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Third time's the charm: The definitive rediscovery of *Telmatobius halli* Noble, 1938 (Anura, Telmatobiidae) at its historic type locality

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Abstract

Telmatobius halli Noble, 1938 was the first representative of its genus to be described for Chile, but for 80 years no new individuals could be located due to the vagueness with which its type locality was described. The type series was collected by one of the members of the International High Altitude Expedition to Chile (IHAEC) that took place in 1935. Recently, three studies successively claimed to have rediscovered the type locality in different places. The third study proved, considering the chronicles of the IHAEC, that the actual locality is Miño, at the origin of the Loa River. In the contemporary herpetological literature, there are no records of *Telmatobius* from this locality. In this study, we provide additional documentary antecedents and graphic material that corroborate that the mentioned location is indeed the historic type locality of *T. halli*. Additionally, we describe the recently discovered *Telmatobius* population from Miño, whose external characteristics are consistent with the description of *T. halli*, and the environment it inhabits. Furthermore, we performed a molecular phylogenetic analysis that strongly suggests that *T. halli* (from Miño), *T. dankoi* and *T. vilamensis*, all known only from their type locality in Chile, are conspecific. Neither of the populations from the previously proposed rediscoveries grouped with the one from the genuine type locality. We discuss the implications that these findings have for the taxonomy, biogeography and conservation of the populations from the extreme south of the distribution of the genus in Chile.

Keywords

Amphibia, Chile, Loa River, lost frog, phylogeny, Puna

Introduction

The genus *Telmatobius* Wiegmann, 1834 is one of the few anuran taxa that has managed to diversify in the high Andes (Barrionuevo 2017), so its representatives exhibit a series of physical and physiological adaptations that allow them to survive in such harsh climatic environments (e.g. Ruiz et al. 1983; Reider et al. 2020). In fact, it includes one of the highest-dwelling frog species, *Telmatobius marmoratus* (Duméril and Bibron, 1841), which has been reported from up to 5,400 m (Reider et al. 2020). Currently, there are 63 recognized species in this genus (Frost 2021), which distribute throughout a variety of ecosystems alongside the Andes, between approximately 1°S and 30°S (Barrionuevo 2017). The biogeographical consequences of the uplifting of the Andes during the late Pliocene and Pleistocene and paleoclimatic processes, such as the repeated formation and evaporation of extensive lakes, have been proposed to be responsible for the diversification of the fauna in the Puna highlands, the driest section of the Central Andes (e.g. Collado et al. 2011; Vila et al. 2013; Sáez et al. 2014). Thus, vicariance seems to be a reasonable explanation for the divergence of the *Telmatobius* from this arid region, taking into account their strongly aquatic habits (Barrionuevo 2017) and the hostile environments that have evolved around the watercourses.

In Chile, nine species of *Telmatobius* (seven of them endemic) are currently recognized (Fabres et al. 2018; Correa 2019), although Sáez et al. (2014) questioned the presence of *Telmatobius peruvianus* Wiegmann, 1834 in Chilean territory. Furthermore, Sáez et al. (2014) suggest that *Telmatobius dankoi* Formas, Northland, Capetillo, Nuñez, Cuevas, and Brieva, 1999 and *Telmatobius vilamensis* Formas, Benavides, and Cuevas, 2003 might be conspecific (see also Fabres et al. 2018) and point out the low genetic divergence between *Telmatobius philippii* Cuevas and Formas, 2002 and *Telmatobius frontiensis* Benavides, Ortiz, and Formas, 2002. Despite these taxonomic uncertainties, the number of known populations of the genus in Chile has increased substantially over the last decade (e.g. Sáez et al. 2014; Victoriano et al. 2015; Fibla et al. 2017; Lobos and Rojas 2020 — see Correa 2019). Undoubtedly, a greater sampling effort will bring up even more discoveries, yet the accessibility and the conditions for fieldwork in the region are challenging.

Like in the case of other Chilean amphibian genera (*Alsodes* Bell, 1843; *Eupsophus* Fitzinger, 1843) (Blotto et al. 2013; Correa and Durán 2019), the taxonomy of the genus *Telmatobius* is complex, due to high levels of intrapopulation and interpopulation variation in morphological features (e.g. Trueb 1979; Wiens 1993; De la Riva et al. 2005; Barrionuevo 2017), especially in characters that have been used for diagnosis in the description of some species (De la Riva et al. 2005). Thus, molecular studies have played an important role in the systematics of this taxonomic group in Chile during the past few years (Sáez et al. 2014; Victoriano et al. 2015; Fibla et al. 2017, 2018 — reviewed by Sáez and Méndez 2020). Nonetheless, a clear species delimitation has not been accomplished yet, and surely a more integrative approach (e.g. Padial et al. 2010) is required to solve the taxonomic problems mentioned above.

Among the endemic species of Chile, *Telmatobius halli* Noble 1938 stands out for its complex taxonomic history. Dr Frank Gregory Hall collected the type series (adults and larvae) in the context of the International High Altitude Expedition to Chile (IHAEC), an endeavor that took place in 1935 and whose principal purpose was to study the effects of low-oxygen environments of high elevation on the human physiology and the body's acclimatization response (Keys 1936b). Three years after the expedition, Dr Gladwyn Kingsley Noble, from the American Museum of Natural History, described the

specimens he had received from Hall and named the species after its collector. There has been considerable confusion regarding *T. halli* and most part of it must be ascribed to Noble's vague definition of the type locality as "Warm spring near Ollagüe, Chile, 10,000 ft. altitude" (Correa 2021). Throughout the years, a few populations had been assumed to belong to *T. halli* (Capurro 1954, 1955; Cei 1962, 1986; Veloso et al. 1982; Northland et al. 1990; Núñez and Gálvez 2015), but were later revised and described as new species (*T. dankoi*, Formas et al. 1999; *T. vilamensis*, Formas et al. 2003) or assigned to another taxon, like in the case of the populations from Ascotán Salt Flat, treated as *T. cf. philippii* by Lobos et al. (2018) (Fig. 1). Furthermore, anurans found at Tatio, San Pedro de Atacama were described as the subspecies *T. halli edentatus* (Capurro 1955), but Cei (1962) identified the specimens in question as *Rhinella spinulosa* (Wiegmann, 1834).

Formas et al. (2003) redescribed *T. halli* based on the type material from the American Museum of Natural History (AMNH) and differentiated it from *T. dankoi* and *T. vilamensis* using morphological evidence. Over the last three decades, significant efforts have been made to locate the type locality of *T. halli* (Formas et al. 2003, 2005; IUCN 2015). These expeditions were infructuous in terms of clarifying the whereabouts of *T. halli*, but led to the description of new species (*Telmatobius philippii*, Cuevas and Formas 2002; *T. fronteriensis*, Benavides et al. 2002) and the discovery of a series of undetermined populations (*Telmatobius* sp. from Ascotán and Carcote salt flats; Sáez et al. 2014) in the area surrounding Ollagüe (Fig. 1).

Recently, two contributions — Fibla et al. (2018) and Cuevas et al. (2020) — independently claimed to have rediscovered *T. halli*. Bibliographic sources describing the IHAEC's activities were used in both studies, but each focused on different known populations of *Telmatobius*. Thus, Fibla et al. (2018) assigned the southernmost populations of *T. chusmisensis* Formas, Cuevas, and Nuñez, 2006 (sensu Sáez et al. 2014) to *T. halli* (Copaquire, Choja, Chijlla), while Cuevas et al. (2020) did the same with a population from the Carcote Salt Flat (specifically, from the hot spring Aguas Calientes) (Fig. 1A, B). Previously, a Carcote population (coordinates not specified) was considered as *Telmatobius* sp. by Sáez et al. (2014) or *T. cf. philippii* by Lobos et al. (2018). According to the molecular phylogenetic analysis of Sáez et al. (2014), the only one where all of these populations were included, they are nested in different clades — the *T. pefauri* (former *T. zapahuirensis*, see Fibla et al. 2017) and *T. hintoni* species groups (not recovered in the most recent analysis by Barrionuevo 2017) — respectively, so they clearly do not correspond to the same taxon. Nevertheless, the opposing hypotheses of Fibla et al. (2018) and Cuevas et al. (2020) were refuted by Correa (2021), who demonstrated, also using bibliographic sources, that the frog was first found near a warm swimming pool in Miño, a location at the source of Loa River, at the western foot of Miño Volcano (Fig. 1C). In the literature, there are no other reports of *Telmatobius* populations neither from Miño nor from the upper Loa basin.

Altogether, 83 years after its description and despite the multiple recent hypotheses about the location of its type locality and identity, *T. halli* is still a lost frog and no specimens have ever been seen since the collection of the type series (Correa 2021). So, the main goal of this contribution is to describe the *Telmatobius* population found in Miño, the place recently identified as the true type locality of *T. halli* (Correa 2021). We provide a general description of the location, some observations on adults and tadpoles and basic information on the quality of their habitat. Furthermore, we performed a phylogenetic analysis to shed light on the systematic relationships among the population of Miño, the ones recently proposed as being *T. halli* (Copaquire, Choja, Chijlla and Carcote Salt Flat) (Fibla et al. 2018; Cuevas

et al. 2020) and other *Telmatobius* species, which, prior to their description, had been postulated to be *T. halli* (*T. vilamensis* and *T. dankoi*) (e.g. Veloso et al. 1982).

Materials and methods

Archival evidence

The diary of Ross McFarland, one of the members of the IHAEC, was requested from the Ross A. McFarland Collection in Aerospace Medicine and Human Factors Engineering at the Wright State University Archives. The diary is listed as “Box 63, Folder 5: Ross McFarland’s Diary (May 1935–September 1935)” in the collection’s inventory (Hoffman and Ritchie 1987: 29). From the same collection, we obtained the video footage recorded by McFarland during the expedition (Items 2213, 2217 and 2218; Hoffman 1987: 113), which shows a swimming pool at the source of Loa River. Individual frames were extracted from the video and panoramic views of the four different positions of the cameraman were generated, using the open-source software HUGIN - Panorama photo stitcher (version 2019.2.0).

Study area

On October 31, 2020, a field trip to the site called Miño (21°12'S, 68°40'W; 3900 m elevation; Calama Commune, El Loa Province, Antofagasta Region, Chile) was performed to locate the frog population that was described as *T. halli* (Correa 2021). The historical reference for this search was the swimming pool and other features of the landscape that appear in the recordings made by McFarland.

As biosecurity measures to prevent the spreading of chytridiomycosis and other infectious diseases, we disinfected car tires, boots and utensils with F10 Super Concentrate Disinfectant (Health and Hygiene Pty.) at a concentration of 1:250 (Webb et al. 2007).

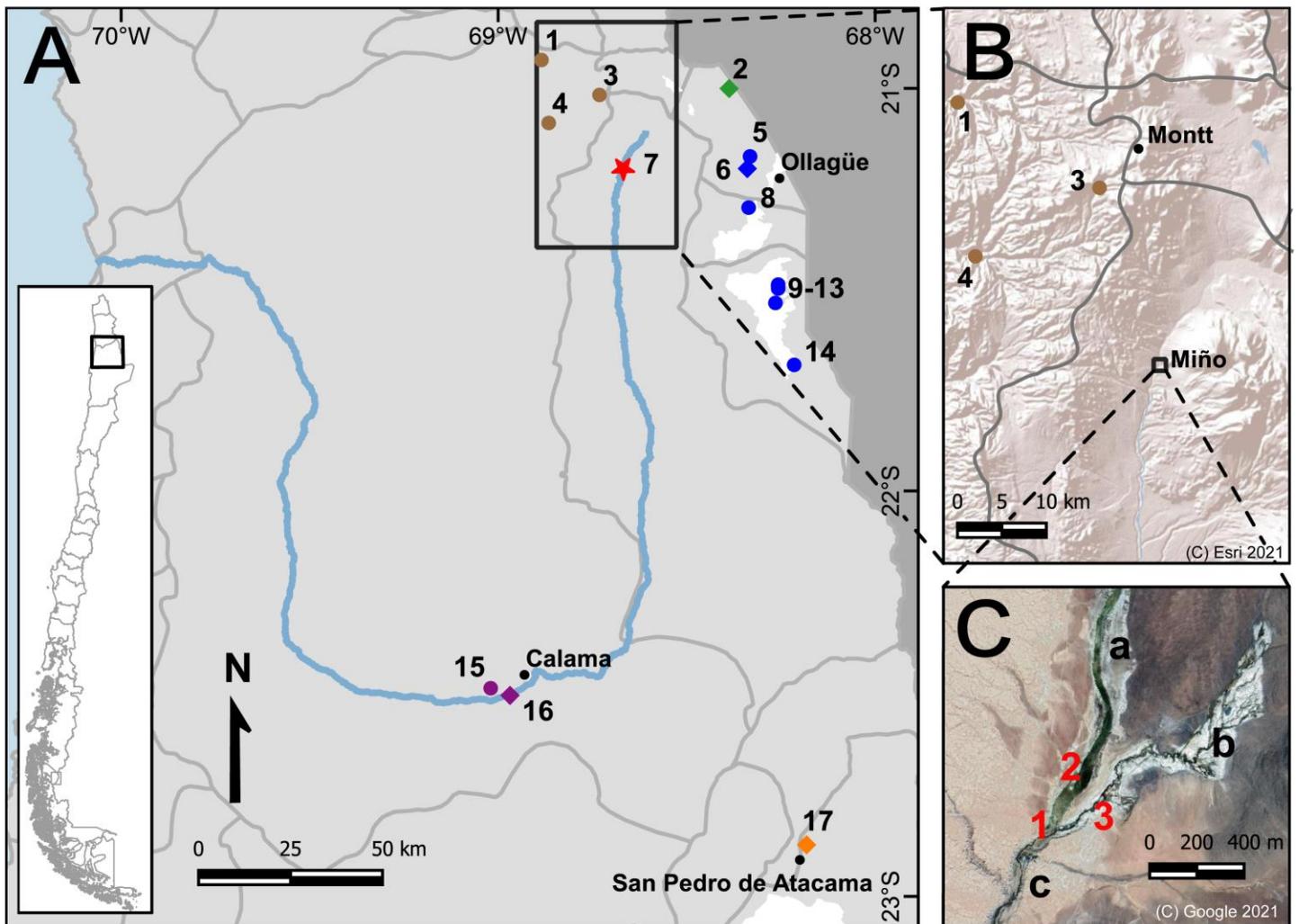


Figure 1. Geographic context of this study. **A** Distribution of all *Telmatobius* populations known from the southern range of the genus in Chile (20°55' – 22°55'S). The localities are listed in Table 1 according to their numeration on the map. Light grey area = Chilean territory, dark grey area = Bolivian territory, grey lines = limits of the sub-basins, blue line = Loa River, red star = study site (Miño), brown marks = *T. chusmisensis*, blue marks = *T. philippii* and *T. cf. philippii*, green mark = *T. fronteriensis*, purple marks = *T. dankoi*, orange mark = *T. vilamensis*, diamonds = type localities. **B** Topographic relief of the surroundings of Miño. Grey lines = limits of the sub-basins. Montt is the name provided by the IHAEC for the Collahuasi Copper Mine. **C** Satellite image of Miño. 1) Concrete pool, 2) ruins of mining settlement, 3) sampling point, a) Miño River, b) Nacimiento Creek, c) Loa River.

Table 1. Currently known *Telmatobius* populations from the southern range of the genus in Chile (20°55' – 22°55'S). The locations are enumerated from north to south (see map of Fig. 1). Bold letters denote type localities. Asterisk (*) indicates that the elevation was obtained from Google Earth. Elevations are expressed in m a.s.l. Note that the specific names assigned to Copaquire, Quebrada Chijlla, Quebrada Choja and Aguas Calientes populations correspond to the taxonomy prior to the proposals of Fibla et al. (2018) and Cuevas et al. (2020).

Number on map	Species	Locality	Elevation	Reference
1	<i>T. chusmisensis</i>	Copaquire	3,540*	Sáez et al. 2014
2	<i>T. fronteriensis</i>	Puquios	4,150	Benavides et al. 2002
3	<i>T. chusmisensis</i>	Quebrada Chijlla	4,550*	Sáez et al. 2014
4	<i>T. chusmisensis</i>	Quebrada Choja	3,500*	Sáez et al. 2014
5	<i>T. philippii</i>	Quebrada del Inca	3,800	Cuevas and Formas 2002
6	<i>T. philippii</i>	Amincha	3,800	Cuevas and Formas 2002
7	<i>T. halli</i>	Miño	3,900*	this study
8	<i>T. cf. philippii</i>	Aguas Calientes ¹	3,717	Cuevas et al. 2020
9–14	<i>T. cf. philippii</i>	Ascotán Salt Flat (springs 2, 3, 5, 6, 7 and 11)	~3,720	Lobos et al. 2018
15	<i>T. dankoi</i>	Ojo de Opache (introduced there in 2019)	1,960*	Lobos and Rojas 2020
16	<i>T. dankoi</i>	Las Cascadas	2,260	Formas et al. 1999
17	<i>T. vilamensis</i>	Vilama River	2,250*	Formas et al. 2003

¹There are several publications prior to Cuevas et al. (2020) that include specimens of a population of *Telmatobius* sp. of the Carcote Salt Flat (Sáez et al. 2014; Fibla et al. 2017, 2018), but none of them specify the coordinates or a precise site within the salt flat. Only in Lobos et al. (2020), the presence of a population of *Telmatobius* sp. in the Carcote Salt Flat is mentioned, whose coordinates fall very close to the Cuchicha spring (not shown in the map of Fig. 1A), located ~1.9 km NE of Aguas Calientes.

Ecology

We made a general description of the study area, considering the topography of the landscape and more specific conditions at microhabitat level. We measured the stream dimensions at various points and took air and water temperatures at different times of the day. The composition of the adjacent vegetation along the stream was ascertained and a nocturnal survey was undertaken to detect possible sympatric amphibians.

Both, adults and larvae, identified as *Telmatobius*, were collected during the daytime from the stream using a hand net. The sampling site was about 300 m upstream from the pool identified as the historical place where *T. halli* was collected (see details in Results). The animals were measured, photographed and finally released back to the capture site. Each individual was handled separately with an unused pair of disposable nitrile gloves (Thomas et al. 2020). To avoid possible toxic effects, the gloves were rinsed and the rinse water was discarded away from the watercourse (Cashins et al. 2008).

In order to obtain bioacoustic data, an AudioMoth recording unit (Hill et al. 2019) was placed beside the stream, at a spot where adult individuals had been sighted during sampling. The device recorded continuously between 8 p.m. and 7 a.m., but we did not obtain vocalizations that could be unquestionably attributed to *Telmatobius* calls.

In the course of the night, the AudioMoth took a measurement of the air temperature every 15 minutes, but the sensor only has an accuracy of $\pm 3^{\circ}\text{C}$ (Open Acoustic Devices 2020). Water temperature was taken with a digital thermometer.

Morphometrics

Seven morphometric features were measured on 11 adult specimens (Watters et al. 2016): snout-vent length (**SVL**), head width (**HW**), head length (**HL**), inter-orbital distance (**IOD**), inter-nostril distance (**IND**), foot length (**FL**) and tibia length (**TL**). FL and TL were assessed on the right hindlimb. In the case of the tadpoles ($n = 9$), body length (**BL**) and total length (**TTL**) were measured (Altig 2007) and the development stages (Gosner 1960) were determined. All measurements were taken using a vernier caliper to the nearest 0.05 mm.

Sampling and obtaining DNA sequences

Three tadpoles (Gosner stages 36–37) were anesthetized, immersing them in a buffered solution of MS-222 (0.2%) (Mitchell 2009) and a small portion of the membrane was cut from the caudal fin. After recovery from the anesthesia, they were released at the collection site. The tissue sample was stored in 96% ethanol until DNA extraction.

The DNA was extracted with a commercial kit (Promega ReliaPrep™ gDNA Tissue Miniprep System, Madison, WI) following the manufacturer's instructions. We obtained fragments of two mitochondrial genes with different degrees of variation, 16S rRNA and cytochrome b (cytb), the same fragments that were used in the phylogenetic analyses of Sáez et al. (2014). The reagent mixtures, reaction conditions and primers used in the PCRs are detailed in Sáez et al. (2014) and references therein. Electropherograms were edited with the program Bioedit v7.1.3 (Hall 1999). Substitution saturation of the sequences was assessed with DAMBE7 (Xia 2018). Sequences were deposited in GenBank (accession numbers pending).

Phylogenetic analysis

The sequences of both fragments were aligned with MUSCLE (Edgar 2004) and the alignments were then inspected by eye. A Bayesian phylogenetic analysis was performed with the program MrBayes v3.2.7 (Ronquist et al. 2012), in which all *Telmatobius* species from Chile and all known populations of the genus geographically close to Miño were included (Appendix 1). Both gene fragments were concatenated, but a reversible-jump Markov Chain Monte Carlo method for exploring the space of all General Time Reversible sub-models, plus gamma and proportion of invariable sites parameters, was applied independently to each fragment. The analysis consisted of two groups of four Markov chains that run independently for 20 million generations, sampling every 1,000 generations. The first 25% of generations was conservatively discarded as burn-in after observing the stationarity of ln-likelihoods of trees in Tracer v1.7.1 (Rambaut et al. 2018). Convergence and mixing of chains were assessed by examining values of average standard deviation of split frequencies (ASDSF) and expected sampling sizes (ESS) and Potential Scale Reduction Factor (PSRF) for all parameters. Trees were rooted with

one specimen of *Telmatobius sibiricus* De la Riva and Harvey, 2003, a representative of the *T. bolivianus* species group (Sáez et al. 2014; Barrionuevo 2017), which constitutes the sister clade of the three species groups present in Chile (Sáez et al. 2014).

Results

The type locality

Like it is pointed out in Correa (2021), according to the chronicles of the IHAEC by Keys (1936a, 1936b) and Dill (1979, 1980), the collection site of the type series of *T. halli* was the surroundings of a concrete swimming pool filled with warm water at the source of the Loa River (Figs 2, 3). Here, we provide the additional historical evidence extracted from the diary and the video recording of Ross McFarland that allowed us to identify the exact spot of the type locality. In the diary entry for Sunday, June 23, 1935, he wrote: “Trip in cars to hot springs at source of Rio Loa with Mr. Bell, Watson & Packard. Swimming & walk in green valley.” (McFarland 1935) (Fig 4). The diary also confirms that the date of the departure of the IHAEC from Collahuasi (railway station Montt) (Fig. 1B) back to Ollagüe was Tuesday, June 25, 1935. As stated in Fibla et al. (2018), this means that the original collection date was June 23 and not June 25, as specified by Noble (1938).

Regarding McFarland’s video material (see Suppl. material 1), the mountain in the background of the takes can easily be identified, even using Google Earth’s perspective view, as Miño Volcano, because of a characteristic bulge in its profile. Although strong erosion events have reshaped part of the landmarks, multiple rock formations of the canyon walls still remain identical and corroborated the congruence of the place with respect to the one depicted in the video (Fig. 2).

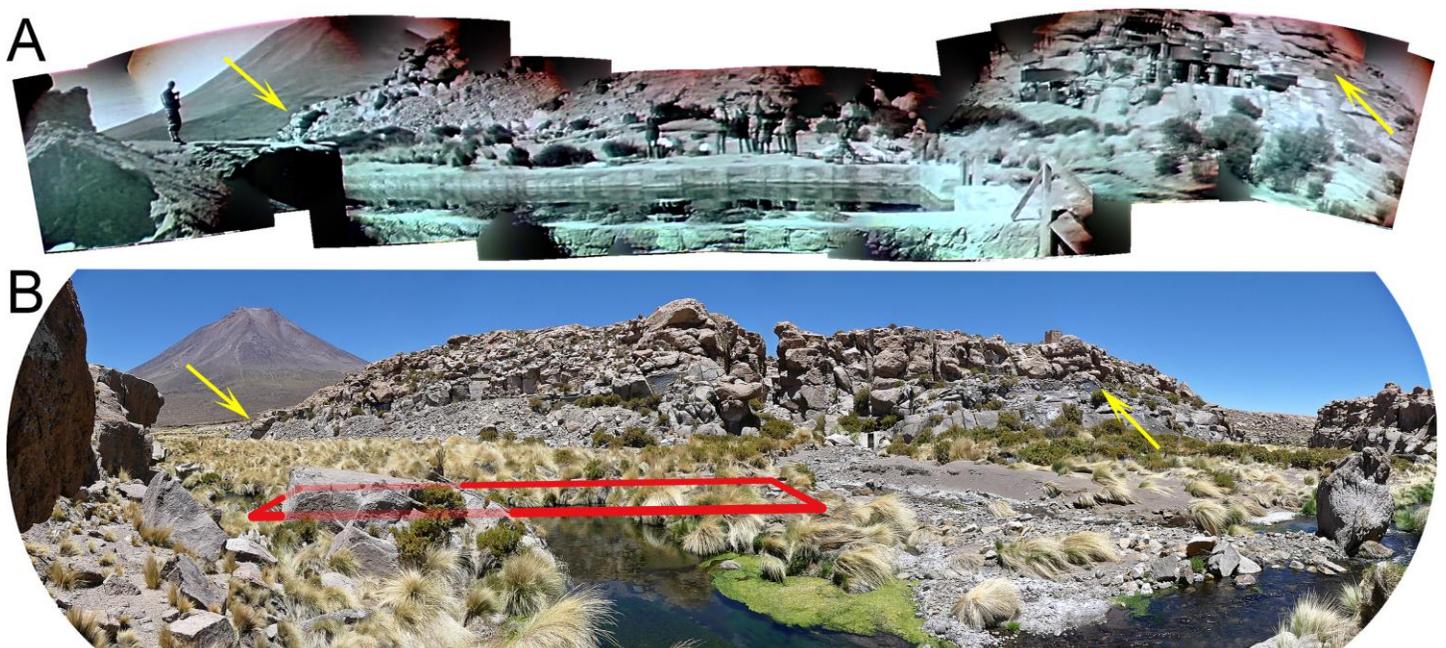


Figure 2. Historic and current panoramic view of the area surrounding the concrete swimming pool in Miño. **A** Panorama extracted from video footage from the IHAEC, 1935. Yellow arrows indicate rock formations that are easily recognizable. **B** Current state of the habitat. Red rectangle = location of the concrete pool. The mountain in the left background is Miño Volcano.

As expected, the remains of the mentioned concrete swimming pool were found at 21°12'01"S, 68°40'09"W (3,900 m) (Fig. 3). Even though the stream broke through the lower end of the pool's wall and the bottom is filled with sand, most of the boundaries are still in place and it is evident that the structure corresponds to the one shown in the recording. The pool is rectangular, approximately 6.5 m wide, 20 m long and between 1.5 and 2 m deep. The sidewalls are made of stones, joined together with concrete, while the upper and lower walls are massive concrete blocks. There are other more recent concrete structures inside the stream, one immediately above the pool and another one about 300 m upstream.



Figure 3. Historic and current state of the concrete swimming pool in Miño. **A** Panorama extracted from video footage from the IHAEC, 1935. Yellow arrows indicate the upper and lower pool walls. **B** Same view in 2020.

Habitat description

The Loa River originates mainly from meltwater from throughout its upper drainage basin, where snow accumulates during austral winter. Several temporal ravines also gather the characteristic precipitations during the austral summer months (December to March), known as Altiplanic winter (Berenguer and Cáceres 2008; Delsouc et al. 2020). Lower down and descending from the east, there also are some important permanent affluents fed by aquifers.

For the first few kilometers, the riverbed is a broad and dry wadi named Miño River. Only about 4 km north of Miño, the arid riverbed gradually turns greener and ends in a small bog with grass tussocks,

covering an area of about 5 ha. No significant water flow was registered during this time of the year (late October). At Miño, there are some well-preserved ruins of an old mining camp from the 18th and 19th centuries at both sides of the bog (Berenguer and Cáceres 2008), serving as an easily recognizable landmark (Fig. 1C).

From this point on, the river bears the name Loa, as it receives its first permanent tributary, the “Estero Nacimiento” creek (Berenguer and Cáceres 2008). This spring emerges at the head of a small ravine of about 1.3 km in length, a place called Ojos del Miño (21°11'43"S, 68°39'40"W) (Flores 2001) (Fig. 1C).

Below the confluence, the river suddenly turns into a pronounced canyon with vertical cliffs. The concrete pool is located precisely at the beginning of the canyon. Soon after, the river gets a little broader, forming larger natural ponds and sections with rapids. The canyon goes on in a similar manner for almost 100 km, until reaching the Conchi water reservoir.

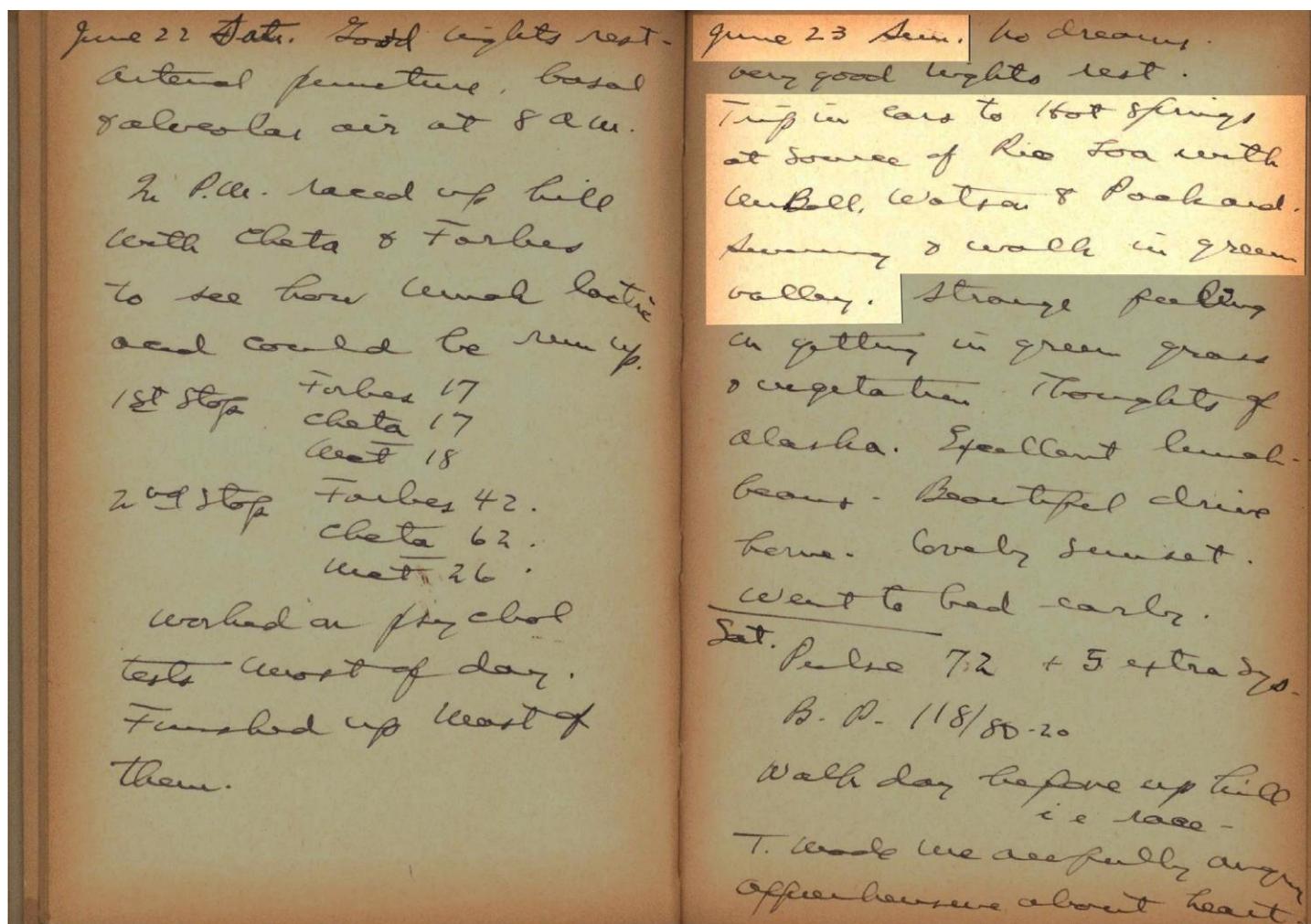


Figure 4. Extract from the diary Ross McFarland wrote in 1935 during the IHAEC

Microhabitat and ecology

At the sampling point, the current of the Nacimiento Creek flows rapidly, though the terrain is not very steep. The stream is between 2.5 and 5 m broad and 25 to 50 cm deep. The water is clear and the bottom is mostly sandy with some stones and scarce detritus at the bends. The margins are almost entirely covered with vegetation, mainly *Festuca chrysophylla* Phil. and a few bushes of *Parastrephia lucida* (Meyen) Cabrera. The overhanging grass cushions are ideal refugia for the frogs, forming at

times gallery-like cavities along the riverbank. At some points inside the stream, patches of *Myriophyllum aquaticum* (Vell.) Verdc. can be found, alternating with mats of undetermined filamentous green algae.

At the pool site, the bottom is also sandy; however, there is a little more mud and detritus, probably coming from the bog and consequently a more abounding aquatic vegetation. The stream at the exit of the pool measures about 4 m in width and 50 cm in depth. Downstream from the pool, the vegetation coverage at the banks decreases a bit, which leaves fewer shelters for the frogs. In fact, a lower population density was detected there.

Adults of *T. halli* were found mainly under the tussocks, where they shared their refugia with other adults and larvae. On one occasion, 11 adults and one tadpole were captured from below the same plant. Tadpoles also exhibit gregarious habits, but somehow seem to prefer to shelter inside the aquatic vegetation, at the bottom of the stream. Still, they are not absent under the cushions at the riverbank. Most of the observed larvae were at about the same development stage (Gosner stage 36–37); however, two specimens were younger (Gosner stages 27 and 33). Directly inside the pool, there were very few *Telmatobius* tadpoles and only one adult was found a few meters below the outlet. At the deepest point of the pool, there was a dead adult of the species.

During the daytime, two adults of *Rhinella spinulosa* were found under the riparian vegetation in the pool and after nightfall, numerous individuals of these toads were observed outside the water along the stream. A small ravine, adjacent to the pool, was occupied by hundreds of *Rhinella* larvae in semi-lentic, shallow puddles, which are ideal for their development. Additionally, one specimen of *Pleurodema marmoratum* (Duméril and Bibron, 1840) was found walking around at night; hence, all three potential anuran species were present in the area. Since no case of syntopy between the Chilean *Telmatobius* has been reported, no other congener is expected to be encountered in Miño.

Temperature

In the afternoon (05:00 p.m.), the air temperature was 21.8°C, almost equal to the water temperature at the outlet of the pool (21.4°C). In contrast, in the morning (8:00 a.m.) the air temperature was -2.4°C, while water temperatures at the pool and the sampling site were 19.0°C and 20.7°C, respectively. After sunset, the air temperature dropped quickly to around -11.0°C (00:30 a.m.) and remained alike until dawn. The minimum value was -13.1°C at 03:30 a.m. The water temperature, which is generally higher than that of other localities of the genus (Lobos and Rojas 2020) and which remains more or less constant (19–21.4°C), is consistent with the description of the original capture site (“a warm spring”; Noble 1938).

Table 2. Morphometrics of adults of *Telmatobius halli* from Miño. All measurements are expressed in millimeters. Measurements of the holotype (AMNH A-44753) and one of the paratypes (AMNH A-44754) were taken from Formas et al. (2003); SVL = snout-vent length, HW = head width, HL = head length, IOD = inter-orbital distance, IND = inter-nostril distance, FL = foot length, TL = tibia length.

Variable	Adults (n = 11)			Holotype	Paratype
	Mean	Min	Max		
SVL	42.94	38.95	57.15	57.06	48.04
HW	13.34	11.65	19.80	18.75	16.58
HL	12.76	11.00	17.80	16.50	14.27
IOD	4.06	3.30	5.75	6.04	4.91
IND	2.87	2.20	4.20	3.65	3.03
FL	22.15	20.10	29.15	40.21	32.27
TL	18.90	17.00	21.55	24.03	20.26

Table 3. Morphometrics of larvae of *Telmatobius halli* from Miño. All measurements are expressed in millimeters; TTL = total length, BL = body length.

Tadpoles (n = 9)			
Gosner stage	n	TTL (Mean)	BL (Mean)
27	1	58.35	24.00
33	1	97.95	30.75
36	5	97.38	38.39
37	2	97.00	39.10

Morphology

Overall, *T. halli* is a medium-sized frog (Table 2), with a depressed body, thin forelimbs and anterodorsolaterally orientated eyes (Fig. 5). In dorsal view, the head is slightly broader than long (HL/HW = 0.96), but narrower than the body. On average the head length is 29.65% of SVL. The snout tends to be long but truncated in dorsal view, although it can be rather elliptical in some individuals. In lateral view, the snout profile is quite variable, as it can be flat with a rounded tip or short and acuminate. *Telmatobius halli* presents a very smooth skin with minuscule granules, which in some specimens are almost absent on the dorsum. In other cases, they can be more evident on the limbs, flanks, or even covering the ventral surface. Mature males have very small spines associated with the granules, in addition to conspicuous, black nuptial pads on their thumbs. The coloration of dorsum and extremities can be described as a broad spectrum of brown, olive and yellowish speckles that alternate with dark, almost black spots or marks. Some frogs have fewer dark spots and the brown colors predominate, others show extensive dark areas (Fig. 5). The ventral coloration is lighter, with shades of cream or pink, mixed with yellow areas or white dots (Fig. 5E). A noteworthy character is the light, yellow annulus around the eyes of some specimens (Fig. 6), a trait that is shared with *T. dankoi* and *T. vilamensis* (von

Tschirnhaus, pers. obs.), but not with other Chilean congeners. Loose skin folds at the posterior part of the thighs can be more or less developed, but seem more frequent in corpulent individuals and mature males. Another highly variable character is the extent of the interdigital membrane. All examined animals had fully webbed toes, but while in some cases the webbing was barely distinguishable towards the tips of the phalanges, others presented very prominent lateral fringes. The tadpoles are large and robust (97.27 mm at Gosner stages 36–37) (Table 3), with a thick, pointed tail (Tail length = 1.52x BL; stages 36–37) and show about the same pigmentation patterns as adults, but with entirely smooth skin (Fig. 5F).

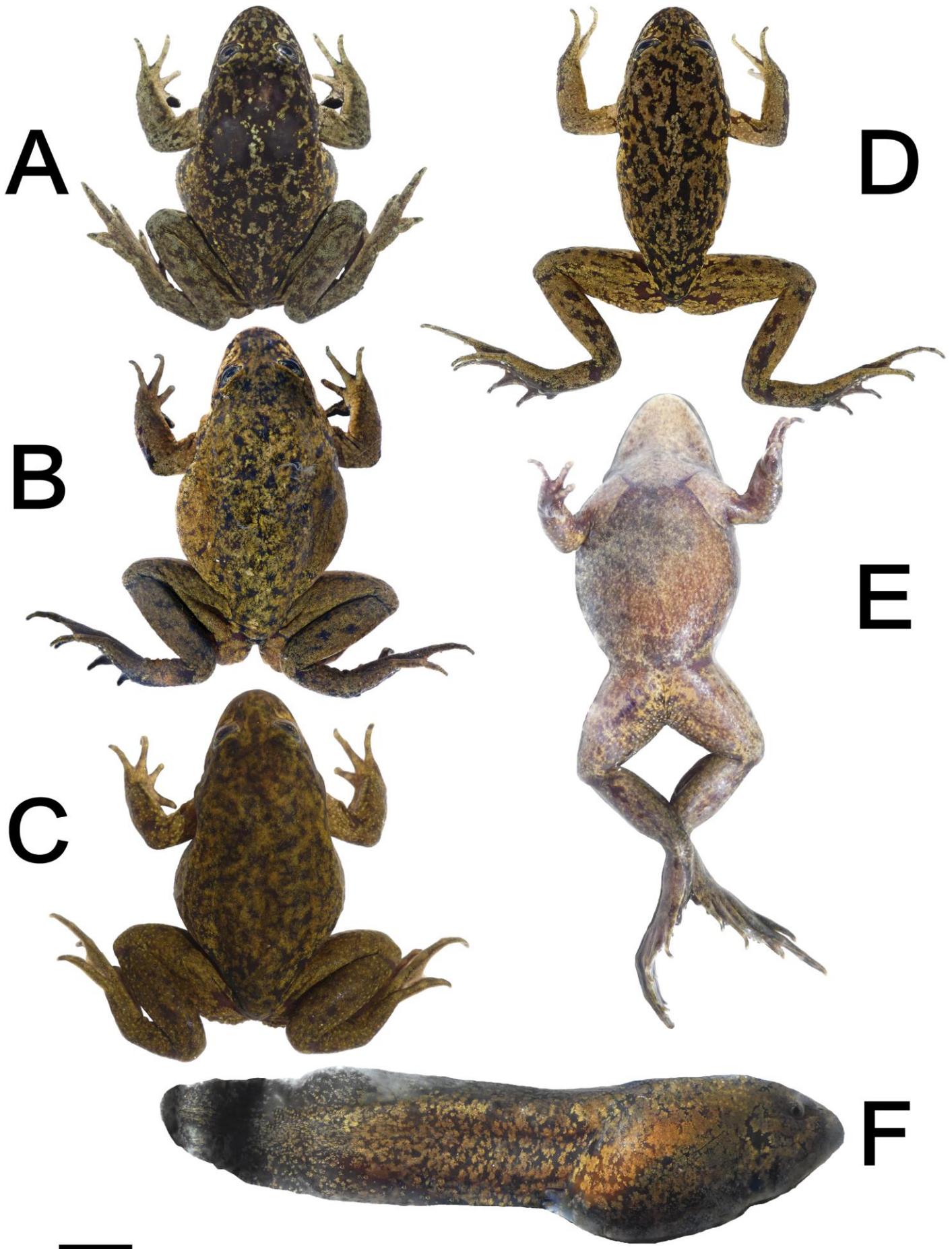


Figure 5. Selected specimens of *Telmatobius halli* from Miño. **A–D** Dorsal view of adult specimens, showing variation in coloring patterns. **E** Ventral view of the specimen from C. **F** Tadpole; scale bar: 1 cm (A–F).



Figure 6. Adult specimen of *Telmatobius halli* from Miño. Scale bar: 1 cm

DNA sequences and phylogenetic analysis

We obtained an alignment of 568 nucleotide sites for the fragment 16S and an alignment of 975 for the cytb, the same lengths of the sequences that we obtained for both fragments of the three tadpoles of *T. halli* from Miño. However, both alignments were incomplete because the sequences of several specimens included from previous studies are shorter, particularly some fragments of the cytb of the *T. marmoratus* group from De la Riva et al. (2010). The topology of the Bayesian consensus tree is congruent with those obtained by Sáez et al. (2014) and Fibla et al. (2017), recovering the three species groups (*T. marmoratus*, *T. hintoni* and *T. pefauri*) present in Chile, although the last one with low support (posterior probability, pp < 0.95) (Fig. 7). Also, the relationships among species and populations within groups are consistent with those studies; for example, the close relationship among populations of Ascotán and Carcote salt flats + *T. philippii* + *T. fronteriensis* and between *Telmatobius pefauri* Veloso and Trueb, 1976 and the clade made up of *T. dankoi* + *T. vilamensis* (although in this case with low support, pp = 0.75). In our analysis, the three samples of *T. halli* group with *T. dankoi* and *T. vilamensis* with the maximum support (pp = 1). All the specimens of *T. dankoi* (n = 4) and *T. vilamensis* (n = 5) make up a polytomy with two of the tadpoles of *T. halli* (L2 and L3), which constitutes the sister group of the third tadpole (L1) (Fig. 7). The polytomy results from the fact that the sequences of all these specimens are identical in their entirety (the 1,543 sites of both fragments), while the separation of the tadpole L1 is due to two differences in the cytb fragment.

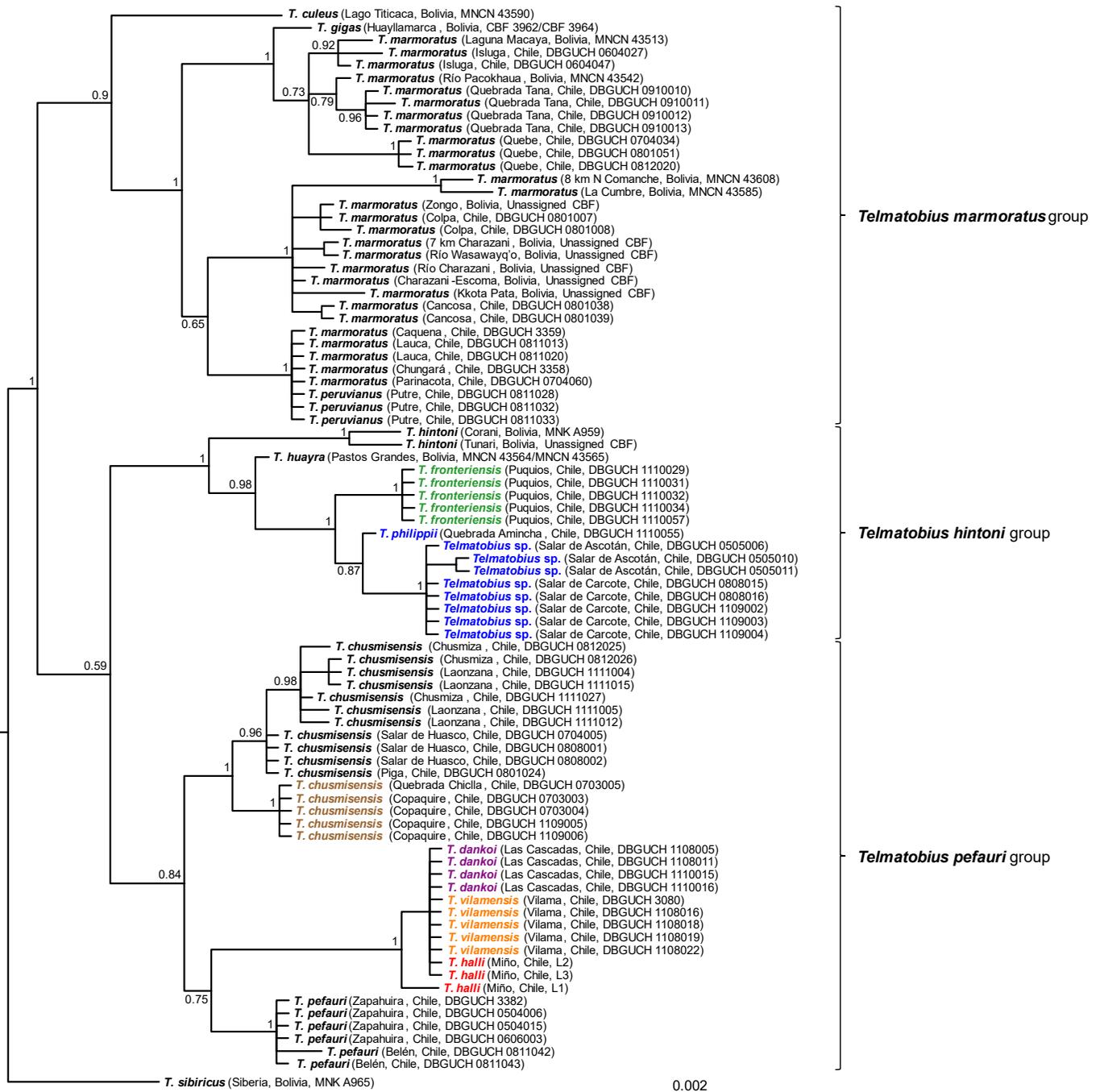


Figure 7. Bayesian consensus tree (50% majority-rule) of the mitochondrial genes, showing the relationships among Chilean *Telmatobius*. The specimens of the species and populations of the extreme south of the distribution of the genus in Chile are highlighted with the same colors of the map in Figure 1A. The values next to the nodes correspond to the posterior probabilities of the Bayesian analysis. The scale bar below the tree represents the expected substitutions per site along the branches. Identification of species and populations follows the taxonomy prior to Fibla et al. (2018) and Cuevas et al. (2020).

Discussion

The discovery of a *Telmatobius* population at the origin of the Loa River (Miño) definitely solves one of the most persistent enigmas of Chilean herpetology: the location of the type locality of *T. halli*. This riddle persisted for more than eighty years because of the uncritical acceptance of the inherently vague description of the type locality by Noble (1938). However, the solution came from a careful analysis of publications and other documentary sources where some of the members of the IHAEC described their activities and the place and circumstances in which the amphibians were collected (Correa 2021). It can be argued that both Fibla et al. (2018) and Cuevas et al. (2020) applied that same strategy, but

paradoxically both reached different (and incorrect) conclusions about the location. In the case of Fibla et al. (2018), some key sources in which the place is explicitly described were not consulted, while in the case of Cuevas et al. (2020), more importance was given to the characteristics of the place they hypothesized as the type locality (Aguas Calientes) than to the information contained in the documentary sources.

Cuevas et al. (2020) defined five conditions to validate Aguas Calientes as the type locality of *T. halli*: “1) the place should be a thermal spring, 2) presence or ruins of a concrete swimming pool in the area, 3) have a small oasis with abundant vegetation, 4) be 3,000 ft (~900 m) down of Collahuasi (Montt) and 5) be located near to Ollagüe.” The measurements and observations made here show that Miño fulfills the first four conditions, while the new sources consulted confirm that the fifth one does not apply to *T. halli*.

The Loa River at Miño has an almost constant water temperature of around 20°C, even at prolonged ambient temperatures below the freezing point, which suggests geothermal activity and matches well with the literature on the type locality of *T. halli* (Keys 1936a, 1936b; Noble 1938; Dill 1980). This temperature is similar to that of the collection site in Copaquire (19°C), the purported type locality of *T. halli* according to Fibla et al. (2018), but lower than that of Aguas Calientes (27.7°C). Only two other species of *Telmatobius* are known to inhabit warm or thermal waters, *T. fronteriensis* in Puquios (originally found in a small thermal pond with a water temperature of 22.9°C, Benavides et al. 2002) and *T. cf. philippii* in several springs at the Ascotán Salt Flat (Lobos et al. 2018). In the latter case, the water temperature varies widely between springs and seasons, but in general, spring water has medium to high temperatures compared to the air. In contrast to the water temperature, at Miño we observed a significant fluctuation range between the air temperatures at day and those at night (34.9°C), which could have been even higher, considering that we did not log the temperature data for the entire day. The constant water temperature may benefit the species, as it serves as a buffer for the thermal oscillations of the environment and prevents thermal stress. Nevertheless, the temperature might not be constant throughout the year, as snowmelt increases the flow rate during thaw season.

We were able to verify on the ground two other conditions defined by Cuevas et al. (2020): the presence of ruins of a concrete swimming pool and an oasis of vegetation. Although Cuevas et al. (2020) point out that there is a pool in Aguas Calientes that was built in 2012 on a previous construction, we show that in Miño there are the ruins corresponding to the concrete pool where the members of the IHAEC swam on June 25, 1935 (Fig. 3). Regarding the oasis of vegetation, we only have the description of Dill (1980) (“a flourishing green oasis”) and that of McFarland’s diary (“green valley”). Both descriptions fit well the current appearance of the area where the Loa River is born (Figs 1C, 2B), suggesting that the vegetation of the place has not changed much since the time of the expedition. The vegetation extends along the riverbed for more than a kilometer upstream from the ruins of the swimming pool and continues downstream along the Loa river canyon, so the place is much more than only a “small oasis” as described by Cuevas et al. (2020).

The elevation of the type locality of *T. halli* is one of the problematic aspects of the description provided by Noble (1938). Fibla et al. (2018) estimated that the site would be at about 4,000 m a.s.l., considering only the indications given by Dill (1979), while Cuevas et al. (2020) indicated that Aguas Calientes is located at 3,717 m. The altitude of our study site at Miño (3,900 m) was not measured in situ but obtained from Google Earth. Neither of these values matches the one Noble (1938) pointed out in the

species description: 10,000 ft (3,048 m). Cuevas et al. (2020) tried to explain this difference by alluding to an underestimation of 610 m in the actual elevation of the Aucanquilcha mine that was reported by members of the expedition (e.g. Keys 1936b; Keys et al. 1938). However, that explanation does not take into account that the data for most of the other reported places (Chuquicamata, Ollagüe, Collahuasi and Punta de Cerro) differ by less than 100 m from the altitudes that can be obtained, for example, from Google Earth. To further complicate this matter, the four chronicles that describe the Sunday trip to the source of the Loa River indicate different heights for that place. In fact, David B. Dill provided two different heights for Montt, 16,400 ft (~4,999 m) and 15,440 ft (~4,706 m) (Dill 1979, 1980, respectively), although in both cases he indicated that the site where the concrete pool was located was 3,000 ft (~916 m) lower. Ancel Keys instead specified the heights of the pool directly: 3,700 m (Keys 1936a) and 12,000 ft (~3,658 m; Keys 1936b). All these measurements should not be taken as absolute, as they seem a little roughly estimated and were indeed stated in a more anecdotal part of the publications. Among all the available values, the statement of Dill (1980) (12,440 ft = ~3,792 m) is the closest to that of Miño and it is further supported as his specification of the height of the former camp of the Collahuasi mine at the Montt railroad station (20°58'35"S, 68°41'20"W) matches very well the value from Google Earth. This explanation still does not solve the reason why Noble (1938) established that the type locality was at 10,000 ft above sea level, yet it only adds to the general impreciseness of the geographic information in his description.

The fifth condition of Cuevas et al. (2020), the proximity to Ollagüe, is the other problematic aspect of the description of the type locality given by Noble (1938) because there is no place that could be considered close to this town that is at 10,000 ft. In fact, the closest places to Ollagüe with that altitude are about 70 km to the west (in a straight line), on the other side of the Loa River. This is one of the reasons why searches for the species around Ollagüe were unsuccessful (Formas et al. 2003, 2005; IUCN 2015) and why Cuevas et al. (2020) concluded that the type locality is located only 12 km southwest of that town (Fig. 1A), but at a higher altitude. Thus, the suggestion from Fibla et al. (2018) that Noble might have used the location from which the specimens were sent as the type locality seems plausible to us.

In the chronicles of the IHAEC, there is little information about the population of *Telmatobius* from Miño. Dill (1979, 1980) only mentions that Frank G. Hall collected some specimens and that one of them proved to be a new species of amphibian. Keys (1936a) gives more details, indicating that many frogs and tadpoles were found in temperate ponds. This is consistent with the description of the species since the type series consists of five adult females, one immature female and six tadpoles. Currently, there seems to exist an abundant and healthy population, as frogs were found at several spots along the stream. This suggests that the environmental conditions at the site are similar to those at the time of the expedition.

The adults and tadpoles observed in Miño present external characteristics congruent with the description of *T. halli* (Noble 1938). Adults have almost completely smooth skin and a long and flattened snout. In addition, the general coloration, brown and olive with darker irregular spots and the size of the adults and tadpoles is compatible with the type series. Among the internal characteristics, which we did not examine, it is necessary to evaluate in the future the presence or absence of maxillary and premaxillary teeth since it is one of the features that motivated the description of the species. On the other hand, it is necessary to reevaluate the presence of postfemoral folds in the type series. Noble

(1938) does not mention anything about this trait in the original description, but Formas et al. (2003), in the redescription of the species, explicitly indicate that it lacks folds. However, in the photographs of the holotype (see fig. 6A in Fibla et al. 2018 and fig. 3E, F in Cuevas et al. 2020) this trait seems to be present. All of the adults that we observed in Miño, both males and females, present postfemoral folds, although they are more developed in males.

This is the first study to include the population that was originally described as *T. halli* in a phylogenetic analysis. Although this analysis was performed only with mitochondrial sequences (nuclear markers have not yet been included in phylogenetic analyses of the genus), it includes all Chilean species of the genus and all known populations that are geographically close. *Telmatobius halli* forms a highly supported clade with the two endemic species from the extreme south of the genus distribution in Chile, *T. dankoi* and *T. vilamensis*. Furthermore, the sequences (both genes) of two of the three specimens of *T. halli* are identical to those of these two species. Only one of these two specimens shows two differences in cytochrome b with respect to all the specimens that make up the clade. This result, together with the morphological and biogeographic evidence, strongly suggests that *T. halli*, *T. dankoi* and *T. vilamensis* are conspecific.

The possible synonymy between *T. dankoi* and *T. vilamensis* had already been pointed out by Sáez et al. (2014) and reaffirmed by Fabres et al. (2018). These species not only have identical mitochondrial sequences but also have common morphological characteristics that support their close affinity (coloration, size, flattened snout, presence of postfemoral folds, absence of vomers), some of which are also shared with *T. halli*. The geographic context is also relevant in this case. *Telmatobius halli* inhabits the same watershed (Loa River) as *T. dankoi*, while the only known population of *T. vilamensis* is found in the Salar de Atacama basin, which is southeast of the Loa River basin (Fig. 1A). If in the future, the conspecificity hypothesis receives more support, all these populations should be called *T. halli* and we further suggest adopting the vernacular name of *T. dankoi* (Loa Water Frog), as it has gained popularity and would represent the species appropriately.

The possible conspecificity of these three species also has important consequences for the conservation of these populations due to the current critical situation of *T. dankoi* and *T. vilamensis*. In 2019, the only known stream where *T. dankoi* inhabits almost completely dried up, resulting in the loss of approximately 90% of the total population of the species (Lobos and Rojas 2020). On the other hand, individuals of *T. vilamensis* have not been observed again in the Vilama River (the only known locality of the species) after a flash flood destroyed the site in 2016 (Lobos and Rojas 2020). Therefore, if these three species are conspecific, Miño would be the only known locality for this taxon with an apparently large population and an unaltered environment. In 2005, the Chilean government started the legal process for the creation of the National Reserve Alto Loa, but the efforts were not carried on and this protected area does not exist yet (Tomás Gerö, CONAF, pers. comm.). Our findings could be an excellent opportunity to resume the task, especially taking into consideration the attention which *T. dankoi* received in the international media in 2019 (Lobos and Rojas 2020).

Currently, based on the scarce and incomplete information available for this species, *T. halli* is listed as Data Deficient by the IUCN (IUCN SSC Amphibian Specialist Group 2015) and as Critically Endangered by the Chilean government (MMA 2019). For this last categorization, in which the uncertainty of the location of the type locality is recognized, it was assumed that the species: has an area of occupancy of about 1 km², is known from a single locality and its habitat is deteriorating due to

excessive use of water and the threat of the chytrid fungus (according to observations in other species of the genus in Chile). In this context, the description of the new population of Miño and the environment where it inhabits constitute fundamental information to reassess the conservation status of *T. halli*, but several aspects must be investigated in greater depth.

Up until now, there seems to exist very little anthropic disturbance at the location described in this work and the place appears to be visited only occasionally by anglers, off-road enthusiasts and mountaineers. Since the times of the IHAEC, it has been a recreational area mainly for the mine staff and, according to locals, still in the 1990s, the spot was sporadically visited by workers from the nearby mines. Accessing the site is very difficult and an increase in tourist activity is unlikely to happen. The valley is very pristine with no visible pollution signs. There is a vehicular track, that crosses the riverbed, which means that there could occur an occasional roadkill or minor contamination with motor oil or fuel; however, given the remoteness of the location not many vehicles pass through. Furthermore, it has yet to be evaluated if the intense nearby mining activity at the Collahuasi and Quebrada Blanca copper mines poses an imminent threat to the *Telmatobius* population, for instance, if contamination with heavy metals could occur through industrial dust dispersion (e.g. Csavina et al. 2012) or if potential upcoming projects demand water extraction for mining processes.

As mentioned above, other species of *Telmatobius* have been found infected with *Batrachochytrium dendrobatidis* (Bd) in northernmost Chile and there is an ongoing spread of chytridiomycosis southwards the Andes (Solís et al. 2015). Now that the type locality of *T. halli* has been rediscovered, most certainly other herpetologists will visit the place and special attention has to be taken to avoid contamination with the pathogen. Precaution is even more imperative, given the fact that Miño is at the headwaters of the Loa River and Bd could easily expand to other putative populations downstream (Johnson and Speare 2005).

Introduced salmonids are another well-known threat for native amphibians in Chile (Soto-Azat et al. 2015). A recent study (Lobos et al. 2020) reports the presence of *Oncorhynchus mykiss* (Walbaum, 1792) in several locations of the upper Loa, being Sapunta the nearest sampling point to the source (approx. 18 km). No salmonids were detected during the fieldwork, but given that they already have colonized the rest of the river, their presence in Miño is quite probable. The highest record of the rainbow trout in the mentioned study is 4,560 m in Misitune (18°22'S), which means that elevation would not be an impediment to the potential expansion of the invasive fish into the habitat of *T. halli*.

Besides these anthropic influences, it is also necessary to consider natural factors that could constitute a threat to the population. The extreme north of Chile is affected by intense precipitations during the so-called Altiplanic winter, which generates flash floods and landslides, having a negative impact on the biota. This phenomenon reduces significantly the riparian vegetation (Paicho-Hidalgo et al. 2015) on which the frogs of the genus *Telmatobius* heavily depend, probably for shelter from UV radiation and predators. An example of this type of catastrophic event is what happened in the Vilama River (see above). A similar case is Amincha, type locality of *T. philippii*, where the effects of a recent swelling of the creek were observed in February 2018 (von Tschirnhaus, pers. obs.). The vegetation was severely damaged, and even though a few living specimens were detected, it took a long time to locate them. Paicho-Hidalgo et al. (2015) pointed out that the ecological resilience of these ecosystems allows quick revegetation, still, such an event in the habitat of *T. halli* could diminish the population and make it more

vulnerable to other stresses. Comparing the current rock formations to those from the 1935 recordings suggests that destructive erosion events do occur in Miño.

All these threats, alone or in combination, could potentially lead to the extinction of *T. halli* if this species were restricted only to the source of the Loa River. Therein lies the importance of surveying the Loa River for the presence of *Telmatobius*, particularly its upper portion, where the watercourse and the surroundings are seemingly untouched for several kilometers, and of establishing the taxonomic status of the Miño population with respect to *T. dankoi* and *T. vilamensis*. In a broader context, the resolution of these aspects would contribute significantly to the taxonomy, biogeography and conservation of the *Telmatobius* populations of Chile.

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Appendix 1

Specimens of *Telmatobius* included in the phylogenetic analysis. For each specimen, species, locality (country), collection number or label, GenBank accession number (for each DNA fragment) and source of the sequences are indicated. Identification of specimens follows the taxonomy prior to Fibla et al. (2018) and Cuevas et al. (2020). The names of the localities are in Spanish, as they appear in the respective publications.

Species	Locality	Collection number or label	cytb	16S	Source
<i>T. culeus</i>	Lago Titicaca (Bolivia)	MNCN 43590	GU060589	GU060554	De la Riva et al. (2010)
<i>T. gigas</i>	Huayllamarca (Bolivia)	CBF 3962 (cytb) / CBF 3964 (16S)	GU060593	GU060558	De la Riva et al. (2010)
<i>T. marmoratus</i>	Laguna Macaya (Bolivia)	MNCN 43513	GU060600	GU060565	De la Riva et al. (2010)
<i>T. marmoratus</i>	Isluga (Chile)	DBGUCH 0604027	KJ562938	KJ563008	Sáez et al. (2014)
<i>T. marmoratus</i>	Isluga (Chile)	DBGUCH 0604047	KJ562939	KJ563009	Sáez et al. (2014)
<i>T. marmoratus</i>	Río Pacokhaua (Bolivia)	MNCN 43542	GU060602	GU060567	De la Riva et al. (2010)
<i>T. marmoratus</i>	Quebrada Tana (Chile)	DBGUCH 0910010	KJ562944	KJ563014	Sáez et al. (2014)
<i>T. marmoratus</i>	Quebrada Tana (Chile)	DBGUCH 0910011	KJ562945	KJ563015	Sáez et al. (2014)
<i>T. marmoratus</i>	Quebrada Tana (Chile)	DBGUCH 0910012	KJ562946	KJ563016	Sáez et al. (2014)
<i>T. marmoratus</i>	Quebrada Tana (Chile)	DBGUCH 0910013	KJ562947	KJ563017	Sáez et al. (2014)
<i>T. marmoratus</i>	Quebe (Chile)	DBGUCH 0704034	KJ562941	KJ563011	Sáez et al. (2014)
<i>T. marmoratus</i>	Quebe (Chile)	DBGUCH 0801051	KJ562942	KJ563012	Sáez et al. (2014)
<i>T. marmoratus</i>	Quebe (Chile)	DBGUCH 0812020	KJ562943	KJ563013	Sáez et al. (2014)
<i>T. marmoratus</i>	8 km N Comanche (Bolivia)	MNCN 43608	GU060603	GU060568	De la Riva et al. (2010)

<i>T. marmoratus</i>	La Cumbre (Bolivia)	MNCN 43585	GU060605	GU060570	De la Riva et al. (2010)
<i>T. marmoratus</i>	Zongo (Bolivia)	Unassigned CBF	GU060607	GU060572	De la Riva et al. (2010)
<i>T. marmoratus</i>	Colpa (Chile)	DBGUCH 0801007	KJ562896	KJ562971	Sáez et al. (2014)
<i>T. marmoratus</i>	Colpa (Chile)	DBGUCH 0801008	KJ562897	KJ562972	Sáez et al. (2014)
<i>T. marmoratus</i>	7 km Charazani (Bolivia)	Unassigned CBF	GU060608	GU060573	De la Riva et al. (2010)
<i>T. marmoratus</i>	Río Wasawayq'o (Bolivia)	Unassigned CBF	GU060610	GU060575	De la Riva et al. (2010)
<i>T. marmoratus</i>	Río Charazani (Bolivia)	Unassigned CBF	GU060609	GU060574	De la Riva et al. (2010)
<i>T. marmoratus</i>	Charazani- Escoma (Bolivia)	Unassigned CBF	GU060611	GU060576	De la Riva et al. (2010)
<i>T. marmoratus</i>	Kkota Pata (Bolivia)	Unassigned CBF	GU060612	GU060577	De la Riva et al. (2010)
<i>T. marmoratus</i>	Cancosa (Chile)	DBGUCH 0801038	KJ562889	KJ562964	Sáez et al. (2014)
<i>T. marmoratus</i>	Cancosa (Chile)	DBGUCH 0801039	KJ562890	KJ562965	Sáez et al. (2014)
<i>T. marmoratus</i>	Caquena (Chile)	DBGUCH 3359	KJ562891	KJ562966	Sáez et al. (2014)
<i>T. marmoratus</i>	Lauca (Chile)	DBGUCH 0811013	KJ562892	KJ562967	Sáez et al. (2014)
<i>T. marmoratus</i>	Lauca (Chile)	DBGUCH 0811020	KJ562893	KJ562968	Sáez et al. (2014)
<i>T. marmoratus</i>	Chungará (Chile)	DBGUCH 3358	KJ562894	KJ562969	Sáez et al. (2014)
<i>T. marmoratus</i>	Parinacota (Chile)	DBGUCH 0704060	KJ562895	KJ562970	Sáez et al. (2014)
<i>T. marmoratus</i>	Putre (Chile)	DBGUCH 0811028	KJ562898	KJ562973	Sáez et al. (2014)
<i>T. marmoratus</i>	Putre (Chile)	DBGUCH 0811032	KJ562899	KJ562974	Sáez et al. (2014)

<i>T. marmoratus</i>	Putre (Chile)	DBGUCH 0811033	KJ562900	KJ562975	Sáez et al. (2014)
<i>T. hintoni</i>	Corani (Bolivia)	MNK A959	GU060594	GU060558	De la Riva et al. (2010)
<i>T. hintoni</i>	Tunari (Bolivia)	Unassigned CBF	GU060596	GU060561	De la Riva et al. (2010)
<i>T. huayra</i>	Pastos Grandes (Bolivia)	MNCN 43564 (cytb) / MNCN 43565 (16S)	GU060599	GU060563	De la Riva et al. (2010)
<i>T. fronteriensis</i>	Puquios (Chile)	DBGUCH 1110029	KJ562884	KJ562959	Sáez et al. (2014)
<i>T. fronteriensis</i>	Puquios (Chile)	DBGUCH 1110031	KJ562885	KJ562960	Sáez et al. (2014)
<i>T. fronteriensis</i>	Puquios (Chile)	DBGUCH 1110032	KJ562886	KJ562961	Sáez et al. (2014)
<i>T. fronteriensis</i>	Puquios (Chile)	DBGUCH 1110034	KJ562887	KJ562962	Sáez et al. (2014)
<i>T. fronteriensis</i>	Puquios (Chile)	DBGUCH 1110057	KJ562888	KJ562963	Sáez et al. (2014)
<i>T. philippii</i>	Quebrada Amincha (Chile)	DBGUCH 1110055	KJ562901	KJ562976	Sáez et al. (2014)
<i>Telmatobius</i> sp.	Salar de Ascotán (Chile)	DBGUCH 0505006	KJ562912	KJ562986	Sáez et al. (2014)
<i>Telmatobius</i> sp.	Salar de Ascotán (Chile)	DBGUCH 0505010	KJ562913	KJ562987	Sáez et al. (2014)
<i>Telmatobius</i> sp.	Salar de Ascotán (Chile)	DBGUCH 0505011	KJ562914	KJ562988	Sáez et al. (2014)
<i>Telmatobius</i> sp.	Salar de Carcote (Chile)	DBGUCH 0808015	KJ562925	KJ562995	Sáez et al. (2014)
<i>Telmatobius</i> sp.	Salar de Carcote (Chile)	DBGUCH 0808016	KJ562926	KJ562996	Sáez et al. (2014)
<i>Telmatobius</i> sp.	Salar de Carcote (Chile)	DBGUCH 1109002	KJ562927	KJ562997	Sáez et al. (2014)

<i>Telmatobius</i> sp.	Salar de Carcote (Chile)	DBGUCH 1109003	KJ562928	KJ562998	Sáez et al. (2014)
<i>Telmatobius</i> sp.	Salar de Carcote (Chile)	DBGUCH 1109004	KJ562929	KJ562999	Sáez et al. (2014)
<i>T. chusmisensis</i>	Chusmiza (Chile)	DBGUCH 0812025	KJ562873	KJ562952	Sáez et al. (2014)
<i>T. chusmisensis</i>	Chusmiza (Chile)	DBGUCH 0812026	KJ562874	KJ562953	Sáez et al. (2014)
<i>T. chusmisensis</i>	Laonzana (Chile)	DBGUCH 1111004	KJ562919	KJ562989	Sáez et al. (2014)
<i>T. chusmisensis</i>	Laonzana (Chile)	DBGUCH 1111015	KJ562922	KJ562992	Sáez et al. (2014)
<i>T. chusmisensis</i>	Chusmiza (Chile)	DBGUCH 1111027	KJ562875	KJ562954	Sáez et al. (2014)
<i>T. chusmisensis</i>	Laonzana (Chile)	DBGUCH 1111005	KJ562920	KJ562990	Sáez et al. (2014)
<i>T. chusmisensis</i>	Laonzana (Chile)	DBGUCH 1111012	KJ562921	KJ562991	Sáez et al. (2014)
<i>T. chusmisensis</i>	Salar de Huasco (Chile)	DBGUCH 0704005	KJ562935	KJ563005	Sáez et al. (2014)
<i>T. chusmisensis</i>	Salar de Huasco (Chile)	DBGUCH 0808001	KJ562936	KJ563006	Sáez et al. (2014)
<i>T. chusmisensis</i>	Salar de Huasco (Chile)	DBGUCH 0808002	KJ562937	KJ563007	Sáez et al. (2014)
<i>T. chusmisensis</i>	Piga (Chile)	DBGUCH 0801024	KJ562940	KJ563010	Sáez et al. (2014)
<i>T. chusmisensis</i>	Quebrada Chiclla (Chile)	DBGUCH 0703005	KJ562930	KJ563000	Sáez et al. (2014)
<i>T. chusmisensis</i>	Copaquire (Chile)	DBGUCH 0703003	KJ562931	KJ563001	Sáez et al. (2014)
<i>T. chusmisensis</i>	Copaquire (Chile)	DBGUCH 0703004	KJ562932	KJ563002	Sáez et al. (2014)
<i>T. chusmisensis</i>	Copaquire (Chile)	DBGUCH 1109005	KJ562933	KJ563003	Sáez et al. (2014)
<i>T. chusmisensis</i>	Copaquire (Chile)	DBGUCH 1109006	KJ562934	KJ563004	Sáez et al. (2014)
<i>T. dankoi</i>	Las Cascadas (Chile)	DBGUCH 1108005	KJ562880	KJ562955	Sáez et al. (2014)

<i>T. dankoi</i>	Las Cascadas (Chile)	DBGUCH 1108011	KJ562881	KJ562956	Sáez et al. (2014)
<i>T. dankoi</i>	Las Cascadas (Chile)	DBGUCH 1110015	KJ562882	KJ562957	Sáez et al. (2014)
<i>T. dankoi</i>	Las Cascadas (Chile)	DBGUCH 1110016	KJ562883	KJ562958	Sáez et al. (2014)
<i>T. vilamensis</i>	Río Vilama (Chile)	DBGUCH 3080	KJ562902	KJ562977	Sáez et al. (2014)
<i>T. vilamensis</i>	Río Vilama (Chile)	DBGUCH 1108016	KJ562903	KJ562978	Sáez et al. (2014)
<i>T. vilamensis</i>	Río Vilama (Chile)	DBGUCH 1108018	KJ562904	KJ562979	Sáez et al. (2014)
<i>T. vilamensis</i>	Río Vilama (Chile)	DBGUCH 1108019	KJ562905	KJ562980	Sáez et al. (2014)
<i>T. vilamensis</i>	Río Vilama (Chile)	DBGUCH 1108022	KJ562906	KJ562981	Sáez et al. (2014)
<i>T. halli</i>	Miño (Chile)	L2	pending	pending	This study
<i>T. halli</i>	Miño (Chile)	L3	pending	pending	This study
<i>T. halli</i>	Miño (Chile)	L1	pending	pending	This study
<i>T. pefauri</i>	Zapahuira (Chile)	DBGUCH 3382	KJ562908	KJ562982	Sáez et al. (2014)
<i>T. pefauri</i>	Zapahuira (Chile)	DBGUCH 0504006	KJ562909	KJ562983	Sáez et al. (2014)
<i>T. pefauri</i>	Zapahuira (Chile)	DBGUCH 0504015	KJ562910	KJ562984	Sáez et al. (2014)
<i>T. pefauri</i>	Zapahuira (Chile)	DBGUCH 0606003	KJ562911	KJ562985	Sáez et al. (2014)
<i>T. pefauri</i>	Belén (Chile)	DBGUCH 0811042	KJ562923	KJ562993	Sáez et al. (2014)
<i>T. pefauri</i>	Belén (Chile)	DBGUCH 0811043	KJ562924	KJ562994	Sáez et al. (2014)
<i>T. sibiricus</i>	Siberia (Bolivia)	MNK A965	GU060615	GU060580	De la Riva et al. (2010)
