

Description of the tadpoles of *Telmatobius platycephalus* and *Telmatobius pinguiculus* from montane regions of Argentina

J.S. Barrionuevo¹ & D. Baldo^{1,2}

¹Instituto de Herpetología, Fundación Miguel Lillo, San Miguel de Tucumán, Argentina

²Laboratorio de Genética Evolutiva y Molecular, Facultad de Ciencias Exactas Químicas y Naturales, Universidad Nacional de Misiones, Argentina

The tadpoles of two species of the genus *Telmatobius* (*T. platycephalus* and *T. pinguiculus*) from montane regions of Argentina are described. The larvae of both species are characterized by bodies that are oval in dorsal view and depressed in lateral aspect. In each, the snout is rounded in dorsal and lateral profiles; the labial tooth row formula is 2(2)/3(1) and a short, sinistral spiracle is directed posterodorsally. The tadpoles of *T. platycephalus* are larger than those of *T. pinguiculus*; they also lack a row of mental submarginal papillae and the nares are dorsally oriented instead of dorsolaterally.

Key words: Anura, Ceratophryidae, external larval morphology, montane frogs

INTRODUCTION

The genus *Telmatobius* Wiegmann contains 58 species (Frost, 2008; Barrionuevo & Baldo, 2009) that are distributed in the Andes, from Ecuador to Argentina (Lavilla & De la Riva, 2005). These aquatic or semi-aquatic frogs occupy different montane freshwater habitats, ranging from cloud-forest streams at 1000 m elevation, to deglaciated ponds at about 5200 m (De la Riva, 2005; Seimon et al., 2006). Currently, populations of *Telmatobius* are experiencing dramatic declines (Merino-Viteri et al., 2005; Barrionuevo & Ponssa, 2008).

The taxonomy of *Telmatobius* has been complex since the early works of Parker (1940) and Vellard (1951, 1953, 1955, 1960, 1969), probably because of the lack of obvious morphological diagnostic characters, the high degree of intraspecific variation that blurs species boundaries and the presumed absence of an advertisement call (Trueb, 1979; Díaz, 1982). Little is known about the biology of this genus of secretive frogs, which lives in some of the highest and inaccessible places in the neotropics. The eggs are laid in a mass of jelly attached to submerged rocks (Lavilla & Barrionuevo, 2005; Merino-Viteri et al., 2005). The large, free-living tadpoles are usually found all year round as they have been suggested to reproduce continuously (Ceï, 1949; Pisanó, 1955; Díaz, 1982), and the larval period can last more than a year (Formas et al., 2005).

Telmatobius platycephalus (Lavilla & Laurent 1988a) inhabits permanent streams in the Salinas Grandes–Laguna de Guayatayoc basin in the Argentinean Puna region. *Telmatobius pinguiculus* (Lavilla & Laurent, 1988b) inhabits permanent streams in Sierras de Fiambalá, Catamarca province. The latter species morphologically resembles *T. pisanoi* and *T. scrocchii* (Barrionuevo, pers.

obs.), which occur nearby at Campo El Arenal in Catamarca province and at Valle de Yokavil in Tucumán province, respectively.

Although the tadpoles of 30 species of *Telmatobius* have been described, many of the earlier descriptions consist of only brief comments about external morphology (e.g. Koslowsky, 1895; Fernández, 1926; Schmidt, 1928; Noble, 1938; Parker, 1940; Vellard, 1946). Recent descriptions of tadpole external morphology available from the literature are more detailed (Trueb, 1979; Lavilla, 1984; Díaz & Valencia, 1985; Lavilla & De la Riva, 1993; Cuevas & Formas, 2002; De la Riva & Harvey, 2003; Formas et al., 2003, 2006; Merino-Viteri et al., 2005; Aguilar et al., 2007a). Some of them include observations on anatomy such as descriptions of the chondrocranium and associated musculature, and buccopharyngeal characters (Fabrezi & Lavilla, 1993; Lavilla & De la Riva, 1993; Aguilar & Pacheco, 2005; Aguilar et al., 2007b; Vera Candioti, 2007, 2008). Lavilla (1985) proposed two informal groups within *Telmatobius* based on the configuration of the oral disc in the larvae. In the “meridional group” (Argentinean species), the larvae have a row of submarginal papillae in the mental area, whereas the “septentrional group” (extra-Argentinean species) lacks this row.

Larval external morphology is known for ten of the 15 Argentine species of *Telmatobius*. In this contribution we describe for the first time the external morphology of *Telmatobius platycephalus* and *T. pinguiculus* tadpoles from this country.

MATERIALS AND METHODS

Specimens used in the descriptions are deposited in FML (Fundación Miguel Lillo), and MLP DB (Diego Baldo Collection, Museo de La Plata). The following samples were

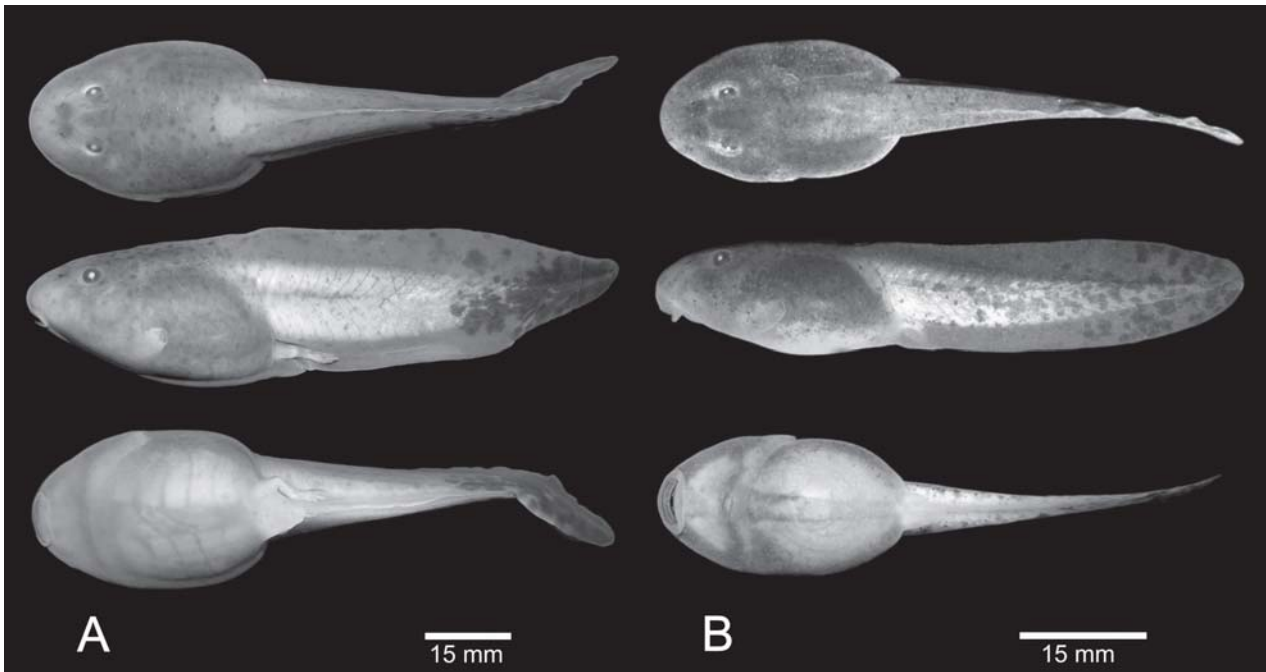


Fig. 1. A) Tadpole of *Telmatobius platycephalus* (stage 38) from Casabindo, Departamento Cochinocha, Jujuy, Argentina (MLP DB 4730), in dorsal, lateral and ventral views; and B) tadpole of *Telmatobius pinguiculus* (stage 35) from Puesto Lagunillas, Sierras de Fiambalá, Departamento Tinogasta, Provincia de Catamarca, Argentina (FML 22280), in dorsal, lateral and ventral views.

used for tadpole descriptions: *Telmatobius platycephalus* (MLP DB 4730), $n=3$, stage 38, collected at Casabindo, Departamento Cochinocha, Provincia de Jujuy, Argentina ($22^{\circ}59'35''$ S; $66^{\circ}00'47''$ W) on 5 January 2006 by Diego Baldo, Andrés Brunetti, Andrea Dallagnol and Daiana Ferraro; *T. pinguiculus* (FML 22280), $n=10$, stages 33–35, collected at Puesto Lagunillas, Sierras de Fiambalá, Departamento Tinogasta, Provincia de Catamarca, Argentina ($27^{\circ}26'32''$ S; $67^{\circ}20'9''$ W) on 23 March 2006 by Sebastián Barrionuevo. Additional specimens examined are listed in Appendix I.

Morphological terminology follows that of Lavilla (1988) and Altig & McDiarmid (1999). Tadpole developmental stages follow those of Gosner (1960). Tadpoles were measured with calipers to the nearest 0.1 mm. Six measurements were recorded following the methods of Altig & McDiarmid (1999): total length (TL), body length (BL), tail length (TaL), maximum tail height (MTH), internarial distance (IND, measured between the internal edges of narial apertures) and tail muscle height (TMH). Thirteen additional measurements were recorded following the procedures of Lavilla & Scrocchi (1986): body maximum width (BMW), body width at nares (BWN), body width at eye level (BWE), body maximum height (BMH), rostrispiracular distance (RSD, measured horizontally from tip of the snout to the posterior edge of the spiracular tube), frontonasal distance (FN, from the tip of the snout to the anterior edge of nares), eye–nostril distance (END, from the posterior edge of nares to the anterior edge of eyes), nostril major axis (N), eye diameter

(E), extranasal distance (EN, distance between external edges of nares), intraorbital distance (IO, distance between interior edges of eyes), oral disc width (OD) and dorsal gap length (DG).

RESULTS

Telmatobius platycephalus Lavilla & Laurent 1988a

Tadpole external morphology (Fig. 1A). The larvae of *Telmatobius platycephalus* belong to the benthic ecomorphological guild (Section II: A: 1) of McDiarmid and Altig (1999), as revised from Altig & Johnston (1989). Body length less than 40% of total length (mean BL/TL = 0.37 ± 0.02); body shape oval in dorsal view; with maximum body width at posterior portion of head or at abdominal region. Body slightly depressed in lateral view (mean BMH/BMW = 0.93 ± 0.11); ventral contour of body flat at level of the head, and convex posteriorly, dorsal contour distinctly convex from anterior edge of oral disc to posterior border of eyes, and slightly convex from behind eyes to origin of dorsal fin. Snout rounded in dorsal and lateral views. Nares not protuberant, oval, dorsolaterally oriented and situated dorsally (mean EN/BWN = 0.39 ± 0.03), closer to eye than snout (mean FN/END = 1.97 ± 0.04). Eyes relatively small (E/BWE = 0.15 ± 0.01), oriented dorsolaterally, and situated dorsally (IO/BWE = 0.27 ± 0.01). 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 slight ridge, and visible in dorsal and lateral views; its opening is oval, located below body midline, its diameter being smaller than tube diameter, opening only visible in lateral view. Intestinal asae central. Vent tube dextral, with opening not visible laterally, concealed by fold of vent tube wall; right wall attached anteriorly to ventral fin. Tail large (mean $TaL/TL = 0.64 \pm 0.003$), with well-developed musculature, not reaching tail tip. Tail axis straight, and tail tip rounded. Dorsal and ventral fins of similar height; dorsal fin not extending onto body; ventral fin starting at end of vent tube; both fins almost as high as body height (mean $MTH/BMH = 1.01 \pm 0.04$). Edge of each fin subparallel for first and second thirds, and convex in posterior third; in one specimen, dorsal origin of dorsal fin abrupt. Oral disc (Fig. 2A) anteroventral, transversally elliptical; medium-sized (mean $OD/BMW = 0.38 \pm 0.04$), not emarginated, and with large dorsal gap (mean $DG/OD = 0.51 \pm 0.02$) in marginal papillae, with no mental gap. Marginal papillae simple, small, longer than wide, subconical; arranged in single or single alternated row in anterior (upper) labium; arranged in single alternate, or occasionally double row in posterior (lower) labium. Submarginal papillae larger than marginal ones; few and scattered in supra-angular region, but denser in angular and infra-angular regions. Submarginal papillae in mental area absent. Jaw sheaths robust, wider than high, finely serrated, and almost entirely pigmented. Free margin of upper jaw sheath widely arch-shaped, with lateral process 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 narrow.

Tadpole coloration. In preservative, body greyish brown, tail tan, dorsal and ventral fins translucent. Skin

with small dark flecks. Large, dark blotches on the fins at tip of tail, more intensely pigmented in one specimen; venter transparent, internal organs visible; eyes black; perinasal region darker than surrounding areas.

Tadpole measurements. Range of measurements of three tadpoles (average in parentheses): TL: 79.0–91.2 (85.0), BL: 30.8–32.5 (31.6), TaL: 50.5–58.9 (54.7), BMW: 20.9–24.5 (22.5), BWE: 16.8–19.5 (17.9), BWN: 12.3–13.7 (12.9), BMH: 18.1–19.9 (19.2), TMH: 10.3–12.3 (11.3), MTH: 18.4–20.8 (19.3), RSD: 20.2–22.3 (21.3), FN: 5.9–6.9 (6.3), END: 3.0–3.6 (3.2), IND: 3.5–4.1 (3.7), IO: 4.5–5.3 (4.8), EN: 4.9–5.1 (5.0), E: 2.5–2.8 (2.6), N: 0.9–1.0 (0.9), OD: 7.4–8.8 (7.9), DG: 3.6–4.5 (4.0).

***Telmatobius pinguiculus* Lavilla & Laurent 1988b**

Tadpole external morphology (Fig. 1B). The larvae of *Telmatobius pinguiculus* belong to the benthic ecomorphological guild (Section II: A: 1) of McDiarmid & Altig (1999), as revised from Altig & Johnston (1989). Body length longer than one third of total length (mean $BL/TL = 0.36 \pm 0.01$); body shape oval in dorsal view with slight constriction behind the spiracle; maximum body width located at posterior portion of the head anterior to spiracle. Body slightly depressed in lateral view (mean $BMH/BMW = 0.92 \pm 0.03$); ventral contour slightly convex, dorsal contour convex from anterior edge of oral disc to posterior border of eyes, and almost straight from behind eyes to origin of dorsal fin. Snout rounded in dorsal and lateral views. Nares not protuberant, rounded or oval, dorsally positioned (mean $EN/BWN = 0.32 \pm 0.03$) and laterally oriented, closer to eye than snout (mean $FN/END = 2.36 \pm 0.02$). Eyes relatively small ($E/BWE: 0.16 \pm 0.00$), ori-

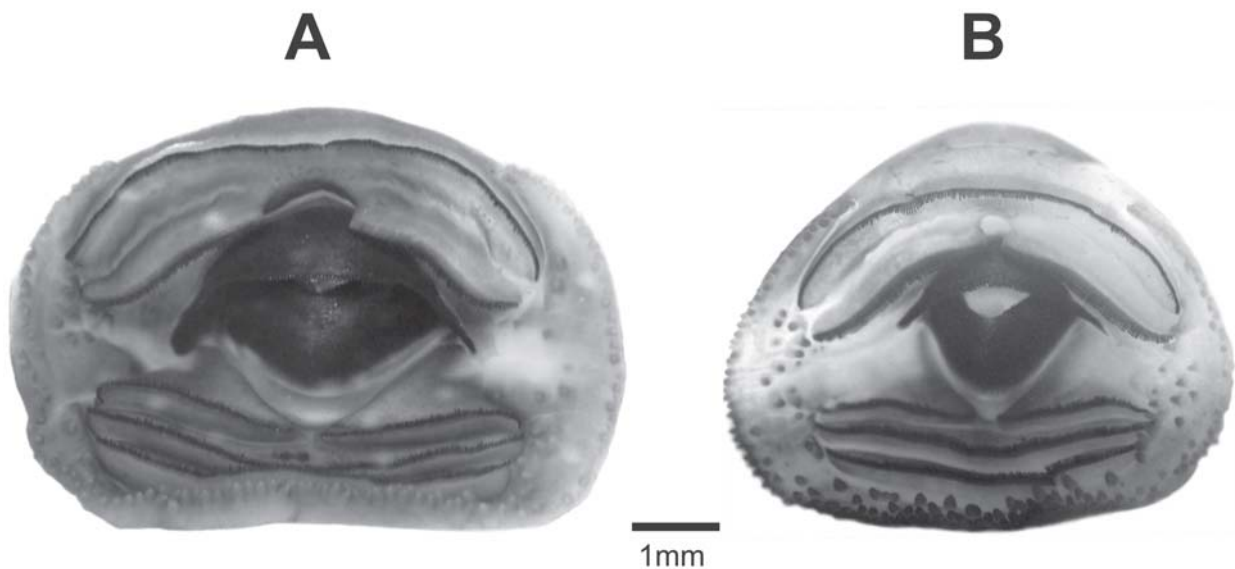


Fig. 2. A) Oral disc of a tadpole of *Telmatobius platycephalus* (stage 38) from Casabindo, Departamento Cochinocha, Jujuy, Argentina (MLP DB 4730). B) Oral disc of a tadpole of *Telmatobius pinguiculus* (stage 35) from Puesto Lagunillas, Sierras de Fiambalá, Departamento Tinogasta, Provincia de Catamarca, Argentina (FML 22280). Scale bar = 1 mm.

Table 1. Measurements (mm) of the tadpoles at different Gosner stages of *Telmatobius pinguius*, providing mean±SD and range at stage 33. Variables are defined in the text.

	Stage 33 (n=5)	Stage 34 (n=1)	Stage 35 (n=1)
TL	57.8±2.4 (56.4–62.1)	60.8	64.1
BL	21.3±0.5 (21.0–22.0)	22.3	22.8
TaL	36.3±2.0 (35.1–39.8)	38.6	41.7
BMW	12.1±0.6 (11.5–13.1)	12.9	12.7
BWE	11.5±0.7 (10.7–12.2)	11.2	11.8
BWN	8.5±0.4 (8.0–9.1)	8.5	11.2
BMH	10.7±0.4 (10.0–10.9)	10.5	10.5
TMH	7.0±0.4 (6.5–7.6)	6.9	7.3
MTH	10.5±0.3 (10.0–10.8)	10.3	11.1
RSD	14.1±0.4 (13.5–14.7)	14.1	14.3
FN	4.4±0.2 (4.2–4.7)	4.4	4.7
END	1.9±0.1 (1.8–2.0)	2.1	1.8
IND	2.8±0.1 (2.7–3.0)	2.6	2.8
IO	3.1±0.1 (2.9–3.2)	3.2	3.1
EN	3.6±0.1 (3.5–3.6)	3.4	3.6
E	1.8±0.0 (1.7–1.8)	1.9	2.0
N	0.5±0.1 (0.5–0.6)	0.5	0.5
OD	6.1±0.3 (5.8–6.6)	5.7	6.5
DG	3.0±0.2 (2.8–3.2)	2.6	2.9

ented dorsolaterally and situated dorsally (IO/BWE = 0.27±0.00). 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 slight ridge, and visible in dorsal and lateral views; opening visible in dorsal and lateral views, oval, located below body midline, its diameter being smaller than tube diameter. Intestinal asae central. Vent tube dextral, with opening not visible laterally, concealed by fold of vent tube wall; right wall attached anteriorly to ventral fin. Tail large (mean TaL/TL = 0.63±0.01), with well-developed musculature, not reaching tail tip. Tail axis straight, and tail tip rounded. Dorsal and ventral fins of similar height; dorsal fin not extending onto body; ventral fin starting at end of vent tube; both fins almost as high as body height (mean MTH/BMH = 0.99±0.02). Edge of each fin subparallel for first and second thirds, and convex in posterior third. Oral disc (Fig. 2B) anteroventral, transversally elliptical; medium sized (mean OD/BMW = 0.52±0.05), not emarginated, and with large dorsal gap (mean DG/OD = 0.50±0.01) in marginal papillae, with no mental gap. Marginal papillae simple, small and longer than wide, subconical; arranged in a single or single alternated row in the anterior (upper) labium, and arranged in single alternate or occasionally double row in posterior (lower) labium. Submarginal papillae larger than marginal ones; few and scattered in supra-angular region, but denser in angular and infra-angular regions. Submarginal papillae in mental area forming a row. These papillae are widely separated from each other, and are clearly distinct from mental marginal papillae. Jaw sheaths robust, wider than deep, finely serrated, and al-

most entirely pigmented. Free margin of upper jaw sheath widely arch-shaped, with lateral process 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 narrow.

Tadpole coloration. In preservative, body grayish brown, tail tan, dorsal and ventral fins translucent. Skin with small dark flecks. Large dark blotches present in tail musculature and at posterior third of fin; venter transparent, internal organs visible; eyes black; perinasal region darker than surrounding areas.

Tadpole measurements. Range of measurements of seven tadpoles (average in parentheses): TL: 56.4–64.1 (59.1), BL: 21.0–22.8 (21.7), TaL: 35.1–41.7 (37.4), BMW: 11.5–13.1 (12.3), BWE: 10.7–12.2 (11.5), BWN: 8.0–11.2 (8.9), BMH: 10.0–10.9 (10.6), TMH: 6.5–7.6 (7.0), MTH: 10.0–11.1 (10.5), RSD: 13.5–14.7 (14.1), FN: 4.2–4.7 (4.5), END: 1.8–2.1 (1.9), IND: 2.6–3.0 (2.8), IO: 2.9–3.2 (3.1), EN: 3.4–3.6 (3.5), E: 1.7–2.0 (1.8), N: 0.5–0.6 (0.5), OD: 5.7–6.6 (6.1), DG: 2.6–3.2 (2.9).

Measurements for each of stages 33–35 are given in Table 1.

DISCUSSION

Adult *Telmatobius platycephalus* and *T. pinguius* are easily distinguished from each other, but their tadpoles are quite similar. Tadpoles of both species have the same labial tooth row formula, 2(2)/3(1), also shared by all described tadpoles of *Telmatobius* (Lavilla, 1985, 1988; Vera Candiotti, 2008), with the exception of the rheophilous larvae of *T. atahualpai* (Aguilar et al., 2007b). The morphological similarity of *Telmatobius* tadpoles has already been noted by Aguilar & Pacheco (2005) based on buccopharyngeal characters and by Vera Candiotti (2008) in her studies of the larval chondrocranium and musculature. Comparison of the larvae of *T. pinguius* with those of *T. pisanoi* (FML 4609) and *T. scrocchii* (FML 5535) revealed that there are apparently no external characters that unequivocally distinguish these species.

Telmatobius platycephalus can be distinguished from *T. pinguius* by 1) the larger size of *T. platycephalus*; 2) the more dorsal orientation of the nares in *T. platycephalus*; and 3) the absence of a row of mental submarginal papillae in *T. platycephalus*. Although we describe these tadpoles at different developmental stages (*T. pinguius* at stages 33–35 and *T. platycephalus* at stage 38) due to availability of fresh material, the size difference was maintained when we compared total length in additional specimens of *T. pinguius* (FML 5536) at stage 38. Relative size differences of tadpoles from different *Telmatobius* populations at comparable stages were noted by Fernández (1926), who erroneously assigned a heterogeneous sample that included several species from northwestern Argentina to *T. aemaricus*. Actually, Fernández studied, among others, tadpoles of *T. pisanoi* from Caspinchango in Calchaquí Valley, Catamarca Province; the total length of larvae of *T. pisanoi* is up to 63 mm, and tadpoles of *Telmatobius rubigo* (Barrionuevo & Baldo, 2009) from Yoscaba, Jujuy Province, which are somewhat larger, reach a length of 112 mm. The size differ-

ences reported by Fernández parallel those that we observed between *T. pinguiculus* (up to 68.08 mm) and *T. platycephalus* (up to 91.2 mm), and hence it would be of great interest to evaluate size differences in *Telmatobius* tadpoles in a phylogenetic framework.

As proposed originally by Lavilla (1985), the geographic distribution of the “meridional” and “septentrional” groups of *Telmatobius* did not overlap; all species in the meridional group were restricted to Argentina while all species in the septentrional group were northern, from Bolivia and northern Chile to Ecuador. After the descriptions of the tadpole of *T. espadai* (originally described as the tadpole of *T. bolivianus*: Lavilla & De la Riva, 1993; De la Riva, 2005) and *T. yuracare* (De la Riva, 1994) from central Bolivia, the distributions of the two groups overlapped slightly. Moreover, the present description of the tadpole of *T. platycephalus* from Argentina with a larval morphology corresponding to the septentrional group, complicates even more the distributional pattern presented by Lavilla (1985). The monophyly of the two groups of *Telmatobius* proposed by Lavilla (1985) should be tested by a phylogenetic analysis of these fascinating montane anurans.

ACKNOWLEDGEMENTS

We acknowledge the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) for doctoral scholarships to both authors. We are grateful to C. Abdala, A. Brunetti, A. Dallagnol, J. M. Díaz Gómez, D. Ferraro, S. Quinteros and the Medanitos Community for their help during fieldwork. SB acknowledges CONICET for Grant PIP (5780) and Universidad Nacional de Tucumán (CIUNT 26/G315). We acknowledge ANPCyT for Grant PICT-O (37035). DB acknowledges ANPCyT for Grant PICT (16-35045) and PICT (06-233). We thank Klaus Borteirensen for his comments and assistance with the English version. Finally we are grateful to Linda Trueb, César Aguilar and Florencia Vera Candiotti for valuable comments and suggestions made on the manuscript.

REFERENCES

- Aguilar, C. & Pacheco, V. (2005). Contribución de la morfología bucofaríngea larval a la filogenia de *Batrachophrynus* y *Telmatobius* (Anura: Leptodactylidae). In *Estudios sobre las Ranas Andinas de los Géneros Telmatobius y Batrachophrynus* (Anura: Leptodactylidae), 219–238. Lavilla, E.O. & De la Riva, I. (eds). Valencia: Asociación Herpetológica Española, Monografías de Herpetología 7.
- Aguilar, C., Lundberg, M., Siu Ting, K. & Jimenez, M. (2007a). Nuevos registros para la herpetofauna del departamento de Lima, descripción del renacuajo de *Telmatobius rimac* Schmidt, 1954 (Anura: Ceratophryidae) y una clave de los anfibios. *Revista Peruana de Biología* 14, 209–216.
- Aguilar, C., Siu-Ting, K. & Venegas, P. (2007b). The rheophilous tadpole of *Telmatobius atahualpai* Wiens, 1993 (Anura: Ceratophryidae). *South American Journal of Herpetology* 2, 165–174.
- Altig, R. & Johnston, G.F. (1989). Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpetological Monographs* 3, 81–109.
- Altig, R. & McDiarmid, R.W. (1999). Body plan. Development and morphology. In *Tadpoles: The Biology of Anuran Larvae*, 24–51. McDiarmid, R.W. & Altig, R. (eds). Chicago: University of Chicago Press.
- Barrionuevo, J.S. & Baldo, D. (2009). A new species of *Telmatobius* (Anura, Ceratophryidae) from Northern Jujuy Province, Argentina. *Zootaxa* 2030, 1–20.
- Barrionuevo, J.S. & Ponssa, M.L. (2008). Decline of three species of the genus *Telmatobius* (Anura: Leptodactylidae) from Tucumán Province, Argentina. *Herpetologica* 64, 47–62.
- Cei, J.M. (1949). Sobre la biología sexual de un batracio de grande altura de la región andina (*Telmatobius schreiteri* Vellard). *Acta Zoologica Lilloana* 7, 467–488.
- Cuevas, C. & Formas, J.R. (2002) *Telmatobius philippii*, una nueva especie de rana acuática de Ollagüe, norte de Chile (Leptodactylidae). *Revista Chilena de Historia Natural* 75, 245–258.
- De La Riva, I. (1994). A new aquatic frog of the genus *Telmatobius* (Anura: Leptodactylidae) from Bolivian cloud forests. *Herpetologica* 50, 38–45.
- De la Riva, I. (2005). Bolivian frogs of the genus *Telmatobius* (Anura: Leptodactylidae): synopsis, taxonomic comments, and description of a new species. In *Estudios sobre las Ranas Andinas de los Géneros Telmatobius y Batrachophrynus* (Anura: Leptodactylidae), 65–101. Lavilla, E.O. & De la Riva, I. (eds). Valencia: Asociación Herpetológica Española, Monografías de Herpetología 7.
- De la Riva, I. & Harvey, M.B. (2003). A new species of *Telmatobius* from Bolivia and a redescription of *T. simonsi* Parker, 1940 (Amphibia: Anura: Leptodactylidae). *Herpetologica* 59, 127–142.
- Díaz, N.F. (1982). Estrategia reproductiva de *Telmatobius marmoratus* (Anura: Leptodactylidae) del altiplano chileno. In *El Hombre y los Ecosistemas de Montaña. Vol I. La Vegetación y los Vertebrados Inferiores de los Pisos Altitudinales entre Arica y el Lago Chungará*, 317–327. Veloso, A. & Bustos, E. (eds). Montevideo: Proyecto MAB 6-UNEP-UNESCO.
- Díaz, N.F. & Valencia, J. (1985). Larval morphology and phenetic relationships of the chilean *Alsodes*, *Telmatobius*, *Caudiverbera* and *Insuetophrynus* (Anura: Leptodactylidae). *Copeia* 1985, 175–181.
- Fabrezi, M. & Lavilla, E.O. (1993). Anatomía del condrocáneo en larvas de tres especies de *Telmatobius* del grupo meridional (Anura: Leptodactylidae). *Physis* 48B, 39–46.
- Fernández, K. (1926). Sobre la biología y reproducción de batracios argentinos. Segunda parte. *Boletín de la Academia Nacional de Ciencias de Córdoba* 29, 271–320.
- Formas, J.R., Benavides, E. & Cuevas, C. (2003). A new species of *Telmatobius* (Anura: Leptodactylidae) from Río Vilama, northern Chile, and the redescription of *T. halli* Noble. *Herpetologica* 59, 253–270.
- Formas, J.R., Cuevas, C.C. & Núñez, J.J. (2006). A new species of *Telmatobius* (Anura: Leptodactylidae) from Northern Chile. *Herpetologica* 62, 173–183.

- Formas, J.R., Veloso, A. & Ortiz, J.C. (2005). Sinopsis de los *Telmatobius* (Amphibia, Anura, Leptodactylidae) de Chile). In *Estudios sobre las Ranas Andinas de los Géneros Telmatobius y Batrachophrynus (Anura: Leptodactylidae)*, 103–114. Lavilla, E.O. & De la Riva, I. (eds). Valencia: Asociación Herpetológica Española, Monografías de Herpetología 7.
- Frost, D.R. (2008). *Amphibian Species of the World: An Online Reference, Version 5.1* (6 June, 2008). Electronic database accessible at <http://research.amnh.org/herpetology/amphibia/index.php>. New York: American Museum of Natural History.
- Gosner, K.L. (1960). A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16, 183–190.
- Koslowsky, J. (1895). Batracios y reptiles de la Rioja y Catamarca, recogidos durante los meses de febrero a mayo de 1895. *Revista del Museo de La Plata* 6, 333–344.
- Lavilla, E.O. (1984). Larvas de *Telmatobius* (Anura: Leptodactylidae) de la Provincia de Tucumán (Argentina). *Acta Zoologica Lilloana* 38, 69–79.
- Lavilla, E.O. (1985). Diagnósis genérica y agrupación de las especies de *Telmatobius* (Anura: Leptodactylidae) en base a caracteres larvales. *Physis* 43, 63–67.
- Lavilla, E.O. (1988). Lower Telmatobiinae (Anura: Leptodactylidae): generic diagnoses based on larval characters. *Occasional Papers of the Museum of Natural History, The University of Kansas, Lawrence, Kansas* 124, 1–19.
- Lavilla, E.O. & Barrionuevo, J.S. (2005). El género *Telmatobius* (Anura: Leptodactylidae) en la República Argentina: una síntesis. In *Estudios sobre las Ranas Andinas de los Géneros Telmatobius y Batrachophrynus (Anura: Leptodactylidae)*, 115–165. Lavilla, E.O. & De la Riva, I. (eds). Valencia: Asociación Herpetológica Española, Monografías de Herpetología 7.
- Lavilla, E.O. & De La Riva, I. (1993). La larva de *Telmatobius bolivianus* (Anura: Leptodactylidae). *Alytes* 11, 37–46.
- Lavilla, E.O. & De la Riva, I. (eds) (2005). *Estudios sobre las Ranas Andinas de los Géneros Telmatobius y Batrachophrynus (Anura: Leptodactylidae)*. Valencia: Asociación Herpetológica Española, Monografías de Herpetología 7.
- Lavilla, E.O. & Laurent, R.F. (1988a). Deux nouvelles espèces du genre *Telmatobius* (Anura: Leptodactylidae) en provenance de El Moreno (Province de Jujuy, Argentina). *Alytes* 7, 77–89.
- Lavilla, E.O. & Laurent, R.F. (1988b). A new species of *Telmatobius* (Anura: Leptodactylidae) from Catamarca (Argentina). *Alytes* 7, 90–96.
- Lavilla, E.O. & Scrocchi, G.J. (1986). Morfometría larval de los géneros de Telmatobiinae (Anura: Leptodactylidae) de Argentina y Chile. *Physis* 44, 39–43.
- McDiarmid, R.W. & Altig, R. (1999). Research: materials and techniques. In *Tadpoles: The Biology of Anuran Larvae*, 7–23. McDiarmid, R.W. & Altig, R. (eds). Chicago: University of Chicago Press.
- Merino-Viteri, A., Coloma, L.A. & Almendáriz, A. (2005). Los *Telmatobius* de los Andes de Ecuador y su disminución poblacional. In *Estudios sobre las Ranas Andinas de los Géneros Telmatobius y Batrachophrynus (Anura: Leptodactylidae)*, 9–37. Lavilla, E.O. & De la Riva, I. (eds). Valencia: Asociación Herpetológica Española, Monografías de Herpetología 7.
- Noble, G.K. (1938). A new species of the frog genus *Telmatobius* from Chile. *American Museum Novitates* 973, 1–3.
- Parker, H.W. (1940). Percy Sladen Trust Expedition to Lake Titicaca under the leadership of Mr. H. Cary Gilson, M.A.–XII–Amphibia. *Transactions of the Linnean Society of London* 3, 203–216.
- Pisanó, A. (1955). Notas ecológicas sobre la vida larvaria de *Telmatobius schreiteri*. *Ciencia e Investigación* 11, 86–91.
- Schmidt, K.P. (1928). The Chilean frogs of the genus *Telmatobius*. *Revista Chilena de Historia Natural* 32, 98–105.
- Seimon, T.A., Seimon, A., Daszak, P., Halloy, S.R.P., Schloegel, L.M., Aguilar, C.A., Sowell, P., Hyatt, A.D., Konecky, B. & Simmons, J.E. (2006). Upward range extension of Andean anurans and chytridiomycosis to extreme elevations in response to tropical deglaciation. *Global Change Biology* 13, 288–299.
- Trueb, L. (1979). Leptodactylid frogs of the genus *Telmatobius* in Ecuador with the description of a new species. *Copeia* 1979, 714–733.
- Vellard, J. (1946). El género *Telmatobius* en la República Argentina. *Acta Zoologica Lilloana* 3, 313–326.
- Vellard, J. (1951). Estudios sobre batracios andinos. I. El grupo *Telmatobius* y formas afines. *Memorias del Museo de Historia Natural Javier Prado* 1, 1–89.
- Vellard, J. (1953). Estudios sobre batracios andinos. II. El grupo *marmoratus* y formas afines. *Memorias del Museo de Historia Natural Javier Prado* 2, 1–53.
- Vellard, J. (1955). Estudios sobre batracios andinos. III. Los *Telmatobius* del grupo *jelskii*. *Memorias del Museo de Historia Natural Javier Prado* 4, 1–28.
- Vellard, J. (1960). Estudios sobre batracios andinos. VI. Notas complementarias sobre *Telmatobius*. *Memorias del Museo de Historia Natural Javier Prado* 10, 1–20.
- Vellard, J. (1969). Les *Telmatobius* de groupe *marmoratus*. *Bulletin du Muséum National d'Histoire Naturelle* 40, 1110–1113.
- Vera Candiotti, M.F. (2007). Anatomy of anuran tadpoles from lentic water bodies: systematic relevance and correlation with feeding habits. *Zootaxa* 1600, 1–175.
- Vera Candiotti, M.F. (2008). Larval anatomy of Andean tadpoles of *Telmatobius* (Anura: Ceratophryidae) from northwestern Argentina. *Zootaxa* 1938, 40–60.

Accepted: 1 April 2009

APPENDIX 1**Additional specimens examined**

Telmatobius pinguiculus. Argentina: Catamarca: Tinogasta: La Ciénaga: FML 5536 (6 specimens, stages 35–38).

Telmatobius pisanoi. Argentina: Tucumán: Tafí del Valle: Ruta provincial N° 307 Kilometro 98: FML 4609 (18 specimens, stages 34–38).

Telmatobius schrocchii. Argentina: Catamarca: Andalgalá: El Ingenio, Campo El arenal: FML 5535 (10 specimens, stages 35–38).

Telmatobius rubigo. Argentina: Jujuy: Santa Catalina: El Queñoal: FML 21157 (9 specimens, stages 33–37).

