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Morphological variation of *Telmatobius atahualpai* (Anura: Telmatobiidae) with comments on its phylogenetic relationships and synapomorphies for the genus

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Abstract

Morphological variation of *Telmatobius atahualpai* (Anura: Telmatobiidae) with comments on its phylogenetic relationships and synapomorphies for the genus. *Telmatobius atahualpai* was described on the basis of a subadult female and three juveniles. A new diagnosis and a description of the adult skeleton of specimens from two localities are provided. We also comment on synapomorphies of the genus and on possible phylogenetic relationships of *T. atahualpai* with other members of the genus.

Keywords: Central Andes, diagnosis, morphology, osteology, skeleton.

Resumen

Variación morfológica de *Telmatobius atahualpai* (Anura: Telmatobiidae) con comentarios sobre sus relaciones filogenéticas y sinapomorfías del género. *Telmatobius atahualpai* fue descrita en base a una hembra subadulta y tres juveniles. Se proporciona una nueva diagnosis y una descripción del esqueleto adulto de especímenes que proceden de dos localidades. También hacemos comentarios sobre sinapomorfías del género y la posible relación filogenética de *T. atahualpai* con otros miembros del género.

Palabras Claves: Andes Centrales, diagnosis, esqueleto, morfología, osteología.

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Resumo

Variação morfológica em *Telmatobius atahualpai* (Anura: Telmatobiidae), com comentários sobre suas relações filogenéticas e sinapomorfias para o gênero. *Telmatobius atahualpai* foi descrita com base em uma fêmea subadulta e três juvenis. Apresentamos aqui uma nova diagnose e uma descrição do esqueleto do adulto feita a partir de espécimes de duas localidades. Tecemos ainda comentários sobre sinapomorfias do gênero e sobre a possível relação filogenética de *T. atahualpai* com outras espécies congenéricas.

Palavras-chave: Andes Centrais, diagnose, esqueleto, morfologia, osteologia.

Introduction

The anuran genus *Telmatobius* Wiegmann, 1834 comprises 60 species distributed from Ecuador to Argentina and Chile (Aguilar and Valencia 2009, Barrionuevo and Baldo 2009). Members of this genus are aquatic and semiaquatic inhabitants of lakes, streams, and wetlands in the Andes, between 1000 and more than 5200 m (De la Riva 2005, Seimon *et al*. 2007). *Telmatobius* is a monophyletic group and includes the two formerly recognized species of *Batrachophrynus* Peters, 1873 (Aguilar and Valencia 2009).

Telmatobius atahualpai Wiens, 1993, is endemic to the Cordillera Central in northern Peru and it is considered as Data Deficient by IUCN (2010). It was described on the basis of a subadult female and three juveniles (Wiens 1993). Allocation of *T. atahualpai* in *Telmatobius* was difficult because putative synapomorphies suggested by Wiens (1993) were absent in the original sample. During the past two decades, the authors collected adults and tadpoles of this species, and recently, Aguilar *et al.* (2007) described its tadpole. With the aim of updating our knowledge of this poorly known, endemic frog, we provide a revised diagnosis and a description of the skeleton of *T. atahualpai,* along with an hypothesis of its possible relationships with its congeners, and comments on synapomorphies of the genus.

Materials and Methods

The external morphology of 12 specimens of *Telmatobius atahualpai* was examined, and a male and a female were prepared as skeletons. We examined additional specimens of other *Telmatobius* species deposited at the Departamento de Herpetología, Museo de Historia Natural de San Marcos (MUSM) and Museum of Natural History, The University of Kansas (KU) (Appendix I). Data for *T. colanensis* Wiens, 1993; *T. degener* Wiens, 1993; *T. hockingi* Salas and Sinsch, 1996; *T. ignavus* Barbour and Noble, 1920; *T. necopinus* Wiens, 1993; *T. sanborni* Schmidt, 1954; *T. thompsoni* Wiens, 1993; and *T. timens* De la Riva, Aparicio and Ríos, 2005 were obtained from species descriptions and species accounts (Wiens 1993, Salas and Sinsch 1996, De la Riva 2005, De la Riva *et al.* 2005). Terminology for external features follows that of De la Riva *et al.* (2005) and the toe-webbing formula follows that of Savage and Heyer (1967) as modified by Myers and Duellman (1982) and the prepollex is considered the first digit following Galis *et al.* (2001). Twelve measurements were recorded from specimens to the nearest 0.1 mm with callipers. They are abbreviated as follows: SVL (snout-vent length); HLEN (head length; posterior corner of jaw to tip of snout); HWID (head width; from posterior corner of jaw); ENOS (eye-nostril distance; from posterior corner of eye); IND (internarial distance); IOD (interorbital distance);

EYE (eye diameter); HNDL (hand length; proximal edge of outer palmar tubercle to tip of third finger); THBL (thumb length; proximal edge of inner palmar tubercle to tip of thumb); RDL (radio-ulnar length; elbow to distal edge of outer palmar tubercle); FOOT (foot length; proximal edge of inner metatarsal tubercle to tip of Toe IV); and TIBL (tibia length; knee to heel). The number of spicules on the surface of the nuptial pad was estimated at a magnification of 50× and in 1-mm^2 squares following the technique of Sinsch *et al.* (2005). Cleared-and-stained skeletons were prepared using the technique of Dingerkus and Uhler (1977). Terminology of osteological features follows that of Duellman and Trueb (1986). Cartilaginous features stained poorly and are reported as not visible in the description. Tadpoles were staged following the developmental table of Gosner (1960).

Results

*Morphological Variation (*N = *12; 6 males, 5 females, 1 juvenile)*

Specimen measurements are presented in Table 1. Head slightly narrower than body; head wider than long (HLEN 73.0–90.1% HWID); head length 26.8–32.3% SVL; HWID 34.0–38.9% SVL; nostril not protuberant, located at anterior terminus of snout; canthus rostralis indistinct, short, slightly concave in dorsal profile, elevated in lateral profile; loreal region concave; snout short, bluntly rounded; eyes anterolateral, protuberant or not, placed on top of head; EYE 31.1–42.2% HLEN; tympanic membrane absent and tympanic annulus not visible externally; supratympanic fold well developed; lips not flared. Maxillary and premaxillary teeth fanglike, embedded in labial mucosa; dentigerous processes of vomers closer to subcircular choanae than to each other; processes medial to choanae oriented perpendicular to anteroposterior axis of skull (with slight posteromedial inclination), each process bearing 1–5 fanglike teeth embedded in buccal lining for most of their lengths. Tongue large, subcircular, shallowly notched or not posteriorly attached through half or two-thirds of its length anteriorly, free posteriorly. Vocal slits absent.

Forelimbs robust in males, slender in females; relative lengths of fingers: IV > V ≥ II > III; webbing and lateral fringes absent; tips of fingers spherical; inner palmar tubercle oval, depressed, or not; inner palmar tubercle usually slightly

Table 1. Measurements (in mm) of specimens of *Telmatobius atahualpai*. Mean ± SD are followed by the range in parenthesis. See text for abbreviations.

Metric	Males (*N* = 6)	Females (*N* = 6)	Juvenile (*N* = 1)
SVL	59.2 ± 4.9 (52.1–63.5)	58.8 ± 3.9 (54.5–64.8)	51.0
HLEN	17.7 ± 0.9 (17.0–19.0)	16.3 ± 0.7 (15.5–17.4)	16.2
HWID	21.6 ± 1.6 (18.7–23.3)	21.0 ± 1.5 (19.3–22.7)	19.6
ENOS	4.1 ± 0.4 (3.4–4.5)	3.8 ± 0.4 (2.6–4.2)	2.9
IND	4.2 ± 0.6 (3.0–4.6)	4.2 ± 0.5 (3.7–4.4)	4.2
IOD	4.4 ± 0.6 (3.5–5.0)	4.5 ± 0.7 (3.4–5.2)	4.1
EYE	6.4 ± 0.5 (5.7–6.9)	6.2 ± 0.6 (5.6–6.9)	5.8
HNDL	16.4 ± 1.5 (15.0–18.6)	15.3 ± 0.6 (14.4–16.0)	14.2
THBL	10.5 ± 1.1 (9.5–12.0)	9.9 ± 0.7 (8.8–10.5)	8.6
RDL	16.8 ± 1.8 (15.2–19.6)	15.2 ± 1.5 (13.8–17.2)	13.3
FOOT	30.2 ± 3.1 (25.4–33.4)	26.8 ± 1.2 (25.5–28.3)	27.4
TIBL	28.1 ± 3.1 (25.2–32.4)	24.2 ± 0.4 (23.7–24.7)	25.3

larger than outer, subcircular (outer palmar tubercle larger in MUSM 15978, 15984, and 19683); one round, indistinct subarticular tubercle proximally on each finger (larger tubercle on Finger II); distal subarticular tubercles barely discernible on Fingers IV and V; supernumerary palmar tubercles absent (supernumerary palmar tubercle present in outer margin of inner palmar tubercle in MUSM 15978, 19478, and 19683); nuptial spines large, conical, keratinized on dorsal and lateral surfaces of thumb, 1 or 2 spines per mm^2 (Figure 1). Hindlimb length (FOOT + TIBL) 81.7–103.3% SVL; relative lengths of toes; IV > III ≥ V > II > I; webbing formula (range followed by mode): **I** (2^{-}–$2^{½}$; 2^{-})–($2^{¼}$–$2^{½}$; $2^{½}$) **II** ($1^{½}$–$1^{¾}$; $1^{½}$)–(3^{-}–3^{+}; 3^{+}) **III** ($1^{¾}$–$2^{⅓}$; 2^{-})–(3^{-}–$3^{⅔}$; $3^{½}$) **IV** (3^{-}–$3^{½}$; $3^{⅓}$)–($1^{¼}$–2^{+}; $1^{⅔}$) **V;** webbing diminishing distally to form fringes along lateral margins of toes (fringe of outer margin of Toe V well developed in MUSM 15979, 15980, and 19684); tips of toes spherical, approximately equal in size to fingertips; inner metatarsal tubercle distinct, ovoid; outer metatarsal tubercle present or absent, subarticular tubercles round, mostly distinct, distributed on toes, as follow: I(1), II(1), III(2), IV(3), V(2); plantar supernumerary tubercles absent (large supernumerary plantar tubercle present between inner and outer plantar tubercles in MUSM 15978); tarsal fold distinct or indistinct extending approximately half or two-thirds the length of tarsus, confluent distally with fringe along inner margin of Toe I.

Skin smooth; keratinized spicules absent from parts of the body other than nuptial excrescences; cloacal opening round or oval, unornamented, placed at upper level of thigh; transverse fold of skin dorsal to cloacal opening (absent in MUSM 15976, 15978–79, and 19683).

Color in Preservative

Gray or brown, with or without light brown or yellow to off-white speckling on face, dorsum, and/or dorsal surfaces of limbs; slightly paler gray or brown ventrally (with paler speckling on throat, flanks and/or undersides of limbs); tips of fingers and toes yellowish cream; palmar and plantar tubercles gray or pale gray.

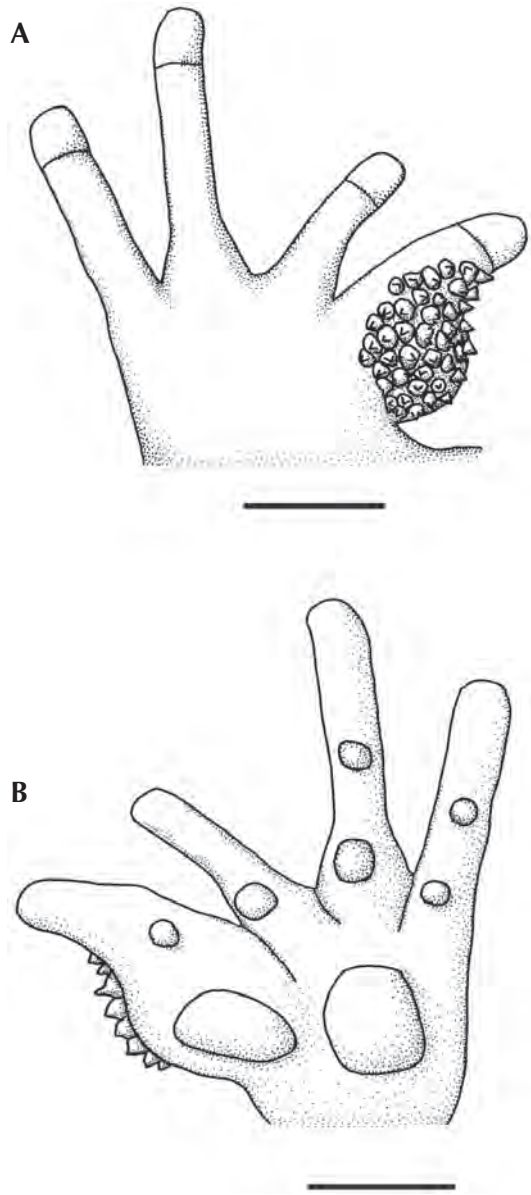

Figure 1. Dorsal (**A**) and ventral (**B**) views of left hand of a male of *Telmatobius atahualpai* (MUSM 15979). Scales = 5 mm. Drawing by K. Siu-Ting.

Figure 2. Female *Telmatobius atahualpai* from Río Abiseo National Park in lateral (**A**) and ventral (**B**) views (MUSM 15976). Lateral view (**C**) of a male *T. atahualpai* from Laguna El Plomo (MUSM 19499). Photographs by A. Catenazzi (A, B) and P. Venegas (C).

Color in Life

The dorsum is gray with minute yellow spots or black with gold or greenish-gold reticulations (Figure 2A, C); the venter is uniformly dark gray or gray (Figure 2B); iris dull bronze. One tadpole at Gosner Stage 42 (MUSM 19602) also has a greenish-gold reticulation on the dorsum (Aguilar *et al*. 2007).

Osteology

Skull moderately depressed, well ossified (Figure 3A, B); sphenethmoid, broadly exposed dorsally, anterior portion widely separated from posterior borders of nasals; prootic well ossified, fused with exoccipital dorsally and ventrally; exoccipital ossified dorso- and ventromedially; frontoparietals not fused posteriorly; fronto-parietal fenestra moderately broadly separated

(~1/3 braincase width) in male and V-shaped in female, and more extensive in male than in female. Fenestra shape determined by the degree of medial development of paired frontoparietal bones. Mineralization of the taenia tecti transversalis affects separation into an anterior frontal and a posterior parietal fontanelle. Anterior margin of frontal fontanelle formed by sphenethmoid at a level approximately one-fourth posterior of length of orbit; posterior margin of fontanelle at a level of anterior margin of crista parotica (male) or approximately one-fourth anterior on length of orbit (female); nasals subtriangular, broadly separated medially from each other, with maxillary process that is broadly separated from the pars facialis of the maxilla, broadly separated from sphenethmoid; pars facialis of maxilla with a small preorbital process; neopalatines long, slightly arcuate, tapered (male) or not (female) medially, in contact laterally with pterygoid and medially with sphenethmoid, broadly separated medially; parasphenoid robust, cultriform process widest at its base with margins tapering to irregularly truncate anterior terminus that is widely separated from, and posterior to, neopalatines; parasphenoid alae large, not perpendicular to cultriform process and not in contact with medial ramus of pterygoids anterolaterally; pterygoid robust, with anterior ramus extending to level of and overlapping neopalatine dorsally; inner margins of rami describing a smooth curve between maxilla and otic capsule. Lateral margins of anterior and posterior rami slightly curved; medial ramus of pterygoid short, articulating with prootic; maxillary arch complete; quadratojugal moderately long; palatoquadrate ossified ventrally; otic ramus of squamosal shorter than zygomatic ramus (similar in size in female); zygomatic ramus long, slim, and directed medially (short, not slim and not medially oriented in female); plectrum with pars interna plectri, pars media plectri thin (absent in one side of female) and pars externa plectri not visible; tympanic ring and operculum not visible; maxilla and premaxilla dentate; teeth pedicellate, monocuspid, fang-like; number of teeth in premaxilla (7/6) (female 7) and in maxilla (18/19) (female 22); posterior half of maxilla slim and straight in lateral view; alary process of premaxilla uniform in width and bifurcate distally, the distal halves of alary processes laterally divergent from one another in frontal view and forming an acute angle with the maxilla in lateral view; vomers small, with slender prechoanal and postchoanal processes, prechoanal process much longer than postchoanal process; dentigerous process of vomer bearing teeth; coronoid process of the angulosplenial well developed and separated from articular.

Hyoid plate and larynx cartilages as well as hyale, anterior, anterolateral and posterolateral processes not visible; posteromedial processes long and well ossified.

Pectoral girdle arciferal (Figure 3C); omosternum not visible; sternum heavily mineralized (male) or slightly mineralized (female); procoracoid and epicoracoid cartilages heavily mineralized in female; clavicle fused with scapula; coracoids well developed, not juxtaposed medially; epicoracoid and procoracoid calcified; scapula bicapitate; suprascapula with cleithrum bifurcate and distal portion mostly calcified.

Eight procoelous, nonimbricate presacral vertebrae (Figure 3D); transverse processes of Presacrals II–IV moderately expanded and long, relative widths of transverse processes: III > IV > II; sacral diapophyses nearly round with width of base being about two-thirds width of distal margin of diapophysis; diapophyses oriented slightly posterodorsal to longitudinal axis of vertebral column; articulation of sacrum with urostyle bicondylar; urostyle bearing a dorsal crest that extends over the anterior three quarters of its length; ilia cylindrical, long; pubis completely ossified and fused indistinguishably with illium and ischium.

Humerus of male robust (Figure 3E), flattened, with well-developed ventral, medial, and lateral crests, latter two crests continuing anteriorly as a single crest nearly reaching the head of the humerus in male; medial and lateral

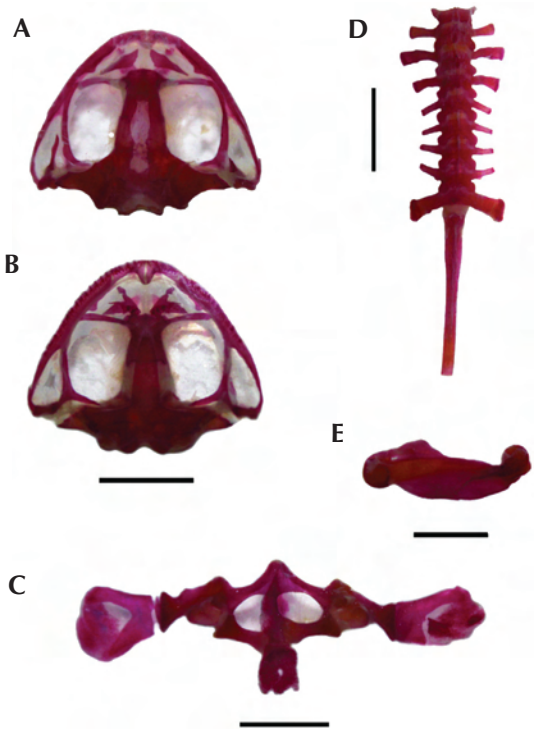

Figure 3. Osteology of male *Telmatobius atahualpai* (MUSM 19499): Dorsal (**A**) and ventral (**B**) views of skull, (**C**) pectoral girdle, (**D**) vertebral column and (**E**) ventral humerus. Scales = 10 mm.

crest absent and ventral crest small in female; phalangeal formula of hand 2-2-3-3; bony nuptial tuberosity is present on the medial surface of Metacarpal I in male; terminal phalanges knobbed; prepollex with two ossified elements, distal element less ossified in female; phalangeal formula of foot 2-2-3-4-3; prehallux with three ossified elements, distal element less ossified in female.

Revised Diagnosis

Telmatobius atahualpai can be distinguished from other Peruvian species of *Telmatobius* by the following combination of characters: (1) snout-vent length up to 63.5 mm in males and 64.8 mm in females; (2) head, in lateral profile, moderately high and with bluntly rounded snout; (3) head rounded in dorsal view; (4) upper lips not flared and not notched medially; (5) gland posterior to mandibular commissura present; (6) tympanic annulus not visible externally; (7) forelimb of males moderately robust, without humeral spine; (8) dermal fringes of fingers absent, nuptial spines large, conical; nuptial pad on dorsal surface of thumb separated from inner palmar tubercle; (9) toes moderately webbed, plantar surface without spicules; (10) tarsal fold present; (11) skin on dorsum and flanks smooth; (12) in life, dorsum gray or brown with greenish-gold or metallic green flecks; (13) belly gray or brown, unpatterned; (14) iris light gray without flecks; (15) tadpole with labial tooth row formula (LTRF) 3/6-7(1), oral disc with submarginal mental papillae and completely bordered by marginal papillae.

Telmatobius atahualpai differs from *T. arequipensis* Vellard, 1955, *T. culeus* (Garman, 1876), *T. intermedius* Vellard, 1951, *T. jelskii* (Peters, 1876), *T. marmoratus* (Duméril and Bribon, 1841), *T. peruvianus* Wiegmann, 1834, and *T. sanborni* (character states of these species in parentheses) by lacking flared upper lips with a medial notch (upper lips flared and notched medially). *Telmatobius atahualpai* can be distinguished from *T. brachydactylus* (Peters, 1873), *T. brevipes* Vellard, 1951, *T. brevirostris* Vellard, 1955, *T. carrillae* Morales, 1988, *T. hockingi, T. ignavus, T. macrostomus* (Peters, 1873), *T. mayoloi* Salas and Sinsch, 1996, and *T. thompsoni* by having large nuptial spines that are separated from the inner palmar tubercle (small nuptial spines in contact with inner palmar tubercle). It differs from *T. brachydactylus, T. carrillae, T. macrostomus,* and *T. mayoloi* by having a tongue that is free posteriorly (tongue completely attached to floor of mouth), and from *T. brachydactylus, T. carrillae,* and *T. macrostomus* by having premaxillary, maxillary, and vomerine teeth (edentate). *Telmatobius atahualpai* can be distinguished from *T. colanensis, T. degener, T. latirostris* Vellard,

1951, *T. necopinus, T. punctatus* Vellard, 1955, *T. timens,* and *T. truebae* by its dorsal color, which is black or brown with greenish flecks in life (greenish flecks absent). It has less webbing between Toes IV and V than does *T. colanensis* (extensive webbing), and differs from *T. latirostris* and *T. truebae* by having a bluntly rounded snout in lateral profile (sloping snout in lateral profile). *Telmatobius atahualpai* has a smooth dorsum, whereas *T. punctatus* has a tuberculate dorsum, and the ventral surfaces of its limbs are pale gray or brown, whereas those of *T. timens* are orange. It differs from *T. degener* in having a nuptial pad separated from inner palmar tubercle, teeth on premaxilla (nuptial pad in contact with inner palmar tubercle; premaxilla edentate), and in the osteological characters mentioned by Wiens (1993).

Distribution and Habitat

The species occurs in the Cordillera Central of northern Peru from the northwestern corner of San Martin Department to southern Amazonas Department between 3100 and 3600 m (Figure 4; Wiens 1993, Lehr 2005, von May *et al.* 2008). Adult *Telmatobius atahualpai* were found in Laguna Quintecocha (06˚51'30.0" S, 77˚42'00" W; 3130 m) on 19 November 2003, and in Laguna El Plomo (06˚51'03.2" S, 77˚43'00" W; 3300 m) on 22 November 2003. In Laguna Quintecocha, *T. atahualpai* was found by day and night on the forest floor or in streams in humid montane forest, as well as in areas of bunchgrass (*Calamagrostis, Festuca,* and *Stipa* spp.). In Laguna El Plomo, *T. atahualpai* was collected from a stream that crosses bunchgrass areas surrounded by patches of elfin forest. In Laguna Quintecocha, *T. atahualpai* was sympatric with *Telmatobius truebae* Wiens, 1993, but the species occupy different habitats; *T. truebae* was only found at night along the shore of the swampy vegetation of the lake and surrounding wetlands.

In Río Abiseo National Park, adults were collected along small creeks or near wet rock walls in the cloud forest or in the transition zone between the wet puna grassland and the cloud forest. Adults were collected in the Abiseo watershed (7˚58'14.44" S, 77˚19'37.48" W; 3160 m) on 22 July 2000, and in the Montecristo watershed (7˚39'48.00" S, 77˚27'21.00" W; 3100 m) on 29 June 1999. The conservation status of these populations and the ones from Quintecocha and El Plomo is unknown. The fungus *Batrachochytrium dendrobatidis,* which causes chytridiomycosis in amphibians and has been implicated in declines of *Telmatobius* species in the Andes (Seimon *et al.* 2007, Catenazzi *et al.* 2011), has been detected in populations of *Atelopus patazensis* near Río Abiseo National Park (Venegas *et al.* 2008). The presence of this fungus could pose a significant threat to the conservation of *T. atahualpai* within the Park.

Discussion

When Wiens (1993) described *Telmatobius atahualpai,* he lacked adult specimens, male exemplars, and skeletal material. He proposed two putative synapomorphies for *Telmatobius* that could not be verified based on the specimens available to him—viz., posterior fusion of the frontoparietals and restriction of nuptial spicules to Finger II; these synapomorphies were not derived from a phylogenetic analysis. In a phylogenetic analysis of 15 species of *Telmatobius* (*T. atahualpai* included) and based on adult and larval morphological characters, Aguilar and Valencia (2009) proposed synapomorphies for the *Telmatobius* species that they examined. In adults, the tongue is partially free posteriorly and the frontoparietals are fused posteriorly. (However this character should be examined more thoroughly because of the obscure relationship of the frontoparietals with the underlying mineralized cartilage [L. Trueb pers. comm.]). In larvae, the oral disc is not emarginated and submarginal lateral papillae form a continuous row on both labia; in the oral cavity the infralabial lateral papillae are shaped like compressed palps with projections in the

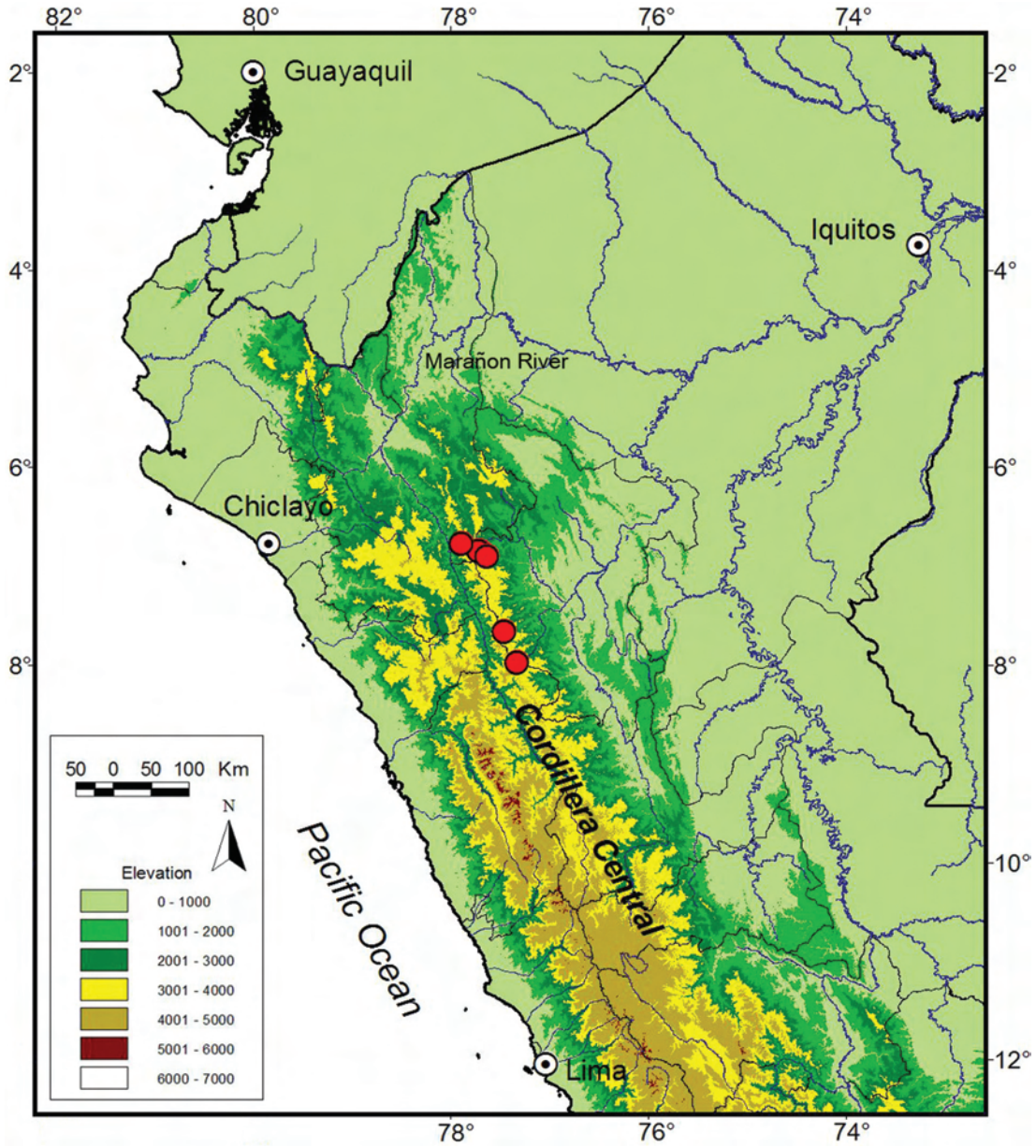

Figure 4. Distribution of *Telmatobius atahualpai* in northern Peru.

free margin of papillae and there are as many as three lingual papillae. In addition, the chondrocranium lacks a commissura quadrato orbital. These authors suggested that these larval features, which characterize all species of *Telmatobius* for which tadpoles are known, might be synapomorphies of the genus (Aguilar and Valencia 2009). Moreover, *T. atahuapai* has fanglike teeth

embedded in the labial mucosa—a feature that was considered a putative synapomorphy of *Telmatobius* by Trueb (1979) and not included in the analysis of Aguilar and Valencia (2009).

The relationship of *Telmatobius atahualpai* to its congeners is unclear. Aguilar and Valencia (2009) could not resolve relationships among *T. atahualpai, T. brevipes, T. brevirostris, T. latirostris, T. rimac,* and *T. truebae*. However, among the species from northern Peru, *T. atahualpai* may be related to *T. colanensis, T. latirostris, T. necopinus,* and *T. truebae;* all of these taxa lack corneal spines in the skin other than nuptial spines, have large nuptial spines on thumb pad of males and a thumb pad that is discrete from the inner palmar tubercle (Wiens 1993).

An understanding of several interesting evolutionary questions awaits the resolution of intrageneric relationships in *Telmatobius.* For example, Cei (1986) proposed that species of *Telmatobius* inhabiting forests from western Argentina to southeastern Ecuador are living relicts of early steps in the colonization of the high Andes. Is *T. atahualpai* part of a monophyletic group formed by species that live in forest habitats and that are basal (i.e., relicts) to highland *Telmatobius* species in central Andes? Like *T. atahualpai,* members of the *T. verrucosus* Group (*T. espadai,* De la Riva 2005; *T. sanborni,* and *T. verrucosus,* Werner 1899) have rheophilous larvae and occupy forest and subparamo habitats (De la Riva 2005, Aguilar *et al*. 2007). The *T. verrucosus* Group is basal to all species of *Telmatobius* in a phylogenetic tree based on mitochondrial sequence data (De la Riva *et al.* 2010). Members of the *T. bolivianus* Group (*T. bolivianus* Parker, 1940; *T. simonsii* Parker, 1940; *T. sibiricus* De la Riva and Harvey 2003; and *T. yuracare* De la Riva 1994) are also forest species and basal to the remaining species of Bolivian *Telmatobius* that live at higher elevations in puna, altiplano, and dryer habitats (De la Riva *et al.* 2010). These findings are consistent with Cei (1986)'s hypothesis. However, additional information is required before this hypothesis can be tested. There are at least two additional species of *Telmatobius* having rheophilous tadpoles that live in forest habitats in the Peruvian departments of Huánuco and Pasco, but the identities of the larvae cannot be determined because the tadpoles were not found together with adults. Moreover, distributional data are lacking for species of *Telmatobius* on the Amazonian slopes of the Andes of central and southern Peru (De la Riva *et al.* 2005). Thus, new field data and a better knowledge of phylogenetic relationships are needed to test Cei's hypothesis that montane forest *Telmatobius* species in Peru are relicts of the lineage that later diversified during the colonization of the high Andes.

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Appendix I. Specimens Examined.

Telmatobius arequipensis—PERU: Arequipa: Riachuelo Characato, MUSM 3906–07 (females), MUSM 3903–04, MUSM 3910–11, MUSM 3913–14 (males). Arequipa, MUSM 3916 (female), MUSM 3915, MUSM 3917–18 (males). Yura, MUSM 6774–75 (females), MUSM 6776 (male). MUSM 12577 (female), 12578–79 (males).

Telmatobius atahualpai—PERU: Amazonas: N slope Abra Barro Negro, 28 km SSW Leimebamba, KU 212485 (Holotype), 28.3 km SW Leimebamba, KU 182084 (Paratype). San Martín**:** Provincia de Mariscal Cáceres: Laguna Quintecocha, MUSM 19478–79 (males), Laguna El Plomo MUSM 19499 (male, skeleton). San Martín: Río Abiseo National Park, MUSM 15976, MUSM 15978, MUSM 19682–83 (females), MUSM 15983 (female, skeleton), MUSM 15979–80, MUSM 19684 (males), MUSM 15984 (subadult).

Telmatobius brachydactylus—PERU: Junín: Lago Junín, MUSM 0112, MUSM 0104, MUSM 0488, MUSM 0490–0492, MUSM 0494–95, MUSM 0497 (females), MUSM MUSM 0088, MUSM 0098, MUSM 0449, MUSM 0452, MUSM 0470, MUSM 0489, MUSM 0493, MUSM 7115, MUSM 11032, MUSM 11039, MUSM 11060, MUSM 1334 (males), MUSM 0498 (subadult).

Telmatobius brevipes—PERU: La Libertad: Huamachuco, MUSM 3742, MUSM 3749 (females), MUSM 3743–44, MUSM 6186 (males), MUSM 3740 (subadult).

Telmatobius brevirostris—PERU: Huánuco: Ambo, Caina, MUSM 7666–67 (females), MUSM 7669 (subadult). Chasqui, MUSM 7676 (male), 7677 (subadult). Tomayrica, MUSM 20468–69 (females). Chaglla MUSM 20464, MUSM 20466 (juveniles).

Telmatobius carrillae—PERU: Ancash: Yuraccyacu, MUSM 1528, MUSM 1545, MUSM 3934 (females), MUSM 1544, MUSM 3932–33 (males). Huikia, MUSM 6661, MUSM 6664, MUSM 6680–81 (females), MUSM 6667, MUSM 6672, MUSM 6682–84 (males).

Telmatobius culeus—BOLIVIA: Isla del Sol, MUSM 7770 (female), MUSM 7769 (male). PERU: Arequipa: Saracocha, MUSM 12565–67 (males). Puno: Río Juliaca, MUSM 7789, MUSM 7816, MUSM 7820–22, (females), MUSM 7767, MUSM 7817 (males). Lagunillas, MUSM 7806 (female), MUSM 7786, MUSM 7792, 7823–24, (males). Juliaca, Río Coata, MUSM 7771–72 (males). Chicuito, Río Llave, MUSM 7755 (male). Desaguadero, MUSM 12296–99 (males).

Telmatobius intermedius—PERU: Ayacucho: Puquio, MUSM 3754–55 (females), MUSM 3752–53 (males).

Telmatobius jelskii—PERU: Ayacucho: La Mar, Tambo, MUSM 7646–47, MUSM 7651 (females), MUSM 7648–50 (males). Parinacochas, MUSM 12909 (female), MUSM 12907 (male). Huancavélica: Huancavélica, MUSM 7639–41(males). Junín: Huancayo, MUSM 16862, MUSM 16865, MUSM 16883 (males). Jauja, MUSM 16851 (female), MUSM 16769, MUSM 16773, MUSM 16786 (males).

Telmatobius latirostris—PERU: Cajamarca: Cutervo, MUSM 3734–36, MUSM 3738 (females), MUSM 3733, MUSM 7866 (males). Chorro Blanco, MUSM 0960 (male).

Telmatobius macrostomus—PERU: Junín: Lago Junín, MUSM 0001, MUSM 0009, MUSM 0044, MUSM 0292, MUSM 0294–96 (females), MUSM 0016, MUSM 0061, MUSM 0374–76, MUSM 0118, MUSM 0250, MUSM 0253, MUSM 0266, MUSM MUSM 0293, MUSM 0376, MUSM 0474, MUSM 0477 (males), MUSM 0039, MUSM 0049 (subadults). Pasco: Ninacaca, MUSM 18536 (female).

Telmatobius marmoratus—BOLIVIA: La Paz: Calacoto MUSM 3920, MUSM 3925, MUSM 3927 (males). PERU: Cusco: Urubamba, Laguna Chincheros, MUSM 7690 (female), MUSM 7689, MUSM 7692–93, MUSM 7691 (subadult). Urubamba, MUSM 7687–88, MUSM 12323 (males). Tinta, MUSM 12896 (female). Puno: Juli, Pomata, MUSM 7758, MUSM 7764 (females), MUSM 7765, MUSM 12373 (males). Huancurcuchu, MUSM 12267 (female), MUSM 12014–15, MUSM 12024, MUSM 12302 (males). Desaguadero, MUSM 12342 (male). Hacienda Checayani MUSM 10937 (male).

Telmatobius mayoloi—PERU: Ancash: Aguascocha, MUSM 20479–80 (males). Catac, MUSM 20478, MUSM 20486, MUSM 20488 (males). Conococha, MUSM 20470–74 (females). Pachacoto, MUSM 20489 (female).

Telmatobius peruvianus—PERU: Tacna: Caplina, MUSM 19606–19608 (females), MUSM 19604–05, MUSM 19609 (males). Torata, MUSM 12418 (female).

Appendix I. *Continued.*

Telmatobius punctatus—PERU: Huánuco: Santa María del Valle, MUSM 7681 (male). Without data MUSM 19610–11 (males).

Telmatobius rimac—PERU: Ancash: Ocros, MUSM 12509 (female), MUSM 12489, MUSM 12495, MUSM 12552 (males). Lima: Marcahuasi, MUSM 12817 (female). Canta, MUSM 12459–60, MUSM 12629 (females), 12458 (male).

Telmatobius timens—PERU: Cusco: Manu National Park, MUSM 20858, 20883, AMNH 153100–01.

Telmatobius truebae—PERU: Amazonas: Bongara, MUSM 12365, MUSM 12367–68 (females), MUSM 6185, MUSM 12366, MUSM 12369–70 (males), MUSM 6183–84, MUSM 12364 (subadults).