis* group (GALLARDO 1961, DUELLMAN & SCHULTE 1992) and our examination of its holotype did not contradict this view, as it

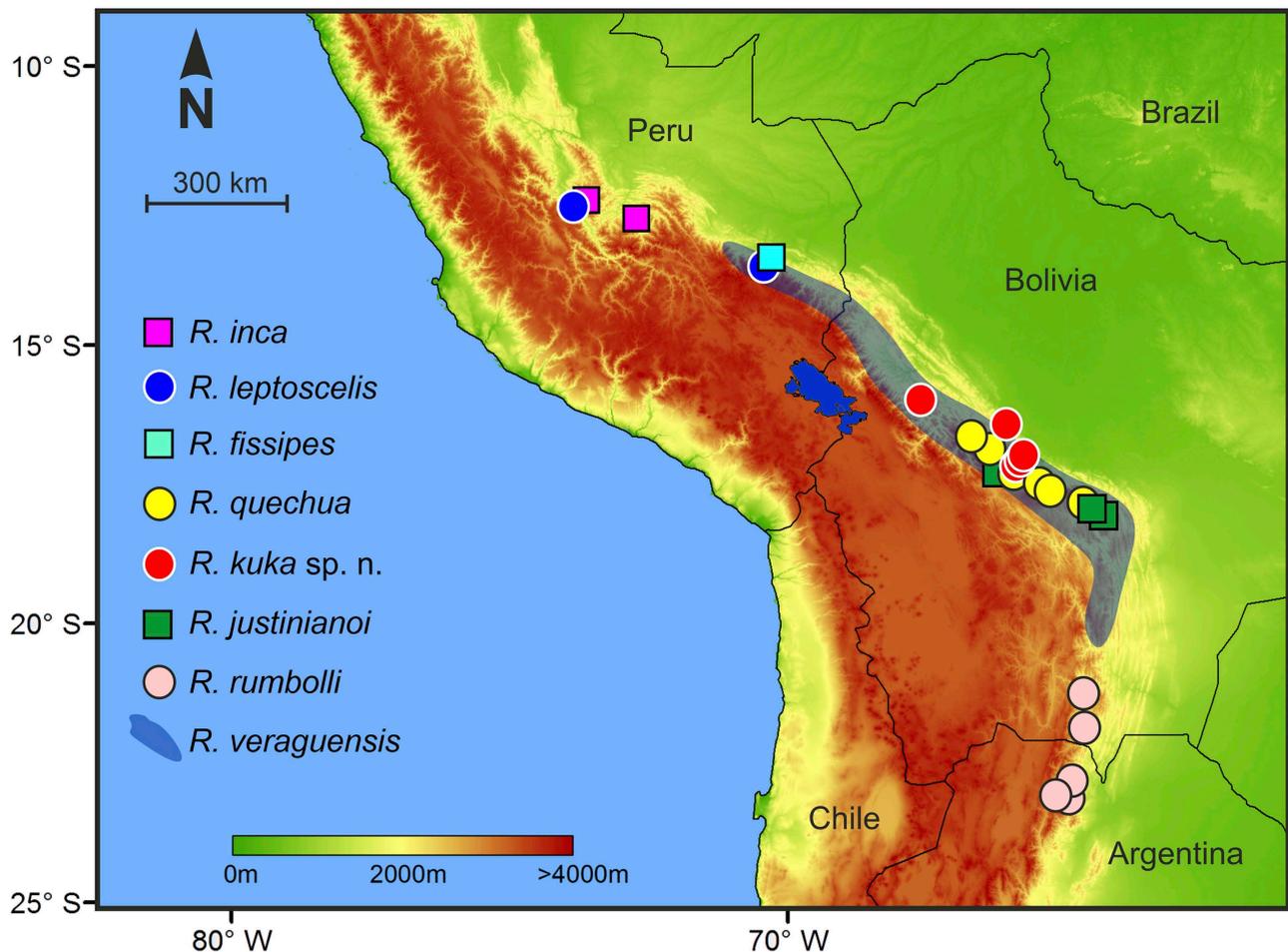


Figure 11. Schematic map of west-central South America showing the approximate known distribution of species in the *Rhinella veraguensis* species group as inferred from original literature sources, photographic records, and examined museum specimens. Broadly overlapping symbols may correspond to the same locality.

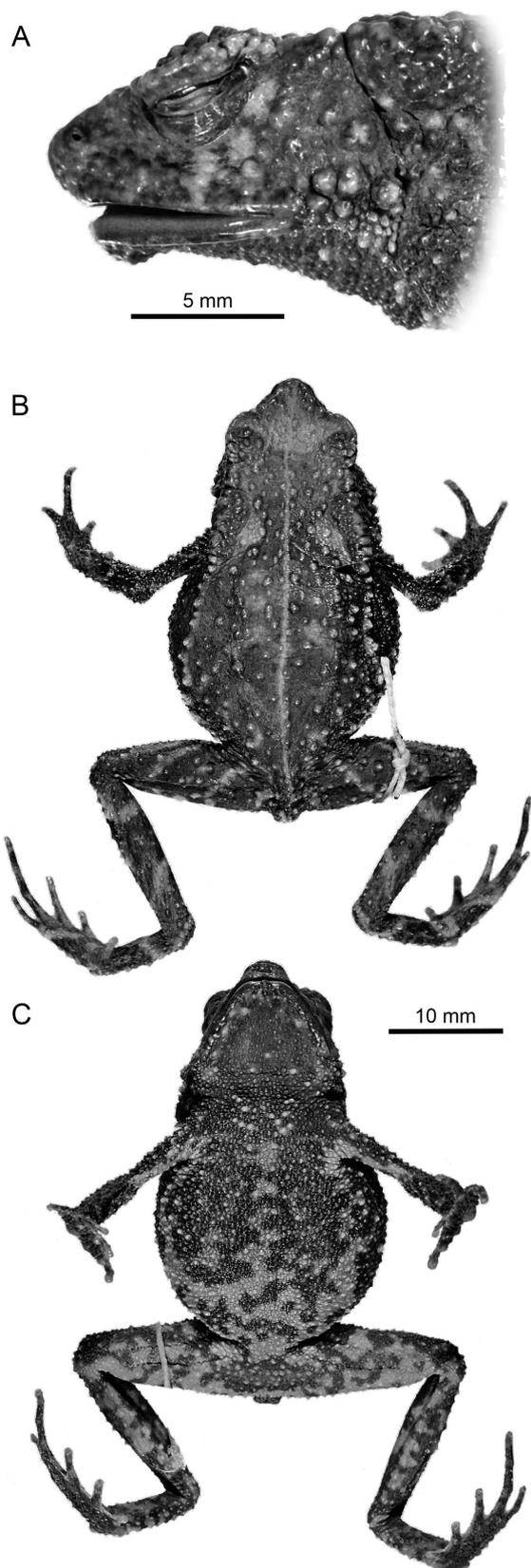


Figure 12. Preserved holotype of *Bufo fissipes* (BMNH 1947.2.20.64): (A) head in lateral profile; (B) dorsal view; (C) ventral view.

shares several morphological traits common in this species group (Fig. 12). However, we cannot exclude that *R. fissipes* might actually be more closely related to species of the *R. festae* group. Several species morphologically assigned to the *R. veraguensis* group in the original publications, like *R. aborescandens*, *R. chavin*, *R. tacana* and *R. yanachaga* (DUELLMAN & SCHULTE 1992, LEHR et al. 2001, 2007, PADIAL et al. 2006), were later demonstrated to actually represent members of the *R. festae* species group based on molecular data (CHAPARRO et al. 2007, CUSI et al. 2017, CASTILLO-URBINA et al. 2021, PEREYRA et al. 2021).

The allocation of the Bolivian Chapare populations to *R. leptoscelis* by PADIAL et al. (2009) was reasonably justified, as indeed the Bolivian specimens share many morphological characters with *R. leptoscelis* (see Diagnosis). However, as revealed by our molecular analysis, *R. leptoscelis* and the Bolivian populations are only distantly related (Fig. 1) and exhibit the greatest uncorrected pairwise distance (7.8%) among our samples of species in the *R. veraguensis* group. In summary, our study revealed substantial evidence for the specific distinctness of the Bolivian populations, neither representing *R. fissipes* or *R. leptoscelis*, nor any other species of *Rhinella*, justifying our description as a new species.

The barely supported sister relationship of *R. kuka* and *R. rumbolli* perhaps remains questionable to some extent. In addition to more comprehensive phylogenetic analyses, the discovery of the tadpole of *R. kuka* could probably provide additional evidence. The larvae of four species in the *R. veraguensis* group have been described so far. The larvae of three species (*R. chrysophora*, *R. quechua*, *R. veraguensis*) are gastromyzophorous and exhibit a well-developed abdominal sucker as an adaptation to lotic conditions, like known for larvae of species in the bufonid genus *Atelopus* (MCCRANIE et al. 1989, CADLE & ALTIG 1991, AGUAYO et al. 2009). However, the tadpole of *Rhinella rumbolli* lacks such an abdominal sucker (HAAD et al. 2014).

Interestingly, the possible sister relationship of central Bolivian *R. kuka* to the distantly distributed *R. rumbolli* from northern Argentina would be paralleled by a similar case in the strabomantid genus *Oreobates*. KÖHLER & PADIAL (2016) found *Oreobates yanucu*, occurring in sympatry with *Rhinella kuka* in the Bolivian Chapare region, to be most closely related to *Oreobates berdemenos* from the Yungas in Provincia Jujuy, northern Argentina. Possible explanatory scenarios for a close connection of the Yungas forests in central Bolivia and northern Argentina are non-obvious and require further studies on the biogeographical history of these biomes.

Although *Rhinella kuka* is probably more widespread in the Bolivian Yungas than currently known, its habitat is likely threatened by ongoing degradation (DE LA RIVA & REICHLER 2014). In addition, *R. kuka* may suffer from invasive spreading pathogens, like the amphibian skin fungus *Batrachochytrium dendrobatidis*. At least, BARRIONUEVO et al. (2008) reported chytridiomycosis in *R. quechua* tadpoles from Sehuencas, Carrasco National Park, Bolivia, which is close to the type locality of *R. kuka*, although at higher el-

evation (ca. 2500 m a.s.l.). Furthermore, anuran individuals (including *R. quechua*) in the Yungas de Cochabamba were documented to partly suffer from massive infestation by trombiculid mites, with so far unknown impact on respective populations (WOHLTMANN et al. 2006). The known distribution of *R. kuka* is covered by protected areas (Carrasco and Isiboro Sécure National Parks), but there is little knowledge about the current status of populations. However, according to the ongoing decline in the extent and quality of its habitat and suspected population declines in related species occurring in the same general area, such as *R. justinianoi*, we propose a IUCN Red List category of 'Vulnerable' for *R. kuka*.

In general, all potentially vulnerable species in the *R. veraguensis* group deserve more in depth study on population density as well as life and natural history, as very little is known about their ecology and reproductive biology. Apart from the described tadpoles (MCCRANIE et al. 1989, CADLE & ALTIG 1991, AGUAYO et al. 2009, HAAD et al. 2014), oviposition mode and egg clutch structure were only reported for *R. rumbolli* (PEREYRA et al. 2015). For none of the species currently considered to be part of the *R. veraguensis* group have vocalizations been reported. During our own fieldwork in Bolivia, we never heard calls emitted by these toads, even in places where they were relatively abundant and amplexant couples and gravid females were present. This may lead to the assumption that species in the *R. veraguensis* group are 'voiceless'. The same has been hypothesized for members of the *R. festae* species group, with males of several species being known to lack vocal slits and a vocal sac (e.g., CASTILLO-URBINA et al. 2021), until BATALLAS & BRITO (2022) described calls of *R. festae*. In 2016, J. M. PADIAL and collaborators (unpubl.) recorded a single and hard to hear call of *R. leptoscelis* during fieldwork in the Cordillera Vilcabamba, Peru. This finding suggests that species in the *R. veraguensis* group may in fact communicate acoustically, although apparently in a rather secretive way when compared to most other groups of *Rhinella*, or perhaps at times when field herpetologists are rarely present in the habitat such as in the early morning.

During investigation of the status of certain populations of species in the *R. veraguensis* group, we again came across the problematic taxon *Bufo pleuropterus*, described by SCHMIDT (1857, 1858) from an apparent juvenile specimen with 25 mm SVL (type locality "Grenzgebiet von Bolivia gegen Peru, in etwa 3000 [feet?] Höhe"). This taxon was largely neglected in the taxonomic literature since its synonymization with *R. margaritifera* by PETERS (1873). As already discussed by LÖTTTERS & KÖHLER (2000), its allocation as a synonym of *R. margaritifera* is highly questionable. The status of *R. margaritifera* received some recent attention by the rediscovery of two syntype specimens (MILTO & BARABANOV 2011, LAVILLA et al. 2017) and the subsequent designation of a lectotype by PEREYRA et al (2021). As currently understood, *R. margaritifera* is a species exhibiting well-developed supratympanic crests and has the first finger longer than the second. These characters are absent in the type specimen of *Bufo pleuropterus* (see SCHMIDT

1858, LÖTTTERS & KÖHLER 2000) and although being a juvenile, from our experience relative finger length is unlikely to change during ontogenesis in *Rhinella* species. In addition, character traits typical for most species in the *R. margaritifera* group, such as a lateral row of enlarged tubercles, are lacking in the type of *Bufo pleuropterus*. Given its morphological characters and overall appearance (see LÖTTTERS & KÖHLER 2000: Fig. 6), it appears rather evident that *B. pleuropterus* is not conspecific with *Rhinella margaritifera* and consequently we remove it from its synonymy and allocate it to the genus *Rhinella*, considering it a valid species, *Rhinella pleuroptera* (SCHMIDT, 1857). The external morphology of *R. pleuroptera* suggests a possible relationship with the *R. veraguensis* species group sensu PEREYRA et al. (2021). The holotype of *R. pleuroptera* (KM 1030) shares external morphological characters with *R. inca* from southeastern Peru (type locality "Huadquinia, Peru, about 5,000 feet altitude"; holotype USNM 49557), namely similar head and snout shape, skin on ventral surfaces homogeneously covered with rounded to conical tubercles, and first finger about equal in length to second (see also SCHMIDT 1858, STEJNEGER 1913). Future research is needed to elucidate the relationships of *R. pleuroptera* and its possible conspecificity with *R. inca*, both taxa supposedly originating from montane forests of southeastern Peru (see SCHMIDT 1858, STEJNEGER 1913, LÖTTTERS & KÖHLER 2000).

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Supplementary data

The following data are available online:

Supplementary Table S1: Species, GenBank accession numbers, voucher specimens, and locality information for 16S rRNA sequences used in the genetic analysis.

Appendix

Specimens examined

Rhinella acutirostris: “flumen Amazonum” (= Amazon River, Brazil), ZSM 1147/0 (holotype).

Rhinella chavin: Peru: Huánuco: Palma Pampa, 20 km south-east of Chaglla, 3010 m, MUSM 20028 (holotype).

Rhinella chullachaki: Peru: Huánuco: Cordillera Azul, La Cumbre, 1780 m, MUSM 40293 (holotype), MUSM 40292, ZSM 237/2019 (paratypes).

Rhinella dapsilis: Ecuador: Napo: Cando, Cabañas Pimpilala, QCAZ-A17719 (field no. SC 3509).

Rhinella fissipes: Peru: Puno: Carabaya, Santo Domingo, 6000 feet, BMNH 1947.2.20.64 (holotype).

Rhinella gnustae: Argentina: Jujuy: Rio Grande, MACN 4775 (holotype; photos only).

Rhinella inca: Peru: Huadquinia, 5000 feet, USNM 49557 (holotype); Peru: Cusco: Kimbiri River, 1100 m, MNCN 44405.

Rhinella iserni: Peru: Pasco: Yanachaga-Chemillén National Park, Quebrada San Alberto, 1950 m, MUSM 31097 (holotype of *Rhinella yunga*).

Rhinella justinianoi: Bolivia: Santa Cruz: El Chape, 2050 m, MNK-A 950 (holotype); Bolivia: Cochabamba: Karahuasi, 1800 m, ZFMK 72657; Bolivia: Cochabamba: old Chapare road (cf. *justinianoi*), 1650 m, ZFMK 72600–72602; 2250m, ZFMK 72621.

Rhinella leptoscelis: Peru: Puno: Carabaya, Santo Domingo, 6500 feet, BMNH 19075.7.32 (holotype); Peru: Puno: Santo Domingo de Carabaya, 1658 m, MHNC 5975–76; Peru: Cuzco: Kimbiri River, 1550 m, MNCN 44406.

Rhinella lilyrodriguezae: Peru: San Martín: Bellavista: Alto Biavo: ca. 20 km from Park Rangers Center N° 53 “Shapaja” of the Cordillera Azul National Park, MUSM 32204 (holotype), MUSM 32201, 32205–32206, 32211, 32213 (paratypes); Peru: Huánuco: Consuelo village, MUSM 26511.

Rhinella pleuroptera: “Grenzgebiet von Bolivia gegen Peru, in etwa 3000 Höhe” (= southern Peru; see LÖTTERS & KÖHLER 2000), KM 1030 (holotype; photos only).

Rhinella quechua: Bolivia: Cochabamba: Parjacti, 83.2 km by road NE Cochabamba on road to Villa Tunari, USNM 257799 (holotype of *Bufo echinodes*); Bolivia: Cochabamba: Sehuencas, 2200 m, ZFMK 60255–60274, ZFMK 66835–66836; Bolivia: Cochabamba: Incachaca, 2500 m, CM 4225 (holotype); 2300 m, ZFMK 66939–66941; Bolivia: Cochabamba: old Chapare road, 1400 m, ZFMK 72622; Bolivia: Cochabamba: 12.7 km by road E of Enpalme along road to Karahuasi, 2150 m, MNK-A 953 (holotype of *Bufo amboroensis*).

Rhinella rumbolli: Argentina: Salta: Arasayal, MACN 7456 (holotype; photos only); MACN 7453 (paratype; photos only).

Rhinella spinulosa: possibly Peru or Bolivia, NMW 16521 (syn-type of *Bufo simus*); Peru: Puno: Arapa, 4500 m, MWNH 153/1 (lectotype of *Bufo spinulosus arapensis*).

Rhinella stanlarii: Bolivia: Cochabamba: road to San Onofre, 1900 m, CBF 3346 (holotype), USNM 257797–257798, ZFMK 67097 (paratypes); Bolivia: Cochabamba: km 96.7 on road from Cochabamba to Villa Tunari, 1967 m, USNM 257796 (paratype); Bolivia: Cochabamba: km 115 on road from Cochabamba to Villa Tunari, 1850 m, ZFMK 60464 (paratype); Bolivia: Cochabamba: km 36 on old Chapare road, 1600 m, ZFMK 67096 (paratype); Bolivia: Santa Cruz: La Hoyada, 1700 m, ZSM 144/1999 (paratype).

Rhinella veraguensis: Peru: Marcapata valley, BMNH 1947.2.21.23 (neotype; concurrently lectotype of *Bufo ockendeni*); Bolivia: Santa Cruz: 29 km E of Guadalupe, 1600 m, ZFMK 66850–66851; Bolivia: Santa Cruz: La Yunga de Mairana, 2300 m, ZFMK 66880; Bolivia: Cochabamba: old Chapare road, 1250 m, ZFMK 72555–72558; 1300–1500 m, ZFMK 72574–72575; 1650 m, ZFMK 72590–72592; Paracti, 1900 m, ZFMK 80039.

Rhinella yanachaga: Peru: Pasco: Oxapampa: Yanachaga-Chemillén National Park, W side of the Cordillera Yanachaga near Río San Alberto, 2600 m, MUSM 19994 (holotype).