



The tadpole of *Telmatobius fronteriensis* (Anura, Telmatobiidae), from Puquios, western of the Andes Range, northern Chile

C.C. Cuevas¹, J.R. Formas² & C. Azat-Soto³

¹Departamento de Ciencias Biológicas y Químicas, Universidad Católica de Temuco, Temuco, Chile

²Laboratorio de Zoología, ICML, Universidad Austral de Chile, Valdivia, Chile

³Sustainability Research Centre & Ph.D. Program in Conservation Medicine, Faculty of Life Sciences, Universidad Andrés Bello, Santiago de Chile

INTRODUCTION

Frogs of the genus *Telmatobius*, Wiegmann, are typical inhabitants of high Andean aquatic environments, such as small streams, thermal springs, lakes and lagoons (Lavilla & De la Riva, 2005). This diverse taxon (63 species; Frost, 2023) extends from the south of Ecuador to the North of Argentina, and its altitude ranges from 1,000 to 5,000 m.a.s.l. (Barrionuevo, 2017; Cei, 1986). The taxonomy of this genus has been considered remarkably complex due to low interspecific and intraspecific variations (De la Riva, 2005; Barrionuevo, 2017). Seven endemic species have been described in the Chilean Andes Range's western slopes: *T. chusmisensis*, *T. dankoi*, *T. fronteriensis*, *T. halli*, *T. pefauri*, *T. philippii* and *T. vilamensis*. Among these species, only the larva of *T. fronteriensis* is unknown, which prevents a better understanding of the importance of larval morphology for the systematics of the genus; so their tadpole is described for the first time in this work.

The morphological characters of anuran tadpoles have been successfully used for taxonomic purposes (Larson & de Sá, 1998; Aguilar & Pacheco, 2005; Aguilar & Valencia, 2009; Aguilar et al., 2007). Thus, Lavilla (1985; 1988) and Altig & McDiarmid (1999b) redefined the genus *Telmatobius* considering larvae's external characters. Consequently, based on the oral morphology of tadpoles, Lavilla (1985) proposed two phenetic groups in *Telmatobius* species: "the meridional" and the "septentrional" groups. On the other hand, Sáez et al. (2014), based on molecular analyses, studied the phylogenetic relationships of central Andes *Telmatobius* species in Chile and Bolivia, showing they form three phylogenetic groups: the *Telmatobius marmoratus* group, widespread in the Chilean and Bolivian Altiplano; the *Telmatobius hintoni* group, including the species *T. philippii*, *T. fronteriensis* and *T. huayra*, occurring in the south-western Altiplano of Chile and Bolivia; and the *Telmatobius pefauri* group, a new clade which includes *T. chusmisensis*, *T. dankoi* and *T. vilamensis*, restricted to the western slopes of the Andes in Chile.

In this study, we describe for the first time the tadpole of *T. fronteriensis*, a small-sized frog (mean snout-vent length 39.28 ± 2.56 mm; Benavides et al., 2002), endemic

to the type locality of Puquios (northern Chile). We also comparatively analysed the external morphology of the larvae of the Chilean species of *Telmatobius*, and we explore the degree of similarities/inequalities that exist among the phylogenetic groups proposed by Sáez et al. (2014) and corresponding species tadpoles. Furthermore, the presence of *Batrachochytrium dendrobatidis* and *Ranavirus* is explored.

MATERIALS & METHODS

Specimens

Five tadpoles and 21 adults of *T. fronteriensis* were captured (permit N° 301/2015 from Agricultural and Livestock Service) in the type locality (Puquios, Fig. 1A). For comparative purposes we analysed the larvae of another six Chilean *Telmatobius* species (data in Table 1). At the time of capture (19–20 October 2015, austral spring), adults (Fig. 1B) and larvae were detected on the edge or in the middle of the stream (Fig. 1C), in cavities or among aquatic vegetation. Five tadpoles of *Telmatobius* species and two adults were euthanised in a solution of 4 g/L of tricaine methanesulfonate and preserved in 10 % formalin for posterior analysis. Tadpoles were assigned to *T. fronteriensis* because no further amphibian species were found in this area and its surroundings. Collected and examined specimens (tadpoles and adults) are housed in the Instituto de Ciencias Marinas y Limnológicas, Universidad Austral de Chile, Valdivia, IZUA. Measurement data of tadpoles are presented in Table 2.

Methods

Larval stages were determined according to Gosner (1960). Measurements and terminology follow Altig & McDiarmid (1999a) for total length (TL), body length (BL), and tail length (TAL); Lavilla & Scrocchi (1986) for body width (BW), body width at the narial level (BWN), body width at eye level (BWE), body height (BH), eye-snout distance (ESD), eye-nostril distance (END), nostril-snout distance (NSD), eye diameter (ED), narial diameter (ND), snout-spiracular distance (SSD) and oral disc width (ODW); Grosjean (2005) for dorsal fin height (DFH) and

Correspondence: Cesar C. Cuevas (cesar.cuevas@uct.cl)

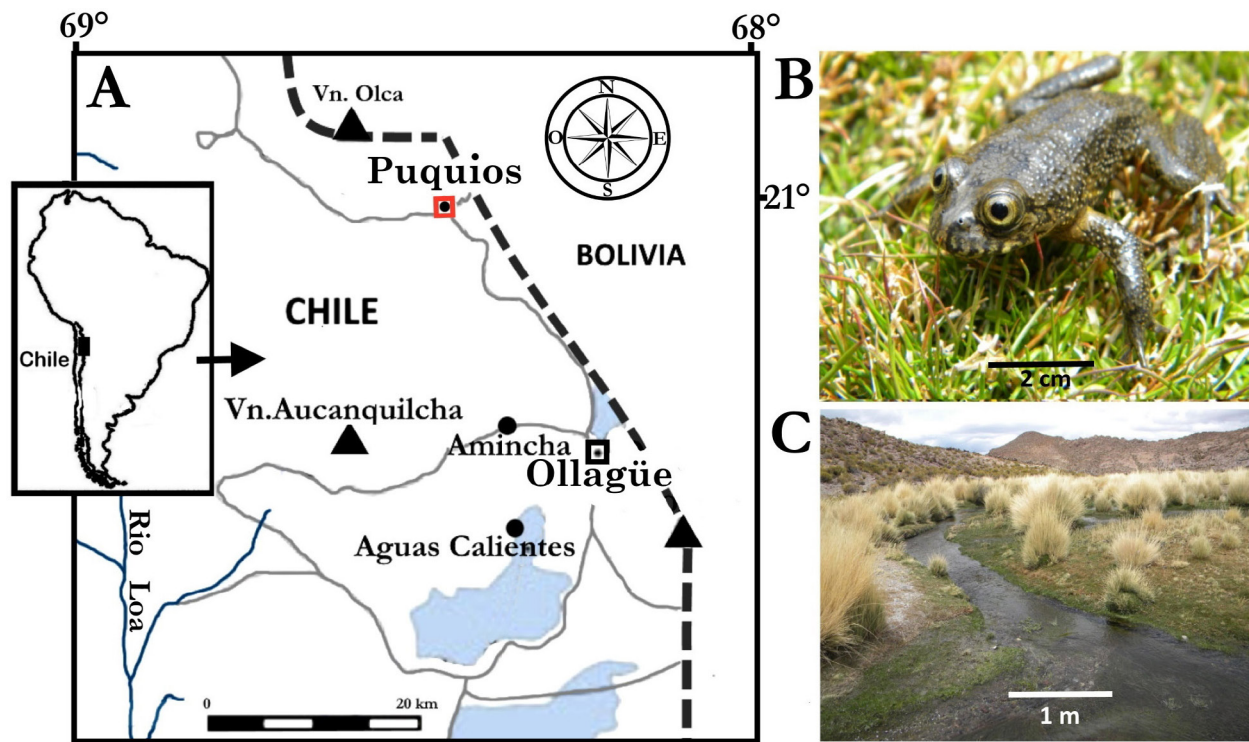


Figure 1. (A) Puquios, type locality of *T. fronteriensis*, (B) Adult male of *T. fronteriensis*, and (C) Stream where adult and tadpoles were captured.

Table 1. Tadpoles of the *Telmatobius* species and capture localities

| Species | Voucher | n | High (m.s.n.m) | Localities/Province/Region | Co-ordinates |
|-------------------------|-----------|---|----------------|--|----------------------------------|
| <i>T. fronteriensis</i> | IZUA 3657 | 5 | 4,104 | Puquios (Type Locality)/El Loa/Antofagasta | 21° 00'08,70" S; 68° 22'42,40" W |
| <i>T. chusmisensis</i> | IZUA 3662 | 5 | 3,365 | Chusmisa/Iquique/Tarapacá | 19° 40'44.92" S; 69° 10'47.26" W |
| <i>T. dankoi</i> | IZUA 3657 | 2 | 2,169 | Las Cascadas/El Loa/Antofagasta | 22° 30'14.75" S; 68° 58'21.67" W |
| <i>T. halli</i> | IZUA 3558 | 2 | 3,717 | Near Ollagüe/El Loa/Antofagasta | 21° 17'49,39" S, 68° 20'08,68" W |
| <i>T. pefauri</i> | IZUA 3657 | 3 | 3,535 | Chapiquiña/Parinacota/Arica y Parinacota | 18° 20'46.60" S; 69° 33'18.67" W |
| <i>T. philipii</i> | IZUA 3657 | 1 | 3,845 | Quebrada de Amincha/El Loa/Antofagasta | 21° 11'55.10" S; 68° 20'09,30" W |
| <i>T. vilamensis</i> * | IZUA 3082 | 5 | 3,110 | Río Vilama/El Loa/Antofagasta | 22° 52'05.80" S; 68° 10'54,90" W |

* Data from Formas et al. (2003)

ventral fin height (VFH). We use the configuration of the spiracle and vent, according to Altig & McDiarmid (1999a). The neuromast topography was named according to Lannoo (1987). The shape of the tail tips was determined following Savage (2002). All measurements were taken to the nearest 0.1 mm. Collected tadpoles and additional 21 adults of *T. fronteriensis* were non-invasive sampled (skin and oral swabs respectively) and tested through specific real-time PCR assays for the presence of two pathogens: *Batrachochytrium dendrobatidis* and *Ranavirus*, following previously described methods (Soto-Azat et al., 2016).

Taxonomic criteria and number of specimens

To avoid nomenclatural confusion, we use the taxonomic proposition of Fibla et al. (2017), which suggests a synonymy involving priority of the name *Telmatobius pefauri* over *T. zapahuirensis*. Consequently, we use *T. pefauri* for

the species and clade previously named *Telmatobius zapahuirensis*. The presence of *T. fronteriensis* in this restricted area (Puquios), and the inaccessibility of this place during some periods of the year prevent the capture of additional individuals. Furthermore, the critical state of conservation of the Chilean species of *Telmatobius* (Lobos & Rojas, 2020) justifies the description of the tadpoles *T. fronteriensis* based on scant material (five tadpoles).

RESULTS

The larvae of *T. fronteriensis* correspond to a morphological generalised type (Orton, 1953) and belong to the benthic ecomorphological guild type of Altig & McDiarmid (1999b). The body length corresponds to 40, 2 % of the total length (BL/TL = 0.40). Body shape oval in dorsal view, with maximum body width at abdominal region.

Table 2. Measurements (mm) of five tadpoles of *T. frontieriensis* (stages according to Gosner, 1960.) Characters are defined in the maintext.

| Specimens Character (mm) | Stages | | | | |
|-----------------------------|--------|------|------|------|------|
| | 32 | 34 | 35 | 36 | 41 |
| TL | 68.5 | 71.1 | 71.5 | 65.2 | 66.0 |
| BL | 26.0 | 25.5 | 28.1 | 24.2 | 23.8 |
| TAL | 42.5 | 46.2 | 43.4 | 41.0 | 42.2 |
| BMW | 12.5 | 15.0 | 18.2 | 19.8 | 14.0 |
| BWN | 9.0 | 9.0 | 10.1 | 9.4 | 9.0 |
| BWE | 17.0 | 12.5 | 14.8 | 12.0 | 11.0 |
| BMH | 17.5 | 14.8 | 14.9 | 12.0 | 11.1 |
| DFH | 4.0 | 4.0 | 4.0 | 2.8 | 2.6 |
| VFH | 3.0 | 3.0 | 2.8 | 1.5 | 2.0 |
| RSD | 17.0 | 15.5 | 19.0 | 20.0 | 13.9 |
| FN | 4.6 | 4.7 | 3.0 | 4.1 | 4.0 |
| END | 2.9 | 2.5 | 3.1 | 2.0 | 2.6 |
| IO | 4.6 | 4.9 | 6.2 | 4.5 | 6.4 |
| E | 1.8 | 1.7 | 2.1 | 2.1 | 2.0 |
| EN | 2.1 | 2.0 | 3.0 | 2.9 | 2.8 |
| OD | 6.1 | 7.0 | 7.8 | 6.0 | 6.0 |
| DG | 4.8 | 4.9 | 5.0 | 3.9 | 3.2 |

The body is slightly rounded in lateral view (BMH/BMW = 0.77); the ventral contour of the body is flat at the level of the head and body (Fig. 2A). The dorsal contour is convex from the oral disc's anterior edge to the eyes' posterior border. In the dorsal view, the snout is slightly rounded (Fig. 2B). The nares are oval without protuberances. Dorsolaterally oriented and situated dorsally (BWN/ BWE = 0.74), closer to the snout than the eye (FN/END = 66.0). Eyes relatively small (E/BWE = 0.10), situated dorsolaterally (IO/BWE = 0.47) (Fig. 2B). The spiracle is single, lateral, sinistral, directed posterodorsally, almost as long as broad, and placed approximately halfway between the snout and posterior margin of the body (Fig. 2A). Its inner wall presents as a slight ridge and is visible in dorsal and lateral views; its opening is oval, located below the body midline, and its diameter is smaller than the tube diameter, opening only visible in lateral view. The inner wall is attached to the body but perfectly distinguishable. Vent tube dextral, with an opening not visible laterally, concealed by a fold of vent tube wall; right wall attached anteriorly to ventral fin (Fig. 2C). The oral disc is anteroventral located and transversally elliptical (Fig. 2D). Medium-sized (OD/BMW = 0.43), not emarginated, and with a medium dorsal gap (DG/OD = 0.62) in marginal papillae; with mental papillae (Fig. 2D). Marginal papillae are simple, small, and conical, arranged in a single row in the anterior (upper) labium; placed in a single row in the posterior (lower) labium. There are 15–16 submarginal papillae in the anterior and posterior lip. The papillae are small, round, or conical with rounded or pointed tips. Submarginal papillae in mental area absent (Fig. 2D). Jaw sheaths are robust, more expansive than high, there are 15–17 /mm of finely serrated triangular

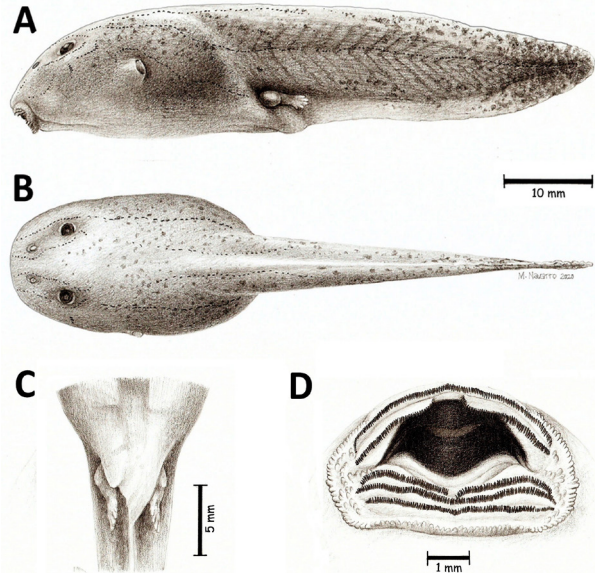


Figure 2. The tadpole of *T. frontieriensis* (IZUA N° 3657, stage 36) – (A) Lateral, (B) dorsal, and (C) ventral views. (D) Oral disc.

serrations on the upper jaw, wide and brown pigmented. The upper jaw sheath is arc-shaped, and the lower jaw sheath is V-shaped. The free margin of the upper jaw sheath is widely arch-shaped, with a short lateral process. Lower jaw sheath V-shaped. The labial tooth row formula 2(2)/3(1); A2 = A1, P1 = P2 > P3; P4; gaps in A-2 and P-1 about 1.0 and 0.5 mm respectively. A2 > A1, P1 = P2 > P34; gaps in A-2 and P-1 about 1.4 and 0.8 mm. Tooth density on A1 23–55 teeth /mm.

The tail is large (TaL/TL = 0.43), with well-developed musculature, almost reaching the tail tip. The tail axis is straight and the tail tip is gently rounded. Dorsal and ventral fins of similar height; dorsal fin not extending onto the body; ventral fin starting at the end of vent tube; both fins almost as high as body height (MTH/BMH = 1.1). Lines of the neuromasts are present on the tail (dorsal and medial) (Fig. 2A), dorsum (dorsal) (Fig. 2B), around the eyes (anterior oral) (Fig. 2B) and belly (ventral).

Tadpole colouration

When the larvae were observed among the aquatic vegetation, they were olive green in colour (Fig. 3). In life, out of the water and exposed to the sun (Fig. 4A,B,C) the body and tail are leaden blues, covered with fine golden spots. In fixative (10% formalin) the body and tail are greyish and the golden colouration disappears.

Natural History Notes

Puquios belongs to the Puna biogeographic province, which is characterised by its aridity, rocky substrate, and xerophytic vegetation: Yareta (*Azorella compacta*) and low grasses and bushes (*Festuca ortophylla*, *Stipa nardoides*). In Ollagüe, a town near Puquios (15 km), the temperature ranges between 1.6 °C (July) and 10.2 °C (January). During two years (1989 and 1998) of observation, no rainfall was recorded, and in the period 1972–2014, only 69.2 mm of rainfall was recorded at the Ollagüe weather



Figure 3. Tadpoles (red arrows) of *T. fronteriensis* under aquatic plants of the genus *Potamogeton*.

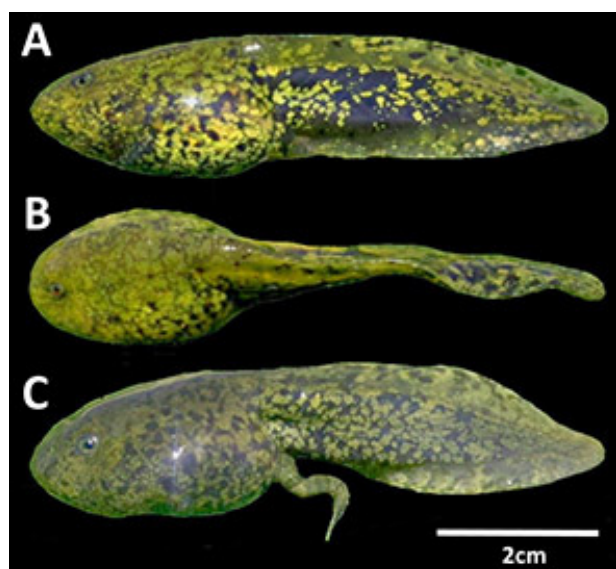


Figure 4. Colour of live larvae. **(A)** Lateral and **(B)** dorsal views of tadpoles of *T. fronteriensis* (stage 31). **(C)** Tadpole of *T. fronteriensis* (stage 39).

station (Sarricolea et al., 2017). On 19 October 2015, in Puquios during fieldwork, between 1230 h and 1300 h the temperature was 20 °C and the humidity was 23.4 %.

Adults and tadpoles of *T. fronteriensis* were captured among the aquatic vegetation (*Potamogeton* sp) of a low-flow stream (3 km long, 1 m wide, and 40 cm deep) (Fig. 3); the water temperature was 22 °C. The bottom consisted of mud (<1 mm), (0.5–2.0 mm) and was large (11–100 mm).

Disease screening

The five collected tadpoles and additional 21 adults, all gave negative results for both *B. dendrobatidis* and *Ranavirus*.

Variation

Among the tadpoles examined we found one (Fig. 4C) that differed from the rest. From the posterior third of the caudal fin, its edge drops steeply. In the other tadpoles, this edge descends gently. During the fieldwork, we found

larvae in different stages of development (Gosner, 1960) which may be evidence of a larval development period of more than one year.

DISCUSSION

Díaz & Valencia (1985) studied the external morphology of four *Telmatobius* species (*T. halli* [specimens from Vilama river now *T. vilamensis*], *T. pefauri*, *T. marmoratus* and *T. peruvianus*) present in Chile, and noted the remarkable homogeneity of their external morphological characteristics. So, the bauplan of these larvae corresponds to a lentic type, e.g. their larvae have in tendency a globular body, median to high fins, a non-robust tail musculature, and a pointed tail end (Altig & McDiarmid, 1999a; Laudor et al., 2021) (See Figs. 2 & 5). In northern Chile, these prevailing morphological traits are frequently found in lentic and lotic environments. Probably because lotic environments do not present great differences in flow compared to lentic environments (generally streams 1 m wide and 20 cm deep, see Fig. 1). This situation differs from those of lotic environments with fast running waters (mountain streams) where highly modified reophilous tadpoles are found, such as *T. espadai* and *T. sanborni* (suctorial oral disc, and tail muscle more robust) (Aguilar et al., 2007). However, in this work, we found variations in some of their external characters. For example, the tadpoles *T. halli* differ from the analysed tadpoles in the following characteristics: the spiracular aperture is rounded, the inner wall is wholly attached to the body wall and the dorsal fin originates in the anterior third of the tail. On the other hand, the BL/TL index ranges between 0.36 (*T. chusmisensis*) and 0.51 (*T. halli*). This comparative analysis showed that at the interspecific level, some characters are "variable" (e.g. spiracle, the tip of the tail) and others "more constant" (e.g. tooth row formula, oral disc emarginate/not emarginate). Thus, to improve the interspecific comparisons of Chilean *Telmatobius* tadpoles, it would be helpful to standardise the characters to be considered (variable/constant, developmental states) so that comparisons help to establish their taxonomic identity and the morphological patterns involved. Some characteristics of those tadpoles are presented in Table 3.

Among the generalised (*sensu* Orton, 1953) *Telmatobius* tadpoles, Lavilla (1985) recognised two well-defined phenetic groups: the first, with only one row of sub-marginal mental papillae ("meridional" group), whereas the second ("septentrional") lacks this row. All species examined in this work belong to the "septentrional" group. Barrionuevo & Baldo (2009) and Barrionuevo (2017) questioned the phylogenetic validity of Lavilla's hypothesis. However, the significance of these structures should be evaluated appropriately.

Sáez et al. (2014) studied the phylogenetic relationships of 19 *Telmatobius* species from the central Andes of Chile and Bolivia, including individuals from 12 undescribed populations of Chile. This analysis based on mitochondrial DNA 16S and cytochrome b shows that the Chilean endemic species belong to two groups (clade) species: (a) the *T. hintoni* (*T. fronteriensis* and *T. philippii*) and

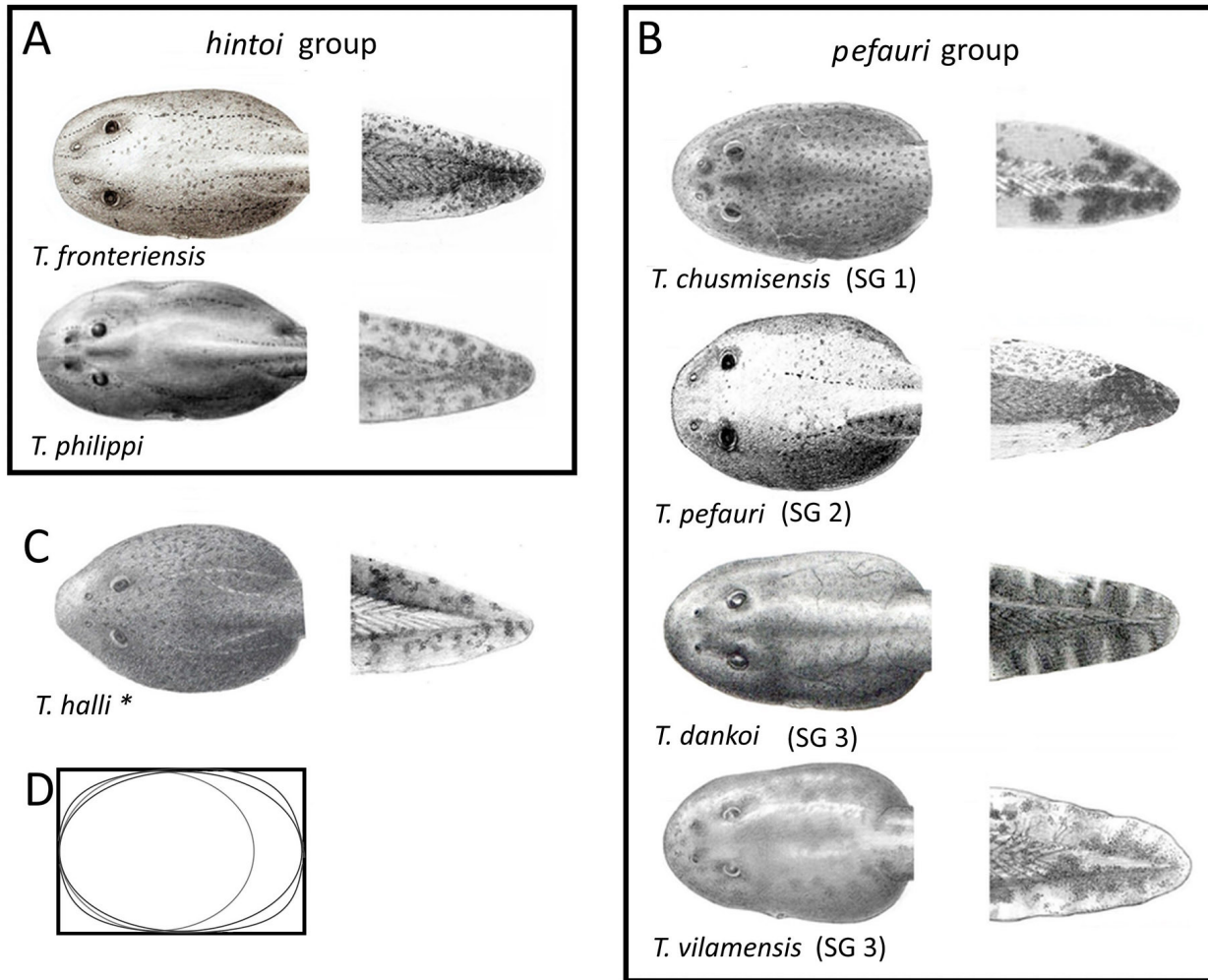


Figure 5. Dorsal view of body and tail tips of seven Chilean endemic *Telmatobius* tadpoles – (A) hintoi group, and (B) pefauri group. (C) *T. halli* not in Sáez et al. (D) Body shape criteria (frame from inside out): rounded, ovoid, rectangular. Drawings (not to scale) taken from original publications, except *T. fronteriensis* and *T. pefauri*. SG Subgroup.

Table 3. External morphological comparisons among the tadpoles of seven Chilean *Telmatobius* species. Stages according to Gosner (1960). BL = body length, LT = total length.

| Species | Stage | BL/ TL | Spiracle: direction and shape of its aperture | Dorsal fin origin | Bodyform | Tip tail form and pigmentation | Source |
|-------------------------|--------|-----------|--|------------------------|--------------------------|--------------------------------------|--------------------------------------|
| <i>T. fronteriensis</i> | 36 | 0.39 | posterior, ovoid | contact the body | ovoid | gently rounded, pigmented | This paper |
| <i>T. philippii</i> | 33 | 0.42 | posterior, ovoid | contact the body | rectangular | gently rounded, gently pigmented | Cuevas & Formas, 2002; This paper |
| <i>T. pefauri</i> | 36 | 0.39 | posterior, ovoid | contact the body | ovoid | gently rounded, pigmented | This paper |
| <i>T. chusmisensis</i> | 36 | 0.40 | posterior, ovoid | contact the body | rectangular | gently rounded, pigmented | Formas et al., 2006; This paper |
| <i>T. dankoi</i> | 37 | 0.36 | posterior, ovoid | contact the body | ovoid | rounded, pigmented | Formas et al., 1999; This paper |
| <i>T. vilamensis</i> * | 35 | 0.44 | posterior, ovoid | contact the body | ovoid | rounded, gently pigmented | Formas et al., 2003 |
| <i>T. halli</i> | 33, 34 | 0.51 | lateral, rounded | anterior third tail | approximately rounded | bluntly pointed, gently pigmented | Cuevas et al., 2020; This paper |

* Data from Formas et al. (2003)

(b) the *T. pefauri*, the latter having three subgroups: the first, *T. chusmisensis*, the second, *T. pefauri*; and the third includes, *T. dankoi* and *T. vilamensis*. This group (b) is restricted to the western slopes of the Andes. In this work tadpoles of the six exclusive Chilean *Telmatobius* species (*T. fronteriensis*, *T. philippi*, *T. chusmisensis*, *T. pefauri*, *T. dankoi* and *T. vilamensis*) were distributed in each group proposed by Sáez et al. (2014) (Fig. 5AB), and their external morphological characteristics compared (Table 3). As a result of this exercise, we observed differences between the members of different groups. For example, the members of the “hintoi” group differ in body shape: ovoid in *T. fronteriensis* and rectangular (elongated) in *T. philippii*. Among the tadpoles of the “pefauri” group, in *T. chusmisensis* (subgroup 1) and *T. pefauri* (subgroup 2) differ just in body form, ovoid (*T. chusmisensis*) and rounded (*T. pefauri*). Finally, both members of subgroup 3 share the body and tail form (ovoid and rounded respectively), however, the tail is gently pigmented in *T. vilamensis*, and strongly pigmented in *T. dankoi*, being the more consistent group respecting Sáez et al. proposition. *Telmatobius halli* (not in Sáez et al., 2014) (Fig. 5C) is the most dissimilar tadpole (body rounded with snout acuminate, tail shape bluntly pointed and the opening of the spiracle tube directed perpendicular to the body wall). These observations showed the differences that exist among the external characters and suggest that heterogeneity is a frequent phenomenon in these tadpoles. Although our observations are preliminary, they suggest that the revision of the criteria of morphological homogeneity should be reconsidered in species of the genus *Telmatobius* tadpoles (and adults).

Telmatobius spp. has been one of the most impacted groups of amphibians by *B.dendrobatidis* (Scheele et al., 2019) and no published information exists on the impacts of *Ranavirus* to this amphibian group. It is likely that the apparent absence of both pathogens (all 26 samples negative) is due to the isolation of the stream used by this species. It is therefore useful to assess the potential threat posed by an unwanted introduction of both emerging pathogens to *T. fronteriensis*. Finally, to increase knowledge of the biology of *Telmatobius* species on the western slope of the Andes in northern Chile, it is convenient to determine the taxonomic identity of the populations analysed by Sáez et al. (2014), describe their tadpoles for a better understanding of the taxonomy of this genus, and thus be able to address future conservation actions.

ACKNOWLEDGEMENTS

We appreciate the comments on the manuscript by Drs. Esteban Lavilla (Fundación Miguel Lillo, Argentina), César Aguilar (Museo de Historia Natural, Perú) and two anonymous referees. The assistance in the field of Mario Ryback and Alexandra Peñafiel is appreciated. Marcos Navarro expertly drew the tadpole of *T. fronteriensis* and Manuel Corvalán determined specific names of aquatic plants. Fieldwork and drawings were supported by project Fondecyt N° 1211587 granted to Claudio Azat.

REFERENCES

- Aguilar, C. & Pacheco, V. (2005). Contribución de la morfología bucofaringea larval a la filogenia de *Batrachophrynus* y *Telmatobius*. In *Monografías de Herpetología Vol. 7: Estudios sobre las ranas andinas de los géneros Telmatobius y Batrachophrynus (Anura: Leptodactylidae)*. Lavilla, E.O., De la Riva, I., Font, E. & Lluch, J. (Eds.). Asociación Herpetológica Española, Valencia, España. 219–238 pp.
- Aguilar, C. & Valencia, N. (2009). Relaciones filogenéticas entre telmatobiinidos (Anura, Ceratophryidae), de los Andes centrales basado en la morfología de los estados larval y adultos. *Revista Peruana de Biología* 16, 43–50.
- Aguilar, C., Lundberg, M., Siu-Ting, K. & Jiménez, M.E. (2007). 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 Biología* 14, 209–216.
- Altig, R. & McDiarmid, R.W. (1999a). Body Plan. Development and Morphology. In *Tadpoles: The Biology of Anuran Larvae*. McDiarmid, R.W. & Altig, R. (Eds.). Chicago: University of Chicago Press. 24–51 pp.
- Altig, R. & McDiarmid, R.W. (1999b). Diversity: Familial and generic characterizations. In *Tadpoles: The Biology of Anuran Larvae*. McDiarmid, R.W. & Altig, R. (Eds.). Chicago: University of Chicago Press. 295–337 pp.
- Barrionuevo, J.S. (2017). Frogs at summits: phylogeny of the Andean frogs of the genus *Telmatobius* (Anura, Telmatobiidae) based on phenotypic characters. *Cladistics* 33, 41–68.
- Barrionuevo, J.S. & Baldo, D. (2009). Descriptions of the tadpoles of *Telmatobius platycephalus* and *Telmatobius pinguiculus* from montane Argentina. *The Herpetological Journal* 19, 21–27.
- Benavides, E., Ortiz, J.C. & Formas, R. (2002). A new species of *Telmatobius* (Anura: Leptodactylidae) from northern Chile. *Herpetologica* 58, 210–220.
- Cei, J.M. (1986). Reptiles del centro, centro-oeste y sur de la Argentina. Herpetofauna de las zonas áridas y semiáridas. In *Monografie IV. Museo Regionale di Scienze Naturali, Turin, Italia*. Mapas. Figuras. Fotografías. Stabilimento Silvestrelli & Capelleto di S. Rosa-Clot e C. Turin, Italia. 527 pp.
- Cuevas, C.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.
- Cuevas, C.C., Formas, J.R., Ryback, M., Peñafiel, A. & Azat Soto, C. (2020). Rediscovery of the enigmatic Andean frog *Telmatobius halli* Noble (Anura: Telmatobiidae), re-description of the tadpole, and comments on new adult’s characters, type locality and conservation status. *Zootaxa* 4834(2), 195–206.
- De La Riva, I. (2005). Sinopsis of Bolivian *Telmatobius*. In *Monografías de Herpetología Vol. 7: Estudios sobre las ranas andinas de los géneros Telmatobius y Batrachophrynus (Anura: Leptodactylidae)*. Lavilla, E.O., De la Riva, I., Font E. & Lluch, J. (Eds.). Valencia: Asociación Herpetológica Española. Valencia, España. 65–101 pp.
- Díaz, N.F. & Valencia, J. (1985). Larval morphology and

- phenetic relationships of the Chilean Alsodes, *Telmatobius*, *Caudiverbera*, and *Insuetoprynus* (Anura: Leptodactylidae). *Copeia* 1985, 175–181.
- Fibla, P., Sáez, P.A., Salinas, H., Araya, C., Sallaberry, M. & Méndez, M.A. (2017). The taxonomic status of two *Telmatobius* frog species (Anura: Telmatobiidae) from the western Andean slopes of northernmost Chile. *Zootaxa* 4250, 301–314.
- Formas, J.R., Northland, I., Capetillo, J., Núñez, J.J., Cuevas, C.C. & Bieva, L.M. (1999). *Telmatobius dankoi*, una nueva especie de rana acuática del norte de Chile (Leptodactylidae). *Revista Chilena de Historia Natural* 72, 427–445.
- Formas, J.R., Benavides, E. & Cuevas, C.C. (2003). A new species of *Telmatobius* (Anura: Leptodactylidae) from Rio 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.
- Frost, D.R. (2023). Amphibian Species of the World: an Online Reference. <https://amphibiansoftheworld.amnh.org/index.php>. Version 6.1. Accessed on 22 September 2022. American Museum of Natural History, New York, USA.
- Gosner, K.L. (1960). A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16, 183–190.
- Grosjean, S. (2005). The choice of external morphological characters and developmental stages for tadpole-based anuran taxonomy: a case study in *Rana (Sylvirana) nigrovittata* (Blyth, 1855) (Amphibia, Anura, Ranidae). *Contributions to Zoology* 74, 61–76.
- Lannoo, M.J. (1987). Neuromast topography in anuran amphibians. *Journal of Morphology* 191, 115–129.
- Larson, P.M. & de Sá, R.O. (1998). Chondrocranial morphology of *Leptodactylus* larvae (Leptodactylidae: Leptodactylinae): its utility in phylogenetic reconstruction. *Journal of Morphology* 238(3), 287–305.
- Laudor, J., Schultze, A., Veith, M., Viertel, B., Elle, O. & Lötters, S. (2021). Morphology of lentic and lotic tadpoles from Madagascar. *BMC Zoology* 6, 28. <https://doi.org/10.1186/s40850-021-00091-9>.
- Lavilla, E.O. (1985). Diagnoses genéricas y agrupación de las especies de *Telmatobius* (Anura: Leptodactylidae) en base a caracteres larvales. *Physis* 105, 63–67.
- Lavilla, E.O. (1988). Lower Telmatobiinae (Anura: Leptodactylidae): generic diagnoses based on larval characters. *Occasional Papers Museum Natural History, University of Kansas* 124, 1–19.
- 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. & Scrocchi, G.J. (1986). Morfometría larval de los géneros de Telmatobiinae (Anura: Leptodactylidae) de Argentina y Chile. *Physis* 44, 39–43.
- Lobos, G. & Rojas, O. (2020). Ecología y conservación en los *Telmatobius altoandinos* de Chile; El caso de la ranita de Loa. Imprenta América Impresores. Valdivia, Chile. 173 pp.
- Orton, G.L. (1953). The systematics of vertebrate larvae. *Systematic Zoology* 2, 63–75.
- Sáez, P., Fibla, P., Correa, C., Sallaberry, M., Salinas, H., Veloso, A., Mella, J., Iturra, P. & Méndez, M.A. (2014). A new endemic lineage of the Andean frog genus *Telmatobius* (Anura, Leptodactylidae) from the western slopes of the central Andes. *Zoological Journal of the Linnean Society* 171, 769–782.
- Sarricolea, P., Meseguer Ruiz, O. & Romero Aravena, H. (2017). Tendencias de la precipitación en el norte grande de Chile y su relación con las proyecciones de cambio climático. *Dialogo Andino* 54, 41–50. <http://dx.doi.org/10.4067/S0719-26812017000300041>.
- Savage, J. (2002). The Amphibians and Reptiles of Costa Rica: A herpetofauna between two continents, between two seas. Bibliovault OAI Repository, the University of Chicago Press. 181 pp.
- Scheele, B.C., Pasmans, F., Skerratt, L.F., Berger, L., Martel, A., Beukema, W., Acevedo, A.A., Burrowes, P.A., Carvalho, T., ... & Canessa, S. (2019). Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. *Science* 363(6434), 1459–1463. Doi: 10.1126/science.aav0379.
- Soto-Azat, C., Peñafiel-Ricaurte, A., Price, S.J., Sallaberry-Pincheira, N., García, M.P. & Cunningham, A.A. (2016). *Xenopus laevis* and emerging amphibian pathogens in Chile. *EcoHealth* 13, 775–783.

Accepted: 6 July 2023