A NEW SPECIES OF TELMATOBIOUS (ANURA: TELMATOBIIIDAE) FROM MONTANE FORESTS OF SOUTHERN PERU, WITH A REVIEW OF OSTEOLOGICAL FEATURES OF THE GENUS

IGNACIO DE LA RIVA1,2,4, LINDA TRUEB3, AND WILLIAM E. DUELLMAN3

1 Museo Nacional de Ciencias Naturales, CSIC, C/ José Gutiérrez Abascal, 28006 Madrid, Spain. E-mail: irriva@mncn.csic.es
2 School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia.
3 Biodiversity Institute, The University of Kansas, Lawrence, Kansas 66045-7561, USA.
4 Corresponding author.

ABSTRACT. We describe a new species of Telmatobius from cloud forests in the valley of the Río Kosñipata in the Cordillera de Paucartambo, Región de Cusco, Peru, where it inhabits roadside ditches and forest streams. The new species is among the larger Telmatobius known. It has a short rostrum and exceedingly long jaw. Males have nuptial excrescences composed of minute, closely spaced spicules. Osteologically, the new species is distinguished by unusual ossification of the endocranium. The sphenethmoid is synostotically united with the prootic and the ossification/mineralization of the dorsal neurocranial roof eliminates the parietal fontanelles, leaving only a small frontal fontanelle. Osteological comparisons are made between the new species and the 24 other species of Telmatobius for which there is information available in the literature. Preliminary evidence suggests that the suspensory apparatus of Telmatobius may have a unique combination of features distinguishing it from that of other anurans. Superficially, the new species resembles members of the Telmatobius bolivianus Group, but its phylogenetic relationships are unknown. Many anurans in the area of the type locality have experienced severe declines, and the new species, not seen since 2007, is considered as Critically Endangered.

KEYWORDS. Amphibia; Anura; Telmatobiidae; Telmatobius mendelsoni sp. nov.; Andes; Peru; Osteology.

INTRODUCTION

The diversity of frogs of the Andean genus Telmatobius in Peru was reviewed recently by Lehr (2005), who recognized 22 species in this country; De la Riva et al. (2005) added another species. Whereas several species occur nearly exclusively in puna highlands or dry valleys (e.g., T. jelskii, T. marmoratus, T. rimac), others inhabit either humid paramo (e.g., T. thompsoni, T. timens) or cloud forest-humid montane forests (e.g., T. colanensis, T. ignavus; Wiens, 1993; De la Riva et al., 2005; Lehr, 2005). Wiens (1993) reviewed the Telmatobius fauna of northern Peru, and that of central Peru was studied by Sinch and Jurasek (1995) and Sinch et al. (1995, 2005); however, the Telmatobius frogs from southern Peru have not been properly addressed. Given the high species diversity of forest-dwelling Telmatobius in both northern Peru (6 species; Wiens, 1993; Lehr, 2005) and Bolivia (8 species; De la Riva, 2005), a comparable species richness is expected in central and southern Peru. But, thus far, only one species of forest-dwelling Telmatobius (T. sanborni) has been reported from southeastern Peru (Región de Puno; De la Riva, 2005; Lehr, 2005).

As noted by De la Riva (2005), intra- and inter-populational variation and the lack of clear diagnostic characters confounds taxonomists working with living Telmatobius. Thus, it is not surprising that taxonomic work based on preserved specimens of the genus is even more difficult; as a consequence, specimens of undescribed species have accumulated on museum shelves. Molecular techniques offer a valuable tool for species recognition and a method for estimating species diversity of Telmatobius. However, the quest for tissue samples for use in genetic studies has proven to be a nearly hopeless task in recent years as populations of forest-dwelling Telmatobius continue to disappear, most likely because of chytridiomycosis (Merino-Viteri et al., 2005; De la Riva and Lavilla, 2008).

There are some clearly diagnosable, distinct species of Telmatobius in several museum collections that should be described based on extant material, because it is unlikely that additional specimens will be found. Among the Telmatobius in southern Peru, there is a large species from cloud forests of the valley of the Río Kosñipata in the Cordillera de Paucartambo in the upper parts of the Parque Nacional Manu and surrounding areas. This species is easily distinguishable from any other Peruvian or Bolivian species, and is described herein.

MATERIAL AND METHODS

Collection codes are: AMNH = American Museum of Natural History, New York, USA; KU = Biodiversity
A new species of *Telmatobius* from Southern Peru

**Institute.** University of Kansas, Lawrence, USA; MHNC = Museo Historia Natural, Cusco, Peru. Specimens in the KU collection were collected in the field, photographed while alive, fixed in 10% formalin, and preserved in 70% ethanol. Drawings were made using a stereomicroscope and camera lucida. We used 10 morphometric variables: snout-vent length (SVL), head length (from rictus to tip of snout; HL), head width (at level of rictus; HW), internarial distance (IND), distance from eye to nostril (END), eye diameter (ED), interorbital distance (ID), eyelid width (EW), tibia length (TL), and foot length (from proximal border of inner metatarsal tubercle to tip of fourth toe; FL). Measurements were taken with digital calipers to the nearest 0.01 mm, and rounded to only one decimal to avoid pseudo precision (Hayek et al., 2001). Osteological observations are based on one female dry skeleton that was prepared in the field. Additional information was provided by a digital x-ray of a preserved male specimen (AMNH 157036). Osteological terminology follows that of Trueb (1973, 1993) and Duellman and Trueb (1986). The format of the diagnosis and description follows De la Riva (2005) with the addition of osteological features. The familial placement of *Telmatobius* follows Blackburn and Wake (2011). Specimens examined are listed in Appendix I.

**Telmatobius mendelsoni** sp. nov.

**Holotype:** KU 173385, adult male from Buenos Aires, Valle del Río Kosñipata, Districto de Kosñipata, Provincia de Paucartambo, Región (Departamento) Cusco, Peru, 13°09′31″S, 71°35′26″W, 2400 m, one of a series collected on 19 January 1977 by William E. Duellman and David C. Cannatella.

**Paratypes:** All from Valle de Río Kosñipata, Districto de Kosñipata, Provincia de Paucartambo, Región Cusco, Peru: KU 162962, juvenile from Río Kosñipata, 4 km SW of Santa Isabel, 13°04′12″S, 71°33′15″W, ca. 1700 m, collected on 11 February 1975 by Dana T. Duellman; KU 173386-88, adult male, adult female, and juvenile respectively, and KU 173505, dry skeleton of adult female, all from Buenos Aires, same data as the holotype; AMNH 157036-37, adult male and adult female, respectively from Pillahuata-Esperanza, 13°10′03″S, 71°35′55″W, 2598 m, collected by Lily O. Rodríguez in 1998; MHNC 4568, adult female from Esperanza, 13°11′05″S, 71°35′21″W, 2850 m, collected by Juan C. Chaparro and Armando Mendoza on 26 January 2003.

**Diagnosis:** (1) Snout-vent length of males to 69.7 mm, females to 79.5 mm; (2) head in profile moderately low, with rounded snout; (3) snout rounded in dorsal view; (4) lips not flared; (5) postcommisural gland present, large; (6) tympanum and tympanic annulus not visible; supratympanic fold robust; (7) forelimb moderately robust, with evident humeral crest and spine in males; (8) nuptial spicules small, closely arranged; nuptial pad on dorsal surface of thumb; a smaller, thin pad of spicules on Finger II; (9) foot not fully webbed, but reaching the base of tips of toes as dermal lateral fringes; palmar and plantar surfaces smooth; (10) tarsal fold present; (11) dorsal skin with small, flat pustules; (12) dorsal surfaces of body and legs dull olive-tan, with or without small dark brown dots; (13) venter dull yellow or olive, ventral surfaces of limbs yellow; (14) iris dull olive with fine black flecks; (15) skull shape characterized by medial head length being less than greatest head width at the level of the quadratojugal-maxillary articulation, and rostrum short, 20% or less than head length; (16) optic fenestra with bony margin; (17) stapes normally developed; (18) frontoparietals separate; and (19) nasals overlapping sphenethmoid, with anterior margins coincident with anterior margin of bony sphenethmoid.

**Comparison with other species:** *Telmatobius mendelsoni* (Fig. 1) cannot be mistaken for other southern Peruvian *Telmatobius*, from which it differs by the combination of characters presented in the diagnosis. More specific comparisons are provided for those species inhabiting forests, those showing a greater external similarity, and those occurring in the Región Cusco. The only two species of *Telmatobius* known from forests and humid paramos in southern Peru are *T. sanborni* (Puno to Bolivia) and *T. timens* (Cusco to Bolivia). The new species is larger than both (SVL females up to 79.5 mm vs. 55.2 mm in *T. sanborni* and 61.0 mm in *T. timens* [De la Riva et al., 2005]) and has a flatter head; in addition, the nuptial excrescences of males (Figs. 2, 3) are composed of small, closely arranged spicules (large or moderately large spicules in *T. sanborni* and *T. timens*, not closely arranged). In addition to *T. sanborni*, the *T. verrucosus* Group contains two other species — *T. espadai* and *T. verrucosus* — both known only from Bolivia. Like *T. sanborni*, these two species differ from *T. mendelsoni* by the size and arrangement of the spicules of the nuptial pads, their bufoniform heads, and the lack of a humeral spine and a tarsal fold. Two nominal species, *T. brevirostris* and *T. punctatus* can be found in forests in the Región Huánuco in central Peru. They
differ from *T. mendelsoni* by their smaller size (maximum SVL of females 61.1 mm and 64.9 mm, respectively, vs. 79.5 mm in *T. mendelsoni*) and coloration of the venter — pale gray or pale green with gray and orange blotches in *T. brevirostris*, and grayish-brown or brown with cream and pale orange blotches in *T. punctatus* (Lehr, 2005) (venter dull yellow or olive and ventral surfaces of limbs yellow in *T. mendelsoni*). Two forest-dwelling species from northern Peru (Región Amazonas), *T. necopinus* and *T. truebae*, superficially resemble *T. mendelsoni*. The new species differs from *T. necopinus* by having a larger external metatarsal tubercle, nuptial pad of males (Fig. 3A) composed by small, closely arranged spicules (large and more greatly spaced spicules in *T. necopinus*), humeral crests or spines, and lower surfaces of limbs yellow. It can be distinguished from *T. truebae*, by having small, closely arranged spicules (large and more greatly spaced spicules in *T. truebae*). Other northern Peruvian species inhabit paramo. Of these, *T. atahualpai* has a black dorsum with greenish-gold flecks in life. *Telmatobius brevipes*, which is equally as large as *T. mendelsoni*, differs from that species by having a pale brown or gray venter and minute nuptial spines on the dorsal, lateral, and ventral surfaces of the thumb. Wiens (1993) presented data for these species, and Lehr (2005) provided color photos. *Telmatobius mendelsoni* has external characteristics similar to two members of the *T. bolivianus* Group, *T. bolivianus* and its sister species, *T. yuracare* (De la Riva, 2005; De la Riva et al., 2010; Discussion). Both species occur in forests and males have humeral spines. However, among other differences, they have fully webbed feet and they are smaller than *T. mendelsoni* (maximum SVL of *T. mendelsoni* females, 79.5 mm vs. 52.7 mm in *T. bolivianus* and 46.0 mm in *T. yuracare*); in addition, they have larger spicules in the nuptial excrescences, and *T. bolivianus* has a bufoniform head, whereas *T. yuracare* has a more flattened head and a markedly short snout. Another species of *Telmatobius* occurs in the high puna and dry valleys of the Región Cusco — *T. marmoratus*. The new species differs from it mainly by its larger size (females maximum SVL 79.5 mm vs. 64.6 mm), smoother skin, flatter head, and presence of humeral crests or spines in males.

**Figure 1.** Coloration of *Telmatobius mendelsoni*. (A) KU 173385 (holotype), male, 69.7 mm SVL; (B) KU 173386, male, 65.2 mm SVL, both from Buenos Aires; photos by W. E. Duellman. (C) MHNC 4568, female, 61.8 mm SVL, Esperanza; photo by J. C. Chaparro. (D) KU 129262, juvenile, 34.3 mm SVL, Río Kosñipata, 4 km SW Santa Isabel. Photo by W. E. Duellman.
Description of the holotype: An adult male with a SVL of 69.7 mm; body moderately robust; head wider than long, its length 30.7% of SVL; head width 38.8% of SVL; head length 76.7% of head width. Head moderately depressed; snout rounded in lateral and dorsal views; nostrils not protuberant, oriented dorsolaterally; internarial distance 15.1% of head width; nostrils closer to tip of snout than to margin of orbit; internarial region slightly convex; eye large, 33.1% of head length; loreal region moderately concave; lips not flared; tympanum and tympanic annulus indistinct; supratympanic fold well developed, extending from behind eye to level of shoulder; distinct dermal fold from supratympanic fold to corner of mouth (obvious on the right side only); postcommissural gland large, round. Maxillary and premaxillary teeth fanglike, embedded in labial mucosa; dentigerous processes of vomer between choanae, bearing two small, fanglike teeth; choanae moderately large, subcircular; tongue rounded, attached anteriorly through about two thirds of its length; vocal slits absent.

Forelimb moderately robust; humeral crest evident through skin (Fig. 2); relative lengths of fingers: I > II < III > IV (Fig. 3A); Finger II notably shorter than Finger IV; palmar webbing absent; tips of fingers spherical; fingers lacking lateral fringes; inner palmar (prepollical) tubercle oval, distinct; outer palmar tubercle slightly larger than inner, rounded; subarticular tubercles rounded; supernumerary palmar tubercles absent, palmar surface smooth; nuptial excrescence on medial surface of thumb, composed by small, keratinized, black spicules closely arranged, forming a pad in contact with inner palmar tubercle; keratinized spicules also covering medial surface of Finger II, forming a fine ridge. Hind limbs moderately robust, long; combined lengths of tibia and foot 96.2% SVL; relative lengths of toes: I < II < III < IV > V (Fig. 3B); Toes III and V about equal in length; toes not fully webbed, but web reaching base of each toe tip as a
Table 1. Measurements of adult *Telmatobius mendelsoni*. KU 173385 is the holotype.

<table>
<thead>
<tr>
<th>Character</th>
<th>KU 173385 ♂</th>
<th>KU 173386 ♂</th>
<th>AMNH 157036 ♂</th>
<th>KU 173387 ♀</th>
<th>AMNH 157037 ♀</th>
<th>MHNC 4568 ♀</th>
</tr>
</thead>
<tbody>
<tr>
<td>SVL</td>
<td>69.7</td>
<td>65.2</td>
<td>66.4</td>
<td>58.2</td>
<td>70.8</td>
<td>61.8</td>
</tr>
<tr>
<td>HL</td>
<td>21.4</td>
<td>21.7</td>
<td>19.3</td>
<td>20.0</td>
<td>21.3</td>
<td>17.7</td>
</tr>
<tr>
<td>HW</td>
<td>27.1</td>
<td>27.3</td>
<td>25.3</td>
<td>25.8</td>
<td>26.5</td>
<td>25.7</td>
</tr>
<tr>
<td>IND</td>
<td>4.1</td>
<td>4.3</td>
<td>4.6</td>
<td>4.5</td>
<td>4.9</td>
<td>4.7</td>
</tr>
<tr>
<td>END</td>
<td>3.8</td>
<td>4.6</td>
<td>4.2</td>
<td>4.4</td>
<td>4.9</td>
<td>4.2</td>
</tr>
<tr>
<td>ED</td>
<td>6.9</td>
<td>6.2</td>
<td>5.8</td>
<td>5.7</td>
<td>6.6</td>
<td>6.0</td>
</tr>
<tr>
<td>ID</td>
<td>4.0</td>
<td>5.0</td>
<td>5.2</td>
<td>5.0</td>
<td>3.6</td>
<td>4.5</td>
</tr>
<tr>
<td>EW</td>
<td>3.8</td>
<td>4.2</td>
<td>4.8</td>
<td>4.8</td>
<td>4.7</td>
<td>3.1</td>
</tr>
<tr>
<td>TL</td>
<td>32.5</td>
<td>32.2</td>
<td>32.0</td>
<td>29.6</td>
<td>32.0</td>
<td>30.1</td>
</tr>
<tr>
<td>FL</td>
<td>34.6</td>
<td>34.1</td>
<td>36.1</td>
<td>29.7</td>
<td>36.6</td>
<td>35.1</td>
</tr>
</tbody>
</table>

Skin on dorsum with scattered, small, flat pustules; keratinized spicules in tympanic region and on postcommissural gland, throat, and inner surface of forelimbs (Figs. 1, 2); loose folds of skin absent; ventral skin smooth; cloacal opening approximately at dorsal level of thighs.

For measurements of all adults, see Table 1.

Coloration: In preservative, dorsal surfaces of head, body, and limbs mostly uniform grayish-brown; venter and throat dirty yellowish-gray; ventral surfaces of limbs cream and gray; tips of digits cream; plantar and palmar surfaces gray. In life, dull olive-tan above, with irregular darker areas especially in scapular region and on head; dark olive-brown spots at night; by day, dorsum dull olive-green with black spots; flanks pale cream; venter dull yellow with bright yellow ventral surfaces of limbs; iris dull olive with fine black flecks (color photograph and Duellman’s field notes).

Variation: Dorsal coloration varies from gray to olive or tan, either nearly uniform or with irregular dark areas (Fig. 1A; holotype), or numerous dark brown pustules, irregularly distributed on the dorsal surfaces of the head and body (Fig. 1C; MHNC 4568). The skin texture varies from almost smooth to quite pustular (AMNH 157036). The cream color on the hind limbs is quite extensive in some specimens (AMNH 157036-37). In life, the coloration of a juvenile (Fig. 1D; KU 162962) was bronze-brown above with abundant small pustules and black flecks; the tips of digits and the subocular region were pale cream, the throat and belly creamy gray, and the ventral surface of the limbs pale orange with gray mottling; the iris was greenish-bronze with black reticulations (photographs and Duellman’s field notes).

Distribution and ecology: *Telmatobius mendelsoni* is known only from elevations of 1700-2850 m in the Kosñipata Valley (Fig. 4), an area covered by lush cloud forest. Individuals were found in roadside ditches and forest streams. The holotype and individuals collected with it were sitting in a shallow roadside ditch with barely flowing water. MHNC 4568 was collected at 21:00 h in a stream bordered by bamboo and bromeliads (Fig. 5).

At the highest elevation, Esperanza, 2850 m, three terrestrial strabomantid frogs were found in sympatry with *Telmatobius mendelsoni* — *Bryophrynella nubilosus*, *Oreobates gemcare* (type locality) and *Psychrophrynella usurpator*. Some of the same species (*Oreobates gemcare* and *Psychrophrynella usurpator*) were found at the type locality at 2400 mm, along with several other species, including *Gastrotheca nebulanastes*, *Hyloscirtus armatus*, *Pristimantis pharangobates*, and *Psychrophrynella bagre‑cito*. Esperanza, at 2850 m, also is the type locality of *Gastrotheca antoniiochoai*. Many more species are sympatric with *T. mendelsoni* at the lowest-known elevation of its range (1700 m); these include six strabomantids of the genus *Pristimantis* (cosnipatae, danae, lindae, mendax, platydactylus, and salapu‑tium), four bufonids (*Atelopus tricolor*, *Rhinella inca*, *R. margaritifera*, and *R. veraguensis*), five centrolenids (*Hyalinobatrachium bergeri*, *H. munozorum*,...
Nymphargus phenax, N. truebae, and Rulyrana spiculata), and three hylids (Hyloscirtus armatus, H. phyllognathus, and Hypsiboas gladiator), plus Gastrotheca testudinea, Hemiphractus heloi, Leptodactylus labrosus, and L. rhodonotus. The distributions of these species are discussed in Duellman and Lehr (2009) and Duellman et al. (1997, 2011).

Etymology: This specific epithet is a patronym honoring Joseph R. Mendelson III. He is among the early, constructive responders to the global decline of anurans (Lips et al., 2004, 2008; Mendelson et al., 2004, 2006; Mendelson and Donnelly, 2011) and the first to apply the term “forensic taxonomist” to himself and others, who sadly must use “forensic tools” (Duellman and Hedges, 2005) to describe taxa that they have every reason to suspect are extinct (Mendelson, 2011a, b). Forensic taxonomy is a regrettable reality that Joe Mendelson, in his role as an active leader of the Society for the Study of Amphibians and Reptiles, international herpetological diplomat, and curator at Zoo Atlanta, has used effectively to focus and leverage attention on the acute need for conservation and biodiversity research on amphibians and reptiles globally.

Osteology

The following description is based on a dry skeletal preparation of a female (KU 173505) with a snout-vent length of 79.5 mm. Hence, the description of cartilaginous elements such as the tympanic annulus, the hyolaryngeal apparatus, and pre- and postzonal pectoral girdle elements was precluded; likewise, the carpal and tarsal elements were not sufficiently well preserved to describe them.

Cranium: General proportions and shape (Figs. 6A, B). — The skull is 25% wider than long (distance from premaxilla to margin of occipital condyle), with the greatest width being at the articulation of the maxilla with the quadratojugal. At the anterior level of the orbit, which is coincident with the planum antorbitale, the skull width is 69% of its greatest width. The greatest height of the skull is in the area of the anterior level of the otic capsule, where the height is about 40% of the skull length. A transverse line projected across the skull at the level of the posterior end of the maxillary arcade demonstrates that the angles of the jaw lie posterior to the level of the occipital condyles, and in lateral aspect (Fig. 6C), it is evident that the upper jaw is deflected ventrally, such that the pars articularis lies notably ventral to the level of the premaxilla. The snout is high (about 60% greatest height of the skull) and sloped posteriorly at about a 30° angle. In either dorsal or ventral view, the angle of the posterior margin of the otic capsule and crista parotica is approximately 30° from the transverse or horizontal plane.

Neurocranium: Although the dry preparation precludes description of cartilaginous parts of the neurocranium, it is obvious that the endocranium is unusually well ossified. The septomaxillae are large and located between the nasals and vomers adjacent to the pars facialis of the maxilla at its anterior terminus. The anterior end of the sphenethmoid lies only slightly posterior to the level of the anterior ends of
the maxillae. The sphenethmoid extends laterally in the region of the planum antorbitale composing approximately the medial third of the wall between the orbit and the olfactory capsule; thus, the orbitonasal foramen is totally enclosed in bone. The sphenethmoid is synostotically united with the prootic; thus, the margins of the optic fenestra, and the oculomotor and prootic foramina are complete in bone. The frontal fontanelle is small, its total length being less than 20% the medial skull length. The anterior border is formed by the ossified sphenethmoid, whereas the posterior border seems to be composed of heavily mineralized cartilage. We assume that during postmetamorphic development, cartilage filled in the parietal foramina of the larval chondrocranium and subsequently was mineralized. Thus, we interpret the remaining fontanelle to be the frontal fontanelle that is bordered posteriorly by the mineralized taenia tecti transversalis.

The fused prootic and exoccipital is equally as well developed as the sphenethmoid. The margin of the foramen magnum is complete in bone. The otic capsule is completely ossified and the crista parotica long, slender, and complete to the head of the squamosal. A slender, dorsolaterally oriented pars media plectri is present; the pars interna plectri is located in the anterodorsal part of the fenestra ovalis. Owing to its absence in this dry specimen, we assume that the operculum probably was cartilaginous.

**Dermal investing bones:** The nasals are slender elements overlapping the anterolateral margins of the sphenethmoid dorsally (Fig. 6A). The bones are broadly separated medially by the anteromedial sphenethmoid and their anterior margins are coincidental with the anterior limits of the sphenethmoid. Each nasal bears a moderate maxillary process that forms most of the anterior margin of the orbit; however, the nasal is distinctly separated from the preorbital process of the maxilla, as well as the pars facialis of that bone (Fig. 6C).

The frontoparietals extend over the dorsolateral parts of the sphenethmoid to terminate at the anterior margin of the orbit; they are broadly separated from the nasals. The frontoparietals are broadly separated from one another medially (Fig. 6A). In the region of the frontal fontanelle, they form the irregular margins of the fenestra, and posterior to it, the medial margins

---

**Figure 6.** Skull of *Telmatobius mendelsoni* (adult female KU 173505, 79.5 mm SVL) in dorsal (A), ventral (B), and lateral (C) aspects. Abbreviations: cr par = crista parotica; epi em = epiotic eminence; exoc = exoccipital; fpar = frontoparietal; fr fon = frontal fontanelle; max = maxilla; min endo = mineralized endocranium; nas = nasal; neopal = neopalatine; opt fen = optic fenestra; orbnas for = orbitonasal foramin; p artic = pars articularis; palquad = palatoquadrate; pmax = premaxilla; pro = prootic; prsph = parasphenoid; pter = pterygoid; qj = quadratojugal; sphen = sphenethmoid; spmax = septomaxilla; sq = squamosal; st = stapes; vom = vomer.
of the frontoparietals are obscured by the mineralization of the endocranial roof that is described above. The bones have a well-developed lamina perpendicularis (Fig. 6C). The posterolateral margins lie medially adjacent to the anterior epiotic eminence. At the junction between the anterior and posterior eminences, the frontoparietal bears an acinate terminus; the posterior border is anteriorly convex, slightly irregular, and overlies the exoccipital at about the midlevel of the otic capsule.

The parasphenoid has relatively short alae that are posterolaterally oriented and widely separated from the medial ramus of the pterygoid, which articulates with the anteroventral margin of the otic capsule (Fig. 6B). The posteromedial process of the parasphenoid is massive and truncate; it occupies the medial floor of the braincase between the occipital condyles and contributes to the bony margin of the foramen magnum. The corpus of the parasphenoid is broad and only slightly narrower than the cultriform process at the level of the optic fenestra. Anterior to the latter, the cultriform process gradually narrows to a truncate terminus at the level of the orbitonasal foramina.

The neopalatines are robust bones underlying the plana antorbitalia. Laterally, each bone articulates with the anterior ramus of the pterygoid along the lingual margin of the pars facialis of the maxilla. The neopalatine is anteriorly convex and has an acute terminus on the lateral sphenethmoid anterior to the orbitonasal foramen (Fig. 6B). The bone forms the posterior margin of the choana. Its ventral surface is smooth.

The vomers slightly overlap the anterolateral margin of the ventral part of the sphenethmoid (Fig. 6B). The vomerine corpus is broad, lacking an anterior process, and widely separated from the maxilla laterally. The long prechoanal process is narrowly separated from the pars facialis of the maxilla and forms the entire anterior margin of the choana. In contrast, the postchoanal process is short, stout, and forms only about half of the medial margin of the choana. The dentigerous process is only moderate in size, bearing four fanglike teeth; the processes are transversely oriented at about the midlevel of the choana and broadly separated from one another.

**Maxillary arcade:** The upper jaw is composed of robust premaxillae, maxillae, and quadratojugals. Both the premaxillae and maxillae bear large, fanglike, pedicellate teeth. The premaxilla has a well-developed alary process that is deflected posteriorly at approximately a 30° angle and the maxilla bears a high pars facialis (Fig. 6C). The maxilla has a short, overlapping articulation with the quadratojugal, which subtends only about the posterior quarter of the subtemporal fenestra (Fig. 6B). The maxillary dental series is short, terminating at about the mid-orbit. The maxilla lacks a distinct pterygoid process, and the partes palatinae of the maxilla and premaxilla are uniformly narrow except for the medial palatine processes of the premaxillae.

**Suspensory apparatus:** Bracing and abutment of the maxillary arcade involves one endochondral element, the palatoquadrate, and three sets of dermal bones — the squamosals, the pterygoids, and the neopalatines, which also provide support for the choanae. The squamosal is not especially well developed (Figs. 6A, C). The otic ramus is short and located at the anterolateral corner of the ossified crista parotica; in life, it probably bordered a narrow band of cartilage along the lateral margin of the crista. An otic plate is absent. The zygomatic ramus is slightly curved in dorsal aspect, and extends anteriorly in the horizontal plane in lateral aspect; the tip of the ramus is deflected ventrally, but the ramus is broadly separated from the maxilla below. The ventral ramus invests the posterolateral margin of the palatoquadrate, which is ossified. The angle described by the margin of the ventral ramus and the horizontal plane of the maxilla is markedly acute — about 52° (Fig. 6C).

The pterygoid is extraordinarily well developed. The medial and posterior rami are about equal in length in ventral aspect (Fig. 6B). The medial ramus articulates with the anteroventral surface of the otic capsule. The posterior ramus articulates with the medial and anterior surface of the ossified palatoquadrate (Fig. 6C). The anterior pterygoid ramus is slightly curved and extends anterolaterally to meet the maxilla; the ramus extends along the lingual margin of the maxilla and articulates with the posterolateral margin of the neopalatine adjacent to the pars facialis of the maxilla.

**Mandible:** The angulosplenial and dentary are compressed to produce a dorsal mandibular flange anterior to the coronoid flange. Although the flange is narrow, it is long, comprising the posterior quarter of the mandible. The dentaries are especially well developed and completely overlap the stout mentomeckelian bones anteriorly. It is unclear whether the dentaries are fused with the mentomeckelians or simply overlap them anteriorly.
Axial column: The vertebral column is composed of eight procoelous vertebrae (Fig. 7A). The neural spines of Presacrals I and II articulate; the remaining presacral vertebrae are nonimbricate. The vertebral width profile is as follows: VIII ≅ VII < II ≅ V ≅ VI < sacrum < IV < III. The transverse processes of Presacrals II and III are markedly expanded, whereas those of Presacral IV are only slightly expanded. The sacral diapophyses are posterolaterally oriented and only slightly expanded, with the base of the diapophysis being more than three-quarters the width of the distal margin. The leading edge of the sacral diapophysis is slightly concave, whereas the posterior margin is straight. The lateral margins are thick and knobby. The urostyle is long, being slightly less than 50% the entire length of the axial column. The urostyle lacks

Figure 7. Postcranial osteology of Telmatobius mendelsoni (adult female KU 173505, 79.5 mm SVL). (A) Axial column in dorsal aspect. (B) Pectoral girdle in ventral aspect. Scapula and suprascapula of left side have been deflected into the ventral, zonal plane; right scapula and suprascapula not shown. Cartilaginous elements are shown in gray. Distal part of sternum is missing and distal omosternum is an estimation. Lateral (C) and dorsal (D) views of pelvic girdle.
The acetabulum is rounded in lateral aspect and forms a prominence that is broad, low, and scarcely evident. The shape of the acetabulum is approximately a 90° angle with the horizontal plane of the ilial shaft. The articulation of the ilium with the ischium is evident, but the synostosis of the pubis with the ilium and ischium obscures the boundaries of the pubis. The acetabulum is deep and distinct. Although generally round, the dorsal margin of the acetabulum bears a small depression that produces an asymmetry of shape.

**Pectoral girdle:** The cartilaginous omosternum and distal sternum are too poorly preserved to describe. The zonal elements of this arciferal girdle are composed of a robust clavicle and coracoid, epicoracoid cartilages with the frog’s left epicoracoid ventrally overlapping the right, and well-developed procoracoid cartilages associated with the medial portions of the clavicles (Fig. 7B). The lateral part of the clavicle is especially well developed; it has a broad articulation with the pars acromialis of the scapula and forms part of the margin of the glenoid fossa. The anterior edge of the clavicle is strongly curved and the part that invests the anterior edge of the procoracoid cartilage is uniform in width; the medial ends of the coracoids are blunt and widely separated from one another near the epicoracoid bridge.

The coracoids are short, stout and widely separated from one another medially by the epicoracoid cartilages (Fig. 7B). The sternal end of the coracoid is not quite as wide as the glenoid end; the width of the glenoid terminus is slightly greater than half the length of the bone and three times the midshaft width. There is a bony articulation between the clavicle and coracoid at the glenoid fossa. Although the posterior cartilaginous part of the sternum is missing, a broad, flat plate of heavily mineralized cartilage lies in the midline posterior to the epicoracoid cartilages.

The scapula is stout, being about one and one-half times the length of the coracoid (Fig. 7B). The medial end bears a robust pars acromialis that articulates with the clavicle and a pars glenoidalis that is about one-third the size of the pars acromialis. The suprascapular end of the scapula is about half the length of the bone and slightly smaller than the zonal end. The posterior margin of the scapula is anteriorly convex, whereas the leading edge bears a thick ridge along its central portion. The cleithrum is thick, well ossified, and synostotically united with the mineralized cartilage of the suprascapula.

**Pelvic girdle:** In dorsal aspect (Fig. 7C), the configuration of the ilial shafts of the pelvic girdle is a narrow U-shape, which is about twice as wide anteriorly as it is at the bases of the shafts. The ilial shaft is simple, with a short, poorly developed dorsolateral crest along the distal third of its length (Fig. 7D). The ilial prominence is broad, low, and scarcely evident. The preacetabulum is rounded in lateral aspect and forms

---

**Discussion**

**Osteological Data**

*Telmatobius* has proven to be a decidedly intractable group for anuran systematists, given the paucity of distinguishing external morphological characters. Lynch (1971) provided the initial osteological diagnosis of the genus, which was modified by Trueb (1979) in her treatment of the Ecuadorian members of the genus. Lynch also provided a useful figure of the cranium of *T. hauthali* (*T. hautholi* fide Lynch). Virtually no further progress was made until Wiens’ (1993) systematic treatment of *Telmatobius* in northern Peru. Wiens redescribed three species and described six new species, including an osteological description of each taxon. These works suggest that despite similarities in external morphology, there are osteological differences; however, in view of the documented intraspecific variation (e.g., Sinch et al., 2005), it is prudent to examine series of specimens when possible. Many more recent descriptions of new taxa, or redescriptions, included valuable osteological descriptions (*T. pinguiculus*-Lavilla and Laurent, 1988; *T. yuracare*-De la Riva, 1994; *T. yuracare*-De la Riva and Harvey, 2003; *T. vilamensis*-Formas et al., 2003; *T. chusmisensis*-Formas et al., 2006; and *T. rubigo*-Barriumeu and Baldo, 2009). Unfortunately, primary systematic revisions that have appeared (e.g., De la Riva, 2005; De la Riva et al., 2010; Correa et al., 2006) did not include osteological descriptions or discussions of osteological character transformations based on phylogenies. A review of the osteological evidence suggests that Sinch et al.’s (2005) determination that osteological characters were of little value may have been somewhat premature; these authors provided illustrations of the crania, hyoids, and partial sterna of several taxa (*T. carrillae*, *T. jelski*, *T. mayoloi*, and *T. rimac*), along with two species of *Batrachophrynus*. Below, we offer some
summary comparisons of T. mendelsoni with the 24 other taxa (more than a third of the 60 named taxa) for which there are data and illustrations in the literature (Appendix II). Our aim is to encourage researchers to include osteological data in their descriptions, and to provide osteological descriptions for taxa lacking this information, as Aguilar et al. (2012) have done recently for T. atahualpai. When comparing taxa, it is important to assure that comparisons of mature adults of the same sex are made. That obviously is not always possible when one extracts data from the literature. Thus, some of the following observations may prove to be incorrect in the future; nonetheless they represent a summary and point of departure for other studies.

Cranium: The skull is broader than long in all taxa except six — carrillae, chusmisensis, dankoi, degener, fronteriensis, ignavus, and vilamensis. The greatest width of the skull usually is at the level of the articulation of the quadratejugal with the maxilla; the greatest width is posterior to this level at the angle of the jaw (pars articularis) in only four species — carrillae, chusmisensis, fronteriensis, and vellardi. The rostrum is notably short in bolivianus, dankoi, ignavus, mendelsoni, philippii, and yuracare (20% or less than skull length), whereas in the remaining taxa it is longer (ca. 25-30% skull length).

The maxillary arcade is complete in all Telmatobius except T. carrillae and T. yuracare, and the maxilla and premaxilla bear fanglike, pedicellate teeth embedded in the labial mucosa. Reports of missing or reduced dentition based on examination of preserved, rather than skeletal specimens, should be accepted with caution because the teeth can be buried in the mucosa (Barrionuevo, pers. comm.). According to Aguilar and Valencia (2009), maxillary, premaxillary, and vomerine teeth are absent in T. carrillae, as well as in Batrachophrynus brachydactylus and B. macrostomus — two taxa that many authors find nested within, or closely related to, Telmatobius (e.g., Aguilar and Pacheco, 2005; Córdova and Descailleaux, 2005; Sinsch et al., 2005; Aguilar and Valencia 2009); they also are absent in T. dankoi. Telmatobius degener differs in lacking teeth on the premaxilla. Vomerine teeth are absent in T. carrillae, chusmisensis, dankoi, and rubigo, and Wiens (1993) noted that vomerine teeth are absent on one or both sides of some individuals of T. brevipes, degener, and truebae. The maxilla is exceptionally short in T. carrillae and T. degener; a transverse line superimposed on a dorsal view of the skull at the level of the pars articularis lies anterior to the otic capsule. In all of the remaining taxa except two (T. cirrhacelis and T. mendelsoni), a similar line transects the otic capsule at the level of the union of the anterior and posterior epiotic eminences or slightly posterior; however, in cirrhacelis and mendelsoni, the line lies posterior to the otic capsule, indicating the extraordinary length of the jaw in these species.

There is substantial variation in the development of the endocranium involving the extent of the ossification/mineralization of the sphenethmoid, prootics, and exoccipital in Telmatobius. In all adult Telmatobius, except T. vilamensis, the halves of the sphenethmoid are fused. The limits of the anterior ossification of the bone usually lie in the region of the nasal bones; however, in T. atahualpai, chusmisensis, cirrhacelis, degener, vellardi, and vilamensis, the bony sphenethmoid terminates at the level of the planum antorbitale at the anterior margin of the orbit. Sphenethmoid ossification extends into the planum antorbitale in all taxa except T. carrillae, chusmisensis, cirrhacelis, vellardi, and vilamensis; its presence in the otherwise poorly ossified T. degener is curious. The posterior limits of the bony sphenethmoid usually lie in the midorbital region, except in T. chusmisensis, cirrhacelis, and vellardi, in which the bone terminates in the anterior part of the orbit. The anterior margin of the optic fenestra is formed in cartilage in all taxa except T. dankoi, fronteriensis, mendelsoni, and thompsoni, in which the margin is bony.

In all taxa except Telmatobius carrillae, chusmisensis, cirrhacelis, vellardi, and vilamensis, the contralateral halves of the exoccipital are fused or otherwise solidly united by mineralization of the cartilaginous neurocranium. The exoccipital is fused to the prootic in all taxa except the latter four. The posterior half of the neurocranial roof is heavily mineralized and parietal foramina are absent in all taxa except T. carrillae, mayoloi, and vilamensis; the latter two taxa are the only known Telmatobius to bear separate parietal and frontal fontanelles. A large frontoparietal fontanelle (representing parietal and frontal fontanelles delimited by the taeniae tecti transversalis and medialis) occurs in T. atahualpai, carrillae, cirrhacelis, degener, and vellardi, and probably in T. chusmisensis and T. truebae. In the remaining taxa, the parietal fontanelles have been obliterated, leaving only a small frontal fontanelle. The frontoparietal bones are clearly distinct from one another medially in only five taxa — T. carrillae, cirrhacelis, mayoloi, mendelsoni, and vellardi. In the remaining taxa, the posteromedial boundaries of the frontoparietals are
obscured by their incorporation into the mineralized roof of the neurocranium.

The nasals in all *Telmatobius* tend to be moderately small, subtriangular bones that lack an articulation with the pars facialis of the maxilla; thus, the anterior margin of the orbit is incomplete in bone. The nasals are moderately separated from one another medially in most taxa. However, the bones are narrowly separated in *T. brevipes*, *cirrhacelis*, *thompsoni*, and *vellardi*, and widely separated in *T. atahualpai*, *dankoi*, *truebae*, and *vilamensis*; the bones are notably small in the latter species. The nasals either overlap the anterior part of the sphenethmoid or the margins of the nasals and bony sphenethmoid are closely juxtaposed in *T. brevipes*, *degener*, *fronteriensis*, *mendelsoni*, *niger*, *oxycephalus*, *rubigo*, and *sibiricus*. In *T. atahualpai*, *cirrhacelis*, *ignavus*, *latirostris*, *necopinus*, *thompsoni*, *truebae*, and *vellardi*, there are moderate to wide separations between the nasals and sphenethmoid, depending on the size of the nasals and the degree of ossification of the sphenethmoid. The extreme condition noted in *vilamensis*, reflects the hypo-ossification of this species.

The development of the plectral apparatus is variable in *Telmatobius*, both at the level of populations and individually. The stapes is reduced to a spherical nubbin of bone in *T. degener*, and is absent in *T. cirrhacelis*, *dankoi*, *fronteriensis*, *pinguiculus*, *vilamensis*, and *yuracare*. In *T. atahualpai*, *cirrhacelis*, *ignavus*, *latirostris*, *necopinus*, *thompsoni*, *truebae*, and *vellardi*, the stapes is present, but varies morphologically from the left to the right side in many individuals. Plectral development is normal in some individuals of *T. truebae*, whereas in others it varies bilaterally, and in *T. chusmisensis* and *T. niger*, the plectral apparatus varies from fully developed to absent. The plectral apparatus has been reported to be present and complete in *T. mendelsoni*, *oxycephalus*, *rubigo*, *sibiricus*, and *vellardi*. However, the accumulated evidence suggests that the presence, absence, and degree of development of the middle-ear apparatus is extraordinarily variable in *Telmatobius*; thus, its condition in any species should be assessed by examination of several individuals of both sexes.

The parasphenoid is a robust bone in all taxa, and in most, the alae tend to be synostotically united with the prootic and exoccipitals; thus, the posterior boundaries of the bone are obscured in many taxa. In two species, *Telmatobius cirrhacelis* and *rubigo*, the cultriform process is markedly long, terminating at the level of the planum antorbitale. In most of the other taxa, it terminates at the level of the orbitonasal foramina; however, in four (*T. atahualpai*, *ignavus*, *latirostris*, and *necopinus*) the cultriform process is noticeably short and terminates in the anterior part of the orbit posterior to the level of the orbitonasal foramina. With respect to shape, in most *Telmatobius*, the base (or “waist”) of the cultriform process is wider that the width of the process at the level of the mid-orbit and the optic fenestra; however, in five (*T. chusmisensis*, *cirrhacelis*, *mendelsoni*, *oxycephalus*, and *vellardi*), these dimensions are equal. The sides of the process usually are slightly convex; however, in *T. ignavus*, *latirostris*, *niger*, *rubigo*, and *vilamensis*, they are straight.

All *Telmatobius* have paired vomers that are broadly separated from the maxillary arcade except *T. dankoi* and *T. vilamensis*, which lack the bones. The vomers are small to moderate sized in most taxa; in *T. chusmisensis*, they are minute, whereas in *T. brevipes*, they are large. The presence/absence of vomerine teeth is described above. In at least one species (*T. rubigo*), dentigerous processes are present, but teeth are absent; in another, *T. chusmisensis*, the dentigerous process of the vomer is absent. *Telmatobius yuracare* differs from its congeners in apparently lacking pre- and postchoanal processes on the vomer. Depending on the anterior extent of the ossification of the ventral sphenethmoid and the size of the vomers, the vomers are broadly separated from the ossified sphenethmoid (*T. chusmisensis*, *cirrhacelis*, *degener*, *fronteriensis*, and *vellardi*), juxtaposed to the anterior margin of the sphenethmoid (*T. atahualpai*, *brevipes*, *ignavus*, *necopinus*, and *truebae*), or overlapping the sphenethmoid (*T. brevipes*, *mendelsoni*, *latirostris*, *niger*, *oxycephalus*, and *sibiricus*).

The suspensory apparatus of *Telmatobius* may have a unique combination of attributes distinguishing it from those of other anurans. First, the anterior ramus of the pterygoid tends to be robust and terminates near the planum antorbitale in all taxa. The anterior ramus is closely associated with the neopalatine in all but the hypo-ossified members of the genus (*T. chusmisensis*, *degener*, *vilamensis*) and the separation between the elements in these taxa seems to reflect the small size of the neopalatine, rather than reduction of the anterior ramus of the pterygoid. In nearly all taxa, the medial and posterior arms of the pterygoid are about equal in length; the medial ramus is longer than the posterior in *T. atahualpai*, *ignavus*, and *sibiricus*, whereas the medial ramus is shorter than the posterior in *T. carrillae*, *rubigo* and *vilamensis*. The relatively short medial ramus articulates with the anterolateral margin of the ventral otic capsule. Owing to mineralization of this region, it is difficult
to determine whether the medial ramus articulates with the parasphenoid ala; in most, it apparently does not.

In nearly all anurans, the ventral terminus of the palatoquadrate cartilage between the quadratojugal and the posterior ramus of the pterygoid becomes mineralized as the pars articularis, the articular surface for the mandible. In many, perhaps most, *Telmatobius*, this area of the cartilaginous palatoquadrate seems to have been replaced by endochondral bone that either articulates with the adjacent quadratojugal or is synostotically united with this dermal element. An elaboration of the pterygoid provides an articulation of this element with the anterior face of the ossified palatoquadrate — a condition that we have not observed in other anurans.

The squamosals of *Telmatobius* are modestly developed. There is a ventral ramus that invests the posterolateral margin of the palatoquadrate. The zygomatic ramus is slender and widely separated from the maxilla. The otic ramus typically is a short spur of bone that resides adjacent to the anterolateral corner of the cartilaginous crista parotica. In no species observed to date is there an otic plate covering the cartilaginous or ossified crista parotica.

*Hyolaryngeal apparatus*: For many species of *Telmatobius* (*T. mendelsoni* included), the hyoid apparatus was not preserved from specimens during the preparation of dry skeletons; thus, information is available for only a few taxa. Nonetheless, it is apparent that the corpus of the hyoid tends to be markedly wider at midlength than it is long — usually by a factor of 2-3 times wider than long. The two exceptions noted are *T. fronteriensis* and *T. chusmisensis*, in which the width and length of the corpus are about equal. Among the remaining taxa, the midlength of the corpus seems to be correlated with the size of the hyoglossal sinus, with a deeper (longer) sinus being associated with a reduced length of the corpus. All have anterolateral and posterolateral processes that tend to be slender, rather than heavy and spatulate. The posteromedial processes are markedly robust and long. Although they lack lateral flanges, they tend to be elaborated anteromedially, and frequently united at the base of the corpus by mineralization. The intrageneric variation in the sizes of the tongues and their attachment to the floor of the mouth suggests that the feeding mechanisms of these anurans should be explored, especially with respect to the nature of their teeth and the unusual configuration of the jaw suspension.

*Axial column*: The vertebral column in *Telmatobius* is composed of eight procoelous presacral vertebrae, with Presacrals II-VIII being non-imbricate. The sacrum has a bicondylar articulation with the urostyle. (Data for other variables are unknown in *T. rubigo* and *T. sibiricus*, for which illustrations are unavailable.) Variation in the presacral portion of the axial column involves the structure of Presacral I and its relationship with Presacral II, as well as the lengths of the transverse processes. The first two presacrals are imbricate in only four taxa — *T. fronteriensis*, *ignavus*, *niger*, and *thompsoni*. They are partially imbricate in *brevipes* and *mendelsoni*, and non-imbricate in the remaining taxa. In one species, *T. cirrhacelis*, the dorsal part of the neural arch of Presacral I is incompletely ossified. Presacral III is markedly wider than Presacral IV in all taxa except *T. chusmisensis* and *T. vilamensis*, in which the transverse processes of the two vertebrae are about equal in length. Presacral III is clearly wider than the sacrum in all taxa except *T. atahualpai*, *degener*, and *latirostris*, in which the structures are about equal in width. These differences reflect the tendency for these frogs to have narrow sacral diapophyses, rather than exceedingly wide transverse processes on the anterior presacrals. Overall, the sacral diapophyses are not dilated or only slightly dilated. Most have a posterolateral orientation. However, the diapophyses are perpendicular to the midline in *cirrhacelis*.

Some patterns emerge in the configuration of the posterior half of the vertebral column in *Telmatobius*. In six taxa (*T. brevipes*, *degener*, * fronteriensis*, *latirostris*, *truebae*, and *vellardi*), the transverse processes of Presacrals V-VIII are relatively short (i.e., lengths about half the width of the central parts of the vertebrae); in all of these taxa the transverse processes are clearly shorter than those of Presacral IV and the sacral diapophyses. A second group of seven taxa (*T. atahualpai*, *chusmisensis*, *cirrhacelis*, *ignavus*, *mendelsoni*, *niger*, and *oxycephalus*) differs from the first group in having longer transverse processes on the posterior presacrals; they are about equal to the overall width of the central parts of the vertebrae. Outliers to these two groups are *T. necopinus*, *thompsoni*, and *vilamensis*. In *necopinus*, the length of the transverse processes on Presacral IV are short and about equal in length to those of the posterior vertebrae; in other features this taxon resembles the first group described. Similarly, *thompsoni* resembles the first group, save for the exceedingly short sacral diapophyses, which are equivalent in length or perhaps shorter than the transverse processes of Presacrals.
V-VIII. The vertebral column of vilamensis seems to be the most deviant. The transverse processes of all presacrals are long, and those of Presacrals II-VII nearly equal in length and wider than the sacral diapophyses.

Pectoral girdle and humerus: Pectoral girdles have been illustrated for only a few taxa of Telmatobius — atahualpai, chusmisensis, fronteriensis, mendelsoni, oxycephalus, sibiricus, simonsi, vilamensis, and yuracare. The girdle is arciferal and in all of these taxa, the anterior part of the sternal plate is heavily mineralized or ossified. The coracoids are moderately short, stout bones that are equally expanded at their sternal and glenoid ends, with the expansion being about twice the width of the midshaft. The clavicles are particularly well developed; each bone provides a wide protective sheath to the leading edge of the procoracoid cartilage, and widens laterally to a broad articulation (and perhaps fusion in some taxa) with the pars acromialis of the scapula; in most taxa there seems to be a bony articulation with the coracoid at the margin of the glenoid fossa.

The scapulae are robust elements in Telmatobius; they tend to be short (not much longer than the coracoids) and thick. The partes acromialis and glenoidalis are well developed, with the pars acromialis having a broad articulation (and sometimes fusion) with the clavicle, and the pars glenoidalis forming a substantial part of the glenoid fossa. In several taxa (e.g., T. atahualpai, chusmisensis, mendelsoni, oxycephalus, and rubigo), the leading (i.e., anterior) edge of the scapula is hypertrophied.

Mineralization of the suprascapular cartilage and zonal elements is pervasive in Telmatobius. Typically the epicoracoid and procoracoid cartilages are partially mineralized, along with the base of the slender omosternum. Likewise, the sternum invariably seems to be heavily mineralized to produce a broad proximal bony plate that bifurcates distally into a pair of broad, stumplike cartilaginous processes.

The humeri of only a few species of Telmatobius have been illustrated. These include T. atahualpai, bolivianus, oxycephalus, rubigo, and yuracare. In these taxa, the humerus of the male bears expanded, laminate medial and lateral crests. In addition, there is a deltoid crest on the venter of the humerus. In T. atahualpai, oxycephalus, and rubigo, the deltoid crest is a moderately expanded plate of bone than extends along the proximal half of the humerus. Male T. bolivianus, mendelsoni, and yuracare differ from the former in having the deltoid crest modified into a massive, recurved spine. This is evident in the X-ray of T. mendelsoni (as well as in Fig. 2) and is well illustrated for T. bolivianus (Lavilla and Sandoval, 1999: fig. 7) and T. yuracare (De la Riva, 1994: fig. 4). The humerus of female T. mendelsoni lacks the laminate medial and lateral crests entirely, and has a modestly developed deltoid crest that lacks a spinous process.

Pelvic girdle: The pelvic girdles of Telmatobius are fairly remarkable in their uniformity. They have round ilial shafts that usually bear a low dorsolateral crest along part of their margin. The ilial prominence is evident in all taxa that have been illustrated. The preacetabular angle in most taxa is about 90°; however, it appears slightly acute in T. ignavus, latirostris, necopinus, and vellardi. There is variation in the development of the ischial crest. It is low (i.e., height of ilial prominence) in T. latirostris and T. vellardi, and high in T. fronteriensis, mendelsoni and vilamensis; in the remaining taxa it is moderate (i.e., slightly higher than ilial prominence). The pubis is mineralized/ossified in all taxa except T. cirrhacelis, vellardi, and vilamensis. The acetabulum varies from subcircular/ovoid (T. necopinus, niger, oxycephalus, vellardi, vilamensis) to cordiform in the other taxa that have been illustrated (T. brevipes, cirrhacelis, degener, fronteriensis, ignavus, mendelsoni, thompsoni, and truebae).

Manus and pes: The carpus and tarsus has only been described for three species of Telmatobius — fronteriensis, oxycephalus, and vilamensis. In each the pattern is the same, with the carpus being composed of the ulnare, radiale, Element Y, Distal Carpal 2, a fused element representing Distal Carpals 3-5, and a prepollex composed of two bones. The tarsus comprises Element Y, Distal Tarsal 1, and a compound bone representing Distal Tarsals 2 and 3. In T. oxycephalus, there is a prehallux composed of a proximal bone and two distal cartilaginous elements.

Relationships

Given the data at hand, the relationships of Telmatobius mendelsoni to other members of the genus cannot be ascertained. We are still far from having a comprehensive phylogeny of Telmatobius, and we lack complete and comparable data for many of the taxa that have been described. De la Riva (2005) defined several species groups within Bolivian Telmatobius; these groups correspond with well-supported
quent field surveys by Catenazzi in 2008, 2009, and until July 2007; the species was not found in subsequent surveys along the road, and it was observed regularly in the area of the Kosñipata valley. It was a common species. It has been described in 2005, 2007; Catenazzi et al., 2010, 2011). Possibly Telmatobius mendelsoni (and T. timens) are not extinct, but their existence remains to be confirmed.

Species of Telmatobius in the puna and dry Andean highlands are known to be infected by Batrachochytrium dendrobatidis (Bd), but populations persist with the fungus, whereas species living in humid paramos and forests seem to have been completely extirpated since the arrival of Bd (De la Riva and Burrowes, 2011). However, Telmatobius mendelsoni has been observed as recently as 2007 and has a considerable elevational range, reaching the lowest elevation of any Peruvian Telmatobius (Lehr, 2005). Therefore, it is possible that some individuals may exist at the lowest elevations, where Bd is less prevalent than at higher elevations. In all, we consider that Telmatobius mendelsoni must be categorized as Critically Endangered following the criteria of the IUCN.

Conservation

In spite of the fact that Kosñipata Valley lies within an immense and important preserved area, Parque Nacional Manu, amphibians there are in peril. Catenazzi et al. (2011) reported a disastrous collapse of amphibian fauna in the upper elevations of the park as a result of chytridiomycosis, which has led to a loss of 36% of the anuran species between 1999 and 2009. Telmatobius are known to be especially susceptible to chytridiomycosis (De la Riva and Lavilla, 2008) and there are several reports of species infected in southern Peru (Seimon et al. 2005, 2007; Catenazzi et al. 2010, 2011). Telmatobius mendelsoni has been known for a long time by herpetologists working in the area of the Kosñipata Valley. It was a common species along the road, and it was observed regularly until July 2007; the species was not found in subsequent field surveys by Catenazzi in 2008, 2009, and 2010 (Catenazzi et al. 2011; A. Catenazzi, in litt.). Likewise, T. timens, which was once common in the upper part of the valley (Abra Acanaco) seems to have vanished as well (Von May et al., 2008; Catenazzi et al., 2011). Telmatobius mendelsoni and T. timens are described as critically endangered in the IUCN Red List.

Resumen

Se describe una nueva especie de Telmatobius de bosques de niebla del valle del Río Kosñipata en la Cordillera de Paucartambo, Región de Cusco, Perú, donde habita en arroyos y cunetas inundadas. La nueva especie está entre los más grandes Telmatobius conocidos. Posee un rostro corto y una larga mandíbula. Los machos tienen callosidades nupciales compuestas de espículas pequeñas y muy juntas. osteológicamente, la nueva especie se distingue por la inusual osificación del endocráneo. El esfenetmoide está sinostóticamente unido con el proótico, y la osificación/mineralización del techo dorsal del neurocráneo elimina las fontanelas parietales, dejando sólo una pequeña fontanela frontal. Se proporcionan comparaciones osteológicas entre la nueva especie y las 24 otras especies de Telmatobius para las cuales hay información disponible en la bibliografía. La evidencia preliminar sugiere que el aparato suspensorio de Telmatobius puede presentar una combinación única de rasgos que lo distinguen de otros anuros. La nueva especie es superficialmente similar a miembros del grupo de Telmatobius bolivianus, pero sus relaciones filogenéticas son desconocidas. Muchos anfibios de la zona de la localidad tipo han sufrido un severo declive, y la nueva especie, no vista desde 2007, se considera Críticamente Amenazada.
ACKNOWLEDGMENTS

We are grateful to A. Catenazzi, J. C. Chaparro, J. S. Barrionuevo, O. Aguilar, and L. O. Rodríguez for providing data on the species described herein; C. Aguilar (MHNC) and D. Kizirian (AMNH) facilitated access to the collections under their care, and D. Kizirian provided a digital x-ray of the new species. The distribution map was prepared by Charles Linkern. This research was funded by projects CGL2005-03156 and CLG2008-04164 of the Spanish Ministry of Science and Innovation (I. De la Riva, Principal Investigator), and finished during a sabbatical year at James Cook University funded by Programa Nacional de Movilidad de Recursos Humanos del Plan Nacional de I-D+i 2008-2011. Duellman’s fieldwork was supported by grants (GB 42481 and DEB 76-09986) from the National Science Foundation, USA.

LITERATURE CITED


APPENDIX I

Specimens examined

*Museum codes:* The Natural History Museum, London, United Kingdom (BMNH); Colección Boliviana de Fauna, La Paz, Bolivia (CBF); Field Museum of Natural History, Chicago, USA (FMNH); Museum of Natural History, The University of Kansas, Lawrence, USA (KU); Museo de Historia Natural, Cusco, Peru (MHNC); Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN); Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia (NK); Smithsonian Institution, National Museum of Natural History, Washington, USA (USNM).

*Telmatobius bolivianus* – BOLIVIA: La Paz: Chaco, BMNH 1940.4.3.83 (holotype); Chusipata, CBF 2072 (holotype of *Telmatobius ifornoi*); Río Unduavi, MNCN 43547, 43592-93.

*Telmatobius necopinus* – PERU: Amazonas: east slope of Abra Pardo de Miguel, 39 km ENE Pomacochas, KU 212482 (holotype), 212481, 212483 (paratypes).


*Telmatobius sibiricus* – BOLIVIA: Cochabamba: Río Chua Kocha, NK A965 (holotype), MNCN 23830-32 (paratypes); El Empalme, NK A3573 (paratype).

*Telmatobius simonsi* – BOLIVIA: Chuquisaca: Sucre, BMNH 1947.2.1493 (holotype), 1947.2.1495-96 (paratypes); Cochabamba: 3 km S Epizana, KU 160130-34; Santa Cruz: Vallegrande, NK A229-30; El Chapé, MNCN 23833.


*Telmatobius yuracare* – BOLIVIA: Cochabamba: Sehuencas, NK A511-13 (paratypes); La Siberia, MNCN 16645; Río Apaza, MNCN 16646; Incachaca, MNCN 43552.
### Appendix II

Species descriptions and accounts that include osteological illustrations of *Telmatobius*. A dash indicates absence of illustrations from which determinations could be made.

<table>
<thead>
<tr>
<th>Species of Telmatobius</th>
<th>Skull</th>
<th>Hyoid</th>
<th>Vertebral column</th>
<th>Pectoral girdle</th>
<th>Pelvic girdle</th>
<th>Humerus</th>
<th>Hand and foot</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>atahuallpa</em></td>
<td>Aguilar et al., 2012</td>
<td>—</td>
<td>Aguilar et al., 2012</td>
<td>—</td>
<td>Aguilar et al., 2012</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>carrillae</em></td>
<td>Sinsch et al., 2005</td>
<td>Sinsch et al., 2005</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>chusmisensis</em></td>
<td>Formas et al., 2006</td>
<td>Formas et al., 2006</td>
<td>Formas et al., 2006</td>
<td>Formas et al., 2006</td>
<td>—</td>
<td>Formas et al., 2006</td>
<td>—</td>
</tr>
<tr>
<td><em>cirrhacelis</em></td>
<td>Trueb, 1979</td>
<td>—</td>
<td>Trueb, 1979</td>
<td>—</td>
<td>Trueb, 1979</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>fronteriensis</em></td>
<td>Benavides et al., 2002</td>
<td>Benavides et al., 2002</td>
<td>Benavides et al., 2002</td>
<td>Benavides et al., 2002</td>
<td>—</td>
<td>Benavides et al., 2002</td>
<td>—</td>
</tr>
<tr>
<td><em>haithali</em></td>
<td>Lynch, 1971</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>jelskii</em></td>
<td>Sinsch et al., 2005</td>
<td>Sinsch et al., 2005</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>mayoloi</em></td>
<td>Sinsch et al., 2005</td>
<td>Sinsch et al., 2005</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>mendelsoni</em></td>
<td>This study</td>
<td>—</td>
<td>This study</td>
<td>This study</td>
<td>This study</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>niger</em></td>
<td>Trueb, 1979</td>
<td>—</td>
<td>Trueb, 1979</td>
<td>—</td>
<td>Trueb, 1979</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>oxycephalus</em></td>
<td>Barriónuevo, MS</td>
<td>Barriónuevo, MS</td>
<td>Barriónuevo, MS</td>
<td>Barriónuevo, MS</td>
<td>—</td>
<td>Barriónuevo, MS</td>
<td>—</td>
</tr>
<tr>
<td><em>rimac</em></td>
<td>Sinsch et al., 2005</td>
<td>Sinsch et al., 2005</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>rubigo</em></td>
<td>Barriónuevo and Baldo, 2009</td>
<td>Barriónuevo and Baldo, 2009</td>
<td>—</td>
<td>Barriónuevo and Baldo, 2009</td>
<td>—</td>
<td>Barriónuevo and Baldo, 2009</td>
<td>—</td>
</tr>
<tr>
<td><em>sibiricus</em></td>
<td>De la Riva and Harvey, 2003</td>
<td>De la Riva and Harvey, 2003</td>
<td>—</td>
<td>De la Riva and Harvey, 2003</td>
<td>—</td>
<td>De la Riva and Harvey, 2003</td>
<td>—</td>
</tr>
<tr>
<td><em>simonsi</em></td>
<td>De la Riva and Harvey, 2003</td>
<td>De la Riva and Harvey, 2003</td>
<td>—</td>
<td>De la Riva and Harvey, 2003</td>
<td>—</td>
<td>De la Riva and Harvey, 2003</td>
<td>—</td>
</tr>
<tr>
<td><em>vellardi</em></td>
<td>Trueb, 1979</td>
<td>—</td>
<td>Trueb, 1979</td>
<td>—</td>
<td>Trueb, 1979</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>vilamensis</em></td>
<td>Formas et al., 2003</td>
<td>Formas et al., 2003</td>
<td>Formas et al., 2003</td>
<td>Formas et al., 2003</td>
<td>—</td>
<td>Formas et al., 2003</td>
<td>—</td>
</tr>
<tr>
<td><em>yuracare</em></td>
<td>De la Riva, 1994</td>
<td>De la Riva, 1994</td>
<td>—</td>
<td>De la Riva, 1994</td>
<td>—</td>
<td>De la Riva, 1994</td>
<td>—</td>
</tr>
</tbody>
</table>