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Revisiting the systematics of the *Ranitomeya uakarii* complex (Anura: Dendrobatidae) with the description of a new species from the Fitzcarrald Arch of Peru and Brazil

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Abstract

A new species of *Ranitomeya* from Amazonian lowland forests in western Brazil and southeastern Peru is described and named. This species was formerly considered to be an outlying population of *R. uakarii* on the southern periphery of its distribution. We analyze new and existing phylogenomic data and infer that the new species is not part of nor closely related to *R. uakarii,* but is sister to a clade including *R. benedicta* and a lineage referred to here as *R.* aff. *benedicta*. The new species can be distinguished from all other *Ranitomeya* by its distinctive color pattern, with thin yellow stripes on the dorsum, complete dorsolateral stripes, a complete labial stripe, and a single middorsal stripe that extends from the vent, forks into two stripes anterior to the orbital sockets and merges with dorsolateral stripes, forming a large yellow ring on the top of snout. There are four *Ranitomeya* species that look similar and co-occur in the general distribution of the new species (*R. hwata*, *R. sirensis*, *R. variabilis*, and *R. toraro*). The new species can be distinguished from all of them by the combination of a complete middorsal stripe and a round black rostral spot. Given the few and temporally scattered known records, the new species appears to be naturally rare, which raises concern regarding its conservation status.

Resumo

Uma nova espécie de *Ranitomeya* das florestas da baixa Amazônia, no oeste do Brasil e sudeste do Peru, é descrita e nomeada. Esta espécie era considerada uma população periférica de *R. uakarii*, no limite sudeste de sua distribuição. Nós analisamos novos e existentes dados filogenômicos e inferimos que esta nova espécie não pertence ou é intimamente relacionada a *R. uakarii*, mas sim irmã de um clado composto por *R. benedicta* e uma linhagem aqui referida como *R.* aff. *benedicta*. A nova espécie distingue-se de todas as demais *Ranitomeya* por seu padrão de coloração distinto, apresentando finas linhas amarelas no dorso, linhas dorsolaterais completas, uma linha labial contínua, e uma linha mediana dorsal única, que se estende desde a região cloacal, bifurca anteriormente às órbitas e se conecta às linhas dorsolaterais, formando um grande anel amarelo no topo do focinho. Quatro espécies de *Ranitomeya* se assemelham e coocorrem na mesma área geral de distribuição da nova espécie (*R. hwata*, *R. sirensis*, *R. variabilis* e *R. toraro*). A nova espécie pode ser distinguida de todas elas pela combinação da linha mediana dorsal completa e a mancha preta rostral circular. Com poucos registros

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conhecidos e temporalmente espaçados, a nova espécie aparenta ser naturalmente rara, levantando preocupações quanto ao seu estado de conservação.

Resumen

Se describe una nueva especie de *Ranitomeya* de los bosques amazónicos de tierras bajas del oeste de Brasil y sureste de Perú. Anteriormente, esta especie se consideraba como una población periférica de *R. uakarii*, en el límite sureste de su distribución. Analizamos datos filogenómicos nuevos y existentes e inferimos que la nueva especie no forma parte de *R. uakarii*, ni está cercanamente relacionada a ella, sino que es hermana de un clado que incluye *R. benedicta* y un linaje al que nos referimos aquí como *R.* aff. *benedicta*. La nueva especie puede ser distinguida de las otras especies de *Ranitomeya* por su distintivo patrón de coloración, que posee líneas delgadas amarillas en el dorso, líneas dorsolaterales completas, una línea labial completa y una única línea mediodorsal que se extiende desde la cloaca, se bifurca en dos líneas anteriores a las orbitas oculares y se une con las líneas dorsolaterales, formado un gran anillo amarillo en la parte superior del hocico. Hay cuatro especies de *Ranitomeya* que se asemejan y co-ocurren en la distribución general de la nueva especie (*R. hwata*, *R. sirensis*, *R. variabilis*, y *R. toraro*). La nueva especie puede ser distinguida de todas ellas por la combinación de una línea mediodorsal completa y una mancha rostral negra y redonda. Dados los pocos registros conocidos y dispersos en el tiempo, la nueva especie aparenta ser naturalmente rara, lo que genera preocupación sobre su estado de conservación.

Key words: dendrobatid frogs, poison frogs, ultraconserved elements, UCE, mitogenome

Introduction

Lowland Amazonian dendrobatid frogs remain understudied, particularly those near the eastern border of Peru into western Brazil (Koch *et al.* 2025; Mônico *et al.* 2025; Twomey *et al.* 2025). Intensified sampling in this region over the past two decades, combined with molecular phylogenetic analyses, has revealed several new species of *Ranitomeya* and dramatically restructured existing taxonomic boundaries (Twomey & Brown, 2009; Koch *et al.* 2025; Mônico *et al.* 2025; Twomey *et al.* 2025).

Since its orogeny in the late Pliocene (ca. 4 mya), the Fitzcarrald Arch has been a major geomorphic feature of southwestern Amazonia that may have shaped diversification processes. The Fitzcarrald Arch has been gradually rising due to subduction of the Nazca Ridge, caused by east-west volcanoes that pushed the Nazca oceanic tectonic plate below the S. American tectonic plate (Espurt 2007; Espurt *et al.* 2007; Espurt *et al.* 2008a, b; Regard *et al.* 2009; Espurt *et al.* 2010; Mora *et al.* 2010). At the start of the Pliocene, river drainages were largely identical to those of present-day South America, with the exception of the upper drainages of the Rio Acre and Rio Madre de Dios in southern Peru. The bulge of the Fitzcarrald Arch blocked the northward flow of the Acre and Madre de Dios systems into the Peruvian Amazon, causing these two drainages to flow to the southeast, into the Rio Purus and Rio Madeira (via Rio Madre de Dios systems). The consequences of these landscape changes on the biota remain poorly known; although some studies have explored their influences on fishes, reptiles, and mammals (Salas-Gismondi *et al.* 2007; Albert *et al.* 2012; Tejada-Lara *et al.* 2015).

The *Ranitomeya reticulata* group is an assemblage of six described species that are small in size (14–21 mm; Brown *et al.* 2011); most species have black dorsal coloration with bright orange to red dorsal patterning that is concentrated or brightest at their head. The *R. reticulata* group is relatively young, with most species diverging during the early Pleistocene (ca. 2.1–1.3 mya; Muell *et al.* 2022), after the formation of the Fitzcarrald Arch (Espurt 2007). This group has two biogeographic hotspots in Peruvian Amazonia: 1) the forests around Iquitos (containing *Ranitomeya reticulata* (Boulenger, 1884), *Ranitomeya uakarii* (Brown, Schulte & Summers, 2006), and *Ranitomeya ventrimaculata* (Shreve, 1935)), and 2) around eastern San Martin and nearby Loreto (containing a group of closely related, allopatric species: *Ranitomeya fantastica* (Boulenger, 1884); *Ranitomeya benedicta* Brown, Twomey, Pepper & Rodriguez, 2008; and *Ranitomeya summersi* Brown, Twomey, Pepper & Rodriguez, 2008). The *Ranitomeya reticulata* group has been subject to some taxonomic flux in the past decades, with the descriptions of *R. uakarii, R. summersi,* and *R. benedicta* in the late 2000s (Brown *et al.* 2006, 2008), and synonymies of *Ranitomeya ignea* (Melin, 1941) (considered a junior synonym of *R. reticulata*) and *Ranitomeya duellmani* (Schulte, 1999) (considered a junior synonym of *R. ventrimaculata*) (Brown *et al.* 2011).

One species in this group, *R. uakarii* was described from a locality within the Tamshiyacu-Tahuayo Reserve along Quebrada Blanco, in the North-Central lowlands of Amazonian Peru. The species diagnosis was based on its unique coloration pattern (paired parallel dorsolateral lines: yellow oblique lateral lines and red to orange dorsolateral lines), advertisement call (a nearly continuous long series of soft buzz-like notes), and molecular phylogenetic relationships, that suggested it was not conspecific with *R. ventrimaculata* (at that time referred to as *Dendrobates duellmani*) but closely related to an undescribed species (then referred to as "*D. ventrimaculatus* 1"; Brown *et al.* 2006) and *R. fantastica* (referred to as *D. fantasticus*; Brown *et al.* 2006). Subsequent phylogenomic studies have unequivocally supported these taxonomic circumscriptions (Muell *et al.* 2022; Santos *et al.* 2009; Twomey *et al.* 2023).

Since the description of *R. uakarii*, individuals from many other localities in Peru, Brazil, Colombia, and Guyana have been considered conspecific based on either molecular phylogenetic relationships or similar external morphology (Brown & Twomey *et al.* 2011). While these were initially treated as a single, widespread species (Brown & Twomey *et al.* 2011), recent phylogenomic studies revealed that the taxonomic diversity in this group is underestimated, and that *R. uakarii* is paraphyletic, with four individuals being more closely related to *R. benedicta* (Muell *et al.* 2022). Here, we reevaluate the taxonomic diversity within the *R. reticulata* group (including the *R. uakarii* complex) based on phylogenomics and increased sampling, and describe a new species previously considered to be *R. uakarii*.

Materials and methods

Morphological data acquisition

Specimens were morphologically examined in the Sam Noble Oklahoma Museum of Natural History (OMNH), USA, and Museo de Historia Natural San Marcos, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM). Two specimens were originally deposited in Museu Paraense Emílio Goeldi, Pará state, Brazil (MPEG), but were in the collections at OMNH at the time of this study. Nineteen morphometric measurements were made with mechanical calipers and a micrometer to the nearest 0.1 mm, following Myers (1982) and Brown *et al.* (2006): snout-vent length (SVL), femur length from vent to lateral surface of knee (FL), tibia length from heel to lateral surface of knee (TL), knee-knee distance with both legs extended straight (KK), foot length from proximal edge of metatarsal tubercle to tip of toe IV (FoL), hand length from proximal edge of metacarpal tubercle to tip of longest finger (HaL), head length from most exposed corner of occipitum to tip of snout (HL), head width between tympanum (HW), body width under axillae (BW), upper eyelid width (UEW), interorbital distance (IOD), internarial distance (IND), horizontal tympanum diameter (TD), horizontal eye diameter (ED), distance from outer corner of eye to tympanum (DET), length of finger I from proximal edge of median palmar tubercle to tip of finger disc (L1F), length of finger II from proximal edge of median palmar tubercle to tip of finger disc (L2F), width of disc of finger III (W3D), and width of finger 3 just below disc (W3F). Sex was determined by the presence of vocal slits.

Molecular analyses

Sequence acquisition

We acquired 60 samples for our phylogenetic analyses; 23 from a previous study (Muell *et al.* 2022) (Appendix 1). We included three outgroup samples representing *Ranitomeya defleri* Twomey & Brown, 2009, and at least one terminal from every recognized species of the *R. reticulata* group: five *R. benedicta,* 20 *R. fantastica*, two *R. reticulata*, 19 *R. summersi*, seven *R. uakarii*, two *R. ventrimaculata*, two samples sister to *R. benedicta,* but resembling *R. uakarii* (herein referred to as *R.* aff. *benedicta*) and two samples sister to *R. benedicta* + *R.* aff. *benedicta*, which represent the new species described herein.

Samples consisted of toe-clippings preserved in 95% ethanol. For each one, we extracted genomic DNA with the Qiagen DNeasy Blood and Tissue Kit (Valencia, CA) and quantified yield with a Qubit 3 fluorometer (ThermoFisher Scientific). We sent extracted DNA to RAPiD Genomics (Gainesville, FL, USA), who performed sequence capture and Illumina sequencing of ultraconserved elements (UCEs) following Faircloth *et al.* (2012). The samples were enriched with the Tetrapods-UCE-5Kv1 set of 5,472 probes, targeting 5,060 UCE loci (Faircloth *et al.* 2012). All corresponding sequences are available for download at https://doi.org/10.5281/zenodo.18775813.

Read quality trimming, sequence assembly, and alignment

For the UCE dataset, we performed most bioinformatic steps in the software package PHYLUCE v1.7.0 (Faircloth 2016). We trimmed raw reads using Illumiprocessor v2.0.6 (Faircloth *et al.* 2013), a Python-based wrapper for the program Trimmomatic v0.36 (Bolger *et al.* 2014). We assembled the trimmed reads with SPAdes (Prjibelski *et al.* 2020) implemented in PHYLUCE. We mapped contigs to UCE loci using PHYLUCE, retaining loci found at least once in any sample. In total, we retained 2,842 UCE loci. We then performed per-locus alignments with MAFFT 7 (Katoh & Standley, 2013), implemented within PHYLUCE. We filtered for matrix incompleteness by only retaining loci present in 75% or more of taxa.

When mitochondria-rich tissues such as muscle or liver are sequenced for UCEs, off-target sequencing reads originating from mitochondrial DNA are frequently generated as byproducts and are often abundant enough to allow for assembly of complete mitochondrial genomes (mitogenomes) (Raposo do Amaral *et al.* 2015). We first mapped the fastq file of each sample against a reference mitogenome of *Ranitomeya amazonica* (Schulte, 1999) (AF3590, unpublished data of LJCLM). We used the algorithm BWA-MEM implemented in the software package Burrows-Wheeler Alignment Tool (BWA; Li 2012), which aligns reads to a reference genome (mitogenome in this study) by identifying maximal exact matches (MEM). We then produced a consensus mitogenome for each sample using the program Analysis of Next Generation Sequencing Data (ANGSD) (Korneliussen *et al.* 2014). We used the following ANGSD command: *angsd-doFasta 4-doCounts 1-minQ 20-minMapQ 30-remove_bads 1-uniqueOnly-setMinDepth 2-iupacRatio 0.2-i.* Our selected parameters retained sites covered by at least 2 reads with a base quality ≥ 10 and a mapping quality ≥ 20, selecting for the most common base. This allowed for less strict parameters with a major allele consensus to retain a single consensus sequence per sample.

Phylogenetic inferences

We performed a maximum likelihood (ML) analysis on the partition UCE dataset using IQ-TREE v1.6.5 (Nguyen *et al.* 2015). All UCE loci were concatenated into a single alignment, and the resulting matrix was partitioned by UCE loci. To determine the best-fit nucleotide substitution model for each locus, we used the ModelFinder Plus option (-m MFP) (Kalyaanamoorthy *et al.* 2017). Node support was evaluated with 10,000 ultrafast bootstrap replicates (Minh *et al.* 2013) for the UCE data set. We also performed a ML analysis on the mitogenome dataset using 10,000 ultrafast bootstrap replicates, with the ModelFinder Plus option also implemented.

Results

Bioinformatics

We recovered 2,842 UCE loci in at least one sample. The dataset was further filtered for loci present in 75% or more of samples, which reduced the number of loci to 1,881. For the mitogenomes, we assessed the proportion of missing data per individual to evaluate sequence completeness. The average percentage of missing data across samples was 22.12 ± 28.02%, with individual samples ranging from 0.05% to 90.05% missing (prior to filtering).

Molecular phylogenetic relationships

Both phylogenies for the UCE and mitogenome datasets had high nodal support values, and their topologies were overall consistent (Figs. 1 & 2). Both recovered a clade containing *R. benedicta* and *R.* aff. *benedicta* and the new species described herein. In the UCE phylogeny, the *R. benedicta* + related lineages clade was recovered as sister to the clade containing *R. summersi* and *R. fantastica*, which were recovered as reciprocally monophyletic. *Ranitomeya uakarii* is recovered as sister to the clade containing *R. summersi*, *R. fantastica*, *R. benedicta,* and its related lineages. *Ranitomeya reticulata* is recovered as sister to this larger clade, and *R. ventrimaculata* is recovered as sister to all other species in *R. reticulata* group. In contrast, the mitogenome phylogeny recovered the *R. benedicta*

+ related lineages clade as sister to *R. uakarii*, and this clade as sister to the one containing *R. fantastica* and *R. summersi*. Another difference was the positioning of *R. ventrimaculata* and *R. reticulata* as sister species, forming a clade sister to all other species of the *R. reticulata* group. In the mitogenome dataset, *R. summersi*, *R. fantastica* and *R. benedicta* were recovered as paraphyletic, as some samples of *R. summersi* and *R. benedicta* were nested within *R. fantastica* and *R. summersi*, respectively, suggesting episodes of introgression or incomplete lineage sorting among these species. All other taxa were recovered as monophyletic in both analyses. Both molecular phylogenies consistently indicate the existence of two independent lineages closely related to *R. benedicta*, which are phenotypically similar to *R. uakarii.* They also have dramatic morphological differences from *R. benedicta*, a species which lacks dorsolateral, oblique lateral and middorsal lines (vs. present in both lineages), but instead has a brilliant red head with a black mask around the eyes and tympanum (vs. not present in *R.* aff. *benedicta* and the new species described here). The main characteristic that all three (*R. benedicta*, *R.* aff. *benedicta*, and the new species) share is that they are all rarely encountered, a factor likely associated with their similar natural histories (see Discussion). However, given that these lineages are morphologically diagnosable and distinct from *R. benedicta*, we name and describe below the one for which more data are available.

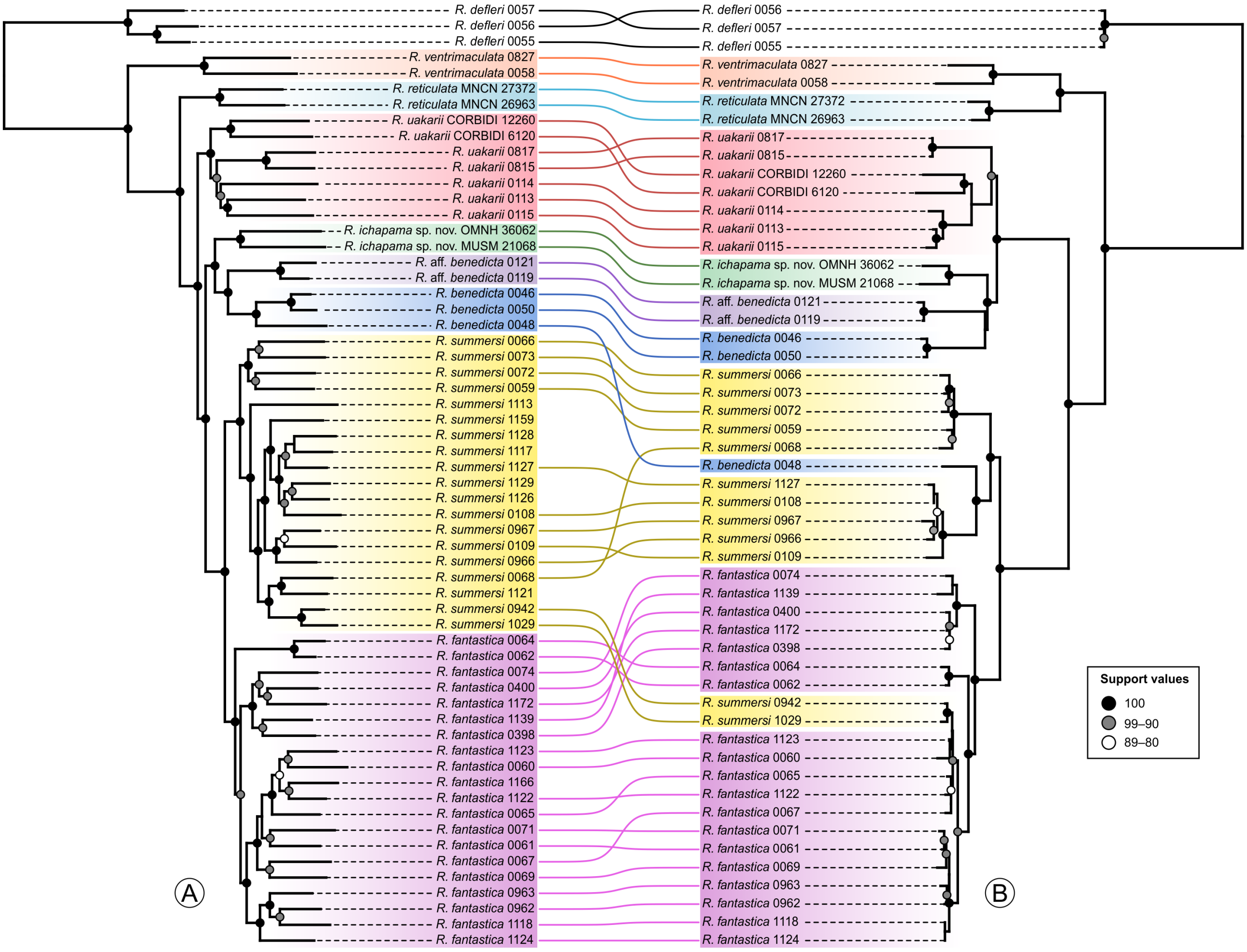

FIGURE 1. Comparison of Maximum Likelihood phylogenetic trees of the *Ranitomeya reticulata* group based on 1,881 nuclear ultraconserved elements (UCE) loci (A) and mitochondrial genome data (B). Node support values correspond to ultrafast bootstrap replicates. Described and undescribed taxa are highlighted in different colors, matching those used in Figs. 2, 6, and 7. Lines between trees connect corresponding terminals.

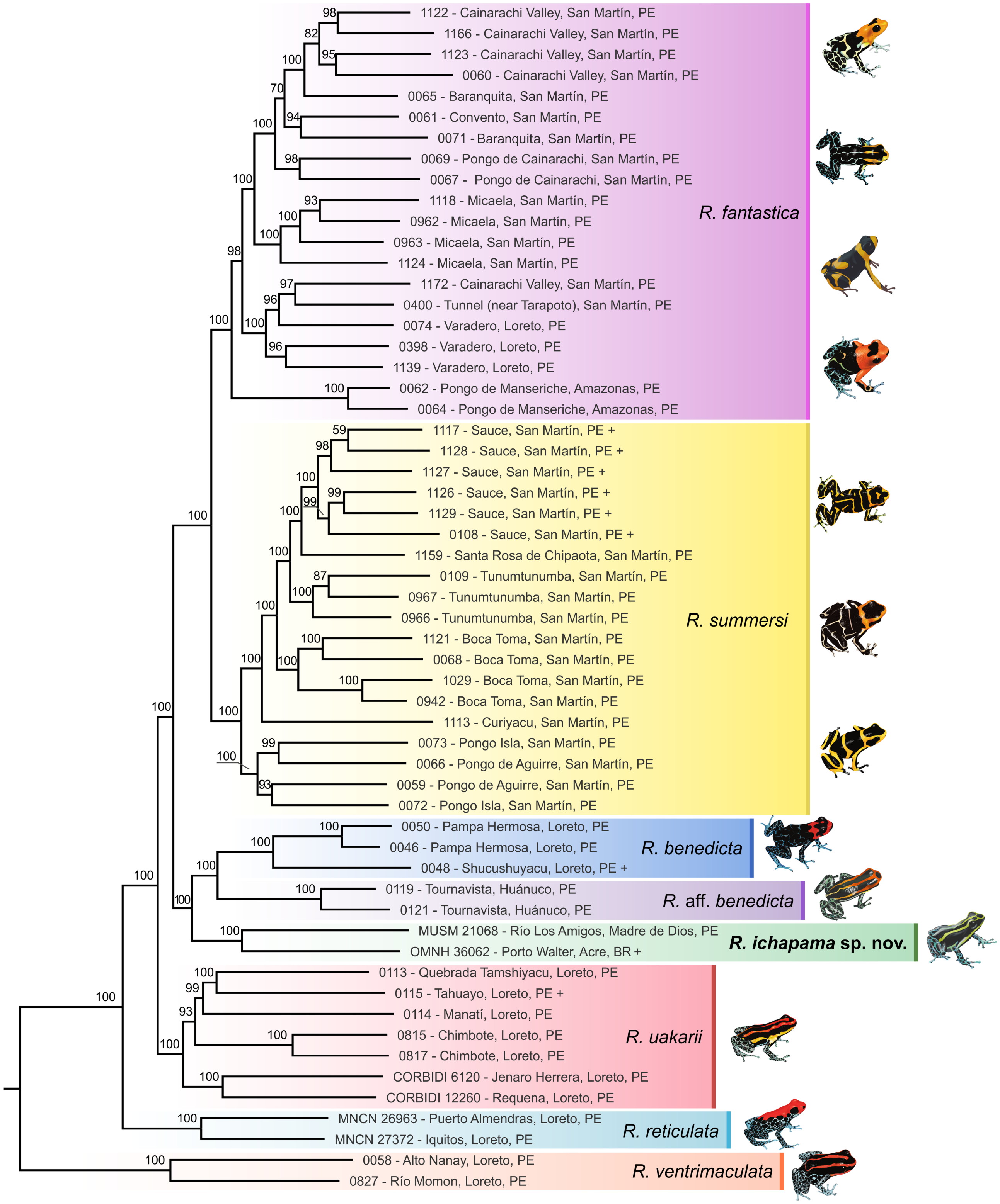

FIGURE 2. Maximum Likelihood phylogenetic tree of the *Ranitomeya reticulata* group inferred from 1,881 nuclear ultraconserved elements (UCE), under a partitioned scheme with the best-fit substitution model selected independently for each locus. Node support values correspond to ultrafast bootstrap replicates. Described and undescribed taxa are highlighted in different colors, matching those used in Figs. 1, 6, and 7. Outgroups were excluded to improve visualization. Terminals with the symbol "+" represent topotypic specimens (Drawings: WXG and T. Kahn).

Species description

Ranitomeya ichapama sp. nov.

Yaminawá Poison Frog

(Figs. 3–5; Table 1)

Dendrobates ventrimaculatus: **de Souza 2003** (in partim) p. 139**, Brown *et al.* 2006** (in partim), **Roberts *et al.* 2006** (in partim)

Ranitomeya ventrimaculata: **Grant *et al.* 2006** (in partim) p. 141–145 (MPEG 12394: appendix 5 p. 239; OMNH 36062: appendix 5 p. 239)**; Santos *et al.* 2009** (in partim) p. 0448–0461(LSUMZ 13755; LSUMZ 13770: supplemental table s3); **de Souza 2009** Plate 16

Ranitomeya cf. *ventrimaculata*: **von May *et al.* 2009** p. 18 Table 1; p. 20; p. 25

Ranitomeya sirensis: **Crnobrna *et al.* 2023** Table 2; p. 438, 441, Fig. 5B

Ranitomeya uakarii: **Brown & Twomey *et al.* 2011** (in partim) p. 56–58 (p. 42 Fig. 11J; p. 51 Fig. 17E; pg. 99 Fig. 43A; p. 116 Appendix I; pg. 119 Appendix II: MPEG 12394; p. 15 'Porto Walter, BR; p. 57 Definition and Diagnosis: (ii) 'Toraro' morph); **von May *et al.* 2010** p. 2; **Catenazzi *et al.* 2013** p. 4 Table 1; p. 10 (MUSM 21068); **Grant *et al.* 2017** (in partim) p. 54 (GenBank accessions DQ502501, DQ502070, DQ502792; appendix.s2); **Muell *et al.* 2022** (in partim) p. 1–10 (p. 3 Fig. 1a: *R.* aff. *uakarii*; Fig. 1b: 0112 Rio Los Amigos, 0159 Brazil; p. 6 Fig. 2: *R.* aff. *uakarii* 'Toraro'; p.7 Fig. 3: *R.* aff. *uakarii* 'yellow'; p. 2–5, 8).

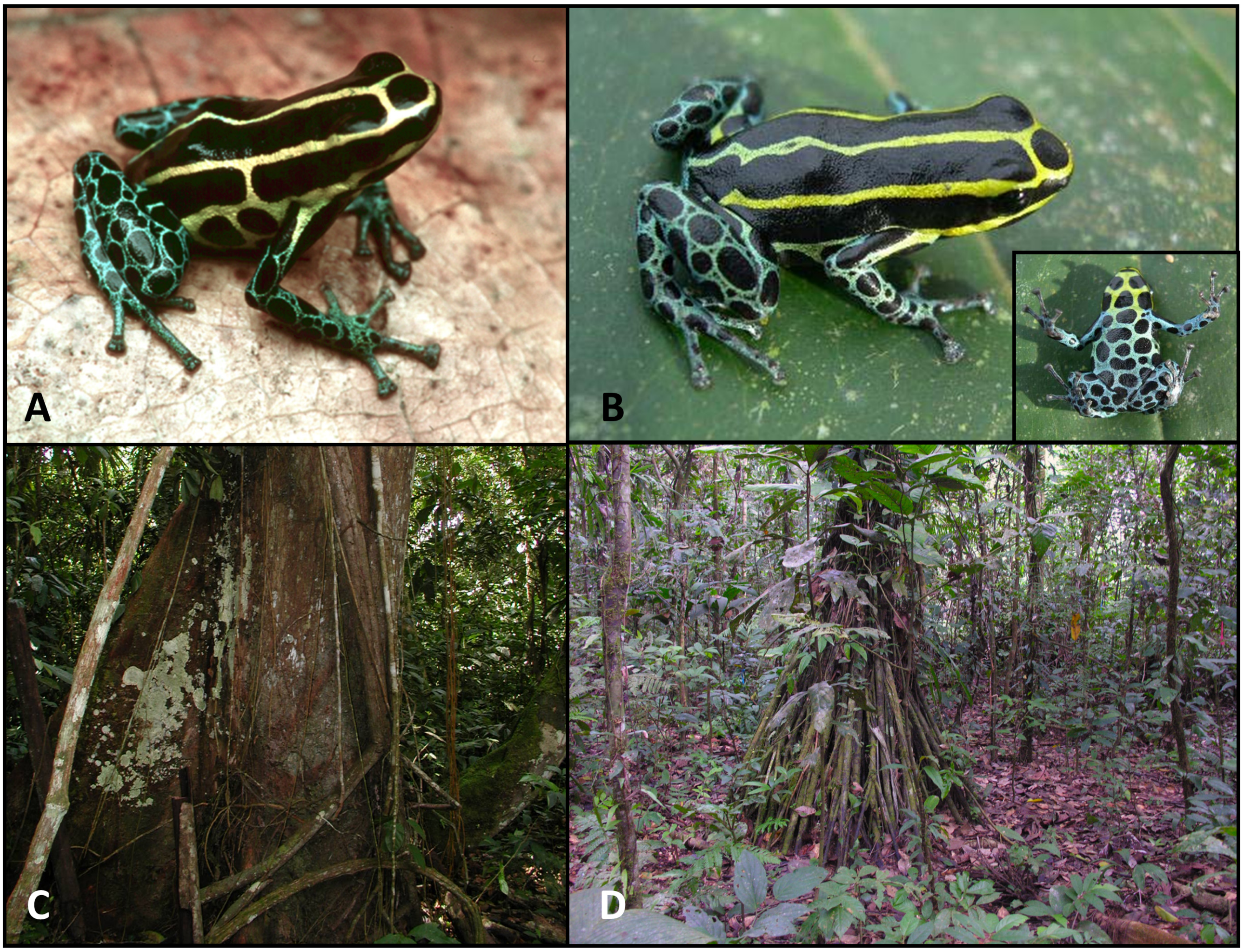

FIGURE 3. *Ranitomeya ichapama* **sp. nov.** from A) Porto Walter, Brazil (paratopotype MPEG 12394, photo J.P. Caldwell) and from B) Los Amigos Biological Station, Peru (paratype MUSM 21068, photo RvM). C) and D) *Terra firme* forest similar to where the only observed specimen of *R. ichapama* **sp. nov.** from Peru was found (C. Mathias Tobler, D. Jennifer M. Jacobs, 2007). The habitat photos were taken approximately 2 km from the discovery location; however, it is similar in appearance to that shown (RvM unpublished data).

FIGURE 4. Dorsal and ventral views of the preserved holotype (left) and paratopotypes (center and right) of *Ranitomeya ichapama* **sp. nov.**

Holotype. OMNH 36062 (field number JPC 13162), an adult female collected by Verônica L. Oliveira on 28 February 1996, in Brazil, Acre state, ca. 5 km west of Porto Walter city, inland from Rio Juruá (8° 15' 31.2" S, 72° 46' 37.1" W, 80 m a.s.l., Fig. 4).

Paratopotypes. Two adult females, MPEG* 12394 (field number JPC 13082) and MPEG* 12395 (field number JPC 13306), collected from 24 February 1996 and 7 March 1996, respectively, by Verônica L. Oliveira (Figs 3 & 4).

Paratype. One adult unsexed voucher, MUSM 21068 (field number RvM 238), collected by R. von May on 13 March 2003, in Peru, Madre de Dios region, Manu province, approximately 3.6 km NW from Los Amigos Biological Station (12° 32 '58" S, 70° 07' 35" W, 282 m a.s.l.).*

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* These specimens were loaned to JLB from the OMNH on 5/2009 and returned on 6/2009. As of August 2025, they remain in the care of OMNH.

Referred specimens. Two adults collected by Roy Santa-Cruz Farfan in 2012 in the Ucayali region, Coronel Portillo province, from San Mateo (08° 11.47′ S, 073° 40.82′ W) and deposited at Natural History Museum of the Universidad San Agustín in Arequipa, Peru (MUSA) (male; MUSA 4296, and female; MUSA 6145) (Crnobrna *et al.* 2023).

Etymology. The specific epithet, '*ichapama'*, is derived from the Yaminawá adjective *Ic̆apa-ma* (pronounced *ee-cha-pa-ma*) meaning "rare" or "few". Here, we use the Yaminawá language to honor the Yaminawá Indigenous people who once occupied much of the range of this species throughout western Brazil and southeastern Peru. The name references the rarity of this species, given its known distribution. Despite ongoing research efforts throughout its range, this species remains one of the most elusive *Ranitomeya*. The name is an invariable noun in apposition to the genus name.

Generic placement. Assigned to the genus *Ranitomeya* due to the combination of the following characteristics: small size (< 20 mm SVL), dorsal coloration conspicuous and bright, with pale limb reticulation, first finger distinctly shorter than the second. Further assigned to the *R. reticulata* group based on molecular phylogenetics (see below for further details).

Definition. A medium-sized species of *Ranitomeya* (adult SVL 13.9–17.2 mm) with dorsal coloration conspicuous, dorsolateral stripes extending to top of thigh, ventrolateral stripes present, brightly colored throat, distinctive pale reticulation on limbs and venter, dorsal skin smooth, finger I greatly reduced and shorter than finger II, finger discs II–IV greatly expanded, disc of finger 2.0–4.0 times wider than finger width, thenar tubercle conspicuous, toe discs III–V moderately expanded, toe webbing absent, maxillary and premaxillary teeth absent.

Dorsal body and head black with complete yellow middorsal and dorsolateral stripes, extending from vent to rostrum and from upper surface of thighs to orbits, respectively. Limbs and venter black with pale to bright green reticulation forming round black spots on limbs and irregular spots on venter. Chin with yellow reticulation outlining typically five black gular spots: two pairs of two small gular spots and a large central spot.

Comparisons. *Ranitomeya ichapama* **sp. nov.** can be distinguished from similar-looking *Ranitomeya* species by two characters in combination: (1) presence of a complete yellow middorsal stripe that extends from the vent to the eye-level (2) presence of a round, black spot on the rostrum. As follows are additional comparisons to species with brightly yellow dorsolateral stripes: *R. defleri*, *R. flavovittata* (Schulte, 1999), *R. hwata* Twomey, Melo-Sampaio, Brown, Castroviejo-Fisher, Gagliardi-Urrutia, Padial, Gutiérrez & Chaparro, 2025*, R. sirensis* (Aichinger, 1991), *R. amazonica*, *R. variabilis* (Zimmerman & Zimmerman, 1988), and *R. toraro* Brown, Caldwell, Twomey, Melo-Sampaio & Souza, 2011 (Fig. 5). *Ranitomeya defleri* and *R. flavovittata* have highly variable dorsal markings consisting of yellow dots and elongated spots (vs. complete middorsal and dorsolateral stripes in *R. ichapama* **sp. nov.**); further, *R. defleri* has characteristic large yellow blotches behind the eyes (absent in *R. ichapama* **sp. nov.**). *Ranitomeya flavovittata* typically has a pale conspicuous yellow spot on the upper surface of each thigh (absent in *R. ichapama* **sp. nov.**).

Some populations of *R. sirensis* are similar in appearance to *R. ichapama* **sp. nov.**; however, all *R. sirensis* possess a large spot that is the same color as the stripe coloration (typically yellow) in the center of the venter (vs. absent in *R. ichapama* **sp. nov.**, Fig. 5). *Ranitomeya variabilis* and *R. amazonica* are fairly variable species and some of their morphs can be similar to *R. ichapama* **sp. nov.**, but *R. ichapama* **sp. nov.** has a complete yellow middorsal stripe that extends from the vent to the eye-level (starting in mid-dorsum in *R. variabilis* and *R. amazonica*). A complete middorsal stripe has been observed in *R. variabilis,* however this is incredibly rare (only 2 individuals of >500 individuals we have observed have this trait).

In southwestern Brazilian Amazonia, the co-occurring *R. toraro* can be distinguished from *R. ichapama* **sp. nov.** by the following characters: 1) absence of a large black spot on the rostrum (present in *R. ichapama* **sp. nov.**, vs. the fusing of black nostril spots, creating the appearance of an upside-down 'U' or 'horseshoe' on the tip of the snout, Fig. 5), 2) a single pair of large black gular spots (vs. typically two smaller pairs in *R. ichapama* **sp. nov.** Fig. 5).

FIGURE 5. Visual comparison to eleven similar-looking or closely related *Ranitomeya*. *Ranitomeya ichapama* **sp. nov.** possess: **i)** a large black spot on the rostrum (absent in other species, often present in *R. variabilis* and *R. amazonica*); **ii)** a uniform colored yellow middorsal stripe that extends from the vent to between eyes (also present in *R. toraro, R. sirensis, R. hwata*, and typically absent in *R. variabilis*) that is roughly the same width across dorsum (iia vs. iib; vs. in some populations of *R. toraro* the stripe at iib is ca. 2x wider than iia and typically bicolored) and splits anterior to eyes fusing with labial stripe (absent in *R. uakarii, R. sirensis, R. hwata, R. amazonica, R. flavovittata*); **iii)** an oblique lateral stripe that is identical to ventral coloration (vs. different color than venter coloration in *R. uakarii, R. amazonica, R. toraro, R. sirensis, R. hwata*); **iv)** occasionally, the dorsolateral and oblique lateral stripes connect (not typically observed in other species, with exception to some morphs of *R. variabilis* (not pictured)); **v)** large yellow spot on center of venter absent (vs. present in *R. sirensis*), and **vi)** two pairs of smaller gular spots on throat (single pair in *R. uakarii, R, defleri, R. benedicta, R. toraro, R. variabilis*; absent in *R. flavovittata, R. sirensis, R. hwata*) as well as a central gular spot between posterior gular spot pair (typically absent in *R. amazonica, R. flavovittata, R. benedicta, R. uakarii, R. variabilis*, *R. sirensis, R. hwata*). Locality of photos and photo credits: *Ranitomeya ichapama* **sp. nov.** (Los Amigos Biological Station, PE; RvM), *R. uakarii* (Tamshiyacu-Tahuayo Reserve along Quebrada Blanco, PE; JLB), *R.* aff. *benedicta* (Tournavista, PE; Tilo Henning), *R. benedicta* (Shucushuyacu, PE; ET and JLB), *R. toraro* (dorsal: Humaitá, Amazonas, BR; P. I. Simões, ventral: near Boca do Acre, Amazonas, BR; M. B. Souza), *R. sirensis* (Los Amigos Biological Station, PE; JLB), *R. hwata* (Reserva Extrativista Arapixi, Amazonas, BR; P. R. Melo-Sampaio), *R. flavovittata,* Tamshiyacu-Tahuayo Reserve along Quebrada Blanco, PE; JLB), *R. varibilis*—left (nearby Contamana, PE; JLB), *R. variabilis*—right (Callanayacu, PE; JLB), *R. amazonica* (nearby Iquitos, PE; JLB), *R. defleri* (near Puerto Córdoba, CO; JLB).

Measurements (in mm) of holotype. SVL 17.2; FL 6.6; TL 7.1; KK 13.8; FoL 6.8; HaL 4.7; HL 5.3; HW 5.5; BW 5.5; UEW 2.6; IOD 2.4; IND 2.0; TD 0.9; ED 2.2; DET 0.4; L1F 1.7; L2F 2.4; W3D 0.9; W3F 0.2. For paratopotype measurements, see Table 1.

TABLE 1. Morphological measurements of holotype and paratopotypes (in mm) of *Ranitomeya ichapama* **sp. nov.** See text for character abbreviations.

Character	**OMNH 36062 (holotype)**	**MPEG 12394**	**MPEG 12395**	**Mean ± SD**
SVL	17.2	17.0	13.9	16.0 ± 1.9
FL	6.6	7.5	6.4	6.8 ± 0.6
TL	7.1	7.9	6.3	7.1 ± 0.8
KK	13.8	14.8	11.7	13.4 ± 1.6
FoL	6.8	7.3	5.8	6.6 ± 0.8
HaL	4.7	4.9	4.0	4.5 ± 0.5
HL	5.3	5.0	4.4	4.9 ± 0.5
HW	5.5	5.3	4.6	5.1 ± 0.5
BW	5.5	6.0	5.0	5.5 ± 0.5
UEW	2.56	2.56	2.33	2.5 ± 0.1
IOD	2.44	2.44	2.00	2.3 ± 0.3
IND	2.00	2.33	2.22	2.2 ± 0.2
TD	0.89	0.78	0.67	0.8 ± 0.1
ED	2.22	2.11	1.89	2.1 ± 0.2
DET	0.44	0.72	0.50	0.6 ± 0.1
L1F	1.67	2.11	1.56	1.8 ± 0.3
L2F	2.44	3.22	2.11	2.6 ± 0.6
W3D	0.89	1.11	0.67	0.9 ± 0.2
W3F	0.22	0.44	0.33	0.3 ± 0.1
SEX	F	F	F	

Description of holotype. In life, dorsal stripes are bright yellow, throat bright yellow, venter and limb coloration is a dull greenish on black body coloration. Head widest at jaw articulation; head slightly narrower than body. Head width equal to head length; head width 32.0% of SVL. Snout acuminate in lateral view, truncate with slight rounding in dorsal view. Nares directed posterolaterally, 1.4 mm from tip of snout; internarial distance 2.0 mm, 36.4% of head width. Canthus rostralis rounded, loreal region flat. Eye–naris distance 1.3 mm, 70.0% of horizontal eye diameter. Tympanum slightly oval, posterodorsal margin hidden by depressor muscle, tympanum 40.0% of eye diameter. Tongue ovoid, attached anteriorly; median lingual process absent. Teeth absent.

Body with three parallel stripes; middorsal stripe bifurcates anterior to eyes and fuses with dorsolateral stripes midway between corner of eye and nares, dorsolateral stripe extends from tip of snout above the eye-edge to form a labial stripe; ventrolateral stripe integrates into ventral reticulate pattern. Skin texture smooth on head and most of dorsum, becoming weakly granular on posterior surface of dorsum and on limbs. Ventral surfaces of body and limbs weakly granular, chin nearly smooth. Forelimbs slender, hand relatively large, 27.3% of SVL. Finger I considerably shorter than finger II when fingers appressed; finger III > II > IV > I. Discs on fingers II, III and IV greatly expanded; disc on finger I small, rounded. No webbing or lateral fringes on hand. Width of disc on finger III 4.0 times width of adjacent phalanx. Outer metacarpal tubercle (= palmar tubercle) large, round, unpigmented; inner metacarpal tubercle (= thenar tubercle) oval, located at base of finger I. Unpigmented proximal subarticular tubercles present at bases of fingers II, III and IV; on finger I tubercle is halfway to tip of digit. Smaller, distal subarticular tubercles present only on fingers III and IV, tubercle diffuse on finger IV. Tubercles raised in lateral view. Dorsal scutes present on all digits.

Length of legs moderate; heels of appressed legs reach level of eyes. Femur and tibia nearly equal in length; tibia 92.3% of femur; knee–knee distance 80.2% of SVL. Relative lengths of appressed toes, IV > III > V > II > I. Toe I short with rounded disc; toes II, IV and V with moderately expanded discs. Unpigmented outer metatarsal tubercle round, raised; unpigmented inner metatarsal tubercle oval, located at base of toe I. Unpigmented outer metatarsal tubercle located laterally at base of fifth metatarsal; unpigmented inner metatarsal tubercle located medially near base of toe I. Weakly defined tarsal keel extends from inner metatarsal tubercle for about one-third length of tarsus; tarsal tubercle absent. Two subarticular tubercles present on toes III and V, one on toes I and II. Three subarticular tubercles on Toe IV, the basal one weakly defined. Toes lack webbing and lateral fringes.

Variation. Based on the three measured type specimens, average adult SVL is 16.0 mm (13.9–17.2 mm). The striping pattern among the known specimens was remarkably consistent with only minor deviations. Two specimens from the type series have the dorsal stripes connected midway into oblique lateral stripes (OMNH 36032 and MPEG 12394; Figs. 3 & 4). This was also the case for the individual pictured by de Souza (2003). In some specimens, the mid-dorsal line becomes more sinuous posteriorly, branching into a reticulated pattern and acquiring bluish tones (MUSM 21068 and the individual pictured by Crnobrna *et al.* (2023), one of the referred specimens). In the third specimen of the type series (MPEG 12395), the central black gular spot is divided, giving the appearance of a sixth spot (Fig. 4).

Color in life. Ground color of dorsum black with three longitudinal stripes; dorsolateral stripes are iridescent yellow; middorsal stripe yellow on back (Fig. 3). Middorsal stripe bifurcates on head and extends anterior to eye fusing with labial stripe, mid-distance between eye-edge and nares. Ventrolateral stripe near the axilla is light blue or greenish blue, then yellow in the groin. Arms, legs, and ventral surfaces with dull green reticulate pattern on black ground color, forming large black round or elongate spots. Iris black.

Color in preservative. Dorsum dark gray with three whitish but distinct longitudinal stripes on body and head. Middorsal stripe bifurcates on head anterior to eye and extends below eye alongside to fuse with labial stripe. Reticulate pattern distinct, in shades of gray, on upper limbs, sides and all ventral surfaces except chin.

Tadpole. Unknown

Vocalizations. Unknown

Distribution and natural history. *Ranitomeya ichapama* **sp. nov.** has been observed at three localities in the western region of the Brazilian state of Acre and three localities in Peru (Figs. 6 & 7). This species likely occurs widely throughout the Fitzcarrald Arch limits; however, further sampling is required to determine the extent of its distribution. Individuals from all localities have been found in undisturbed *terra firme* primary forest or old-growth secondary forest. These forests are not subject to flooding during the rainy season. The habitat at the type locality, according to Caldwell & de Oliveira (1999), consisted of forest dominated by straight-boled hardwood trees, intersected by numerous small streams that rendered the terrain hilly. They also noted a general lack of large tree holes and bromeliads, resources typically important for dendrobatids (Caldwell & de Oliveira 1999). In the other two Brazilian localities, individuals were observed on leaves, branches, and stems of the herbaceous and shrubby vegetation, near temporary pools, bromeliads, and other phytotelm plants (de Souza 2003). Although some individuals were observed in bamboo forests, neither adults nor larvae were found using bamboo culms as oviposition or larval development sites (de Souza 2003). In all three Brazilian localities, *R. ichapama* **sp. nov.** was found co-occurring with *Ranitomeya vanzolinii* (Myers, 1982), which was considerably more commonly encountered (de Souza 2003; J. Caldwell, pers. comm.). In southern Peru, individuals were observed calling and moving in the underbrush and leaf litter during the daytime, and one male was carrying tadpoles on its back (Crnobrna *et al.* 2023). The specimen collected in southern Peru was found during a leaf-litter plot survey in an old-growth terra firme forest site. The habitat features continuous canopy cover, with the understory dominated by palms, vines, shrubs, lianas, and trees of varying diameters. In this locality, *R. ichapama* **sp. nov.** was recorded co-occurring with *R. sirensis*, which was relatively common in *terra firme* sites mixed with woody bamboo (*Guadua weberbaueri*)[**].

Conservation status. Following the IUCN Red List criteria B2ab(i) (IUCN 2012), we suggest *R. ichapama* **sp. nov.** be listed as Vulnerable (VU), as it is known from only six locations with a known extent of occurrence estimated to be less than 20,000 km^2. Further, this species appears to be rare at all known sites. The total geographic

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[**] In early March 2026, post-acceptance of this manuscript, ET discovered one additional specimen of R. ichapama (USNM 537566) in a collection. This specimen is from the Urubamba Lowlands (W 11° 47 ‘ 8” S 72° 41’ 57.1”) and was collected in the early 1990s as part of a RAPID survey. This observation is ca. 300 km west-northwest of the Los Amigos Biological Station voucher in Southern Peru.

extent of this species could dramatically exceed 20,000 km^2, as much of the forests across the Fitzcarrald Arch is largely undisturbed.

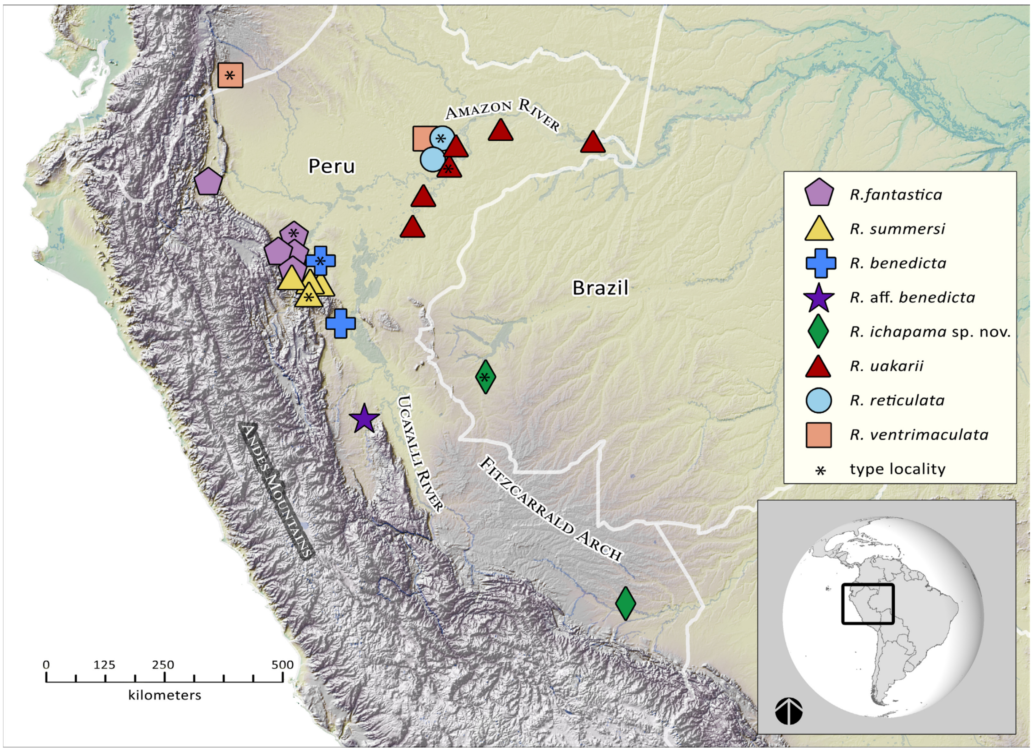

FIGURE 6. Geographic distribution of *Ranitomeya reticulata* group genetic samples analyzed here. *type localities (or nearest to it, if not represented in genetic samples).

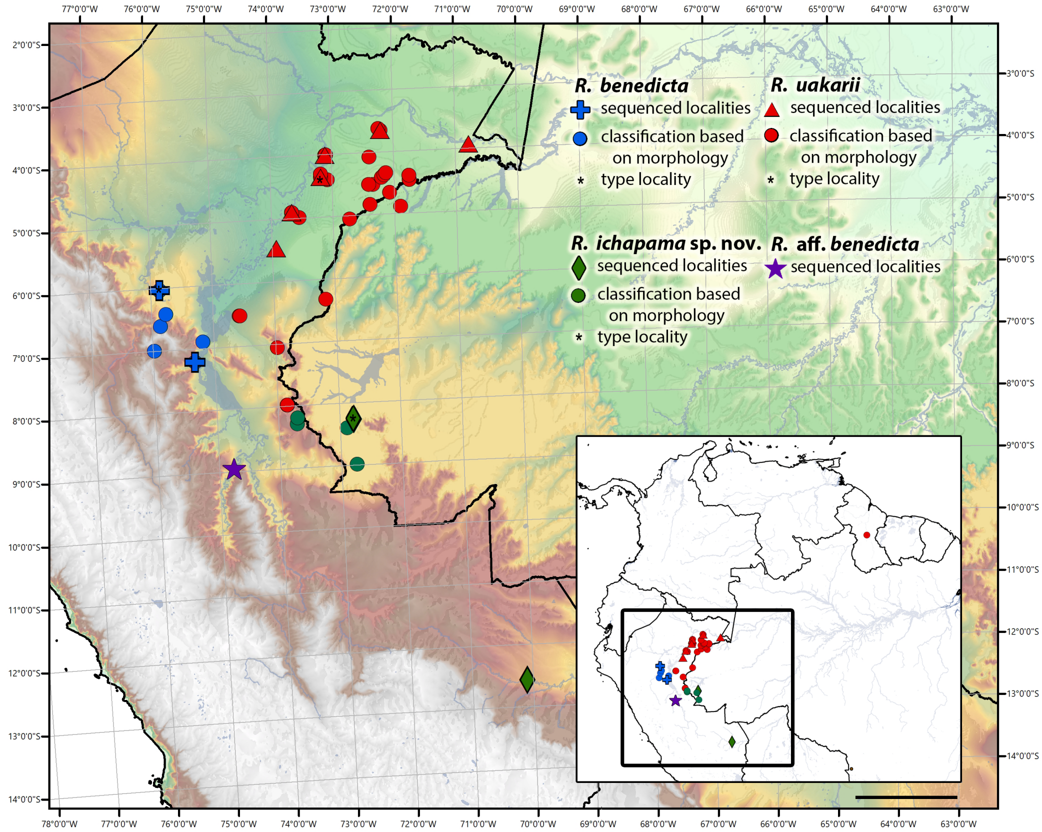

FIGURE 7. Detailed geographic map of known distributions of *Ranitomeya uakarii, R. benedicta, R. ichapama* **sp. nov.**, *and R.* aff. *benedicta* over an altitudinal background. Black bar (in lower right) = 200 km.

Discussion

The available evidence suggests that *R. ichapama* is a genuinely rare species. At the type locality, only three individuals were recorded despite the efforts of four independent, experienced researchers conducting surveys over a 72-day period (Caldwell & de Oliveira 1999). Since the original collection in 1996, no additional specimens have been recorded from this region, although subsequent sampling efforts were limited (but see Fonseca *et al.* 2019, who conducted a similar sampling effort to that of 1996 and have not recorded the species), and the region has undergone substantial deforestation over the years. In the two nearby localities in Brazil, surveys were conducted over 180 and 136 days, and although no abundance data were reported, the available information indicates that the species was found at low frequency (de Souza 2003). In southern Peru, only a single specimen was collected in 2003, and despite additional surveys conducted in 2006, 2007, 2008, 2009, and 2012, no further individuals have been detected (RvM unpublished data). Further, as of November 2025, there is no record of this species on iNaturalist (www.inaturalist.org).

The causes of this apparent rarity remain uncertain, but could be due to naturally low population densities or a patchy distribution associated with uncommon ecological preferences (i.e. the use of higher forest canopy or the use only of large phytotelmata for tadpole nurseries), as reported for the closely related *R. benedicta*, which is also rarely recorded (Brown *et al.* 2008). The consistent co-occurrence of *R. ichapama* with a much more abundant congener may further suggest limited competitive ability for reproductive sites. These hypotheses, however, remain speculative, and additional field studies are needed to clarify the factors underlying this apparent scarcity. The other undescribed lineage within this clade (*R.* aff. *benedicta*) also appears to be rare, and we hope that the formal description of *R. ichapama* encourages further observations and improved knowledge of these elusive lineages.

The evolutionary origins and apparent distribution of *R. ichapama* coincide with the formation of the Fitzcarrald Arch. We advocate for additional scientific surveys throughout the Fitzcarrald Arch, with a primary goal of defining the distribution of this species. A few other *Ranitomeya* are known to occur within this region. *Ranitomeya vanzolinii* appears to occupy forests throughout the Fitzcarrald Arch and likely co-occurs with *R. ichapama* throughout much of its range. At the presumed eastern edge of the distribution, *R. ichapama* co-occurs with *R. toraro*. At the presumed southwestern edge of the distribution, *R. ichapama* co-occurs with *R. sirensis* (*biolat* morph, sensu Brown *et al.* 2011). In the southeast of its presumed distribution, *R. ichapama* could co-occur with *R. hwata* (Twomey *et al.* 2025); however, this has yet to be observed. Given that this species is only known from six localities, the extent to which *R. ichapama* co-occurs with any of these species, as well as other *Ranitomeya* species is unknown.

The phylogenetic placement of species in the *R. reticulata* group remains in flux (Brown *et al.* 2011, Muell *et al.* 2022, Twomey *et al.* 2025). *Ranitomeya ichapama* is sister to a clade containing *R. benedicta* and a frog similar in appearance to *R. uakarii* ("*R.* aff. *benedicta*", also referred to as *R.* aff. *uakarii* Tournavista in Muell *et al.* 2022). These results are consistent with other recent phylogenomic studies (Muell *et al.* 2022, Twomey *et al.* 2023) and suggest that several lineages once presumed to be closely allied with *R. uakarii* are not as similar as once thought (Brown & Twomey *et al.* 2011).

To date, no voucher specimens or call recordings exist of *R.* aff. *benedicta* from near Tournavista, Peru. As such, it is difficult to investigate the taxonomic status of this population. Its taxonomic status is further complicated and remains uncertain, since this lineage is the sister taxon to *R. benedicta,* a species previously thought to be most closely related to *R. fantastica* and *R. summersi,* rather than to *R. uakarii. Ranitomeya* aff. *benedicta* thus could be either an undescribed species or hybrid between *R. benedicta* and another species (i.e. *R. uakarii* / *R. ichapama*). Additional data on this population might provide insight into the taxonomic status of this elusive frog.

Our results also provide the most comprehensive phylogenomic analysis of the relationships of *R. fantastica*, *R. summersi,* and *R. benedicta* to date (Muell *et al.* 2022 had 11 individuals from 10 localities, whereas this study has 44 individuals from 18 localities). The taxonomic revision of *R. summersi* by Muell *et al.* (2022) classified the Boca Toma (from nearby Tarapoto) and lower Huallaga canyon populations as *R. summersi* (populations previously considered *R. fantastica*). We recovered strong phylogenetic support for each taxon (sensu Muell *et al.* 2022), and all species are reciprocally monophyletic in our UCE phylogenetic analysis.

Our mitogenomic analyses largely match our nuclear analyses, except for two likely introgression events involving *R. summersi*. The first likely introgression event is between *R. fantastica* and *R. summersi* from Boca Toma (1029; 0942), a population of *R. summersi* that is isolated from all other sampled ones (Fig. 1). Both *R. summersi* individuals from Boca Toma possess mitochondrial genomes that are more closely related to nearby populations of

R. fantastica (Fig. 1). This observation could help explain some of the past confusion over the taxonomic status of the Boca Toma frogs (Brown *et al.* 2009; Brown & Twomey 2011; Muell *et al.* 2022), which are morphologically intermediate between *R. fantastica* and *R. summersi*—with white limb coloration typically present in *R. fantastica* and the dorsal color/pattern similar to *R. summersi* from the lower Huallaga canyon.

The second likely introgression event is between the *R. summersi* from the lower Huallaga Canyon and *R. benedicta* from Shucushuyacu, where our sample of *R. benedicta* possesses a mitogenome that is more closely related to *R. summersi*. When comparing the *R. benedicta* from Shucushuyacu to *R. benedicta* from Pampa Hermosa, the populations possess different limb patterns (with Shucushuyacu populations possessing dark blue limb and venter reticulation, whereas the Pampa Hermosa populations completely lack limb and venter reticulation). Nearby Callanayacu and Huimbayoc (two towns in the Huallaga Canyon), *R. benedicta* and *R. summersi* have been found in very close proximity to each other. The *R. benedicta* populations from Huimbayoc have orange head coloration (vs. bright red found in all other populations), thus introgression between these two species is completely plausible. Future research is needed to determine if these are historical hybridization events and if they played any role in the unique phenotypes of the *R. summersi* from Boca Toma and the *R. benedicta* from Shucushuyacu and Huimbayoc.

Lastly, our results reaffirm potential risks when basing taxonomic decisions on only mitochondrial data (including complete mitogenomes). Here, likely due to introgression, we identified paraphyletic species in our mitogenome phylogeny that do not reflect current or historically recognized phenotypic species boundaries, whereas the nuclear phylogenies are congruent with such taxonomic hypotheses (this study; Brown *et al.* 2008, 2011; Muell *et al.* 2022, Twomey *et al.* 2025). Thus, we urge taxonomists to proceed with caution when using only mitochondrial data for taxonomic decisions, particularly in dendrobatid frogs.

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APPENDIX 1. Genetic samples of *Ranitomeya* included in the phylogenetic analyses.

Species	Locality	Latitude	Longitude	Seq ID (Voucher)	Source
R. benedicta	Pampa Hermosa, Loreto, PE	-7.2074	-75.3236	0050; 0046	Muell *et al.* 2022
R. benedicta	Shucushuyacu, Loreto, PE	-6.0321	-75.8570	0048	Muell *et al.* 2022
R. aff. *benedicta*	Tournavista, Huánuco, PE	-8.9482	-74.7678	0119; 0121	Muell *et al.* 2022
R. defleri	Caparú, Vaupes, CO	-1.0771	-69.5143	0055; 0056; 0057	Muell *et al.* 2022
R. fantastica	Cainarachi Valley, San Martin, PE	-6.4272	-76.2908	0060; 1122; 1123; 1166, 1172	Muell *et al.* 2022; this study
R. fantastica	Convento, San Martin, PE	-6.2511	-76.3146	0061	this study
R. fantastica	Pongo de Manseriche, Amazonas, PE	-4.5800	-77.9000	0062; 0064	Muell *et al.* 2022; this study
R. fantastica	Pongo de Cainarachi, San Martin, PE	-6.2959	-76.2333	0067; 0069	Muell *et al.* 2022; this study
R. fantastica	Road to Barranquita (km 7), San Martin, PE	-6.2975	-76.2344	0065	this study
R. fantastica	Road to Barranquita (km 7), San Martin, PE	-6.2868	-76.2318	0071	this study
R. fantastica	Varadero, Loreto, PE	-5.6821	-76.4171	0074; 0398, 1139	Muell *et al.* 2022; this study
R. fantastica	Tunnel (near Tarapoto), San Martin, PE	-6.4486	-76.2937	0400	this study
R. fantastica	Road to Micaela (km 5), San Martin, PE	-5.9512	-76.2437	0962; 0963; 1118; 1124	this study
R. ichapama **sp. nov.**	Río Los Amigos, Madre de Dios, PE	-12.5686	-70.0992	0112 (MUSM 21068)	Muell *et al.* 2022
R. ichapama **sp. nov.**	Porto Walter, Acre, BR	-8.2587	-72.7770	0159 (OMNH 36062)	Muell *et al.* 2022
R. reticulata	Puerto Almendras, Loreto, PE	-3.8308	-73.3733	0395 (MNCN 26963)	Muell *et al.* 2022
R. reticulata	Iquitos, Loreto, PE	-4.2030	-73.4796	0417 (MNCN 27372)	Muell *et al.* 2022
R. summersi	Sauce, San Martin, PE	-6.7266	-76.2227	0108; 1117; 1126; 1127; 1128; 1129	Muell *et al.* 2022; this study
R. summersi	Tununtunumba (near Chazuta), San Martin, PE	-6.5449	-76.1100	0966; 0967; 0109	Muell *et al.* 2022; this study
R. summersi	Boca Toma, San Martin, PE	-6.4547	-76.3488	0068; 0942; 1029; 1121	Muell *et al.* 2022; this study
R. summersi	Pongo Isla, San Martin, PE	-6.4373	-75.8847	0072; 0073	Muell *et al.* 2022; this study
R. summersi	Curiyacu (Huallaga Canyon), San Martin, PE	-6.5432	-76.1110	1113	this study
R. summersi	Santa Rosa de Chipaota (Huallaga Canyon), San Martin, PE	-6.5851	-76.0808	1159	this study
R. summersi	Pongo de Aguirre (Huallaga Canyon), San Martin, PE	-6.5717	-75.9640	0059; 0066	this study
R. ventrimaculata	Alto Nanay, Loreto, PE	-3.8400	-73.6200	0058	Muell *et al.* 2022
R. ventrimaculata	Río Momon, Loreto, PE	-3.5474	-73.3796	0827	Muell *et al.* 2022
R. uakarii	Chimbote, Loreto, PE	-3.9302	-70.7800	0815; 0817	Muell *et al.* 2022; this study
R. uakarii	Quebrada Tamshiyacu, Loreto, PE	-4.0091	-73.1008	0113	this study
R. uakarii	Requena (2 Km al NE de Comunidad Nativa Nueva Reforma), Loreto, PE	-5.4674	-73.9345	0505	this study
R. uakarii	Manati, Loreto, PE	-3.6520	-72.2005	0114	Muell *et al.* 2022
R. uakarii	Tahuayo, Loreto, PE	-4.3584	-73.1844	0115	Muell *et al.* 2022
R. uakarii	Jenaro Herrera, Loreto, PE	-4.9039	-73.6681	0455	Muell *et al.* 2022