

Revision of the *Ranitomeya fantastica* species complex with description of two new species from Central Peru (Anura: Dendrobatidae)

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Abstract

We describe two new species of poison frogs (genus *Ranitomeya*) from the central Rio Huallaga drainage and adjacent Cordillera Azul in central Peru. Both species were previously considered to be members of *Ranitomeya fantastica*, a species described from the town of Yurimaguas, Peru. Extensive sampling of putative *R. fantastica* (including near-topotypic material) throughout central Peru, and the resulting morphological and phylogenetic analysis has led us to conclude that *R. fantastica* sensu lato is a complex of three closely related species rather than a single, widely distributed species. The first of these species occurs near the type locality of *R. fantastica* but bears significant dissimilarity to the original type series and forms a monophyletic clade that is distributed throughout an expansive lowland zone between Rio Huallaga and Rio Ucayali. This species is diagnosable by its brilliant red head and advertisement call differences. The second new species has long been considered a color morph of *R. fantastica*, although our analysis shows that it is genetically distinct from even adjacent populations of *R. fantastica*. This species is restricted to the Huallaga Canyon near Chazuta and is primarily diagnosed on the basis of nucleotide sequences, although it does possess additional morphological and vocal characteristics which are distinct from *R. fantastica*.

Key words: *benedicta*, *Dendrobates*, Dendrobatidae, *fantastica*, *Ranitomeya*, *summersi*

Resumen

Se describe dos especies nuevas de ranas venenosas (género *Ranitomeya*) de la cuenca central del Río Huallaga y la Cordillera Azul colindante en el centro del Perú. Ambas especies eran previamente consideradas miembros de *Ranitomeya fantastica*, una especie descrita del pueblo de Yurimaguas, Perú. El muestreo extensivo de *R. fantastica* putativo (incluso cerca a la localidad típica) por todo el centro del Perú, y los análisis morfológicos y filogenéticas, los resultados sugiere que *R. fantastica* sensu lato es un complejo de tres especies cercanamente emparentadas más que una sola especie ampliamente distribuido. La primera de esas especies ocurre cerca a la localidad típica de *R. fantastica* pero tiene una desemejanza significativa a la serie típica original y forma un clado monofilético que está distribuido por una zona de selva baja entre Río Huallaga y Río Ucayali. Esta especie se distingue por su cabeza rojo brillante y diferencias en su canto. La segunda especie ha sido considerada un morpho de *R. fantastica*. Esta especie está restringido al cañón Huallaga cerca Chazuta y se distingue ante todo por su secuencias nucleótidos, aunque tiene características morfológicos y vocales adicionales que son distintos de *R. fantastica*.

Introduction

In 1883, George A. Boulenger, curator at the British Museum (Natural History), documented the first poison frogs in Peru (Boulenger, 1883). Currently, the country boasts over 50 described species in the family Dendrobatidae, i.e. more than one fourth of the world's known dendrobatid species. Boulenger described three species from Yurimaguas, a small town on the lower Rio Huallaga in Amazonian Peru. One of these species, *Ameerega hahneli*, was named after their collector, Paul Hahnel, who had been collecting specimens from north-central Peru. The two other species, originally described as *Dendrobates fantasticus* and *D. reticulatus* (now in the genus *Ranitomeya*), were 'forgotten' to academia until the mid 1970s (Silverstone, 1975; Myers, 1982). Given that almost a century had passed since their original description, much information surrounding the initial collection of these species was lost. For example, we now know that *Ranitomeya reticulata* is restricted to a small area north of Rio Amazonas near Iquitos, over 300 km from Boulenger's given locality of Yurimaguas. Since there is no other known poison frog near Yurimaguas that resembles Boulenger's description of *R. reticulata*, it is likely the original locality is an error. The two other species, *Ameerega hahneli* and *R. fantastica*, can both be found near Yurimaguas, matching the original descriptions by Boulenger.

Ranitomeya fantastica is a phenotypically diverse species, exhibiting over a half a dozen phenotypes (see Fig. 8–10). However, no known population exactly matches those described by Boulenger, which possess a solid-red head mask which extends onto the upper arms. The most notable feature of three of the four type individuals is that they lack a dark chevron between the eyes, a characteristic which has been noted in all nominal *R. fantastica* populations. Despite repeated searches near Yurimaguas, we have been unable to locate a population of *R. fantastica* lacking dark coloration on the head, and we now fear that the exact type population may no longer exist, given that most forests within 25 km of Yurimaguas have been destroyed. However, one population 40 km NW of Yurimaguas along the Rio Paranapura is almost identical (Fig. 8, A–H), with some individuals possessing only a small chevron between the eyes and pale coloration on the upper arms, appearing very similar to the four type specimens (especially individual L, Fig. 10). Given the morphological similarities of the Rio Paranapura population, we consider members related to these individuals to be *R. fantastica* sensu stricto.

We have performed phylogenetic analyses of *fantastica*-like frogs from 14 different localities, which suggest that *R. fantastica* is in fact a species complex comprised of three species rather than a single species. In this paper we clarify the taxonomy of *R. fantastica* group by describing two new species, both formerly considered color morphs of *R. fantastica* (see Lötters *et al.*, 2007). In 2005 we became aware of a frog resembling *R. fantastica* from the lowlands between Rio Huallaga and Rio Ucayali. Although similar in appearance to *R. fantastica*, this frog was found much further east and south than other known populations of *R. fantastica*. Furthermore, an abrupt change in phenotype was apparent between the populations on the western bank of Rio Huallaga near Yurimaguas, and those on eastern bank. We have found additional populations of the new species far south along Rio Ucayali.

The second species described in this paper occurs in the central Huallaga Canyon. This species is a relatively large, robust *Ranitomeya*, which occupies the semi-arid transition zone between seasonal dry forests and premontane forests. This species appears to be adapted to living in the leaf litter and small terrestrial plants. Symula *et al.* (2001) recognized that individuals of *R. fantastica* from the central Huallaga Canyon (our second new species) were "genetically distinct from other populations". They attributed this divergence to a "major barrier" (the Rio Huallaga); however, it has since been discovered that these frogs occur on both sides of the Rio Huallaga. The actual barrier inhibiting gene flow appears not to be a geographic barrier but a reproductive barrier between two species, and despite having adjacent distributions, both species remain morphologically and genetically distinct.

Material and methods

Type material is deposited in the Museo de Historia Natural San Marcos, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM). The following measurements were made with mechanical calipers and a micrometer to the nearest 0.01 mm, following Myers (1982) and Brown *et al.* (2006): snout-vent length (SVL), femur length from vent to lateral edge of knee (FL), tibia length from medial edge of heel to lateral edge 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 tympana (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 checking for the presence of vocal slits. We compared type material for the new species to photos of the *R. fantastica* type series from Yurimaguas (Fig. 10, I–L).

Calling males were recorded with a Sony DCR-JC42 camera and Sony ECM-HGZ1 gun microphone. Calls were analyzed in Raven 1.2 (Charif, 2004) and compared to vocalizations of *R. fantastica* sensu stricto from the Cainarachi Valley. Two tadpoles of each species were preserved in 70 % ethanol for description, and staged according to Gosner (1960). Mouthpart formulas follow McDiarmid & Altig (1999).

Genetic data consisted of 19 individuals from 14 localities of *R. fantastica*-like frogs. Data used in the phylogenetic analysis consisted of three mitochondrial genes: 12s ribosomal subunit, 16s ribosomal subunit and cytochrome b, totaling 1,971 base pairs. Tissue collection, DNA extraction, amplification, and sequence analysis of new samples followed the methods of Roberts *et al.* (2006). Phylogenetic analysis was done using MrBayes 3.12 as described in Twomey & Brown (2008). A total of 8 million generations were run; burn in occurred after 0.6 million generations and total of 7,350 trees were summed to form the final consensus tree. Phylogenetic data were partitioned into five partitions: 12s, 16s, and each codon of cytochrome b. Time of divergence was calculated using an approximate rate of substitution for cytochrome b of 0.8–2.5 % divergence per million years (Lougheed *et al.*, 1999), and the branch lengths of the basal node of each species clade and their most recent common ancestors were estimated from cytochrome b sequences (under a Kimura 2-parameter model).

Morphometric analysis was done with a one-way ANOVA in SPSS 15. A total of 30 individuals were measured (10 *R. fantastica*: 6 from upper Cainarachi Valley, 3 Pongo de Cainarachi, and 1 Varadero; 13 *R. summersi* **sp. nov.**: 4 from Chazuta and 9 from Sauce; 7 *R. benedicta* **sp. nov.**: 5 from Shucushuyacu and 2 from Pampa Hermosa). Given the unbalanced sample sizes, Tukey's B post hoc test was used for pairwise comparisons.

Ranitomeya benedicta, **sp. nov.**

Figures 1, 4, 5, 11

Dendrobates quinquevittatus (non Steindachner): Silverstone, 1975 (partim), p. 33–36, Fig. 14 (drawing), patterns K, L. *Dendrobates fantasticus* (non Boulenger): Schulte, 1999 (partim), pp. 57–69, Fig. 5 pattern K, L (reprinted from Silverstone, 1975).

Holotype. MUSM 26957 (field number JLB07-594), an adult female collected by M. Pepper and E. Twomey near Shucushuyacu (alternative spellings: Shucushyacu and Shucush-yacu), a small town on the east bank of Rio Huallaga near Yurimaguas, Departamento Loreto, Peru; 196 m elevation; January 2006.

Paratopotypes. MUSM 26956, 26958, 26959, 26962 (field numbers JLB07-592, 596, 598 and 600), collected along with the holotype.



FIGURE 1. Drawing of species contained in the *fantastica* complex. Clockwise from left: *Ranitomeya summersi* **sp. nov.**, *R. fantastica* sensu stricto, *R. benedicta* **sp. nov.** Illustration of *R. fantastica* is an artist's rendering of the nominal population from Yurimaguas based on the original type series and recent field work nearby.

Paratypes. MUSM 26960, 26961 (field numbers JLB07-602 and 604), collected by M. Sanchez and E. Twomey on the west bank of Rio Ucayali near Contamana, Departamento Loreto, Peru; 153 m elevation; March 2007.

Etymology. The specific epithet is the feminine form of the Latin word *benedictus*, which means 'blessed'. This name was chosen because the core range of *R. benedicta* occurs in the Pampas del Sacramento ('The Holy Plains') in southern Loreto and eastern San Martin. The name also refers to quick and elusive nature of this species: if one is lucky enough to encounter it (as we were in 2005), one may consider themselves 'blessed'.

Definition and diagnosis. Assigned to genus *Ranitomeya* by the following characteristics: first finger shorter than second, premaxillary and maxillary teeth absent, webbing between toes absent, pale limb reticulation present. A relatively large species of *Ranitomeya* attaining a maximum adult SVL of 20.2 mm. Body and limbs black with blue wash or reticulation, head bright red with black markings over eyes. In some populations, the blue reticulation on the dorsum and legs is diffuse, causing the legs and part of the dorsum to appear uniform blue (Fig. 11, A–E). Ventral ground color black with blue reticulation (discrete or diffuse), underside

of chin red. Teeth absent; first finger shorter than second; disc of third finger 2–2.3 times wider than finger width.

Ranitomeya benedicta can be distinguished from other species of *Ranitomeya* by the combination of a relatively large adult SVL and a characteristic red head. *Ranitomeya reticulata* also possesses red coloration on the head, although this coloration extends well onto the dorsum whereas in *R. benedicta* the red coloration is confined to the head only. Furthermore, *R. reticulata* is smaller than *R. benedicta* (SVL 13.7–16.6 mm vs. 15.0–20.2 mm). *Ranitomeya benedicta* is most similar in external morphology to *R. fantastica* and the second new species, *R. summersi*, described below. *Ranitomeya benedicta* has comparatively shorter hind limbs, with a significantly shorter tibia than *R. fantastica* (mean tibia length/SVL = 0.444 in *R. benedicta*, 0.486 in *R. fantastica*, $P = 0.01$, Fig. 2). Certain color morphs of *R. fantastica* have head coloration approaching red (i.e. bright orange), but never a true red as in *R. benedicta*. Furthermore, the call of *R. benedicta* is much louder (audible from ~8 m vs. ~3 m in *R. fantastica*), decreases in tone in consecutive notes (vs. constant tone across notes in *R. fantastica*) and has shorter pulses than the call of *R. fantastica* (150 ± 20 ms vs. 290 ± 30 ms in *R. fantastica*, Fig. 3). For differences between *R. benedicta* and *R. summersi*, see below. *Ranitomeya benedicta* is distinguished from its closest relatives on the basis of 8 unique unambiguous mitochondrial gene nucleotide site substitutions.

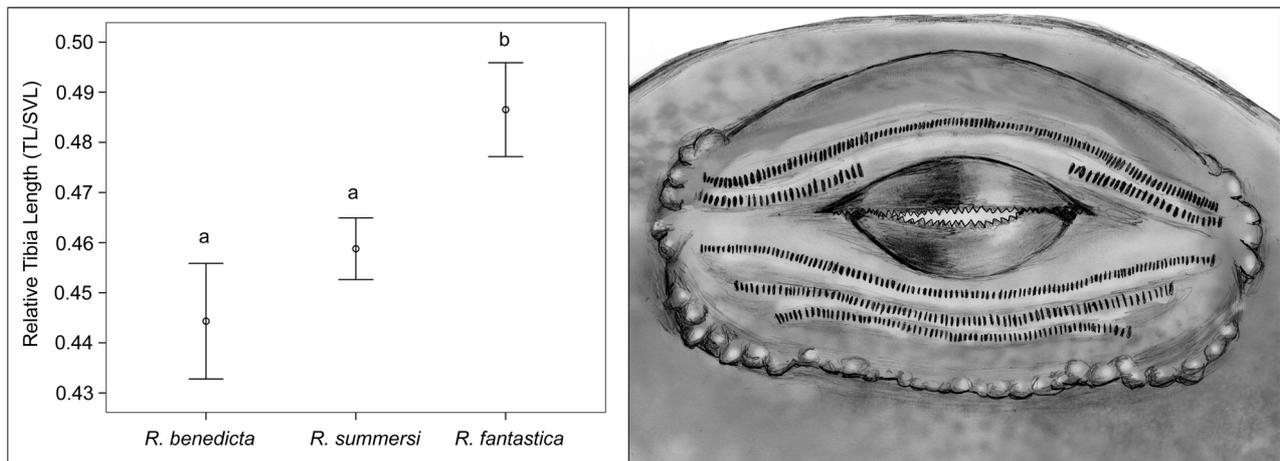


FIGURE 2. Left: Comparisons of tibia lengths for the two new species *R. fantastica*. Error bars represent ± 2 standard errors. *Ranitomeya fantastica* had significantly larger standardized tibia length (Tibia/SVL) than *R. benedicta* and *R. summersi* (One-way ANOVA, SS = 0.009, df = 2, F = 5.654. Between species, $P = 0.008$. Error: SS = 0.022, df = 29) Right: Drawing of tadpole mouthparts of *R. summersi*. Mouthparts of *R. benedicta* and *R. fantastica* sensu stricto are identical.

Measurements (in mm) of holotype. The undissected holotype (Fig. 4) is an adult female as shown by its relatively large size and lack of vocal slits. SVL 17.2; FL 8.1; TL 8.3; KK 15.1; FoL 7.3; HaL 5.0; HL 5.0; HW 5.5; BW 5.5; UEW 2.57; IOD 2.50; IND 2.21; TD 0.75; ED 2.14; DET 0.50; L1F 1.86; L2F 2.86; W3D 0.96; W3F 0.43. Measurements of additional specimens are given in the appendix (Table 1).

Description of holotype. Widest part of head is at jaw articulations. Head width as wide as body. Tongue ovoid; teeth absent. In life, head bright red with comma-shaped black spots over the eyes and tympanum. Red coloration extends posteriorly to level of the axillae; black ground color with blue reticulation on dorsal body. Limbs and digits black, limbs reticulated with blue. Underside of head red, lacking paired gular spots. Venter black with discrete blue reticulation. Nares black surrounded by black spots. Iris black.

In life, skin texture nearly smooth on the dorsal surfaces of the body and head; limbs and rump weakly granular. Venter weakly granular on limbs and body, ventral surface of head nearly smooth. Snout sloping and rounded in lateral profile, round or slightly blunted in dorsal profile. Nares situated at tip of snout and directed laterally; both nares visible from ventral and anterior view but not from dorsal view. Canthus rostralis

rounded, loreal region flat and nearly vertical. Upper eyelid approximately equal in width to interorbital distance; internarial distance roughly equal to eye width. Tympanum round, partially concealed posterodorsally.

Hands relatively large, length 29 % of SVL. Relative length of appressed fingers III > IV \approx II > I; first finger 65 % length of second; finger discs moderately expanded, width of disc on finger III 2.2 times width of adjacent phalanx. An unpigmented median metacarpal tubercle is present on base of palm; inner metacarpal tubercle present near base of finger I but angled posteriorly; unpigmented proximal subarticular tubercles present on base of each digit, except on finger I, where tubercle is part-way up the digit; distal subarticular tubercle visible only on fingers III and IV. All tubercles raised above level of hands; scutes present on dorsal surface of fingers.

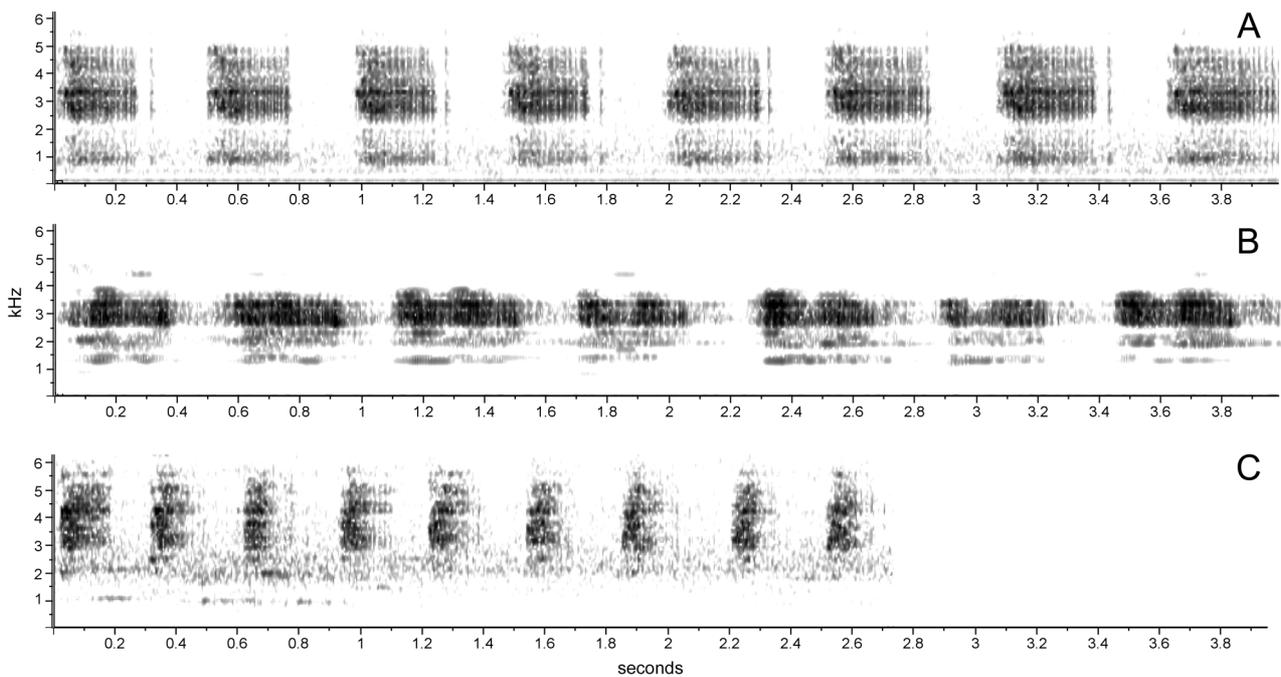


FIGURE 3. Advertisement calls of (A) *R. fantastica* individual from Cainarachi Valley, recording at 24 C, (B) *R. summersi* individual from Sauce, recorded at 24.5 C in captivity, (C) *R. benedicta* individual from Shucushuyacu, recorded at 24 C in captivity.

Hind limbs moderate length, with heel of appressed hind limbs reaching level of eye. Femur and tibia roughly equal in length, tibia 102 % length of femur; knee-knee distance 88 % of SVL. Relative lengths of appressed toes IV > V \approx III > II > I; first toe short with unexpanded disc; second toe with slightly expanded disc, discs on toes III–V moderately expanded. Two unpigmented metatarsal tubercles present on base of foot, one situated medially near base of toe I, the other situated laterally at the base of the fifth metatarsal. Proximal subarticular tubercles present at base of each toe but most notable on toes I and II due to their lack of pigmentation. Toes III and V with two subarticular tubercles, toe IV with three subarticular tubercles. A tarsal keel is present starting below the knee and turning into the medial metatarsal tubercle at the foot. Tarsal tubercle absent; feet and hands lacking webbing and lateral fringing.

Variation. Adults 15.0–20.2 mm SVL, females slightly larger than males: three adult males 15.0–17.5 mm (mean 16.5 mm); four adult females 16.8–20.2 mm (mean 18.4 mm). Widest part of head is at jaw articulations. Head about as wide as body except in two apparently gravid females whose bodies are wider than the head. Head width 92 % of body width in three males (range 80–106 %), 94 % percent of body width in four females (range 74–121 %). Head width 27–34 % of SVL in adults. No apparent sexual dimorphism in external morphology except that males are smaller, possess faint vocal slits on the floor of the mouth, and have a slightly expanded subgular pouch.



FIGURE 4. Type series of *R. benedicta*. (Top L-R: MUSM 26956–26958, Bottom L-R: MUSM 26959–26962).

Live animals bear a diagnostic scarlet-red head with black spots over the eyes. These spots are medially fused in some individuals and form a W-shaped head crest which descends over the eyes creating a face-mask; in most individuals this mask also covers the tympanum. The red coloration on the head extends posterior to level of the axillae; from here the dorsal body coloration changes to a black ground color with blue reticulation. This reticulation is diffuse in some individuals, sometimes to the point of the body appearing uniform blue on the rump. Limbs and digits are colored as the dorsum: individuals with defined dorsal reticulation have limbs reticulated with blue; individuals with diffuse reticulation on the body have either diffuse limb reticulation or limbs colored uniformly blue. Underside of head red, most individuals possessing some amount of black marbling on chin. Venter black with diffuse or discrete blue reticulation. Nares black and surrounded by black spots, these spots are sometimes fused to form a bar across the loreal region.

Hands relatively large, length 24–29 % of SVL. First finger 56–81 % length of second; finger discs moderately expanded in both males and females, width of disc on finger III 2–2.3 times width of adjacent phalanx. Tibia 85–115 % length of femur (mean 99 %); knee-knee distance 81–93 % of SVL (mean 87 %). In preservative, red coloration turning pale pink and blue reticulation turning purple-grey.

Tadpole. One tadpole (captive bred from topotypic parents) was used for the mouthpart description. The body of the tadpole was destroyed after preservation making a full description impossible, but the mouthparts remained intact. Oral disc emarginate, anterior and posterior labia forming flaps free from body wall. Marginal papillae absent on anterior labium except for lateral-most portion (3–4 papillae present), present in one complete row on posterior labium. Papillae white, rounded; submarginal papillae absent. Jaw sheaths deep in longitudinal width, serrate, lacking indentations. Lateral processes short, extending barely past lower jaw. Labial tooth row formula is 2(2)/3. A-1 complete, A-2 with medial gap, same width as A-1. P-1, P-2, and P-3 complete; P-1 and P-2 equal width, P-3 slightly shorter. We examined two *R. fantastica* tadpoles from Tarapoto and the upper Cainarachi Valley (stages 27 and 29) and the mouthparts were indistinguishable from the single *R. benedicta* tadpole.

Vocalizations. The advertisement call is a series of buzz-like notes (Fig. 3). The dominant frequency of the call starts at 4240 Hz and gradually decreases in subsequent notes to 3190 Hz (air temperature 24° C). The notes in the calls were very short with a duration of 150 ± 20 ms (vs. 290 ± 30 ms in *R. fantastica* and 440 ± 30 ms in *R. summersi*); brief pauses between each note lasting 140 ± 20 ms (vs. 200 ± 20 ms in *R. fantastica* and 150 ± 20 ms in *R. summersi*). The ratio of note length to pause length is approximately 1:1 (vs. 1.4:1 in *R. fantastica* and 2.8:1 in *R. summersi*). The call can be heard from as far as ~8 meters which is comparatively loud for a member of the *fantastica* group (vs. 3 m in *R. fantastica* and 1 m in *R. summersi*).

Distribution and natural history. This frog appears to be widely distributed throughout the lowland forest of the Pampas del Sacramento in southern Loreto and eastern San Martin (Fig. 5). The Pampas del Sacramento are enclosed by Rio Ucayali to the east, Cordillera Azul and Rio Huallaga to the west and northwest, and the flooded forests of Pacaya-Samiria to the north. *Ranitomeya benedicta* appears to occur throughout this region in forests over ca. 150 m elevation. The southern margin of its range likely extends at least to Rio Cushabatay, but not reaching Pucallpa, as frequent surveys along the Aguaytia-Pucallpa road since 2006 have failed to encounter any members of the *fantastica* group. *Ranitomeya benedicta* has never been observed west of Rio Huallaga or east of Rio Ucayali, and both rivers appear to be boundaries restricting its westward and eastward distribution, respectively. The Ucayali and the lower Huallaga are generally surrounded by 10–50 km-wide flood plains and wetlands; areas which are inhospitable to most poison frogs and may be more effective barriers than the rivers themselves.

These frogs are most frequently encountered amidst the tangled branches in or near tree-falls. They are extremely alert and agile, and when encountered, immediately flee to the ground and disappear amidst the leaf litter, jumping in erratic spurts. These frogs are rarely encountered and often after days of searching we were only able to find one or two individuals. Their distribution appears to be patchy but in some areas locally abundant. This species appears to favor slightly elevated areas within the forest and have not been found areas

susceptible seasonal flooding. Although *R. benedicta* is primarily a lowland species, individuals have been found in higher elevation areas in the Huallaga Canyon at 315 m and in the upper Cushabatay at 405 m (M. Ramírez Zárate pers. comm.). These records may represent the upper altitudinal limits of this species, although further exploration of the Cordillera Azul may uncover additional montane localities.

In the northwestern extent of its distribution, *R. benedicta* is sympatric with *R. imitator* and *R. ventrimaculata*. Reproduction occurs terrestrially, with clutches of 4–6 grey eggs being laid amongst humid leaves accumulated on the forest floor. Egg development lasts 12–16 days (MSR, pers. obsv.). Tadpoles are transported to larger phytotelmata, such as *Aechmea* bromeliads, and (in captivity) metamorphose in about 100 days (MSR, pers. obsv.). Due to the low phytotelmata abundance in the forests of the Pampas del Sacramento and the observation that *R. ventrimaculata* are the tadpoles most commonly encountered, there is likely strong competition for phytotelmata access, and phytotelmata abundance may be a major limiting factor on population sizes in *R. benedicta* (Donnelly, 1989).

Aside from terrestrial reproduction and foraging, these frogs appear to be arboreal, which could partially explain why they are so difficult to find. Near the village of Shucushuyacu, farmers felling large trees frequently encounter this frog fleeing from the large canopy bromeliads (i.e. *Aechmea*). Timber harvesters along the Rio Ucayali have also reported the same observation.

These frogs also are extremely tolerant of heat. We observed one frog carrying tadpoles across a large, deforested area in full, midday sun (36° C) and was seemingly unaffected.

Conservation status. Under the IUCN Red List criteria (IUCN, 2001), we suggest *R. benedicta* be listed as Vulnerable (VU) under the following criteria (1) we estimate its extent of occurrence at 19,000 km² (although the area of occupancy may be much lower), and ongoing deforestation along the lower Huallaga will reduce the amount of suitable habitat substantially over the coming years, (2) this species is found primarily in undisturbed rainforest and does not occur in areas disturbed by human activity, (3) populations appear to be patchily distributed, and (4) there will be a high demand for this species in the pet trade. This species does occur in a protected area (Cordillera Azul National Park), although the extent to which it occurs there is unknown.

We fear that by describing this species (and others), we are also putting them at risk of illegal smuggling, and expect that there will be a large influx of illegally acquired *R. benedicta* to the North American and European markets over the next few years. This is particularly frustrating for the authors who try to minimize these negative impacts through sustainable harvest and legal exportation (i.e. Understory Enterprises). This organization is concerned with preserving species in their native habitats, while sustainably harvesting individuals for the pet trade. We encourage anyone interested in owning any poison frog to exercise restraint and purchase only sustainably-harvested or captive-bred frogs of legal origin. Further, consumers must understand that when these projects are done correctly; they take a considerable amount of time and money. When a species is illegally smuggled, it reduces the potential market for the legal business, and as a result, reduces the amount of money these organizations can generate for land protection.

***Ranitomeya summersi*, sp. nov.**

Figures 1, 5, 6, 10

Dendrobates quinquevittatus (non Steindachner): Silverstone, 1975 (partim), p. 33–36, Fig. 14 (drawing), patterns G, H. *Dendrobates fantasticus* (non Boulenger): Schulte, 1999 (partim), pp. 57–69, Fig. 5 patterns H, L, Cordillera Oriental, “West flank” and “North spur” morphs, (H and L reprinted from Silverstone, 1975). Symula *et al.*, 2001 (partim), pp. 2415–2420, Fig. 1 photo E, Fig. 3 (phylogenetic tree/drawing). Symula *et al.*, 2003 (partim), table 1 (*D. fantasticus*, Sauce), Fig. 3 (phylogenetic tree/drawing; *D. fantasticus*, Sauce).

Ranitomeya fantastica (non Boulenger): Lötters *et al.*, 2007 (partim), Fig. 592 (photo), pp. 473.

Holotype. MUSM 26994 (field number JLB07-794), an adult male collected by J. Brown and E. Twomey

near the town of Sauce, San Martin, Peru; 6°43' S, 76°15' W; 684 m elevation; 8 July 2007.

Paratopotypes. MUSM 26991-26993 (field numbers JLB07-788, 790, and 792), collected along with holotype.

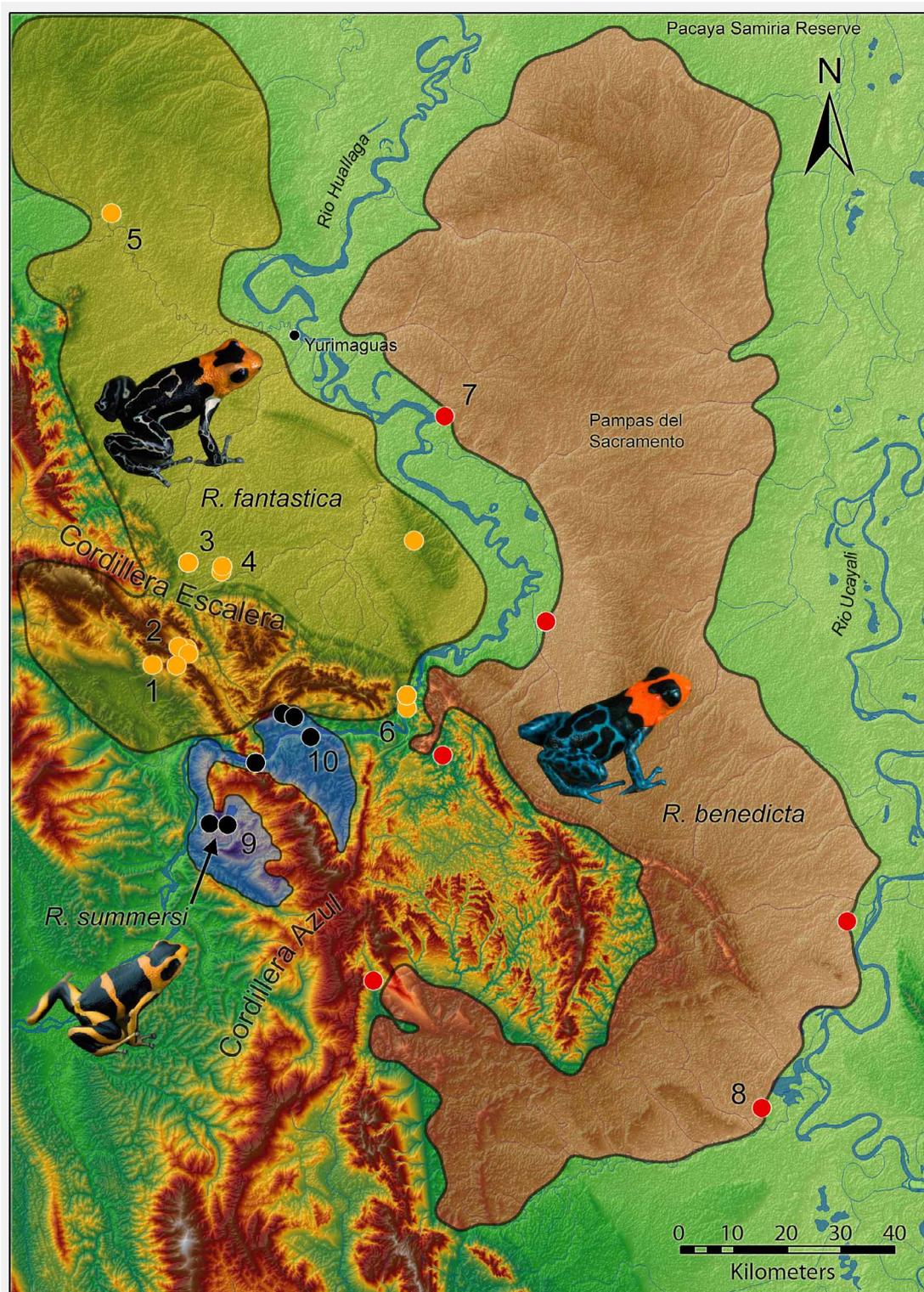


FIGURE 5. Map of known localities and estimated distributions of *R. fantastica*, *R. summersi*, and *R. benedicta*. Because some populations were close together, the 14 sampling localities were simplified into 10 geographic groups. Localities which were included in the phylogenetic analysis are indicated by numbers on the map: (1) Tarapoto; (2) Cainarachi Valley; (3) Convento; (4) Pongo de Cainarachi; (5) Varadero; (6) Lower Huallaga Canyon; (7) Shucushuyacu; (8) Pampa Hermosa; (9) Sauce; (10) Chipaota.



FIGURE 6. Type series of *R. summersi*. (Top L-R: MUSM 26949, MUSM 26967, MUSM 26991, Bottom L-R: MUSM 26992–26994)

Paratypes. MUSM 26949, 26967 (field numbers JLB07-540 and 628), collected by J. Brown and E. Twomey from near Chazuta, Rio Tunumtunumba drainage, San Martin, Peru; 298 m elevation; 11 June 2007.

Etymology. The specific epithet is a patronym for Dr. Kyle Summers, an evolutionary biologist who has studied the evolution, behavior, and ecology of poison frogs for over 25 years, contributing greatly to the knowledge of poison frogs. His work on this species demonstrated conclusively the first case of Müllerian mimicry in vertebrates.

Definition and diagnosis. Assigned to genus *Ranitomeya* by the following characteristics: first finger shorter than second, premaxillary and maxillary teeth absent, webbing between toes absent, pale limb reticulation present. A relatively large species of *Ranitomeya* attaining a maximum adult SVL of 20.4 mm. Body black with one orange cross-band around the sacral region; head black with an orange band outlining the perimeter of the head; face orange with black mask over eyes; limbs primarily black with a longitudinal orange stripe on the dorsal surface. Ventral ground color black with coarse orange marbling, underside of head orange with large black spots. Teeth absent; first finger shorter than second; disc of third finger 2–2.7 times wider than finger width.

Ranitomeya summersi can be distinguished from other species of *Ranitomeya* by the combination of relatively large adult SVL, distinctly bicolored pattern consisting of continuous bands (as opposed to spots or dashes), and a buzz-call. This species is most similar in external morphology to *R. fantastica* and some populations of *R. imitator*. *Ranitomeya summersi* can be distinguished from *R. fantastica* using the following characteristics: shorter hind limbs, with a significantly smaller tibia/SVL ratio (mean tibia length/SVL = 0.458 in *R. summersi*, 0.486 in *R. fantastica*, $P = 0.044$; Fig. 2); the call of *R. summersi* has longer pulses than the call of *R. fantastica* (440 ± 30 ms vs. 290 ± 30 ms in *R. fantastica*, Fig. 3); and the ratio of note length to pause length is 2.8:1 (vs 1.4:1 in *R. fantastica*). All known *R. summersi* individuals possess a bicolored pattern (orange and black), whereas *R. fantastica* typically are tricolored (orange, black, and blue or white) and have reticulated leg netting (see Fig. 8–10). *Ranitomeya summersi* can be distinguished from *R. benedicta* by adult coloration; *R. benedicta* has a red head with blue dorsal and ventral reticulation (compared to the bicolored pattern in *R. summersi* as described above).

Ranitomeya summersi is considered a Müllerian mimic of some sympatric populations of *R. imitator* (Symula *et al.*, 2001 applying the name *Dendrobates fantasticus*) and can be distinguished from these populations by its soft ‘buzz’ call, audible from less than 1 m (vs. loud ‘trill’ call, audible from greater than 5 m in *R. imitator*). In our experience, the black eye-mask of *R. imitator* usually does not cover the tympanum, and the black head spot of *R. imitator* is ovoid, whereas the head spot in *R. summersi* is pentagonal in shape. *Ranitomeya summersi* usually has paired black gular spots, rarely present in *R. imitator*.

This species can be distinguished from its sister taxon, *R. fantastica*, on the basis of 16 unique unambiguous mitochondrial gene nucleotide site substitutions, and can be distinguished from *R. benedicta* on the basis of 20 unique unambiguous mitochondrial gene site substitutions, and is remarkably distant, genetically, to *R. imitator* (see Symula *et al.*, 2001).

Measurements (in mm) of holotype. The undissected holotype (Fig. 6) is an adult male as determined by the presence of vocal slits. SVL 19.5; FL 8.1; TL 8.5; KK 16.7; FoL 8.0; HaL 5.5; HL 5.3; HW 6.3; BW 7.3; UEW 2.86; IOD 1.93; IND 2.29; TD 1.00; ED 2.07; DET 0.50; L1F I 2.07; L2F 3.14; W3D 0.96; W3F 0.36. Measurements of additional specimens are given in the appendix (Table 1).

Description of holotype. Widest part of head is at jaw articulations. Head narrower than body. Head width 86 % of body width. Subgular pouch not visibly expanded. Tongue grey, ovoid, attaching anteriorly; teeth absent. Pattern bicolored; black on the head, body, and limbs, highlighted by several golden orange bands. The head is black and orange, the black confined to the top of the head and around the eyes and tympanum. The black eye mask covers the tympanum and does not connect with the black on top of the head. Dorsum jet black with one incomplete orange cross-band near the sacral region; broken medially left of vertebrae. The hind limbs are black and lack reticulation, but possess a solid orange band extending from the rump over

the femur, down across the anterior surface of the knee, back across the posterior surface of the tibia, and across the posterior surface of the tarsus to the foot. The dorsal surface of the foot is half orange and half black, toes orange. The front limbs are orange dorsally; this orange is fused with the orange on the face. Dorsal surfaces of the hands are both orange and black, fingers orange, finger tips black. Ventrally, the belly is black with irregular and coarse orange marbling. From a ventral aspect, the hind limbs have irregular orange longitudinal bands. Ventral surfaces of the forelimbs are uniformly black. The underside of the head is orange; two well-defined black gular spots laterally. Black bar present on the anterior surface of the snout between the nares. Nares black; iris black.

In life, skin texture granular on the dorsal surfaces of the body and head; dorsal surfaces of limbs weakly granular. Venter weakly granular on belly; limbs and ventral surface of head nearly smooth. Snout sloping and rounded in lateral profile, rounded in dorsal profile. Nares situated at tip of snout and directed laterally; both nares visible from ventral and anterior view but hidden in dorsal view. Canthus rostralis rounded, loreal region slightly concave and vertical. Upper eyelid approximately equal in width to interorbital distance; internarial distance roughly equal to eye width. Tympanum round, partially concealed posterodorsally.

Hands relatively large, length 28 % of SVL. Relative length of appressed fingers III > IV > II > I; first finger 67 % length of second; finger discs moderately expanded, width of disc on finger III 2.6 times width of adjacent phalanx. An unpigmented median metacarpal tubercle is present on base of palm; inner metacarpal tubercle present near base of finger I but angled posteriorly; unpigmented proximal subarticular tubercles present on base of each digit, except on finger I, where tubercle is part-way up the digit; distal subarticular tubercle visible only on fingers III and IV. All tubercles raised above level of hands; scutes present on dorsal surface of fingers.

Hind limbs moderate length, with heel of appressed hind limbs reaching reaching to eye. Femur and tibia roughly equal in length, tibia 105 % length of femur; knee-knee distance 86 % of SVL. Relative lengths of appressed toes IV > III \approx V > II > I; first toe short with unexpanded disc; second toe with slightly expanded disc, discs on toes III–V moderately expanded. Two metatarsal tubercles present on base of foot, one situated medially near base of toe I, the other situated laterally at the base of the fifth metatarsal. Proximal subarticular tubercles present at base of each toe but most notable on toes I and II due to their lack of pigmentation. Toes III and V with two pigmented subarticular tubercles, toe IV with three subarticular tubercles. A faint tarsal keel is present starting below the knee and turning into the medial metatarsal tubercle at the foot. Tarsal tubercle absent; feet and hands lacking webbing and lateral fringing.

Variation. Adults range from 15.5–20.4 mm SVL, females and males roughly equal in SVL. Head width 86 % of body width in type series (range 66–127 %). Head width 30–33 % of SVL in adults. No apparent sexual dimorphism in external morphology except that males tend to be less rotund and possess vocal slits on the floor of the mouth. Subgular pouch not visibly expanded in males.

The black eye mask invariably covers the tympanum and does not connect with the black on top of the head, but the head-black and eye-black can fuse with the black on the dorsum. Dorsum jet black with one orange cross-band near the sacral region. The cross-band is usually complete but in some individuals is broken medially. Some individuals have longitudinal extensions of the cross-band in line with the vertebrae, which can extend up the back, or posteriorly connecting with the orange bands of the hind limbs (Fig. 10, A–G). The dorsal surface of the foot is usually half orange and half black; toes can be either orange or black. Dorsal surfaces of the hands are both orange and black, fingers are usually either all orange or all black. The underside of the head is orange; most individuals have two well-defined black gular spots laterally, in some individuals these spots are medially fused. Most individuals in the type series possess a black bar on the anterior surface of the snout between the nares.

Hands relatively large, length 26–31 % of SVL. First finger 66–76 % length of second; finger discs moderately expanded in both males and females, width of disc on finger III 2–2.7 times width of adjacent phalanx. Femur and tibia roughly equal in length, tibia 100–107 % length of femur (mean 105 %); knee-knee distance

86–93 % of SVL (mean 90 %). In preservative little color change occurs, except that the orange coloration turns to pale gold or white.

Tadpole. A stage 29 tadpole was used for the description (Fig. 2). Total length 19.0 mm, body length 7.6 mm, body width 5.5 mm. Snout rounded when viewed from above; body ovoid in dorsal view. Eyes black, dorsal, angled laterally, pupils white in preservative. Nares not forming tube, situated half-way between eye and tip of snout, directed dorsolaterally. Spiracle sinistral; vent dextral. Tail 3.4 mm in depth measured half-way along length; ventral tail fin begins at tail base, dorsal tail fin begins just posterior to plane of vent opening, ventral and dorsal fins relatively uniform in thickness throughout tail, tapering towards tip. Musculature depth uniform throughout, tapering towards tip, musculature depth 2.0 mm.

The mouth is directed anteroventrally. Oral disc emarginate, anterior and posterior labia forming flaps free from body wall, 2.1 mm in width. Marginal papillae absent on anterior labium except for lateral-most portion (3–4 papillae present), present in one complete row on posterior labium. Papillae white, rounded; submarginal papillae absent. Jaw sheaths deep in longitudinal width, serrate, lacking indentations. Lateral processes very short, extending barely past lower jaw. Labial tooth row formula is 2(2)/3. A-1 complete, A-2 with medial gap, same width as A-1. P-1, P-2, and P-3 complete; P-1 and P-2 equal width, P-3 slightly shorter. In preservative, the head appears light brown. Pigmentation on dorsum is mottled brown with a white ground color. Ventral coloration is white with irregular brown flecking which is most dense near the mouth. Tail musculature brown, fins transparent with brown mottling. Life colors grey. One additional stage 27 tadpole was examined and agrees with this description. Additionally, the above description agrees with two *R. fantastica* tadpoles (see above). Mouthparts are identical between these two species. It appears that tadpole morphology is consistent within the *R. fantastica* species group.

Vocalizations. The advertisement call is a series of soft buzz-like notes, similar to *R. fantastica* (Fig. 3). The notes in the calls are 440 ± 30 ms (vs. 290 ± 30 ms in *R. fantastica*) in duration with brief pauses of 150 ± 20 ms between each note (vs. 200 ± 20 ms in *R. fantastica*). The ratio of note length to pause length is 2.8:1 (vs 1.4:1 in *R. fantastica*). The call is audible from 1 meter (vs. 3 m in *R. fantastica*). The dominant frequency of the call is 2890 Hz at an air temperature of 24° C (vs. 3290 Hz in *R. fantastica* at 24° C). The call of *R. summersi* can be distinguished from *R. benedicta* on the basis of the following parameters: audible from < 2 m (vs. up to 8 m in *R. benedicta*); note length > 400 ms (vs. 150 ± 20 ms in *R. benedicta*), and ratio of note length to pause length is > 2:1 (vs. 1:1 in *R. benedicta*). This call can be distinguished from *R. imitator* in that *R. summersi* has soft buzz-like notes audible from < 2m (vs. loud, trill-like call easily audible from > 5 m in *R. imitator*).

Distribution and natural history. *Ranitomeya summersi* occurs throughout the central Huallaga Canyon (Fig. 5), extending into the southernmost tip of the Cordillera Escalera near Chazuta and to the northwestern edge of the Cordillera Azul. This species occurs on both sides of the Rio Huallaga, extending from Curiyacu westward to Sauce, where they persist in humid recesses of the rocky stream valleys of this semiarid region.

This species is primarily terrestrial and is a denizen of relatively dry secondary and primary premontane forests. They are extremely alert and difficult to detect amidst the leaf litter and rocky terrain they inhabit. The forests they inhabit are characterized by a relatively open canopy and poor, rocky soils, which allows for abundant growth of *Dieffenbachia* in the understory. The relative dryness of the region is conducive to a terrestrial lifestyle, keeping them in contact with the more humid forest floor. *Ranitomeya summersi* is primarily active during the early morning and late afternoon. In midday they are infrequently encountered on the ground, but can be found taking refuge in the humid axils of *Dieffenbachia*. Breeding occurs terrestrially in humid leaf litter; clutch sizes range from 4–9 eggs. Healthy females in captivity are capable of producing clutches every 3 or 4 days when cycled properly. Given the region's aridity, phytotelmata only retain water for a short period each season (MP, pers. obsv.). This truncated breeding season has also been observed in sympatric populations of *R. imitator* (JLB, unpub. data). Tree holes, *Dieffenbachia*, and *Xanthosoma* axils are the preferred pools for tadpole deposition. In captivity metamorphosis occurs between 90 and 110 days.

Conservation status. Under the IUCN Red List Criteria (IUCN, 2001), we suggest *R. summersi* be listed as Endangered (EN) under the following criteria: (1) we estimate the extent of occurrence area of 500 km² or less, most of which is unsuitable habitat, meaning the area of occupancy may be much smaller, (2) deforestation in this area has degraded its habitat, particularly in the Chipaotillo and Tunumtunumba drainages near Chazuta, and will further reduce the amount of suitable habitat for this species in the future, (3) illegal smuggling for the pet trade appears to have caused localized population declines in certain areas. Over the past 30 years, Chazuta has been a staging point for many smuggling operations and populations in close proximity to Chazuta have dramatically declined. However, in the few areas overlooked by illegal collectors, populations appear to be flourishing. The constant encroachment by farmers looking to expand their farms continues to put this frog in increased peril. Unlike *R. imitator*, which will adapt to use agricultural landscapes, *R. summersi* does not appear to adapt well.

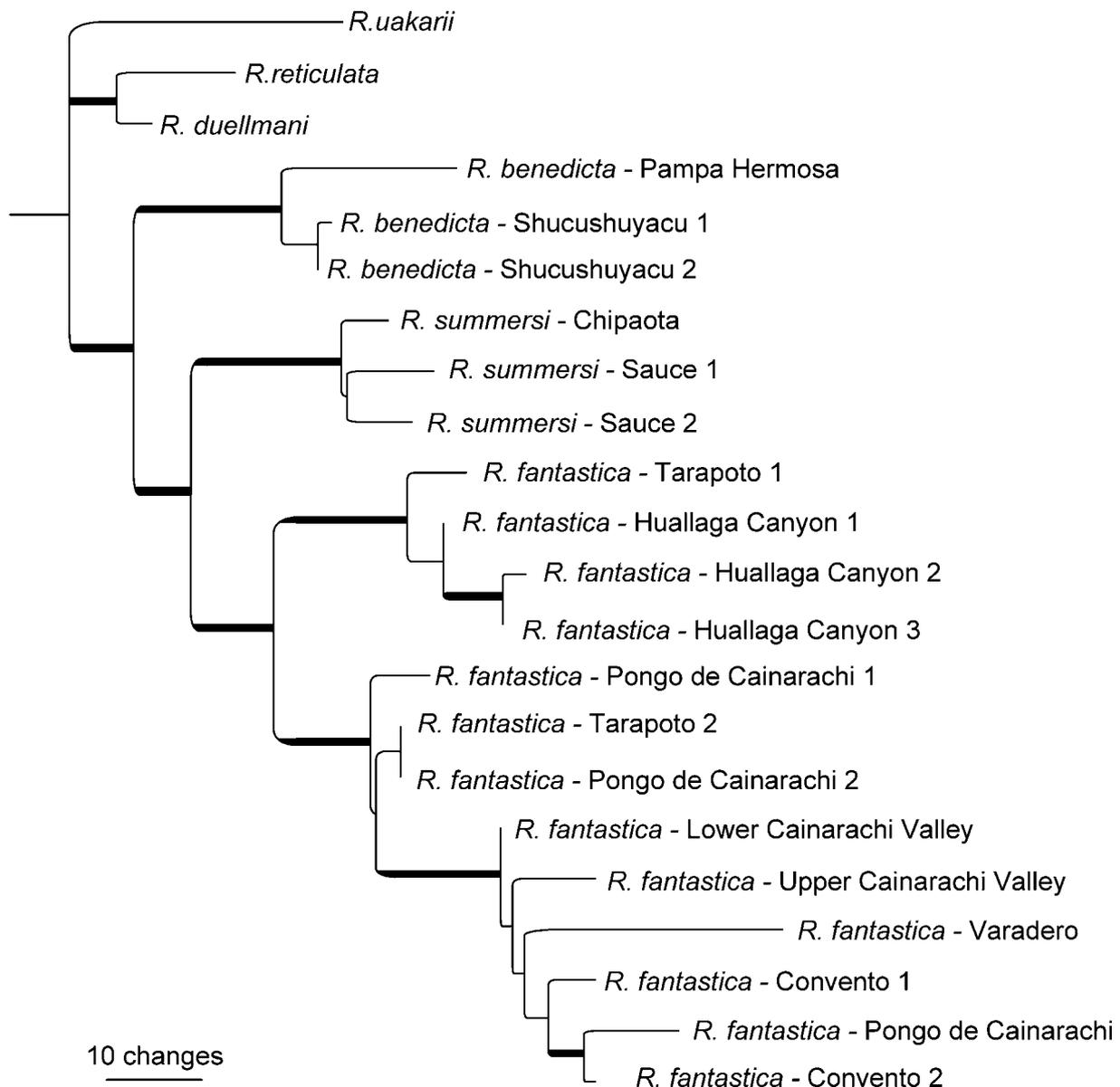


FIGURE 7. Phylogenetic tree from Bayesian analysis. Thick branches indicate posterior probabilities over 80.

Phylogenetics and biogeography

The placement of the *R. benedicta* and *R. summersi* within the genus *Ranitomeya* is supported by molecular phylogenetic data, grouping within the *fantastica* clade (Brown *et al.*, 2006), which contains *R. duellmani*, *R. fantastica*, *R. reticulata*, and *R. uakarii*. Phylogenetic analysis resulted in *R. summersi* as the sister taxon to *R. fantastica*, forming a clade sister to *R. benedicta* (Fig. 7). The phylogenetic relationship of *R. fantastica* and *R. summersi* is consistent with the results of Symula *et al.* (2001). We estimate the time of divergence of *R. benedicta* and *R. summersi* from their most recent common ancestors is between 0.6–2.0 million years and 0.6–1.8 million years, respectively. The estimated time of divergence of *R. fantastica* and its most recent common ancestor (the shared common ancestor of *R. summersi*) is between 0.3–1.0 million years. These estimates do not include the time of divergence within each species (the time since each species diverged from their most recent common ancestor) and when accounted for, the time since each species diverged suggests that all three species diverged during the early Pleistocene (about 1.8 million years ago).

The distribution patterns for both new species are consistent with phylogenetic affinity. The sister clade to *R. benedicta* occurs to the west in the Cordillera Escalera and Cordillera Azul. Within this clade, *R. summersi* occurs in the the central Huallaga Canyon between Sauce and Curiyacu, in the southernmost margin of Cordillera Escalera, and the northwestern Cordillera Azul, while *R. fantastica* generally inhabits the Cordillera Escalera and the lowlands to the north. In the Huallaga Canyon near Chazuta, these three species have been found within 10 km of each other and may occur in sympatry in some areas, although further investigation in the interior Cordillera Azul and Cordillera Escalera is needed. The mechanism of speciation is unclear since no obvious biogeographical barrier seems to play a major role delimiting the distributions of the three species. However, their distributions remain largely isolated, suggesting that these species may have diverged in allopatry, with the Huallaga Canyon representing an area of secondary contact, and each species is locally adapted to a particular area. There are two potential barriers that could help explain their observed distributions. The first is a large area in the northern Cordillera Azul that contains a range of geothermally heated mountains, positioned at the interface of the three species, particularly between *R. summersi* and *R. benedicta*. This area also appears to have reduced contact between two morphs of *R. imitator*, the lowland “yellow-striped” morph and the Huallaga Canyon “orange-blocked morphs”. However, because the level of geothermal activity is probably very dynamic, this area may act to simply reduce gene flow rather than stop it. The second potential barrier, as mentioned previously, is a seasonally-flooding forest along the lower Huallaga. The river is generally surrounded by 10–50 km-wide floodplains and wetlands; areas which are inhospitable to most poison frogs. These areas may have reduced gene flow between the ancestors of *R. fantastica* and *R. benedicta*, and may contribute to the current maintenance of species boundaries.

Under the proposed taxonomy, *R. fantastica* *sensu stricto* is comprised of two main clades: a Huallaga clade and a clade containing all other morphs of *R. fantastica* (Fig. 7, 9–11). The biogeographical patterns within this species are complicated by the phylogenetic placement of two individuals from Tarapoto, one within the Huallaga clade (a population which occurs over 45 km southeast), the other sister to an individual from Pongo de Cainarachi (a population which occurs about 20 km northeast). With the exception of those two individuals from Tarapoto, geographic distance appears to explain most the phenotypic and genetic variation within both *R. fantastica* clades, and adjacent populations appearing more similar and possessing fewer genetic differences than more distant populations.

The Tarapoto population contains the highest level of phenotypic diversity within *R. fantastica*. Some individuals (Fig. 9, A–F) appear almost exactly the same as those from nearby populations in the Cainarachi Valley (Fig. 8, I–Q), whereas others (Fig. 8, G–J) appear similar to either the Huallaga clade of *R. fantastica* or *R. summersi* (Fig. 9, K–O and Fig. 10, A–H, respectively). Given the high levels of illegal frog trafficking stemming from Chazuta, one possible explanation for this discontinuity would be if confiscated Huallaga *R. fantastica* or *R. summersi* were released at this site. Although this event is entirely speculative, other similar

release events have occurred in the past or were attempted by the authorities in charge of animal confiscations. For example, in the late 1980s over 60 *Ameerega silverstonei* were released at km. 20 on the Tarapoto-Yurimaguas road, and in 2007 the same group attempted to release two dozen *Excidobates mysteriosus* outside of Tarapoto (pers. comm. Rainer Schulte). In an attempt to further elucidate this issue, we have searched for populations near Tarapoto although without success. We do have two observations, prior to this study, of individuals from separate localities near Tarapoto, one from San Antonio (8 km from Tarapoto), the other from Ahuashiyacu (4.5 km from Tarapoto). Both individuals resembled *R. fantastica* individuals from the Cainarachi Valley, but unfortunately no tissues or photos were taken. Other, less complicated hypotheses could also explain these morphological patterns, for example, shared morphology due to common ancestry. Increased sampling in these populations and the use of both nuclear and mitochondrial markers could further clarify this issue.

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Appendix tables and figure legends:

TABLE 1. Measurements of the type series of *R. benedicta*.

	MUSM 26956	MUSM 26957	MUSM 26958	MUSM 26959	MUSM 26960	MUSM 26961	MUSM 26962
SVL	19.4	17.2	17.5	20.2	16.8	15.0	17.1
FL	8.3	8.1	8.0	8.8	6.5	7.2	7.5
TL	8.1	8.3	8.4	8.1	7.5	6.8	7.3
KK	16.7	15.1	16.3	17.6	13.7	13.5	14.7
FoL	6.8	7.3	7.3	7.9	5.7	5.6	6.9
HaL	4.8	5.0	5.0	5.0	4.3	3.9	4.7
HL	5.4	5.0	5.9	5.2	4.2	5.6	5.1
HW	5.9	5.5	5.9	6.0	4.6	4.8	5.1
BW	7.9	5.5	7.3	7.5	3.8	4.5	5.7
UEW	3.36	2.57	2.71	2.93	2.21	2.43	2.71
IOD	2.43	2.50	2.86	2.36	2.29	2.21	2.57
IND	2.71	2.21	2.29	2.43	2.00	1.79	2.00
TD	0.79	0.75	1.14	0.71	0.64	0.79	0.71
ED	2.29	2.14	2.21	2.21	2.07	1.93	2.07
DET	0.57	0.50	0.43	0.50	0.43	0.43	0.43
L1F	1.64	1.86	1.71	2.00	1.86	1.71	1.86
L2F	2.93	2.86	2.93	2.93	2.29	2.43	2.71
W3D	0.86	0.96	1.00	0.79	0.71	0.71	1.00
W3F	0.43	0.43	0.43	0.36	0.36	0.36	0.43
SEX	F	F	M	F	F	M	M

TABLE 2. Measurements of the type series of *R. summersi*.

	MUSM 26991	MUSM 26992	MUSM 26993	MUSM 26994	MUSM 26949	MUSM 26967
SVL	17.7	15.5	20.4	19.5	16.7	17.5
FL	7.8	6.8	8.3	8.1	7.7	7.9
TL	8.2	7.5	8.9	8.5	7.7	7.9
KK	16.4	13.7	18.0	16.7	15.5	16.1
FoL	7.9	6.4	8.5	8.0	6.8	7.0
HaL	5.4	4.2	5.9	5.5	4.3	4.7
HL	5.1	4.2	5.6	5.3	5.5	5.1
HW	5.8	5.1	6.6	6.3	5.4	5.3
BW	6.9	6.1	8.4	7.3	4.3	4.8
UEW	2.43	2.21	2.57	2.86	2.29	2.36
IOD	1.93	1.93	2.29	1.93	2.57	2.43
IND	1.89	2.00	2.18	2.29	2.57	2.14
TD	0.71	0.71	1.14	1.00	0.79	1.07
ED	1.93	1.79	2.29	2.07	2.00	2.21
DET	0.43	0.50	0.50	0.50	0.43	0.43
L1F	2.00	1.64	2.14	2.07	2.00	2.07
L2F	2.86	2.29	2.93	3.14	2.64	2.79
W3D	0.79	0.79	1.07	0.96	0.79	1.07
W3F	0.39	0.36	0.43	0.36	0.32	0.43
SEX	F	F	F	M	F	M

TABLE 3. Locality information and Genbank accession numbers for individuals included in the phylogeny.

Species	Locality (region)	12S	16S	CytB
<i>R. benedicta</i>	Pampa Hermosa, Loreto, PE	EU736205	EU736220	EU736190
<i>R. benedicta</i>	Shucushuyacu, Loreto, PE (1)	EU736204	EU736219	EU736191
<i>R. benedicta</i>	Shucushuyacu, Loreto, PE (2)	EU736206	EU736221	N/A
<i>R. duellmani</i>	Napo, EC	AY364566	AY263246	N/A
<i>R. fantastica</i>	Convento, San Martin, PE	AF412442	EU736213	EU736183
<i>R. fantastica</i>	Convento, San Martin, PE	N/A	EU736214	EU736184
<i>R. fantastica</i>	Cainarachi Valley, San Martin, PE (U)	N/A	EU736216	EU736186
<i>R. fantastica</i>	Cainarachi Valley, San Martin, PE (L)	AF4112447	AF412475	EU736193
<i>R. fantastica</i>	Huallaga Canyon, San Martin, PE (1)	EU736200	EU736215	EU736185
<i>R. fantastica</i>	Huallaga Canyon, San Martin, PE (2)	EU736207	AF412468	EU736192
<i>R. fantastica</i>	Huallaga Canyon, San Martin, PE (3)	AF412469	AF412469	EU36194
<i>R. fantastica</i>	Pongo de Cainarachi, San Martin, PE (1)	EU736198	EU736211	N/A
<i>R. fantastica</i>	Pongo de Cainarachi, San Martin, PE (2)	EU736199	EU736212	N/A
<i>R. fantastica</i>	Pongo de Cainarachi, San Martin, PE (3)	N/A	N/A	EU736182
<i>R. fantastica</i>	Tarapoto, San Martin, PE (1)	EU736196	EU736209	EU736181
<i>R. fantastica</i>	Tarapoto, San Martin, PE (2)	EU736197	EU736210	N/A
<i>R. fantastica</i>	Varadero, Loreto, PE	EU736195	EU736208	EU736180
<i>R. reticulata</i>	Puente Itaya, Loreto, PE	AF482772	AF482787	AF482802
<i>R. summersi</i>	Chipaota, San Martin, PE	EU736201	EU736217	EU736187
<i>R. summersi</i>	Sauce, San Martin, PE (1)	EU736202	EU736218	EU736188
<i>R. summersi</i>	Sauce, San Martin, PE (2)	EU736203	AF412473	EU736189
<i>R. uakarii</i>	Tamshiyacu-Tahuayo, Loreto, PE	DQ371305	DQ371316	DQ371335



FIGURE 8. Photos of *R. fantastica*. A–H: Individuals from Varadero, Loreto. I–Q: Individuals from Cainarachi Valley, San Martin.



FIGURE 9. Photos of *R. fantastica*. A–J: Tarapoto, San Martin. K–M: Lower Huallaga, San Martin. P–S: Pongo de Cainarachi, San Martin.

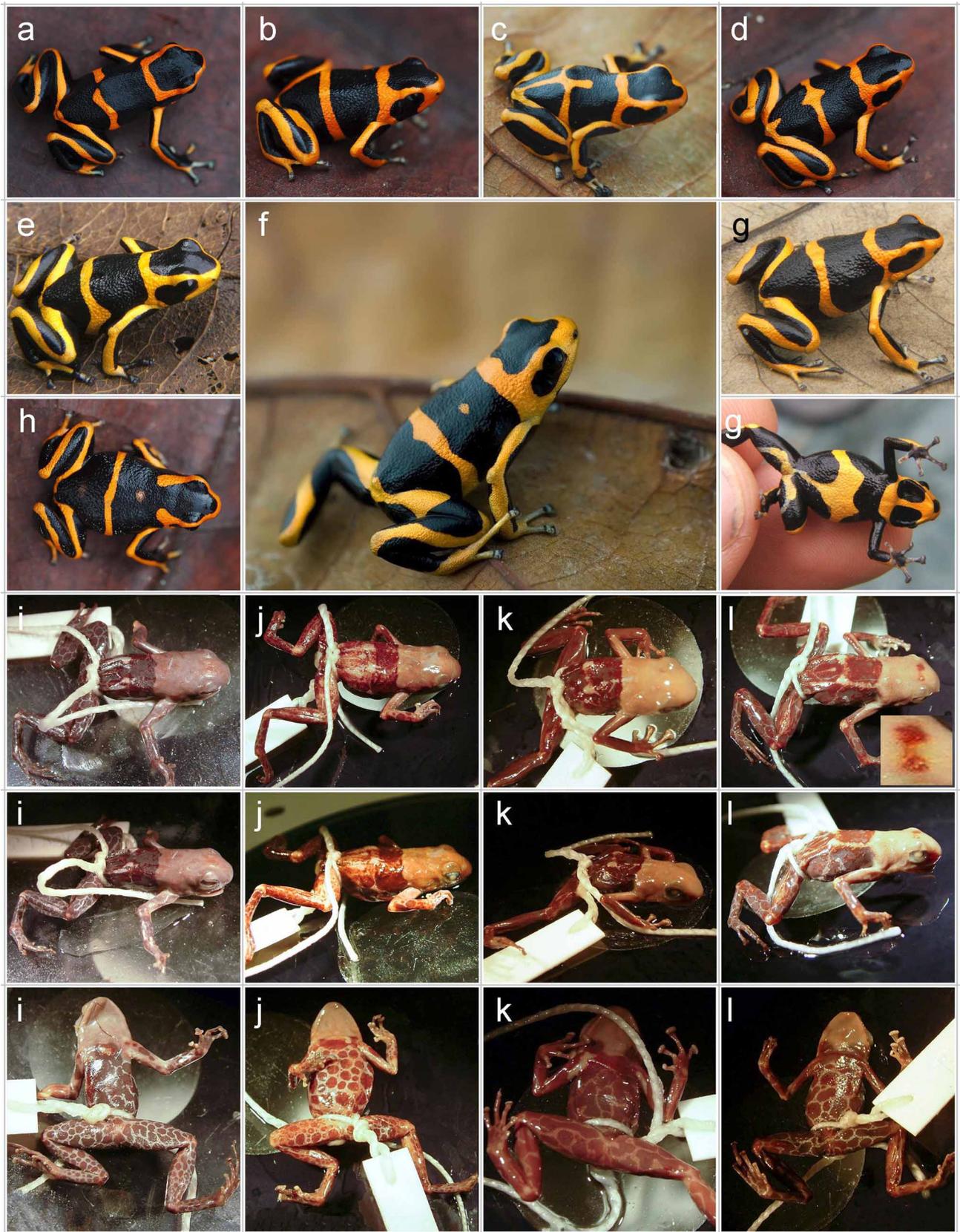


FIGURE 10. Photos of *R. summersi* (A–H). I–L: Type series of *R. fantastica* (1947.2.15.1–4, order not known, photos from Natural History Museum London). Individual L (top): Inset photo in lower-right corner shows close-up of head spotting.



FIGURE 11. Photos of *R. benedicta*. A–E: Individuals from Pampa Hermosa, Loreto F–M: Individuals from Shucushuyacu, Loreto.