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A new species of *Telmatobius* (Anura, Ceratophryidae) from Northern Jujuy Province, Argentina

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Abstract

We describe a new species of frog of the genus *Telmatobius* from Laguna de Los Pozuelos basin in the northernmost region of Argentina in Jujuy province. Osteological, larval and karyological characters are also included. *Telmatobius rubigo* **sp. nov.**, was previously referred as *T. marmoratus*, from which is easily distinguishable by the coloration pattern of adults, metamorphs and tadpoles, and other morphological features. The new taxon is compared with the other species from Argentina and from the neighboring Andean regions of Bolivia and Chile.

Key words: Andean region; *Telmatobius* new species, external morphology, osteology, tadpoles, karyotype

Resumen

Describimos una nueva especie de rana del género *Telmatobius* proveniente de la cuenca de Laguna de Los Pozuelos en el extremo norte de la provincia de Jujuy, Argentina. Incluimos además, una descripción osteológica, larval y cariológica de la especie. *Telmatobius rubigo* **sp. nov.**, fue previamente asignada a *T. marmoratus*, de la cual es fácilmente distinguible por los patrones de coloración de adultos, metamorfos y larvas y algunos otros caracteres morfológicos. El nuevo taxón es comparado con las otras especies de Argentina y de las regiones próximas de los Andes de Bolivia y Chile.

Palabras clave: Región andina, *Telmatobius* nueva especie, morfología externa, osteología, renacuajo**,** cariotipo

Introduction

The genus *Telmatobius* Wiegmann is an important component of the Andean Herpetofauna, reaching some of the highest altitude environments suitable for amphibians at more than 5200 m (Seimon *et al*. 2007). Currently, it comprises 57 aquatic species that occupy different types of mountain freshwater habitats from Ecuador to Argentina (Frost 2008). In Argentina 13 species have been described, especially after R. Laurent prompted the study of the genus in the 1970´s (Laurent 1970a, 1970b, 1973, 1977), which inhabit three distinctive environments: (1) The highlands, Puna or Altiplano; (2) intermediate altitude valleys; and (3) cloud forest above 1300 m. The taxonomy of these frogs has been complex since the early work of Parker (1940) and Vellard (1951, 1953, 1955, 1960, 1969 "1968"), especially due to intrinsic characteristics of *Telmatobius* that includes a lack of clear diagnostic characters and a high degree of intraspecific variation that blur species boundaries. This problem, in addition to the typological criteria for describing species, have

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generated a myriad of subspecies, many of them recently synonymized (Sinsch *el al.* 1995, Benavides *et al.* 2002a). Besides the 13 species endemic from Argentina, many researchers cited *Telmatobius marmoratus* (Duméril and Bibron) for Jujuy province, at Santa Catalina (Parker 1940), Abra Pampa (Cei 1959) and La Quiaca (Gallardo 1962). Gallardo (1962) attributed the specimens cited by Fernández (1926) as *T. aemaricus* Cope, from Villa Cueva (Iturbe) and those considered by Anderson (1906) as *T. jelskii* (Peters) from El Moreno to the species *T. marmoratus* (Lavilla & Barrionuevo, 2005). The specimens from El Moreno were posteriorly described as *Telmatobius hypselocephalus* Lavilla and Laurent and *T. platycephalus* Lavilla and Laurent (Lavilla & Laurent 1989 "1988"). During recent expeditions we collected fresh material of *Telmatobius* in the northernmost region of Jujuy Province in Argentina. The comparison with museum specimens and published descriptions led us to conclude that the populations of *Telmatobius* from the endorheic basin Laguna de Los Pozuelos, Jujuy, previously referred as *T. marmoratus* constitute a new taxon. In the present contribution we described this new species and provided a comparison with other species from Argentina, Southern Bolivia and northern Chile. We also describe the larvae, the karyotype, and we comment the variation and distribution of this new taxon.

Materials and methods

Types and referred specimens are deposited at Fundación Miguel Lillo (FML), Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina (MACN), Museo de La Plata, Argentina (MLP A), and Diego Baldo Collection housed at Museo de La Plata, Argentina (MLP DB). Specimens examined in addition to the new species are listed in Appendix I. We compared the new species described herein mainly with neighboring taxa present in highlands habitats of Northern Argentina (*T. atacamensis* Gallardo, *T.* aff. *marmoratus, T. hypselocephalus* and *T. platycephalus)*, Southern Bolivia (*T. marmoratus, T. huayra* Lavilla & Ergueta-Sandoval) and northern Chile (*T. chusmisensis* Formas, Cuevas and Nuñez, *T. dankoi* Formas, Northland, Capetillo, Nuñez, Cuevas and Brieva, *T. fronteriensis* Benavides, Ortiz & Formas, *T. halli* Noble, *T. phillippi* Cuevas and Formas and *T. vilamensis* Formas, Benavides and Cuevas). We also compared the new taxon with Argentinean species from subparamo valleys and cloud forests (*T. ceiorum* Laurent, *T. contrerasi* Cei, *T. hauthali* Koslowsky, *T. laticeps* Laurent, *T. oxycephalus* Vellard, *T. pinguiculus* Lavilla and Laurent, *T. pisanoi* Laurent, *T. schreiteri* Vellard, *T. scrocchii* Laurent and Lavilla, and *T. stephani* Laurent). The characters of Chilean species were gathered from the original descriptions (Noble 1938, Formas *et al.* 1999, 2003, 2006, Benavides *et al.* 2002b, Cuevas & Formas 2002). The diagnosis and species description follows De la Riva and Harvey (2003) and De la Riva *et al.* (2005). All the measurements done in this work are expressed in milimeters (mm) and were measured with digital callipers to the nearest 0.1 mm. Measurements of adult specimens are: snout-vent length (SVL), head width (HW), head length (HL), eye diameter (ED), interorbital distance anteriorly (IOD), eyelid width (EW), eye-nostril distance (END), internarial distance (IND), snout length (SL), eye-mouth distance (EMD), nostril-mouth distance (NMD), body width (BW), body height (BH), hand length (HAL), radio-ulna length (RUL, from flexed elbow to wrist), radio-ulna width (RUW), femur length (FEL), tibia length (TL), foot length (FOL), web length (WL, from proximal edge of inner metatarsal tubercle to the III–IV toe web), inner metatarsal tubercle length (IMTL), outer metatarsal tubercle length (OMTL).

Webbing formulae are those provided by Savage and Heyer (1967) as modified by Myers and Duellman (1982). The webbing formula in *Telmatobius* generally cannot be scored according to web position between toes I and II with respect to toe II, and between toes II and III with respect to toe III, as there are no subarticular tubercles. That situation was indicated as--in the formula.

The osteological description is based on an adult male (FML 20829) (SVL = 47.0 mm), since the number of specimens collected precluded the use of more individuals. The skeleton of this specimen was stained and cleared following Wassersug (1976).

Larvae description is based on nine specimens (FML 21157), at stages 33–37 (Gosner, 1960), collected at the type locality on 15 January 2005 by Y. Arzamendia, D. Baldo, J. Baldo, S. Barrionuevo, D. Casagranda and A. Dallagnol. These tadpoles were found along with adults of *Telmatobius* sp nov., and no other species of *Telmatobius* was collected at this site. In addition, tadpoles in advanced stages of development and metamorphs exhibit the same dorsal coloration pattern than the adults. Tadpoles were anesthetized and fixed in 10% formalin. Morphological terminology follows Altig and McDiarmid (1999). Nine morphometric variables were recorded following to Lavilla and Scrocchi (1986); total length (TL), body length (BL), tail length (TAL), body width (BW) body height (BH), interorbital distance (IOD, measured between internal margins of pupils) internarial distance (IN, measured between the internal edges of narial apertures), eye-narial distance (EN) and narial-snout distance (NS).

Mitotic and meiotic chromosomes were obtained from cell suspensions of bone narrow, intestine, and testes following Schmid (1978), after an intraperitoneal injection of 0.1 ml of colchicine 0.03% every 10g of body mass, about 18 h before being killed. The individuals karyotyped were one adult male (MLP DB 3614) one subadult female (MLP DB 3621), and two juveniles (MLP DB 3622, 3650), all of them paratopotypes. Chromosome number and morphology were studied on conventional Giemsa stained preparations and observed using a photomicroscope OLYMPUS BX50F-3, and a videocamera SONY ExwaveHAD. Ag-NOR staining method was done following Howell and Black (1980). We used X for basic chromosome number, N for gametic chromosome number, 2N for somatic chromosome number, and FN for fundamental number, as suggested by White (1954). Chromosomes were arranged and classified following Levan *et al*. (1964) as modified by Green and Sessions (1991).

Results

Telmatobius rubigo sp. nov.

(Fig. 1–2)

1926. *Telmatobius aemaricus* (non Cope, 1874): Fernández, 1926: 277 [part.].
1940. *Telmatobius marmoratus* (non Dumeril & Bibron, 1841): Parker, 1940: 207 [part.].
1980. *Telmatobius marmoratus* (non Dumeril & Bibron, 1841): Cei, 1980: 255 [part.].

Holotype. Fundación Miguel Lillo, Tucumán, Argentina. (FML 20828), adult male, from Argentina: Jujuy: Departamento Santa Catalina: El Queñoal (21º52'17.5''S, 66º06'09,2''W, 3966 m a.s.l.), collected on 15 January 2005 by Y. Arzamendia, D. Baldo, J. Baldo, S. Barrionuevo, D. Casagranda and A. Dallagnol.

Paratopotypes. FML 20829 (male, cleared and stained), MACN 39092 (male), FML 20827, MACN 39093, MLP DB 3615, 3621 (females) and FML 20830-5, MACN 39094, MLP DB 3622, 3648 (juveniles), with same data as the Holotype.

Referred specimens. FML 4391 (1 male, 3 females, 1 sub-adult, 2 juveniles), from Argentina: Jujuy: Departamento Rinconada: Cuesta de Fundiciones, northeastern slop (22º29'S, 66º16', 3800 m a.s.l.); FML 2813 (4 males and 2 females); FML 2814 (2 males, 4 females and 1 juvenile); FML 2818 (2 males, 5 females and 1 juvenile), from Argentina: Jujuy: Departamento Santa Catalina: Timón Cruz (22º12'S, 66º10'W, 4200 m a.s.l.), 25 April 1980; FML 4517 (1 male, 3 females and 2 sub-adults), from Argentina: Jujuy: Departamento Santa Catalina: Arroyo Farallón, north of Laguna de Los Pozuelos, 20 January 1989; MLP A 4710 (juvenil), MLP DB 4755-6, 4765, from Argentina: Jujuy: Departamento Santa Catalina: Santa Catalina, Santa Catalina River (21º55'00''S, 66º03'00''W, 3810 m a.s.l.), 6 January 2006; MLP DB 3457-9, 3576-8 (juveniles), from Argentina: Jujuy: Departamento Santa Catalina: Santa Catalina, Santa Catalina River (21º55'00''S, 66º03'00''W, 3810 m a.s.l.), 21 November 2004; 6 January 2006; 4766 (male), 4812 (tadpoles), from Santa Catalina, Provincial Road Nº 5, 2 Km eastearn from Santa Catalina (21º56'58,2''S, 66º02'21,6''W, 3802 m a.s.l.), 6 and 26 January respectively. MLP DB 4760 (tadpoles), from Argentina: Jujuy Province: Santa Catalina Departament: El Queñoal (21º52'17.5''S, 66º06'09,2''W, 3966 m a.s.l.), 7 January 2006.

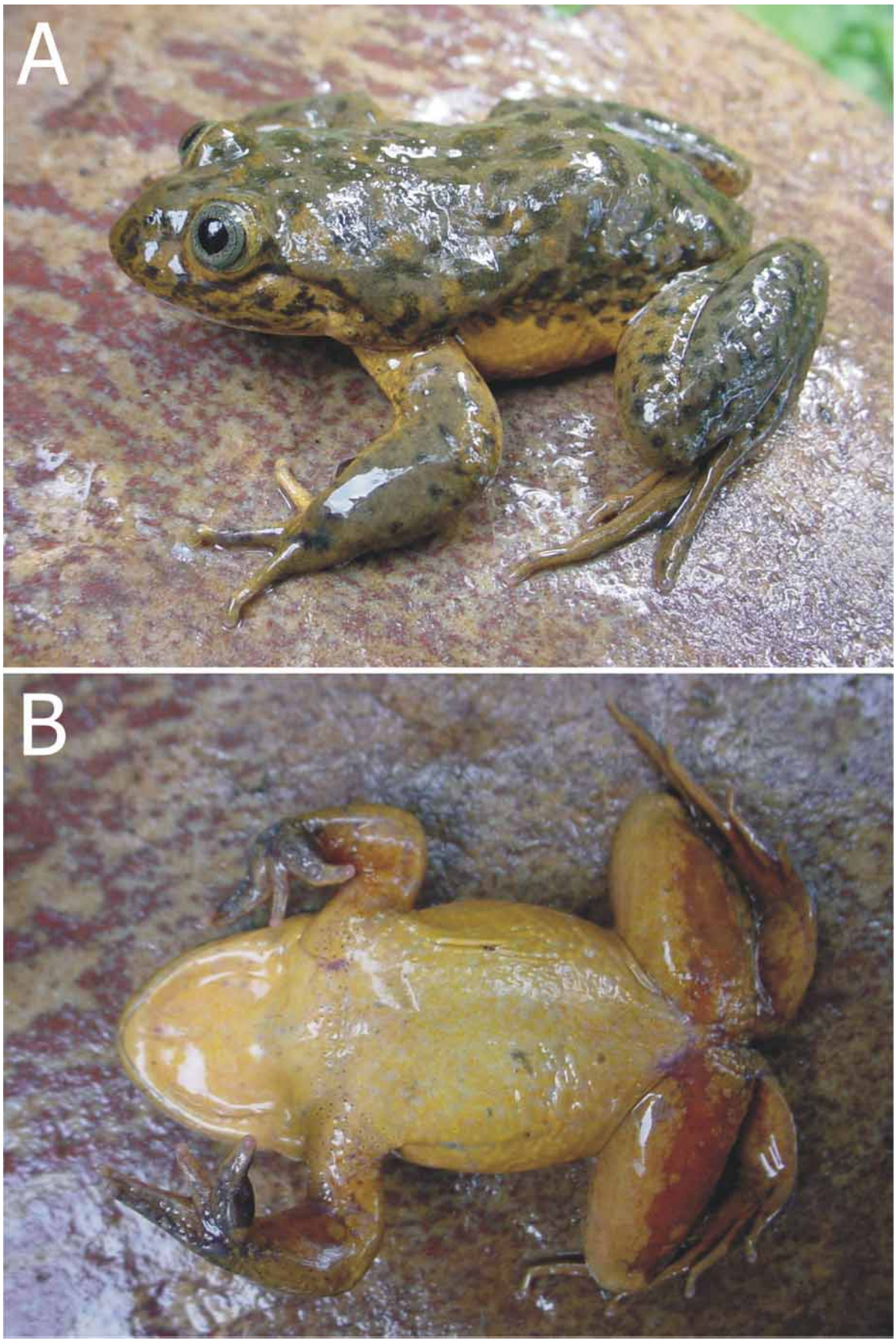

FIGURE 1. (A) Dorsal and (B) ventral view of the holotype of *Telmatobius rubigo* (FML 20828).

FIGURE 2. General dorsal view (A, bar = 10 mm); dorsal (B, bar = 5mm) and (C, bar = 5mm) lateral view of head; right hand (D, bar = 5mm), detail of nuptial excrescences (E, bar = 1mm), and right foot (F, bar = 5mm) of the holotype of *Telmatobius rubigo* (FML 20828).

Etymology. The word *rubigo* is a Latin noun meaning rust, in allusion to the characteristic lichenous rusty blotches in the dorsal skin of this new species. The species name is used as noun in apposition to the genus name.

Diagnosis and comparison with other species. We assign this new taxon to *Telmatobius* genus based on the presence of presumptive synapomorphies as nuptial pad in the thumb only, frontoparietals fused posteriorly (Wiens, 1993) and fanglike teeth embedded in the labial mucosa (Trueb, 1979). *Telmatobius rubigo* can be distinguished from any other species of *Telmatobius* by the following combination of characters: (1) snout–vent length (SVL) of males to 50.4 mm, females to 52.2 mm; (2) head in lateral profile variable (depressed or high) with sloping snout; (3) head subacuminate in dorsal view; (4) upper lips flared, notched medially; (5) postcommisural gland absent or a set of small, separated glands; (6) tympanic annulus visible under the skin in the most of specimens; (7) forelimb of males moderately robust, without humeral spine; (8) dermal fringes of finger variable; base of thumb bearing nuptial pad in contact with the inner palmar tubercle; nuptial spicules small, closely arranged; (9) toes moderately webbed; plantar surface without spicules; (10) tarsal fold present; (11) skin smooth with pustules in the flanks and dorsal surface of thighs; (12) in life greenish-grey dorsum, uniform or with darker gray blotches, always scattered with rusty lichenous blotches; (13) belly pale orange, ventral surfaces of limbs bright orange, yellow and reddish; and (14) iris light grey without flecks; (15) skull well ossified; (16) frontoparietal fenestra bottle shape; (17) zygomatic ramus of squamosal long, slim and bended medially; (18) anterior end of cultriform process irregularly truncate and reaching the level of vomers; (19) posterior half of maxilla slim and straight in lateral view; (20) premaxilar alae inclined posteriorly in lateral view; (21) pars media plectri (columella) very thin; (22) hyoid plate extensively calcified; (23) clavicle and scapula fused; (24) tadpole without intramarginal mental papillae in the oral disc; (25) color in life of larvae brownish with characteristic bright yellow spots.

Telmatobius rubigo differs from all the other species analyzed here by having dorsal skin scattered with rusty orange lichenous blotches, although the color in life of *T. halli* is unknown (Noble, 1938; Formas *et al.*, 2003). *Telmatobius rubigo* differs from *T. atacamensis, T.* aff. *marmoratus, T. huayra, T. marmoratus, T. chusmisensis, T. fronteriensis, T. phillipi* and *T. vilamensis* in exhibiting bright orange and yellow coloration on the ventral skin of limbs. Tympanic annulus is visible externally in the most of the specimens of *T. rubigo* (never visible externally in *T. huayra, T. dankoi, T. fronteriensis, T. halli, T. phillippi,* and *T. vilamensis*). In *Telmatobius rubigo* the spicules in the chest are present only in males, while in *T. atacamensis, T. chusmisensis, T. hypselocephalus* and *T. marmoratus* they can be present in both sexes. These spicules are absent in both sexes in *T. halli* and *T. phillippi*. The upper lip of *Telmatobius rubigo* is notched medially (unnotched in *T. phillippi*), and the nuptial pad is in contact with the inner palmar tubercle (not in contact in *T. phillippi*). *Telmatobius rubigo* has pointed, curved and well developed maxillar and premaxillar teeth which are absent in *T. dankoi* and *T. vilamensis*; premaxillar teeth are absent and maxillar ones are vestigial in *T halli*).

Telmatobius rubigo has a well ossified skull (poorly ossified in *T. chusmisensis, T. platycephalus, T. phillippi* and *T. vilamensis*) and a well ossified *carpus* (which is cartilaginous in *T. chusmisensis*). The vomer in *T. rubigo* is not well developed, as it is in *T. marmoratus, T. atacamensis, T. platycephalus, T. hypselocephalus,* and *T. phillippi.*

The species from subpáramo valleys or cloud forests from Argentina (*T. ceiorum, T. contrerasi, T. hauthali, T. laticeps, T. oxycephalus, T. pinguiculus, T. pisanoi, T. schreiteri, T. scrocchii* and *T. stephani*) differ from *T. rubigo* in exhibiting the following characters: (1) higher heads, (2) eyes more laterally positioned, and closer to the mouth, (3) shorter snout, with the nostrils closer to the tip of snout than to the eyes, (4) superior lip not flared, unnotched medially, (5) nuptial spines larger.

Description of the Holotype (Fig. 1, 2). An adult male, medium-sized, SVL 50.4 (Fig. 2 A). Head length (measured from commissural angle to tip of snout) 33.6% of SVL, wider than long; head width (measured at level of commissural angle) 35.8% of SVL; head length 93.9% of head width; head subacuminate in dorsal view (Fig. 2 B), slightly depressed with sloping snout in lateral profile (Fig. 2 C); nostrils small, not protruding, oriented dorsolaterally, approximately at the same distance to tip of the snout and to the eye;

internarial region convex; *canthus rostralis* indistinct, loreal region slightly concave; upper lips flared, notched medially; maxilla and premaxillae with small curved and pointed teeth, embedded in the labial mucosa; teeth of vomers not visible; small, oval choanae; tongue rounded, attached anteriorly to floor of mouth, free posteriorly for about one-fourth of its length; vocal slits absent; tympanum and tympanic annulus absent; supratympanic fold extending obliquely from behind eye to posterior margin of postcommisural gland and in continuity with suprahumeral fold.

Forelimbs moderately robust; relative length of fingers II < I < IV < III (Fig. 2 D); webbing absent between fingers; tips of fingers swollen; fingers with almost unnoticeable lateral fringes; thenar tubercle large, elliptical, depressed; palmar tubercle rounded, approximately the same size as thenar tubercle; one subarticular tubercle on the base of each finger and at penultimate phalangeal articulation on Fingers II and IV; one round supernumerary tubercle between inner and outer palmar tubercles; palmar surface smooth, without keratinized spicules; base of thumb broadened proximally, bearing a nuptial pad composed of small keratinized, black and conical spicules closely arranged, reaching posterior margin of thenar tubercle, and extending dorsally from the base of thumb to the base of the distal phalange of thumb (Fig. 2 E).

Hind limbs moderately robust; tibia length 44.7% of SVL; tibia length 88.8% of foot length (measured from the proximal border of the inner metatarsal tubercle to the tip of the fourth toe); relative length of toes I < II < III < V < IV (Fig. 2 F); webbing formula I (1 1/2) – (--) II (1 1/3) – (--) III (2 1/3) – (3 3/4) IV (3 1/2) – (2+)V; webbing extending as lateral fringes to tips of toes; tips of toes swollen, approximately of the same size as those of fingers; outer metatarsal tubercles rounded, slighthly smaller than one-fourth size of the elliptical inner metatarsal tubercle; subarticular tubercles rounded and well developed; supernumerary tubercles absent; plantar surface smooth; tarsal fold developed.

Skin of the dorsum and dorsal surface of the head relatively smooth; skin of flanks with pustules, some of them with keratinized tip; some small tubercles are present on the lateral region of the head; dorsal surface of limbs with flat pustules; skin of venter and ventral surfaces of limbs smooth except for keratinized spicules in the chest; cloacal opening unornamented, located just below the dorsal level of thighs.

Coloration of the Holotype (Fig. 1). In life, grey dorsum, with darker gray solid blotches and scattered with orange lichenous blotches; venter pale orange, throat pale pink, ventral surfaces of limbs bright orange, yellow and reddish; iris light grey without flecks. In preservative brownish-gray dorsally with solid darker grey blotches; the belly, throat and the ventral surfaces of limbs are pale cream. The palmar and plantar surfaces are dark gray with the tubercles pale gray.

Measurements of the Holotype. SVL 50.4; HW 18.0; HL 16.9; ED 4.5; IOD 6.6; EW 2.9; END 3.1; IND 3.0; SL 7.5; EMD 3.9; NMD 4.3; BW 19.2; BH 12.4; HAL 12.4; RUL 10.9; FEL 22.0; TL 22.5; FOL 37.6; WL 14.1; IMTL 2.0; OMTL 0.8.

Variation. Range of measurements of 20 adult specimens (average given in parentheses): SVL 39.9–54.0 (47.7); HW 13.9–19.8 (16.9); HL 12.3–17.5 (15.1); ED 4.0–4.9 (4.5); IOD 5.2–7.0 (6.4); EW 1.8–3.2 (2.5); END 2.7–4.5 (3.2); IND 2.5–3.6 (2.9); SL 4.1–7.6 (6.4); EMD 2.8–4.8 (3.8); NMD 3.6–4.9 (4.2); BW 14.5–20.6 (17.9); BH 10.4–16.2 (11.8); HAL 10.4–13.5 (11.7); RUL 8.3–11.2 (10.0); RUW 3.3–5.8 (4.3); FEL 17.4–25.1 (20.8); TL 18.2–24.0 (21.0); FOL 29.6–39.4 (34.3); WL 10.7–14.5 (12.6); IMTL 1.4–2.6 (1.9); OMTL 0.4–1.4 (0.8). As in other *Telmatobius* species head shape in *Telmatobius rubigo* is extremely variable, from moderately depressed with a long snout to a high head with a short snout. The supratympanic fold is strong to almost unnoticeable. The number of vomeral teeth range from 0 to no more than 3, sometimes completely covered by the palatal mucosa. The skin on the flanks is more tuberculate in some specimens, especially those from Cuesta de Fundiciones and in large females from El Queñoal. The skin of specimens from Arroyo Farrallón is similar to those of El Queñoal but whit dorsal skin of thighs being more warty and spiny. The skin in most specimens from Timón Cruz is smooth, occasionally with a few scattered spicules. The tympanic annulus is evident in most of analyzed specimens except in those from Timón Cruz, where the majority has a concealed annulus. The development of webbing varies intra and interpopulationally. The studied adult specimens present some differences in color pattern in life, the ground color can be grey with darker blotches or uniformly greenish. All examined adults specimens share the pattern of rusty lichenous

blotches that is also present in some juveniles and metamorphs (Fig. 3). However, a few juvenile individuals are completely uniform. In preservative the design of dorsum skin is uniformly grayish or grey with darker blotches. The venter is uniformly cream, but in some specimens darker blotches are present in thighs.

FIGURE 3. Paratopotype (juvenile) of *Telmatobius rubigo* showing the characteristic color pattern of lichenous rusty blotches.

The paratopotype MLP DB 3622 has a malformation in the left foot; fingers I, IV and V are malformed and the tip of finger III is atrophied. Sexual dimorphism is evident, mature males have a nuptial pad in the dorsal and ventral surface of thumbs that reach the inner metacarpal tubercles and also have scattered spines in the chest and arms. Those spines are absent in females. The males are smaller than females (SVL: males 39.9–50.4 mm; females: 43.6–54.0 mm), and have more robust forearms (RUW: males 4.2–5.8 mm; females 3.3–5.5 mm.), and more developed webbing (WL/FOL: males up to 58%, females up to 56%).

Osteology (Fig. 4). Skull moderately depressed, well ossified (Fig. 4 A–B); sphenethmoid well ossified, broadly exposed dorsally, anterior portion reaching anterior border of nasals; prootic well ossified, fused with exoccipital dorsally and ventrally, crista parotica consists in a narrow strip of cartilage articulated with otic ramus of squamosal; exoccipital ossified dorso and ventromedially; frontoparietals fused posteriorly; frontoparietal fenestra bottle shaped, extends more than half the length of the orbit. Anterior margin of fontanelle formed by sphenetmoid at a level approximately ¼ posterior on length of orbit; posterior margin of fontanelle at a level approximately ¼ anterior on length of orbit; nasals subtriangular, elongate, close to each other medially, lateral vertex bended backwards, in contact with sphenethmoid; maxillary process of nasal not reaching pars facialis of maxilla; pars facialis of maxilla lacking preorbital process; neopalatines long, straight, slightly tapered medially; in contact laterally with pterygoid and medially with sphenethmoid, broadly separated and not reaching anterior terminus of cultriform process of parasphenoid; parasphenoid

robust, cultriform process irregularly truncate and reaching the level of vomers; alae of parasphenoid large, almost perpendicular to cultriform process and not in contact with medial ramus of pterygoids anterolaterally; pterygoid well developed and robust, anterior ramus extending to level of palatine; inner margins of rami describing a nonsinuous curve between maxilla and otic capsule. Outer margins of anterior and posterior rami forming a slightly curve profile between maxilla and squamosal; medial ramus of pterygoid short, barely contacting prootic by pseudobasal cartilague; maxillary arch complete; quadratojugal moderately long, contacting maxilla but not fused; basal portion of palatoquadrate cartilage mineralized; palatoquadrate cartilage invested by the quadratojugal, posterior ramus of pterygoid, and ventral ramus of squamosal; otic ramus of squamosal shorter and broader than zygomatic ramus; zygomatic ramus long, slim and bended medially; plectral apparatus with pars interna plectri well developed, pars media plectri thin and pars externa plectri cartilaginous; tympanic ring incomplete dorsally; maxilla and premaxilla dentate; teeth pedicellate, monocuspid, fang-like; number of teeth in premaxilla (11/10) and in maxilla (33/34); posterior half of maxilla slim and straight in lateral view; alary process of premaxilla wider at the base, acuminate and bifurcate, the

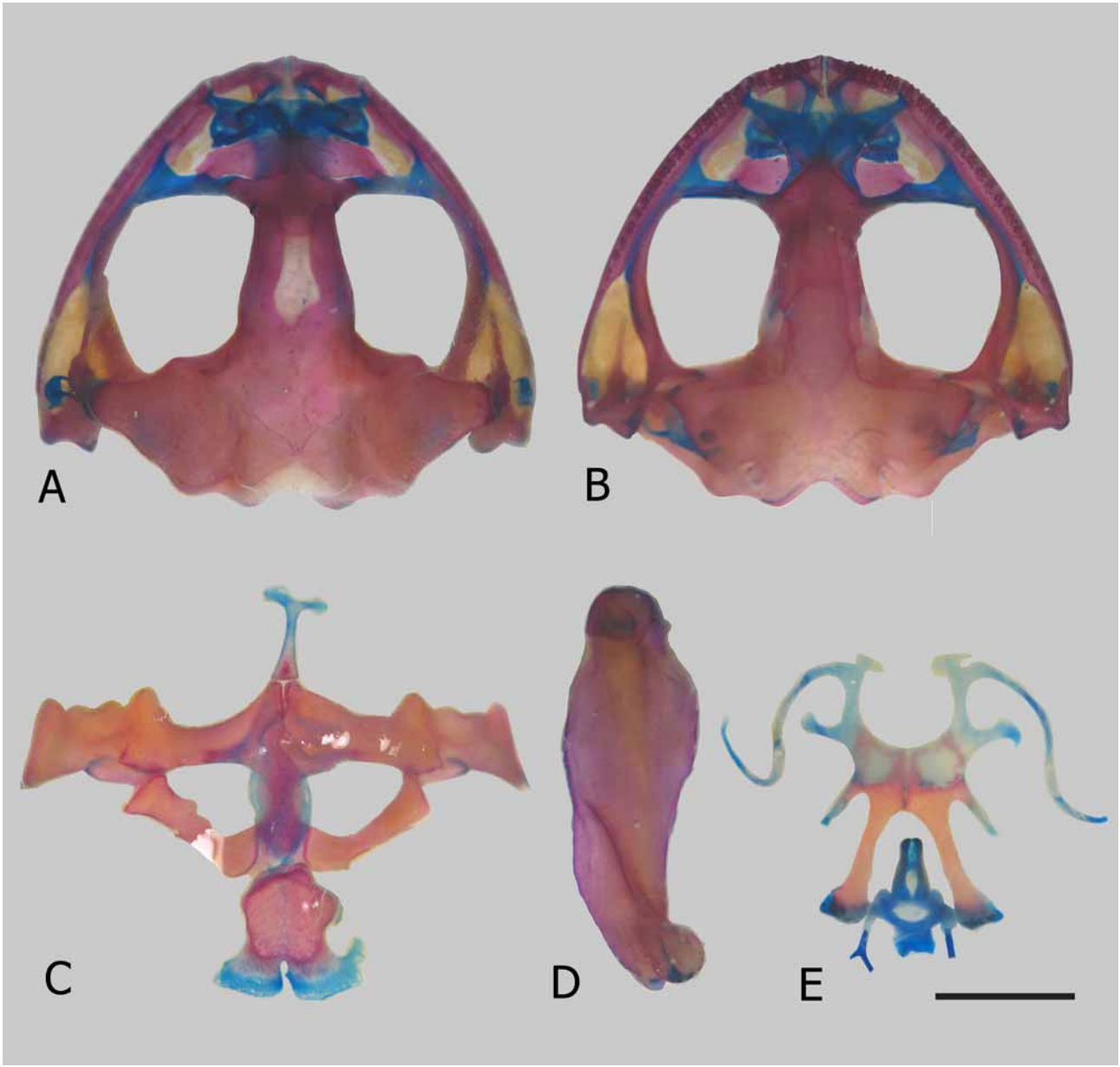

FIGURE 4. Dorsal (A) and ventral (B) view of skull, pectoral girdle (C), right humerus (D) and hyoid apparatus (E) of a paratopotype of *Telmatobius rubigo* (FML 20829).

distal half slightly bended outwards in frontal view; disposed with more than 66º with respect to the maxillary in lateral view; vomers small, with slender prechoanal and postchoanal process; dentigerous process of vomers without teeth in the cleared specimen.

Hyoid plate wider than long (Fig. 4 E), calcified around the bases of the posteromedial processes, which originate inside the plate, and are long and well ossified. Other calcified areas inside the plate are also present; hyale long, sinuous, bearing well developed anterior processes; anterolateral or alar processes moderately long, expanded distally; posterolateral processes straight, divergent respect to midline, approximately as long as anterolateral processes, not expanded distally; esophagic process of aritenoid cartilage broad.

Pectoral girdle arciferal (Fig. 4 C); omosternum cartilaginous, slightly calcified basally; sternum completely ossified, xiphisternon bilobed; clavicle fused with scapula; coracoids well developed, not juxtaposed medially; epicoracoids calcified; scapula bicapitate; suprascapula with cleithrum bifurcate and cartilaginous portion calcified.

Eight procelous presacral vertebrae; transverse processes of presacrals II, III, and IV moderately large, relative width of those transverse processes: III > IV > II; sacral diapophyses moderately expanded, oriented slightly posterodorsal to longitudinal axis of vertebral column; articulation of sacrum with urostyle bicondylar; urostyle bearing small, proximal dorsal crest; ilia cylindrical, long; pubis completely ossified.

Humerus of male robust (Fig. 4 D), flattened, with well developed anteroproximal, medial and ventral crests. The two last crests continue anteriorly as one crest to almost reach the head of the humerus; phalangeal formula of hand 2-2-3-3; terminal phalanges knobbed; prepollex with one basal and four distal elements; basal and three distal elements ossified; phalangeal formula of foot 2-2-3-4-3; prehallux with four elements, basal and one distal elements ossified.

Skull measurements. Skull length 16.5, skull width 17.4; orbit length 5.8; dorsal length sphenetmoid 3.4; ventral length sphenetmoid 4.4; frontoparietal length 9.0; slope angle of alar process of premaxillary in lateral view with respect maxillary 66.55º.

Tadpole external morphology (Fig. 5). The larvae of *Telmatobius rubigo* belongs to the benthic ecomorphological guild (section II: A: 1) of McDiarmid and Altig (1999), as revised from Altig and Johnston (1989). Body length about 40% of total length (BL/TL= 0.38 ± 0.02) (Fig. 5 B); body shape oval in dorsal view (Fig. 5 D–E); with the maximum body width placed at the posterior portion of the head, sometimes at abdominal region. Body depressed in lateral view (BH/BW=0.78 ± 0.06); ventral contour flat to slightly convex, dorsal contour convex from the anterior edge of the oral disc to the posterior border of the eyes, and almost straight from behind the eyes to the origin of the dorsal fin. Snout rounded or slightly truncated in dorsal view, and rounded in lateral view. Nostrils not protuberant, rounded or oval, and situated dorsally, closer to eye than snout (NS/EN= 1.66 ± 0.16). Eyes relatively small, situated dorsolaterally. Spiracle single, lateral, sinistral, directed posterodorsally; almost as long as wide, and placed approximately halfway between snout and posterior margin of body, with its inner wall present as a slight ridge; its opening is oval, placed below body midline, being its diameter smaller than the tube diameter, and visible in dorsal and lateral view. Intestinal assa central. Vent tube dextral, with opening not visible laterally, concealed by a fold of the vent tube wall; right wall attached anteriorly to the ventral fin. Tail large (TAL/TL= 0.62 ± 0.02), with well developed musculature, not reaching tail tip. Tail axis straight, and tail tip rounded. Dorsal and ventral fins of similar depth; dorsal fin not extending onto body; ventral fin starting at the end of vent tube; both fins almost as high as body height. Edge of both fins sub-parallel for the first and second thirds, and convex in the posterior third. Oral disc (Fig. 5 C) anteroventral, transversally elliptical; medium sized, not emarginated, and with a large dorsal gap in the marginal papillae, with no mental gap. Marginal papillae simple, small and longer than wide, sub-conical; arranged in a single or single alternated row in the anterior (upper) labium, and arranged in a single alternate or occasionally double row in the posterior (lower) labium. Sub-marginal papillae larger than marginal ones; few and scattered in supra-angular region, but denser in the angular and infra-angular regions. Sub-marginal infra-angular papillae arranged in short bilateral flaps which run close to the labial teeth ridges, and converge towards the mental region. Some additional sub-marginal papillae are scattered in the mental area, but not forming a complete row. Jaw sheaths robust, wider than deep,

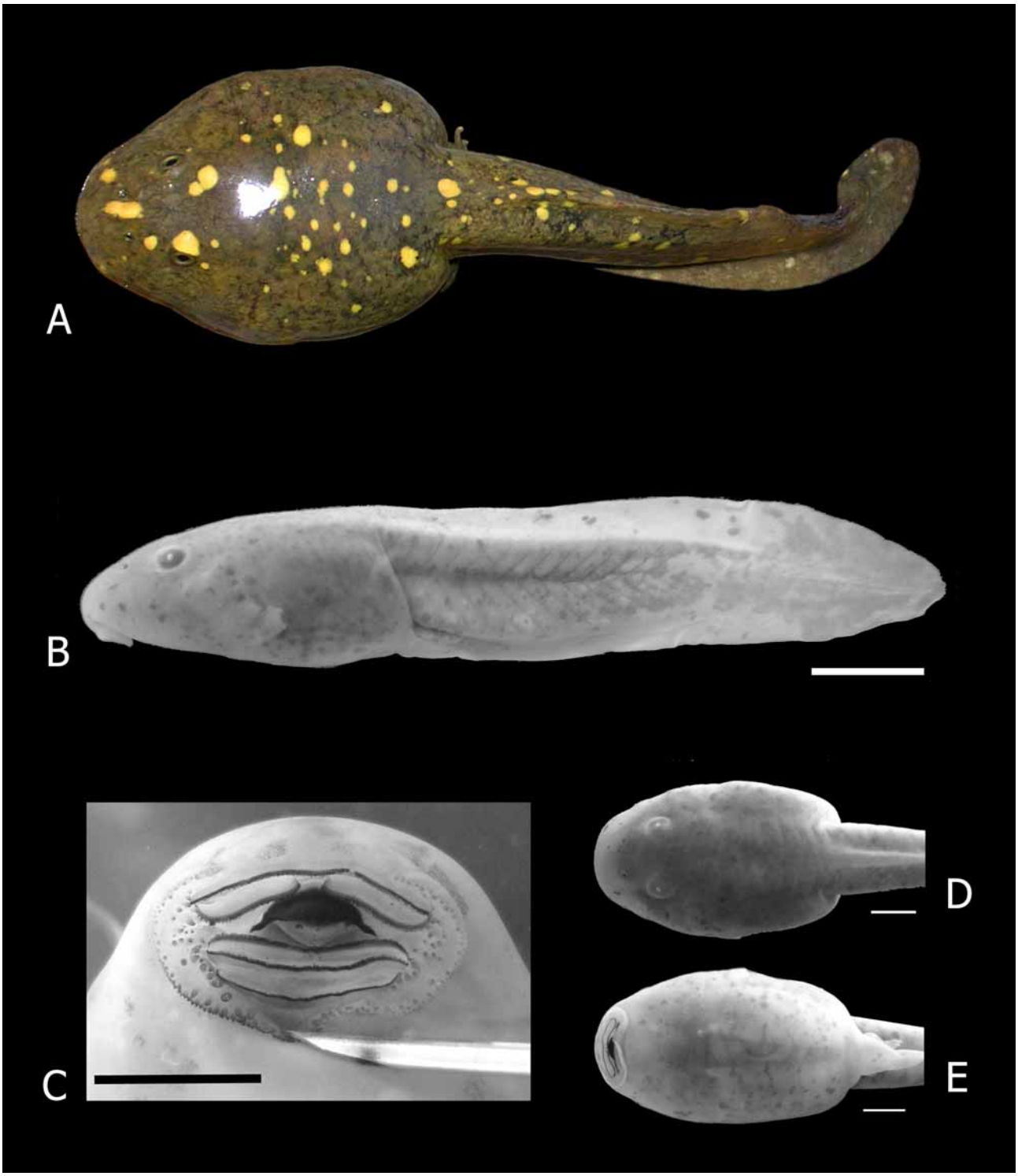

FIGURE 5. Dorsal view of a living tadpole of *Telmatobius rubigo* showing the characteristic yellow blotches (A). Lateral (B, bar = 10mm), dorsal (D, bar = 5mm) and ventral (E, bar = 5mm) view of a fixed tadpole (FML 21157). Detail of the oral disc (C, bar = 5mm).

finely serrated, and heavily pigmented distally for about 2/3 to 1/2 their length. Free margin of the upper jaw sheath widely arch shaped, with lateral processes well developed. Lower jaw sheath V-shaped. Labial tooth row formula (LTRF) 2(2)/3(1). Gap in A2 clearly visible. Medial gap in P1 very narrow. In one specimen (stage 34) there is a small ridge with labial teeth between A1 and A2.

Tadpole coloration (Fig 5 A): In life ground color brown-greenish with rounded bright yellow blotches scattered in the dorsum of body, tail musculature and fins. Iris golden. In preservative, body brown-grayish, tail tan, dorsal and ventral fins translucent. Skin with small darker flecks. In some specimens those flecks are tiny, more numerous and evenly distributed. Large dark blotches are present in the fins at the tip of the tail, more intensely pigmented in some individuals; venter transparent, internal organ visible; eyes black; perinasal region darker than surrounding areas.

Tadpole measurements. Range of measurements of 9 tadpoles (average given in parentheses): TL: 64.4–77.7 (72.0); BL: 25.2–29.7 (27.5); TAL: 39.2–49.6 (44.5); BW: 13.8–17.5 (16.3); BH: 11.9–13.8 (12.7); IOD: 3.8–4.3 (4.0); IN: 2.8–3.2 (3.0); EN: 2.5–3.0 (2.7); NS: 3.9–4.9 (4.5). In Table 1 tadpole measurements are discriminated according to Gosner (1960) developmental stages.

TABLE 1. Measurements (mm) of the tadpoles of *Telmatobius rubigo*, providing mean ± SD and range.

	Stage 33 (n=1)	Stage 34 (n=5)	Stage 35 (n=1)	Stage 36 (n=1)	Stage 37 (n=1)
Total length	72.5	72.0 ± 4.9 (64.4–77.7)	73.6	72.6	69.6
Body length	28.7	27.6 ± 1.6 (25.2–29.7)	26.6	26.8	27.0
Tail length	43.8	44.3 ± 4.0 (39.2–49.6)	47.0	45.8	42.6
Body width	16.0	16.2 ± 1.5 (13.8–17.5)	16.4	15.9	17.0
Body height	13.2	12.7 ± 0.7 (11.9–13.8)	12.3	12.6	12.7
Interorbital distance	3.8	4.07 ± 0.15 (3.9–4.3)	3.8	4.0	4.0
Internarial distance	2.8	3.1 ± 0.1 (2.8–3.2)	3.2	2.9	2.9
Eye-narial distance	3.0	2.7 ± 0.2 (2.6–3.0)	2.5	2.7	2.6
Narial-snout distance	4.4	4.5 ± 0.4 (3.9–4.7)	4.9	4.2	4.6

Karyotype (Fig 6). Chromosome counting from all the samples revealed that *Telmatobius rubigo* has a karyotype composed by 13 biarmed chromosomes pairs (2n = 2x =26) without identifiable sex chromosomes (Fig, 6 A). The first six pairs of the chromosome complement are large and the others seven are small. Pairs 1, 3, 8, 10, 11, 12 and 13 are metacentric, pairs 2, 4, 6, 7 and 9 are submetacentrics, and pair 5 is subtelocentric. The secondary constrictions and Ag-NOR sites were observed on the short arms of both homologues of chromosome pair 6 (Fig. 6 B). All normal stages were observed in meiotic preparations. A notorious bouquet

FIGURE 6. Karyotype of paratopotype of *Telmatobius rubigo* (MLP DB 3622) (A). Sixth chromosome pair bearing the NORs (B).

polarization (Rabl orientation) was observed in Zygotene and early Pachytene, with telomeres grouped in a restricted cluster of the inner membrane of the nuclear envelope (Fig. 7 A). Zigotene cells showed the telomeric regions paired and condensed, and internal regions unpaired and highly discondensed, indicating early stages of synapsis. Thus, the initiation of chromosome pairing was apparently distal and bidirectional (which is also supported by the observation of internal asynaptic loops in bivalentes IIs), give rise to ring IIs with terminal chiasmata in Diakinesis and Metaphase I (Fig. 7 B). In Metaphase II, 13 chromosomes were always observed (Fig. 7 C).

FIGURE 7. Meiotic cells of paratopotype of *Telmatobius rubigo* (MACN 39093): Zygotene showed a bouquet polarization (Rabl orientation) (A); Metaphase I with 13 ring IIs (B); Metaphase II with 13 chromosomes (C).

Geographic distribution and natural history (Fig. 8). This species is only known from a few localities, from the endorheic basin of Laguna de Los Pozuelos (Fig. 8) in the Central Andean Puna Ecoregion (Dinerstein, *et al.* 1995), Jujuy province, Argentina. This basin comprises an area of about 3800 Km^2 between 3600 and 4700 m a.s.l. and collects water of streams of Sierras de Escaya from the east, Sierra de Cochinoca from east and southeast, Sierra de Rinconada from the west, and Sierra de Carahuasi from the west and southwest (Fig. 8) (Cajal *et al*. 1998). The climate of the Puna is cold and dry with average annual temperatures that range between 0–9º C (depending on the altitude), and large daily thermal amplitude (around 30º C) (Tecchi, 1991). Precipitations oscillate between 100 and 500 mm/year, that fall as snow and hail in the winter, and in the summer rains are more common (Cabrera, 1968). At the type locality (El Queñoal) *T. rubigo* inhabits a high altitude permanent stream that flows through a gorge. The riparian vegetation is predominantly characterized by some scattered trees ("queñoas", *Polylepis tomentella*), arborescence cactuses ("cardones" *Thrichocereus* spp.), and tall grasses (*Cortaderia speciosa*) (Fig. 9). This stream crosses the Puna steppe and drains to Santa Catalina river, a tributary of Laguna de Los Pozuelos. Specimens of *T. rubigo* were always found underwater, on permanent high altitude streams. Some specimens were collected under submerged rocks, others while were resting at the bottom of small natural ditches of quiet waters and therefore they were easily detected from the edge of the streams. The few people that live at El Queñoal raise corn, beans and flower crops by the margins of the stream. This locality is about 10 km (straight-line distance) NW from Santa Catalina town. At the type locality and Santa Catalina river *Telmatobius rubigo* is sympatric with *Hypsiboas* sp. (*pulchellus* group) (Hylidae Rafinesque) and *Rhinella spinulosa* (Wiegmann) (Bufonidae Gray).

Discussion

The taxonomic study of *Telmatobius* is problematic. Species of this genus are difficult to differentiate from each other, because the external morphology is highly conservative and, in the other hand, they show considerably intraspecific variation (Lavilla & De la Riva 2005). This problem is especially noticeable among highland or Puna species (De la Riva 2005; Lavilla & Barrionuevo 2005). In addition to this intrinsic

characteristic of *Telmatobius* in the most cases museum specimens are the only available material for most localities. Comparison using fixed specimens is difficult as some relevant characters such as body color

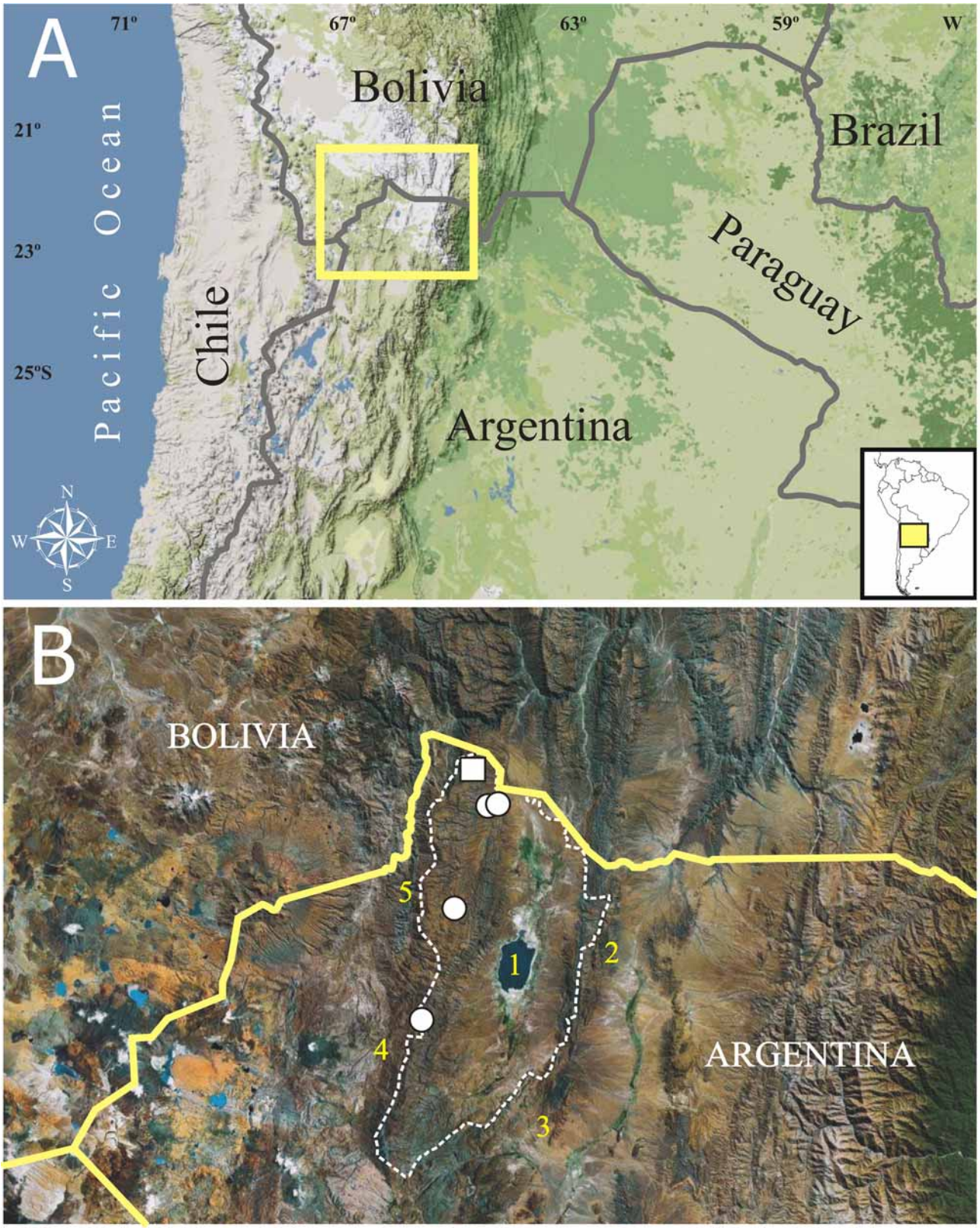

FIGURE 8. Geographic distribution of *Telmatobius rubigo*. (A) Northern Argentina, the study area is marked. (B) Study area, Laguna de Los Pozuelos basin showing type locality (square) and other localities (circles) where *Telmatobius rubigo* was found. Dashed lines delimit the Biosphere Reserve Laguna de Pozuelos. References: 1) Laguna Pozuelos; 2) Sierras de Escaya; 3) Sierras de Cochinoca; 4) Sierras de Rinconada; and 5) Sierras de Carahuasi.

pattern, iris coloration and skin characteristics are sometimes the only way to distinguish among species, but are frequently faded by preservation fluids. As was proposed by De la Riva (2005), some of the Argentinean populations that were traditionally referred as *T. marmoratus* would actually be *T. huayra*. The type locality of *T. huayra* (Campamento Khastor, Provincia Sud Lípez, Departamento Potosí) (Lavilla & Ergueta Sandoval 1995) is close to type locality of *T. rubigo* (108 Km in straight-line distance) but in a different endorheic basin. As discussed above, *T. rubigo* is morphologically different from *T. huayra.* Additionally, this species can be also differentiated from the closest populations of *T.* aff. *marmoratus* of Departamento Yavi, Jujuy. Remarkably, the specimens from Yavi are more similar to *T. marmoratus* from the Titicaca basin, located at approximately 900 km in straight-line distance.

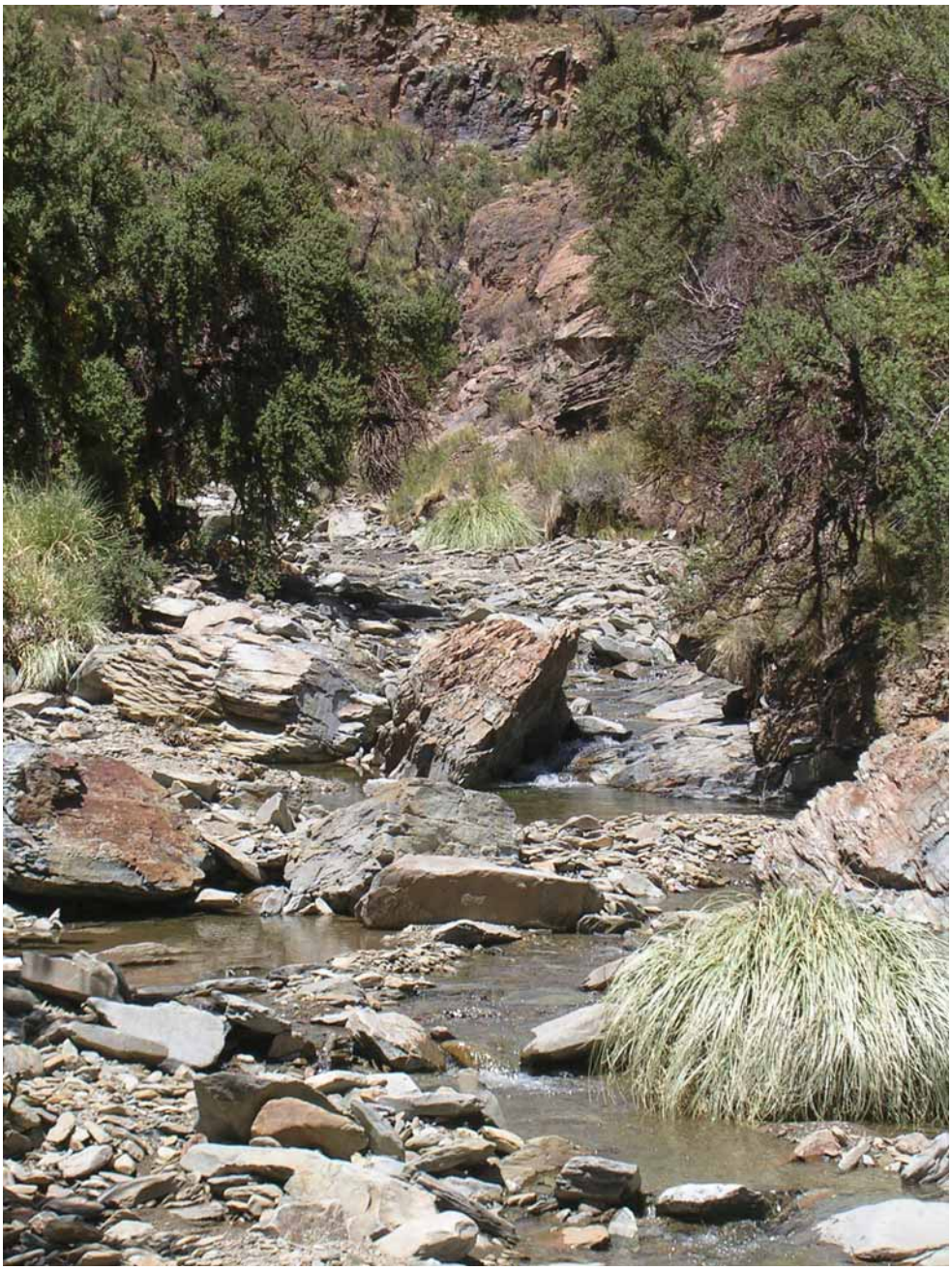

FIGURE 9. Habitat of *Telmatobius rubigo* at type locality.

The LTRF is shared by all described tadpoles of *Telmatobius*, with the exception of the rheophilous larvae of *T. atahualpai* Wiens (Aguilar *et al.* 2007). Traditionally *Telmatobius* larvae were arranged in two groups based on the presence of a mental submarginal row of papillae (Lavilla 1985). The “meridional group” (row

present) comprises all the described Argentinean tadpoles of the genus as was originally stated by Lavilla (1985) (*T.* aff. *marmoratus, T. atacamensis, T. ceiorum, T. hauthali, T. laticeps, T. oxycephalus, T. pisanoi, T. schreiteri*, and *T. stephani*), and *Telmatobius espadai* (Lavilla & De la Riva 1993) and *T. yuracare* (De la Riva 1994) from Bolivia, and *T. vilamensis* from Chile (Formas *et al.* 2003). The "septentrional group" (row absent) comprises the rest of the species with known tadpoles from Bolivia, Chile, Ecuador and Peru. The oral morphology of the larvae of *Telmatobius rubigo* matches with that of the "septentrional group" of Lavilla (1985). The colour pattern of the tadpole of *T. rubigo* is unique among *Telmatobius* since the yellow spots were not described for any other species. These particular yellow spots are similar to that described for adult specimens of *Telmatobius cirrhacelis* Trueb (Merino-Viteri *et al*. 2005), from Ecuador, whose tadpoles are still unknown.

The karyotype is also highly conserved within *Telmatobius*. The seventeen species that were studied to date (*T. arequipensis* Vellard, *T. carrillae* Morales, *T.ceiorum, T. chusmisensis, T. dankoi, T. jelskii, T. laticeps, T. marmoratus, T. oxycephalus, T. pefauri* Veloso and Trueb, *T. peruvianus* Wiegmann, *T. phillippii, T. rimac* Schmidt, *T. rubigo, T. stephanni, T. vilamensis, T. zapahuirensis* Veloso, Sallaberry, Navarro, Iturra, Valencia, Penna, and Diaz) and the two known species of the genus *Batrachophrynus* Peters (nested within *Telmatobius* in some phylogenetic analyses, Aguilar 2006; Barrionuevo unpublished results), have a karyotypic constitution remarkably similar, composed by 26 biarmed chromosomes (Córdova & Deiscailleaux 2005 and references therein; Formas *et al*., 2006). The basic number of 13 chromosomes, highly conserved, is shared by all members of the Ceratophrydae Tschudi (*sensu* Frost *et al*. 2006), *Atelognathus* Lynch, *Batrachyla* Bell, *Chacophrys* Reig & Limeses, *Ceratophrys* Wied-Neuwied, and *Lepidobatrachus* Budgett studied to date (Beçak *et al*. 1967; Barrio & Rinaldi de Chieri 1970; 1971; Díaz & Veloso 1979; Schmid *et al.* 1985; Vieira *et al*. 2006). The presence of NORs in the short arms of the chromosome pair 6 is also apparently very conserved in Telmatobiinae, it is currently known from ten species of *Telmatobius* (*T. arequipensis, T. carrillae, T. chusmisensis, T. dankoi, T. jelskii, T. marmoratus, T. phillippii, T. rimac, T. rubigo,* and *T. vilamensis*) and the two species of *Batrachophrynus* (Córdova & Deiscailleaux 2005 and references therein; Formas *et al*. 2006). The systematic significance of this character state deserves a more extensive evaluation in other subfamilies of Ceratophrydae. Within Batrachylinae the NORs is present in the chromosome pair 6 or 7 in *Batrachyla* (Cuevas & Formas 2008) and it is not known to be present in *Atelognathus*. Its position is variable in Ceratophryinae (*Chacophrys*, *Ceratophrys* and *Lepidobatrachus*). In the diploid forms NORs are allocated in the seventh chromosome pair (Schmid *et al*. 1985; Baldo unpublished data), and in polyploid taxa in the sixth chromosome set (in *Ceratophrys joazeirensis* Mercadal de Barrio) or in seventh and eighth ones [in *Ceratophrys ornata* (Bell)] (Schmid *et al.* 1985; Vieira *et al*. 2006).

After the description of *Telmatobius hypselocephalus* and *T. platycephalus* from El Moreno in Jujuy by Laurent and Lavilla in 1988, the present contributions is a following step to unravel the taxonomic problem of populations classically assigned to *T. marmoratus* of the Northern Altiplano of Argentina.

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Appendix I. Additional specimens examined

Abbreviations for Institutions are: Fundación Miguel Lillo, Instituto de Herpetología (FML), Tucumán, Argentina; Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN), Buenos Aires, Argentina; Museo de La Plata (MLP), Argentina; Colección Boliviana de Fauna (CBF) , La Paz, Bolivia, y Museo de Historia Natural de La Universidad de San Marcos (MHNSM), Lima Perú.

Tematobius aff. *marmoratus*.—**ARGENTINA**: JUJUY: Departamento Yavi: 3 Km N of Inticancha, 25 Km of Yavi (2850 m a.s.l.), FML 3275 (3 specimens); way to Cieneguillas, FML 3291 (9 specimens); Larcas, FML 3274 (14 specimens); Puesto de Cajas (3800 m a.s.l.), FML 2817 (6 specimens); Río Toroara, La Quiaca, FML 3537; Sierra De Santa Victoria, FML 2805; 2809 (8 specimens); Tafna, near to Cuesta de Toqueros, FML 6663, 6675, 6679-80; Yavi, FML 4521 (3 specimens).

Tematobius atacamensis.—**ARGENTINA**: JUJUY: Departamento Susques: Pastos Chicos, near to Sey, FML 02602 (10 specimens). SALTA: Departamento Los Andes: San Antonio De Los Cobres, FML 03252 (3 paratypes); pead bog beetwen San Antonio de los Cobres and Pueblo Nuevo, FML 04505 (28 specimens, 4 cleared and stained).

Tematobius ceiorum.—**ARGENTINA**: TUCUMAN: Departamento Tafí Viejo: Alto de la Perdiz, Cabra Horco, way to Peñas Azules (2300 m a.s.l.), FML 02629 (24 specimens, 4 cleared and stained).

Tematobius contrerasi.—**ARGENTINA**: SAN JUAN: Departamento Jáchal: Quebrada del Madril, Valle del Río Gualcamayo (29º40'27,3"S; 68º48'37,6"W, 3010 m a.s.l.), FML 20813 (specimen cleared and stained), FML 20814-20.

Tematobius hauthali.—**ARGENTINA**: CATAMARCA: Departamento Tinogasta: Arroyo Aguas Calientes, FML 03264/1 (Paratopotype), 03264/9 (Neotype), 03315 (5 specimens cleared and stained**);** Río Aguas Calientes, near to Cazadero Grande (4050 m a.s.l.), FML 03264 (32 specimens).

Tematobius huayra.—**BOLIVIA**: POTOSÍ: Provincia Sud Lípez: Campamento Khastor (22º02'S, 67º08'W, 4600 m a.s.l.), CBF 1221 (Holotype), 1222-3 (paratypes).

Tematobius hypselocephalus.—**ARGENTINA**: JUJUY: Departamento Tumbaya: El Angosto, 6 Km S of El Moreno (3600 m a.s.l.), FML 03767 (Patatype), 03768 (Holotype); El Moreno, (3500 m a.s.l.), FML 03766. (6 Paratypes), 04372 (cleared and stained).

Tematobius laticeps.—**ARGENTINA**: TUCUMÁN: Departamento Tafí del Valle: El infiernillo, FML 1499 (4 specimens cleared and stained); El Infiernillo, east slope, Ruta Provincial Nº 307, Km 84–86, FML 01498 (46 specimens).

Tematobius marmoratus.—**PERÚ**: LA PAZ: Provincia Bautista Saavedra: Charazani, CBF 3621, 3622 (cleared and stained), 3624; Provincia Omasuyos: Huatajata, Lago Titicaca: CBF 2165-66. PUNO: Provincia Azángaro: Guasacona, MHNSM 12163, 12165, 2167 (cleared and stained), 12168, 12172, 12175, 12180, 12182 (all topotypes).

Tematobius oxycephalus.—**ARGENTINA**: JUJUY: Departamento Ledesma: Monument near to San Francisco (1600–1700 m a.s.l.), FML 01369; Quebrada Río Jordán, Parque Nacional Calilegua, FML 03836 (3 specimens cleared and stained); Departamento Valle Grande: Río Jordán (1500 m a.s.l.), FML 02867 (9 specimens, 5 cleared and stained), FML 02883. SALTA: Cerro La Escalera, (3800 m a.s.l.) Orán, FML 00225 (Holotype).

Tematobius pinguiculus.—**ARGENTINA**: CATAMARCA: Departamento Tinogasta: La Ciénaga, Campo El Potrerito (3300 m a.s.l.), FML 03921 (7 paratypes), 04373 (2 specimens cleared and stained).

Tematobius pisanoi.—**ARGENTINA**: Tucumán: Departamento Tafí del Valle: Ruta Provincial Nº 307, Km 93 beetwen Tafí del Valle and Cafayate, FML 2442 (holotype); Quebrada de Los Cardones, Ruta Provincial Nº 307, Km 98; FML 03269 (24 specimens, 4 cleared and stained); Quebrada Río La Tranca, foothills of Sierra de Quilmes, FML 02963 (22 specimens, 4 cleared and stained).

Tematobius platycephalus.—**ARGENTINA**: JUJUY: Departamento Tumbaya: El Angosto, 6 Km S to El Moreno (3600 m a.s.l.), FML 03763 (holotype), 04371 (cleared and stained); San José de Chañi, west slope of Nevado de Chañi (3750 m a.s.l.), FML 03764 (paratype).

Tematobius schreiteri.—**ARGENTINA**: LA RIOJA: Departamento Arauco: Aimogasta, FML 00216 (holotype); Departamento Castro Barros: Quebrada de Anjullón (1800–1900 m a.s.l.), FML 01977. (27 specimens, 4 cleared and stained); Quebrada de Anjullón, Sierra de Velasco (2000–2050 m a.s.l.), FML 01976 (27 specimens).

Tematobius scrocchii.—**ARGENTINA**: CATAMARCA: Departamento Andalgalá: Campo Del Arenal, Loma Redonda, Ruta Provincial Nº 47, Km 1369 or 1436 (2600 m a.s.l.), FML 05772 (9 specimens); El Arenal, (3050 m a.s.l.), FML 01515 (97 specimens, 7 cleared and stained); El Ingenio, Campo El Arenal, Ruta Nº 63, FML 03532 (holotype).

Tematobius stephani.—**ARGENTINA**: CATAMARCA: Departamento Ambato: Cerro Manchao (2300 m a.s.l.), FML 01743 (holotype), 01744 (topotype), 01594. (14 topotypes); La Cumbrecita, Cerro Manchao (2800 m a.s.l.), FML 02765 (11 specimens, 4 cleared and stained).