Frogs at the summits: phylogeny of the Andean frogs of the genus *Telmatobius* (Anura, Telmatobiidae) based on phenotypic characters

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Abstract

A phylogenetic hypothesis for the frogs of the genus *Telmatobius* that includes a comprehensive sample of the morphological and geographical variation is lacking. Obtaining such a hypothesis constitutes the main focus of this contribution. A phylogenetic matrix was generated based on 97 phenotypic characters and 56 terminals. A parsimony analysis of this matrix was performed with TNT. *Telmatobius* is found to be monophyletic and well supported by 11 synapomorphies. Although the consensus tree shows several polytomies, four main groups have been recovered. The well-supported *T. verrucosus* Group includes forest and sub-paramo species from Bolivia and Peru, and is the sister group of the remaining species. The *T. bolivianus* Group includes forest and inter-Andean valley species from Argentina and Bolivia but it is poorly supported. Two supported high-altitude groups have been recovered, the *T. macrostomus* Group from the Central Andes of Peru, and the *T. marmoratus* Group from the Altiplano-Puna Plateau of Argentina, Bolivia, Peru and Chile and its adjacent Pacific and Northern slopes. The synapomorphies proposed for *Telmatobius* are discussed as well as the evolution of some of these synapomorphies and other characters within the genus.
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Introduction

The Andes, one of the highest mountain chains on Earth, is also one of the richest in terms of biological diversity. In this vast region, defined in the sense of Duellman (1999), live not only the highest number of species of anurans of South America but of the world. This anuran richness matches the impressive mosaic of habitats and microhabitats that exist in this vertical world. The greatest part of this diversity is concentrated in the forested and more humid slopes of the tropical Andes. In general, alongside the Andes, as elevation increases, the diversity of anuran species decreases. Contrary to this pattern, the frogs of the genus *Telmatobius* show their richest diversity at the upper limits of the tree line and above. This genus comprises 63 species (Frost, 2015) that are distributed

from Tungurahua Province in Ecuador (approx. 1°S) to San Juan Province in Argentina (approx. 30°S; Lavilla and De la Riva, 2005). Most species live from 3000 to 4000 m above sea level, whereas more than a dozen can live above 4000 m and one of them (*Telmatobius marmoratus*) reaches one of the highest records of altitude for amphibians, 5200 m (Seimon et al., 2007). On the other hand, only eight species have been recorded below 2000 m and just one species (*T. simonsi*) lives around 1000 m (De la Riva and Harvey, 2003). The high-altitude distribution of *Telmatobius* is one of its most distinctive characteristics. The other notable characteristic of these frogs is their remarkable aquatic habits, which inspired its name (Greek *Telmato*: standing water, marsh). This mode of life is especially evident in the species distributed in highland environments such as peat bogs, streams, thermal springs, lakes and lagoons (Parker, 1940a; Vellard, 1951; De la Riva, 2005); species living in montane

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streams of the lower, forested or humid slopes are more independent of water and often are found out of the streams (Vellard, 1951; Laurent, 1970b, 1973; Wiens, 1993; De la Riva, 1994a).

The taxonomy of *Telmatobius* is particularly complex (De la Riva, 2005). The main reason for this is probably the paucity of diagnostic morphological characters to differentiate species and the high level of intraspecific variation (e.g. Parker, 1940a; Vellard, 1951; Trueb, 1979; Lobo Gaviola, 1988; Wiens, 1993; Barrionuevo, 2013). Owing to this intrinsic characteristic of the genus, morphometrics has been widely used in taxonomic studies of *Telmatobius* (Laurent, 1970a,b, 1973, 1977; Trueb, 1979; Wiens, 1993; Sinsch et al., 1995; Benavides et al., 2002). The study of larvae was a main focus in the 1980s, in particular the contributions of Lavilla (1983, 1984a,b, 1985, 1988). Knowledge of the osteology of species of *Telmatobius* is variable, ranging from detailed descriptions (e.g. Trueb, 1979; Lobo Gaviola, 1988; Wiens, 1993; De la Riva, 1994b; Formas et al., 1999, 2003, 2006; De la Riva and Harvey, 2003; Barrionuevo and Baldo, 2009; De la Riva et al., 2012; Barrionuevo, 2013) to simple mentions of few osteological characters (e.g. Peters, 1873; Holmgren, 1933; Andersen, 1978; Jaslow et al., 1988; Fabrezi, 2001a). The existence of a small amount of osteological variability is implied in some studies (Trueb, 1979; Wiens, 1993) whereas this is explicitly stated in others (Lobo Gaviola, 1988; Sinsch et al., 2005). In addition, a wide intraspecific variation in osteological characters has been described (Lobo Gaviola, 1988; Barrionuevo, 2013).

In pre-cladistic studies of *Telmatobius*, some species groups were proposed. Vellard (1951), in a narrative contribution, recognized three groups among Peruvian species based largely on size and habitat (medium-sized stream species, large lake species and medium-sized semi-aquatic species). Vellard suggested that the Peruvian semi-aquatic species "less adapted to highlands and to an aquatic mode of life", together with the Ecuadorian species *T. niger* (including its junior synonym, *T. cinereus*), constitute the "ancestral natural group" of the genus. Laurent (1970b), comparing body proportions and the type of habitat, distinguished three informal groups among species of Argentina ("High-Andean", "Sub-Andean" and "Forest" groups). Largely, the most comprehensive pre-cladistic contribution was the work of Lavilla (1985) who studied larval morphology of 34 taxa of *Telmatobius* from Peru to Argentina. Considering mainly a binary larval character of the oral disc (presence/absence of a row of submarginal mental papillae), Lavilla split the genus in two groups: the "meridional" (=Southern) group (row of submarginal mental papillae present) and the "septentrional" (=Northern) group (row of submarginal mental papillae absent). The species of the "meridional" group were restricted to Argentina, whereas the species of the "septentrional" group were distributed in Bolivia, Chile and Peru.

In the cladistic arena, Wiens (1993), Aguilar and Pacheco (2005), Córdova and Descailleaux (2005) and Sinsch et al. (2005) performed analyses of different small sets of phenotypic characters from a few species of *Telmatobius* from Peru. Subsequently, Aguilar and Valencia (2009) developed a phylogenetic analysis including 15 species of *Telmatobius* also from Peru. Among their results, the placement of *Batrachophrynus* in the synonymy of *Telmatobius* was implied. In this analysis, the relationships within *Telmatobius* were poorly resolved but two clades were recovered: one composed by *T. brachydactylus*, *T. carrillae*, *T. macrostomus* and *T. mayoloi* and other composed by *T. arequipensis*, *T. culeus*, *T. jelskii*, *T. marmoratus* and *T. peruvianus*. De la Riva et al. (2010) analysed 12 species of *Telmatobius* from Bolivia. They included sequences of the mitochondrial genes 16S and cytochrome b (cyt b). In their hypothesis, four species groups were proposed: the *T. verrucosus*, *T. bolivianus*, *T. hintoni* and *T. marmoratus* species Groups. Sáez et al. (2014) re-analysed De la Riva et al.'s (2010) matrix by adding sequences of species and populations from Chile. They found that most species and populations from Chile were nested in the *T. marmoratus* and *T. hintoni* Groups whereas the remaining Chilean species formed a new subclade named as the *T. zapahuirensis* Group.

A phylogenetic analysis of the entire genus is lacking and no morphological synapomorphies are known for most proposed groups. The inclusion of a wide taxon sampling is crucial to understand the whole picture of *Telmatobius* evolution. With more than 60 species distributed in the Andean region, these highly endangered frogs show interesting patterns of variation in morphology and behaviour. Certainly, a comprehensive species-level phylogeny of this genus will provide an evolutionary framework for morphological, biogeographical, behavioural or conservation studies. Thus, the general goal of this contribution is to elucidate the phylogenetic relationships of *Telmatobius* based on phenotypic characters. Although there are sequences of mitochondrial genes (16S and cyt b) available from the analyses by De la Riva et al. (2010) and Sáez et al. (2014), there is low taxon overlap between the present study and those (sequences of both genes available for 12 of the 43 species included here). Nevertheless, a reasonable procedure would be to evaluate simultaneously all available evidence to generate a total evidence phylogenetic hypothesis. For this reason, a multi-authored project is in progress to perform a comprehensive phylogenetic analysis of *Telmatobius* using mitochondrial and nuclear sequences, together with phenotypic characters. In the meantime, the present study communicates the results of the phenotypic study.

Due to the characteristics of *Telmatobius* stated above, to build a morphological matrix of the genus is a challenging task, and requires a more aggressive scrutiny of the morphological diversity than done so far, in the context of a taxon sampling as dense as possible. This taxon sampling represents almost all the geographical and morphological diversity of *Telmatobius*. Hence, the goals of the present study are: (i) to infer relationships among species, and (ii) to discuss the evolution of relevant morphological characters.

Materials and methods

Forty-three of the 63 currently recognized species of *Telmatobius* have been included in this study, representing 68% of the total diversity of the genus. Moreover, species representing the five phylogenetic species groups proposed by De la Riva et al. (2010) and Sáez et al. (2014) were examined as follows: the *T. verrucosus* species Group (3 spp.; *T. verrucosus* included, *T. espadai* and *T. sanborni* not included); the *T. bolivianus* Group (4 spp., *T. bolivianus*, *T. sibiricus*, *T. simonsi* and *T. yuracare*, all included); the *T. marmoratus* Group (4 spp.; *T. culeus*, *T. marmoratus*, *T. peruvianus* included, *T. gigas* not included); the *T. hintoni* Group (4 spp.; *T. hintoni* and *T. huayra* included, *T. philippii* and *T. fronteriensis* not included) and the *T. zapahuirensis* Group (4 spp.; *T. dankoi* and *T. vilamensis* included, *T. chusmisensis* and *T. zapahuirensis* not included).

All species from the two clades obtained by Aguilar and Valencia (2009) were included: the clade composed by *T. brachydactylus*, *T. carrillae*, *T. macrostomus* and *T. mayoloi* and the clade composed by *T. arequipensis*, *T. culeus*, *T. jelskii*, *T. marmoratus* and *T. peruvianus*. Twenty of the 63 species of *Telmatobius* not included in this analysis were unavailable due to their rareness in public collections, their inaccessibility or they have been described only recently. However, the diversity of the group is sampled because the morphological spectrum is covered by the current taxon sampling.

The selection of outgroups was based on recent phylogenetic analyses (Frost et al., 2006; Grant et al., 2006; Pyron and Wiens, 2011; Pyron, 2014). These included exemplar species of the genera *Alsodes*, *Atelognathus*, *Batrachyla*, *Ceratophrys*, *Chacophrys*, *Lepidobatrachus*, *Eupsophus*, *Hylorina*, *Insuetophrynus* and *Pleurodema*. The phylogenetic trees were rooted with *Leptodactylus fuscus*. The total taxon sampling resulted in 56 species including the outgroup. A detailed list of studied material is provided in Appendix 1.

Adult specimens of both sexes were studied to detect sexual dimorphism. Cleared and stained specimens were prepared following the technique of Wassersug (1976). Some species were only available for the study of external morphology. In these few cases, osteological information was obtained from the literature as follows: *T. atahualpai* (Aguilar et al., 2012), *T. mayoloi* (Sinsch et al., 2005), *T. vilamensis* (Formas et al., 2003) and *T. huayra* (Lavilla and Ergueta Sandoval, 1995). Cranial and postcranial osteology follows the terminology used by Trueb (1973, 1993), and laryngeal morphology follows Trewavas (1933). The character describing chromosome number was obtained directly from karyotypes of *Telmatobius oxycephalus*, *T. pisanoi*, *T. pinguiculus*, *T. platycephalus*, *T. marmoratus* and *T. rubigo* (J. S. Barrionuevo, unpublished data) or from the literature (see Appendix 2). Skin histology was studied on 70 histological preparations stained with PAS, Alcian Blue and haematoxylin following Sinsch et al. (2005). For some species, histological characters were codified from the literature (see Appendix 2).

The specimens examined are housed in Fundación Miguel Lillo (FML), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Museo de La Plata (MLP), Museo de Historia Natural de la Universidad Mayor de San Marcos (MHNSM), Colección Boliviana de Fauna (CBF), Museo Nacional de Ciencias Naturales, Madrid (MNCN), Biodiversity Institute, Kansas University (KU), Museum of Comparative Zoology (MCZ), American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), Carnegie Museum (CM) and Zoologische Forschungsmuseum Alexander Koenig (ZFMK).

Ninety-seven phenotypic characters were scored as follows (two continuous and 95 discrete characters, number of characters in parentheses): osteology (58), adult external morphology (20), adult musculature (1), chromosomes (1), skin histology (3), larval external morphology (12) and chondrocranium (2). The distribution of osteological characters is as follows: skull (36), hyoid apparatus (6), vertebral column (1), pectoral girdle (7), forelimb (7), hindlimb (1). Matrix was edited with Mesquite (Maddison and Maddison, 2015). Polymorphic or ambiguous coding for polymorphic characters were employed (Wiens, 1995). Continuous characters were codified following Goloboff et al. (2006). Due to the extreme differences in the magnitude of ranges (3–273 and 1–13), the two continuous characters were rescaled. Missing entries and inapplicable data were coded as a question mark "?". Multistate characters were considered as either nonadditive or additive (see Appendix 2).

A parsimony analysis was performed with the program TNT—Tree Analysis Using New Technology (Goloboff et al., 2008) using equal weights. Shortest trees were found by submitting 1000 random addition sequences to the tree bisection–reconnection branch swapping method (TBR), retaining ten trees per replication. To determine branch support, parsimony

jackknife (Farris et al., 1996) and bootstrap (Felsenstein, 1985) absolute frequencies were calculated with TNT by generating 100 RAS + TBRs per replicate, for a total of 1000 replicates. Although with several caveats, a bootstrap frequency ≥ 70% is considered high (Hillis and Bull, 1993). Transformations on a given node were considered synapomorphies only if they were shared by all most-parsimonious trees (MPTs) ("List common synapomorphies" in TNT). The graphic mapping of characters on the consensus was obtained with the function "common mapping" of TNT.

Results

Appendix 2 provides a list and discussion of the characters. Parsimony analysis of the data matrix (Appendix S1) resulted in 190 MPTs with a score of 328.092. The best length was hit in 21 of the 1000 replicates. The strict consensus from all MPTs is shown in Figs 1 and 2. The conflicts among the MPTs involve relationships both among outgroups and within the ingroup (see below), although the position of the clade containing *Telmatobius* is stable.

The monophyly of the genus *Telmatobius* is well supported by 11 synapomorphies (95% jackknife and 90 bootstrap support, Fig. 2). These synapomorphies (character numbers and state from Appendix 2 in parentheses) are: anterior end of frontoparietals posterior to the level of planum antorbitale (4.1), fang-like premaxillary and maxillary teeth (16.1), monocuspid maxillary and premaxillary teeth (17.0), otic ramus of
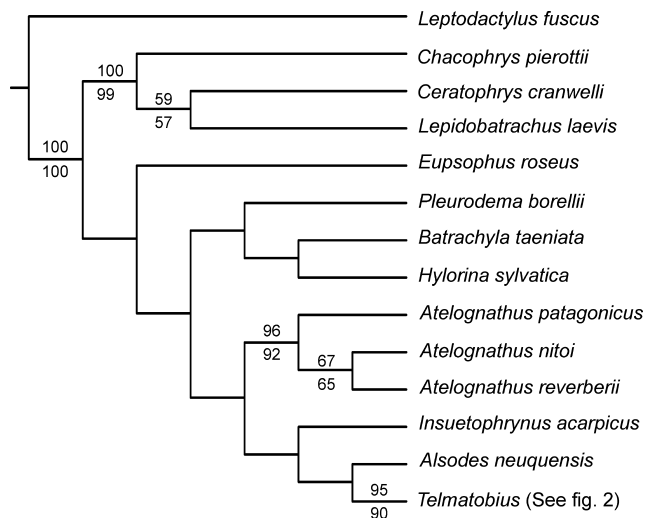

Fig. 1. Strict consensus of the 190 MPTs obtained from the analysis of 97 phenotypic characters. Only outgroups are shown. Numbers above and below nodes indicate, respectively, parsimony jackknife and bootstrapp values over 50%. See Fig. 2 for relationships among species of *Telmatobius*.

squamosal short or incipient (31.0), posteromedial processes invading the hyoid plate and reaching the base of the posterolateral processes (42.2), tongue attached anteriorly to the floor of the mouth more than 70% of its length but with free lateral borders (64.1), sexually mature males with nuptial pad only on Finger II (thumb) (70.0), a single nuptial pad in Finger II (71.0), keratinized spicules in the chest scattered, not forming discrete pads (74.0), skin with serous glands of small granules (type I) (79.1) and skin with a calcified or Eberth-Kastschenko (E-K) layer in the dermis (81.1).

The relationships among species of *Telmatobius* show several conflicts although four main groups have been recovered (Fig. 2). The clade that includes *Telmatobius verrrucosus*, *T. atahualpai* and *T. timens* (87% jackknife and 84% bootstrap support) is the sister taxon of all remaining species of *Telmatobius* (Fig. 2). This group is supported by three synapomorphies as follows: claviform or triangular nasals reduced (2.2), alary process of premaxilla divergent in frontal view (7.1) and absence of medial gap in the second upper labial tooth row (the row most proximal to the mouth) (91.1).

Among remaining species there is a basal polytomy including *Telmatobius thompsoni*, *T. rimac*, *T. necopinus*, *T. latirostris*, *T. brevipes*, the clade of *T. truebae* and *T. niger*, and the other three larger clades (see below).

The clade composed of *Telmatobius bolivianus*, *T. ceiorum*, *T. contrerasi*, *T. hauthali*, *T. laticeps*, *T. oxycephalus*, *T. pinguiculus*, *T. pisanoi*, *T. schreiteri*, *T. scrocchii*, *T. sibiricus*, *T. simonsi*, *T. stephani* and *T. yuracare* is poorly supported by two synapomorphies: alary process of premaxilla directed anterodorsally in lateral view (6.2), and presence of a row of submarginal papillae in the mental region (87.1). The relationships within this clade are poorly resolved with the exception of *T. bolivianus* and *T. yuracare* that were found as sister species.

Telmatobius ignavus and *T. degener* are basal to a clade containing two other subclades. The subclade composed of *T. macrostomus*, *T. brachydactylus*, *T. carrillae* and *T. mayoloi* (73% jackknife and 65% bootstrap support) is supported by the following synapomorphies: frontoparietals not fused in the parietal region (3.0), vomer reduced (20.1) and tongue attached completely to the floor of the mouth (64.3).

The other subclade is composed of *T. arequipensis*, *T. atacamensis*, *T. culeus*, *T. dankoi*, *T. hintoni*, *T. huayra*, *T. hypselocephalus*, *T. jelskii*, *T. marmoratus*, *T. peruvianus*, *T. platycephalus*, *T. rubigo*, and *T. vilamensis*. *T. hintoni*, *T. peruvianus*, *T. jelskii* and *T. arequipensis*. This group is supported by five synapomorphies (74% jackknife and 66% bootstrap support) as follows: anterior end of frontoparietals at the level or close to planum antorbitale (4.0), upper lips with a medial notch at mandibular symphysis (61.1), upper lips covering lower lips laterally (62.1), lower jaw in lateral view
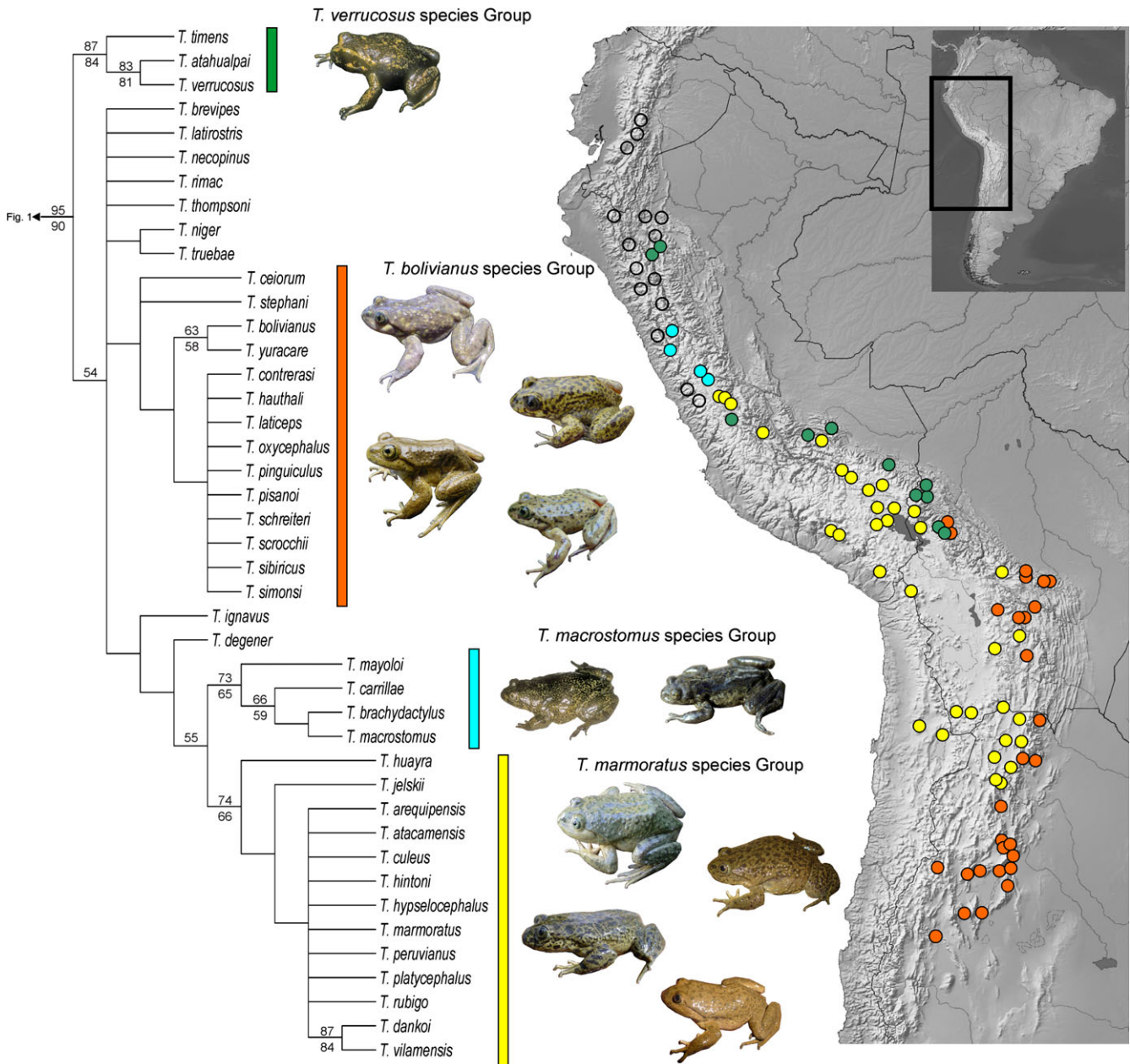
Fig. 2. Strict consensus of the 190 MPTs obtained from the analysis of 97 phenotypic characters. Only relationships among species of *Telmatobius* are shown. Numbers at nodes indicate parsimony jackknife absolute frequencies over 50%. Previous groups proposed by Aguilar and Valencia (2009) and De la Riva et al. (2010) are shown in colours in the cladogram as well as their geographical distribution. See Fig. 1 for relationships of outgroups.

higher posteriorly than anteriorly (63.1), and presence of keratinized spicules in pectoral region in sexually mature males (73.1).

Among outgroup species (Fig. 1), *Alsodes neuquensis* is recovered as the sister species to the clade containing *Telmatobius*. The clade *Alsodes* + *Telmatobius* is poorly supported by five synapomorphies: anterior portion (=pars jugalis) of quadratojugal can reach but not exceed the level of the central part of pterygoid

(18.1), anterior ramus of pterygoid long, reaching the level of neopalatines (29.1), clavicle and scapula fused in males (47.1), crest in the anterior margin of scapula (49.1) and Metacarpal II in males more developed than Metacarpals III, IV and V (53.1).

Insuetophrynus acarpicus is the sister species of the clade containing *Alsodes* + *Telmatobius*. This relationship is poorly supported by two synapomorphies: crista medialis and crista lateralis of the humerus of

males present and well developed (52.1), and two nuptial pads in the thumb and one pad at the base of the inner metacarpal tubercle (71.2). Outside this clade, the three species of *Atelognathus* form a well-supported clade (96% jackknife and 92% bootstrap support). *Pleurodema borellii* forms a clade with *Hylorina sylvatica* and *Batrachyla taeniata* but with low support, whereas *Chacophrys pierottii*, *Lepidobatrachus laevis* and *Ceratophrys cranwelli* form a highly supported clade (100% jackknife and 99% bootstrap support).

Discussion

Morphological variation in the genus *Telmatobius* has been considered to be complex since the pioneering works of Parker (1940a) and Vellard (1951, 1953, 1955). This complexity includes low levels of interspecific variation and high levels of intraspecific variation. This has driven some authors to question the value of morphological characters for establishing phylogenetic relationships in *Telmatobius* (e.g. Trueb, 1979; Wiens, 1993; De la Riva, 2005; Sinsch et al., 2005). Although numerous characters traditionally used in amphibian systematics are polymorphic in *Telmatobius*, a careful scrutiny of morphology has resulted in a good sample of informative characters.

This contribution is, at present, the most comprehensive phylogenetic hypothesis for the genus *Telmatobius*. The monophyly of *Telmatobius* is corroborated and supported by 11 morphological synapomorphies. In previous large-scale phylogenetic analyses, the monophyly of *Telmatobius* was highly supported but no morphological characters were associated with this clade (Pyron and Wiens, 2011; Pyron, 2014). Although the monophyly of *Telmatobius* has been implied or partially corroborated in previous analyses based on phenotypic characters, the design of most of them was not adequate for a reliable test of monophyly. Some analyses included a small number of species (six to nine) and were based on a limited source of evidence (e.g. Aguilar and Pacheco, 2005; Córdova and Descailleaux, 2005; Sinsch et al., 2005).

Aguilar and Valencia (2009) included a larger taxon sampling (15 species) but it was restricted both taxonomically and geographically (only Peruvian species were analysed). In their analysis based on phenotypic characters, the monophyly of *Telmatobius* was partially corroborated and seven synapomorphies were proposed. From these synapomorphies, four were particular to the taxon sampling included by Aguilar and Valencia's (2009) analysis and were not recovered here: frontoparietals fused posteriorly (char. 9.1), oral disc of larvae emarginated (char. 11.1), presence of submarginal lateral papillae in the oral disc (char. 13.3) and absence of quadrato-orbital commissure (char.

22.1). Two synapomorphies describing buccopharyngeal morphology (chars. 16 and 17) were not evaluated here. The only synapomorphy proposed by Aguilar and Valencia (2009) that was confirmed in the present contribution is the character describing the attachment of the tongue to the floor of the mouth (char. 6.), although it is codified differently (see character description in Appendix 2).

Among the published phylogenetic analyses based on DNA sequences, De la Riva et al. (2010) presented a hypothesis restricted to 12 species from Bolivia. The taxon sampling of the outgroup was not adequate for a reliable test of monophyly. They included quite distantly related taxa: *Leptodactylus*, *Psychrophrynella*, *Pristimantis* and *Rana*. The taxon sampling of Sáez et al. (2014) was broader, as they enlarged the matrix analysed by De la Riva et al. (2010) by including eight species from Chile. Although the authors included in the outgroup *Rhinoderma darwinii*, *Insuetophrynus acarpicus*, *Batrachyla taeniata* and *Atelognathus salai*, they do not show the results and there is no subsequent discussion on the monophyly of *Telmatobius*. In fact, they presented the results of an analysis that was rooted on the species of the *T. verrucosus* Group (Sáez et al., 2014).

Outgroup relationships

Alsodes neuquensis is recovered as the sister taxon of *Telmatobius*. This node is supported by six morphological characters. In the context of a precladistic analysis, this relationship had been previously proposed by Lynch (1978) in one of his alternative hypotheses. Previous cladistic analyses of *Telmatobius* included *Alsodes* as outgroup (Aguilar and Pacheco, 2005; Córdova and Descailleaux, 2005; Sinsch et al., 2005; Aguilar and Valencia, 2009). In most of these analyses this sister taxon relationship was recovered although taxon samplings of the outgroups were limited to just a few genera. Darst and Cannatella (2004), using sequences of mtDNA 12S and 16S, found *Alsodes* to be the sister taxon of *Telmatobius*, although subsequent analyses of other authors based on sequences did not support this relationship (e.g. Correa et al., 2006; Frost et al., 2006; Grant et al., 2006; Pyron and Wiens, 2011; Blotto et al., 2013).

Insuetophrynus acarpicus is recovered here as the sister species of the clade *Telmatobius* + *Alsodes*. Wiens (1993) suggested that the presence of an enlarged crista medialis in the humerus is a synapomorphy of the clade *Telmatobius* + *Alsodes*. However, a large crista medialis in males of *Insuetophrynus* (Díaz, 1986) is a synapomorphy (52.1) of the clade *Insuetophrynus* + (*Telmatobius* + *Alsodes*). In analyses based on DNA sequences, *I. acarpicus* has been recovered as the sister species of *Rhinoderma darwinii* (Correa et al., 2006;

Pyron and Wiens, 2011; Blotto et al., 2013; Fouquet et al., 2013; Faivovich et al., 2014; Pyron, 2014). In the hypothesis obtained by Pyron and Wiens (2011), *Telmatobius* is the sister clade of *Atelognathus + Batrachyla* and *Insuetophrynus + Rhinoderma*, although Blotto et al. (2013) detected chimaeras, contaminations and misidentifications in the sequences of *Batrachyla* among others. In the recent hypothesis of Faivovich et al. (2014) and Pyron (2014), the clade *Insuetophrynus + Rhinoderma* is the sister clade of *Telmatobius*. Although *Rhinoderma* was not included in the present analysis, if we evaluate the synapomorphies of *Telmatobius* in relation to the character states in *Insuetophrynus* there would be no variation in the synapomorphies proposed for *Telmatobius*. The only exception is character 4 that describes the level of frontoparietals in relation to the planum antorbitale. The anterior border of the frontoparietals not reaching the level of the planum antorbitale is a synapomorphy of *Telmatobius* (4.1), whereas in *Insuetophrynus* this character is polymorphic (4.0/1).

In several phylogenetic hypotheses based on DNA sequences, Ceratophryinae has been recovered as the sister group of *Telmatobius* (e.g. Wiens et al., 2005; Grant et al., 2006; Blotto et al., 2013; Fouquet et al., 2013; de Sá et al., 2014). In the present analysis, Ceratophryinae and *Telmatobius* are not closely related. However, if we consider the hypothesis of Ceratophryidae as the sister taxon of *Telmatobius*, three of the synapomorphies of *Telmatobius* would be synapomorphies of the clade Ceratophryidae + *Telmatobius*: fang-like (16.1) and monocuspid teeth (17.0) and the calcified layer in the skin (81.1). Moreover, *Ceratophrys* and *Chacophrys* share the presence of the nuptial pad only on Finger II (70.0). Considering the phylogenetic hypothesis of Faivovich et al. (2014) this would be another putative synapomorphy of Ceratophryidae + *Telmatobius*. Another character shared by Ceratophryinae and some *Telmatobius* species is the high degree of mineralization or ossification of the hyoid plate (37.1) as well as the ossification of the base of the posteromedial processes that are invading the hyoid plate (42.2).

Relationships within Telmatobius

The clade formed by *Telmatobius atahualpai*, *T. timens* and *T. verrucosus* is the sister taxon of all remaining species of *Telmatobius*. One of the synapomorphies of this group, the absence of a gap in the keratodonts, is also shared by the two species of the *T. verrucosus* Group not included herein (*T. espadai* and *T. sanborni*, De la Riva et al., 2010). No osteological evidence is available for *T. espadai* and *T. sanborni* to confirm the occurrence of the other two synapomorphies of this group (shape of nasals and

configuration of alary process of premaxillary). However, *T. espadai* and *T. sanborni* share with *T. verrucosus* and *T. atahualpai* some larval characters, such as the oral disc modified as an oral sucker, the lack of intramarginal papillae in the angular area of the oral disc and suprarrostrodonts fused (Lavilla and De la Riva, 1993; Aguilar et al., 2007; J. S. Barrionuevo, pers. obs.). Accordingly, I assigned *T. atahualpai* and *T. timens* to the *T. verrucosus* Group. The species of this group are distributed in the transition between Cloud Forest and Humid Subparamo on the eastern slopes of northern Bolivia and southern Peru and, disjunctly, in northern Peru (Wiens, 1993; De la Riva, 2005; De la Riva et al., 2005; Aguilar et al., 2012).

The *Telmatobius bolivianus* Group (De la Riva et al., 2010) is recovered herein as monophyletic and also includes *T. ceiorum*, *T. contrerasi*, *T. hauthali*, *T. laticeps*, *T. oxycephalus*, *T. pinguiculus*, *T. pisanoi*, *T. schreiteri*, *T. scrocchii* and *T. stephani*. This group is poorly supported herein as well as it is poorly supported in the analysis of De la Riva et al. (2010) based on molecular evidence. The species of this group are distributed in inter-Andean valleys of Argentina and Bolivia, inhabiting streams from montane forests and dry shrublands. Based on published descriptions, *T. edaphonastes* and *T. mendelsoni* presumably would pertain to this group (De la Riva, 1994a; De la Riva et al., 2012).

The clade including *T. brachydactylus*, *T. carrillae*, *T. mayoloi* and *T. macrostomus* was previously recovered by Aguilar and Valencia (2009) and supported the placement of *Batrachophrynus* (the former *B. brachydactylus* and *B. macrostomus*) in the synonymy of *Telmatobius*. In the present study there are two synapomorphies in common with the study of Aguilar and Valencia (2009): tongue completely attached to the buccal floor (64.3) and frontoparietals not fused (3.1). This group was not named previously and herein it will be referred to as the *T. macrostomus* Group. The species of this group are distributed at high altitudes in the Central Andean Wet Puna ecoregion of Peru.

Some authors have related *Telmatobius macrostomus* (as *Batrachophrynus macrostomus*) and *T. brachydactylus* (as *B. brachydactylus* or *Lynchophrys brachydactylus*) to Calyptocephalellidae (*Calyptocephalella + Telmatobufo*). In one of the alternative hypotheses presented by Lynch (1978), the former *Batrachophrynus* (*T. macrostomus + T. brachydactylus*) was the sister taxon of Calyptocephalellidae. The two character states supporting this relationship were the major development of pars palatina of the premaxillary (character 6, Lynch, 1978) and the anterior extension of the cultriform process of parasphenoid reaching the level of neopalatines (character 10, Lynch, 1978). The pars palatina is only enlarged in *T. macrostomus* (possibly associated with its large size) whereas in *T. brachydactylus* it

is similar to the pars palatina of other species of *Telmatobius*. This is also the case of the cultriform process of the parasphenoid which, as in the former members of *Batrachophrynus*, reaches the level of neopalatines in several species of *Telmatobius*.

Burton (1998a,b) provided evidence on finger muscles that would support the relationship of *T. macrostomus* (as *Batrachophrynus macrostomus*) and *T. brachydactylus* (as *Lynchophrys brachydactylus*) with Calyptocephalellidae. These characters are the presence of the hand muscle lumbricalis longus digiti III (LBL III) and the double origin of the muscle lumbricalis brevis digiti III (LBB III). The LBB III may originate: (1) from carpals by a tendon, and/or (2) from tendo superficialis (TS) and the adjacent aponeurosis palmaris (AP). More recently, Aguilar and Valencia (2009) reported and codified the presence of LBL III in *T. arequipensis*, *T. brevirostris*, *T. carrillae*, *T. intermedius*, *T. marmoratus*, *T. rimac* and *T. truebae*. In all these species this character was codified as polymorphic (LBL III absent/present) by Aguilar and Valencia (2009). I could not identify this muscle in any analysed species, except *T. macrostomus*. Instead, I observed a medial slip of LBB III that originates from TS or AP and inserts in the distal phalanx, in a proximal position, in *T. brachydactylus*, *T. carrillae*, *T. ignavus*, *T. laticeps*, *T. macrostomus*, *T. marmoratus*, *T. niger*, *T. simonsi*, *T. truebae* and *T. rimac*. The occurrence of this slip varies intraspecifically, being present or absent. Burton (1998a,b) reported the absence of the medial slip of LBB III and the presence of LBL III in *T. brachydactylus* (as *Lynchophrys brachydactylus*). It is possible that a slip of LBB III originating in the TS or AP and inserting in the basal phalange has been misinterpreted as an LBL III (Burton, 1998a; Aguilar and Valencia, 2009). Thus, LBL III seems to be absent in *Telmatobius*. The only exception is *T. macrostomus* that has a clear LBL III that originates in the TS and inserts in the basal phalanx but in a distal position (in contrast to the medial slip of LBB III that inserts in the basal phalanx but in a proximal position). Consequently, the presence of LBL III would be an autapomorphy of *T. macrostomus*. This species has a unique hand morphology among *Telmatobius*, with unusually long fingers.

The species of the *Telmatobius hintoni*, *T. marmoratus* and *T. zapahuirensis* Groups (De la Riva et al., 2010; Sáez et al., 2014) included here (*T. culeus, T. dankoi, T. hintoni, T. huayra, T. marmoratus, T. peruvianus* and *T. vilamensis*) are recovered as forming a clade plus *T. arequipensis*, *T. atacamensis*, *T. hypselocephalus*, *T. jelskii*, *T. platycephalus* and *T. rubigo*. This clade comprises species mainly distributed in the Altiplano–Puna plateau of Argentina, Bolivia, Chile and Peru. Some species live in the western slopes of the plateau in southern Peru and northern Chile and one species lives at the north of the Altiplano. It is

supported by four synapomorphies. Three of those synapomorphies are non-homoplastic transformations: medial notch in the symphysis of upper lip (61.1), upper lips covering lower lips laterally (62.1) and high lower jaw (63.1). Aguilar and Valencia (2009) recovered the three species of the *T. marmoratus* Group included in their analysis (*T. culeus, T. marmoratus and T. peruvianus*) plus *T. arequipensis* and *T. jelskii*. This clade was supported by four synapomorphies, but there is only one synapomorphy in common with the synapomorphies supporting the Altiplano clade obtained herein: the presence of a notch in the upper lip. The genetic divergence of cyt b sequences among the *T. hintoni*, *T. marmoratus* and *T. zapahuirensis* Groups is extremely small (between 1.9% and 3.8%, De la Riva et al., 2010; Sáez et al., 2014). In addition, the species of these groups cannot be differentiated based on clear morphological characters. I suggest referring these three groups together as the *T. marmoratus* Group.

Within the *Telmatobius marmoratus* Group, as defined herein, most internal relationships are not resolved but *T. vilamensis* and *T. dankoi* are recovered as sister species. The osteological characters distinguishing *T. dankoi* and *T. vilamensis* have led to their description as different species (Formas et al., 1999, 2003) but the sequences of cyt b are identical (Sáez et al., 2014). Interestingly, the main osteological differences relate to characters that reflect different degrees of post metamorphic developmental stages (Barrionuevo, 2013). Considering this, we are facing two possibilities: (i) the specimens used to describe the osteology of *T. vilamensis* in the original description of the species are young individuals, or (ii) phenotypic plasticity, caused presumably by heterochronic processes, are involved in the morphological divergence between these populations (polyphenism). In any case more research is necessary to resolve this problem.

Besides the species belonging to the former recognized *Telmatobius hintoni*, *T. marmoratus* and *T. zapahuirensis* Groups not included here (*T. chusmisensis*, *T. philippii*, *T. fronteriensis*, *T. gigas* and *T. zapahuirensis*), evidence from external morphology suggests that *T. pefauri* (KU 159836) and *T. halli* (AMNH 44753) could be included in the *T. marmoratus* Group.

Skin glands and Eberth Kastschenko layer

Two histological features of the skin resulted in synapomorphies supporting the monophyly of *Telmatobius*. One is the occurrence of serous glands of small granules, called type I (79.1). In most anuran species, only one type of serous glands is present in the skin (Noble, 1931; Toledo and Jared, 1995; Delfino et al., 1998a). This is the case for all species included in the outgroup. In *Telmatobius*, two types of serous glands co-occur in the same species and are referred as type I

and II. This condition was first described for some *Telmatobius* species by Sinsch et al. (2005) and, subsequently, it was found to be widespread in the genus (Barrionuevo, in press). The two types of serous glands are defined by differences in the size of the secretory granules, being small in type I (mean diameter: 1.5 μm, range: 0.8–2.5 μm) and large in type II serous glands (mean diameter: 4.2 μm, range: 2.8–5.9 μm). These are not stages of maturity of the same glands because no intermediate stages have been found between types (Barrionuevo, in press). The coexistence of different types of serous glands not sexually dimorphic or not associated with macroglands is a rare feature among anurans. This has been described in a few species within Bombinatoridae (e.g. Delfino et al., 1982), Bufonidae (e.g. Delfino et al., 1998a), Hylidae (e.g. Delfino et al., 1998b) and Leiopelmatidae (Melzer et al., 2011).

Among outgroup exemplars, the occurrence of type II glands (char. 80.1) is the common condition, whereas the occurrence of type I glands is a synapomorphy of *Telmatobius* (Fig. 3). This feature has just one instance of homoplasy, because type I serous glands are present in *Hylorina sylvatica* although type II glands are absent (Fig. 3).

Within *Telmatobius*, a few species have exclusively serous glands type I. In the context of the present analysis this is the result of independent losses of serous glands type II in *T. bolivianus*, *T. culeus* and the clade *T. carrillae* + *T. brachydactylus* + *T. macrostomus* (Fig. 3). *Telmatobius bolivianus* is the only known species from the *T. bolivianus* Group that lacks type II glands. Curiously, it is also the most aquatic species of that group, together with its sister species, *T. yuracare* (De la Riva, 1994b; De la Riva et al., 2005). Although the condition of skin glands in *T. yuracare* is unknown, based on its phylogenetic position it is possible that *T. yuracare* also lacks type II glands.

Telmatobius culeus is the only species of the *T. marmoratus* Group that lacks type II serous glands. Although all the species of the group are markedly aquatic, the lacustrine *T. culeus* is the most aquatic species of the group (Allen, 1922).

Within the *Telmatobius macrostomus* Group, the most basal species, *T. mayoloi*, has both types of glands, whereas the other three derived species lack glands of type II (*T. carrillae, T. brachydactylus* and *T. macrostomus*). Although the markedly aquatic habits of these species constitute a feature in common with the other species of *Telmatobius* lacking type II glands, the biological significance of the few independent losses of type II glands remains unknown in the genus. Also intriguing is the widespread coexistence of two types of serous glands in the genus (Fig. 3), but with the data at hand is not possible to reach any conclusion.

The other histological character of the skin that resulted in a synapomorphy of *Telmatobius* is the presence of a calcified or Eberth Kastschenko (E-K) layer in the dermis (81.1). The E-K layer is located in the dermis between the stratum spongiosum and the stratum compactum and consists of glycosaminoglycans associated with mineral deposition as calcium (Elkan, 1968; Toledo and Jared, 1993; Katchburian et al., 2001). Its putative function as a defence against desiccation in anurans has been inferred mainly by its occurrence in terrestrial species and its absence in aquatic species, although several exceptions have been reported (Elkan, 1968, 1976; Toledo and Jared, 1993).

The E-K layer proved to be absent in the five species of *Telmatobius* examined by Elkan (1968, 1976). Consequently it was assumed to be absent in the genus. However, its occurrence has been recently confirmed in most *Telmatobius* species studied so far (Barrionuevo, in press). Although the occurrence of the E-K layer is widespread among anurans, in the context of this phylogenetic analysis, it is a synapomorphy of *Telmatobius*. Nevertheless, this may change if the outgroup relationships eventually change (see above). The common mapping of this character shows that the E-K layer is absent in all species of the *T. macrostomus* Group (Fig. 3). Among the species of the *T. marmoratus* Group, the E-K layer is completely absent in *T. culeus* and *T. jelskii*, it is polymorphic in *T. marmoratus* and *T. atacamensis* (present/absent) and it is present in *T. rubigo* and *T. platycephalus* (Fig. 3). In the remaining species of the genus with available data on skin histology, the E-K layer is present.

Nuptial pad variation in Telmatobius

A nuptial pad restricted only to Finger II (thumb) has been corroborated as a synapomorphy of *Telmatobius* (char. 70.0). This was previously suggested as a putative synapomorphy by Wiens (1993). The other synapomorphy related to this structure is that the pad of Finger II is single (char. 71.0; in *Alsodes* or *Insuetophrynus* the nuptial pad of Finger II is double). Basically, the male nuptial pads consist of keratinized epidermal projections (EPs, Luna et al., 2012) arranged at different densities. The density of the EPs depends on the size of each EP and constitutes an informative character in *Telmatobius*. This character has been widely used in taxonomic studies of the genus (Parker, 1940a; Vellard, 1951; Laurent, 1970b, 1973, 1977; Lavilla and Barrionuevo, 2005) as well as in phylogenetic analyses (Sinsch et al., 2005; Aguilar and Valencia, 2009).

In anurans, one of the putative biological roles of the nuptial pads of males is to aid female grasping during amplexus (Lataste, 1876; Boulenger, 1897; Noble, 1931). Variations in the development and morphology of nuptial pads have been related to the environment where the amplexus occurs, varying from
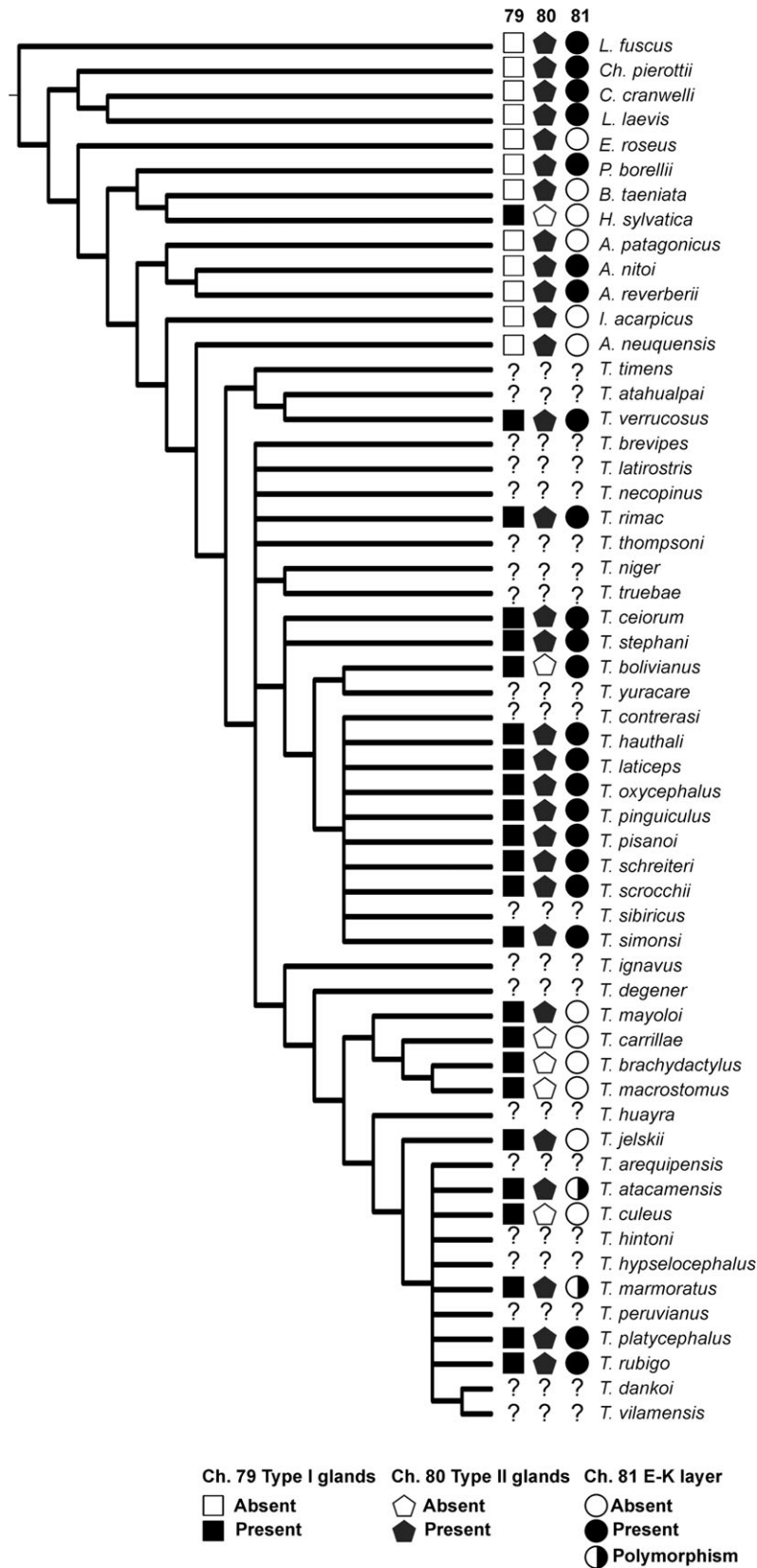
Fig. 3. Taxonomic distribution of three characters from the histological structure of the skin (chars. 79, 80, 81) in *Telmatobius* frogs.

nuptial pads being absent or pad with minute and less keratinized EPs (e.g. amplexus on land) to nuptial pads with large and heavily keratinized EPs (e.g. amplexus in torrent streams) (Liu, 1936; Parker, 1940b). *Telmatobius* is an ideal target to analyse these proposed patterns because the habitats of the species range from torrent streams to calm waters of highland lakes, and development of the nuptial pad varies from a few strong EPs to a myriad of minute EPs. In several cases the association between type of habitat and the morphology of nuptial pads is quite suggestive. For instance, the species of the *T. verrucosus* Group live in steep Andean slopes rivulets (De la Riva, 2005). The males of these species have strong forelimbs and the larvae have characteristics associated with living in fast flowing streams, such as an oral sucker. These species have the largest EPs in the genus. The density of these strongly keratinized EPs is less than $5/mm^2$. Species of the *T. bolivianus* Group living in streams from the slopes of inter-Andean valleys of Argentina such as Cumbres Calchaquíes (*T. pisanoi*, *T. laticeps*), Nevados del Aconquija (*T. scrocchii*), Sierra de Tilcara (*T. oxycephalus*), Sierra de Velasco (*T. schreiteri*) or Sierra de Fiambalá (*T. pinguiculus*) have medium-sized EPs with no more than 25 EPs/mm^2. In general, streams on these slopes are torrential during the wet season and the river beds are rocky. Floods may occur during summer heavy rains (Barrionuevo and Ponssa, 2008). In species of the *T. marmoratus* Group living in the Altiplano and Puna Plateau, for example *T. marmoratus*, *T. rubigo*, *T. culeus*, *T. atacamensis*, *T. platycephalus* and *T. hypselocephalus*, the EPs are smaller and are packed in higher densities (normally 30–60 EPs/mm^2). In these highland environments the streams are, in general, slow flowing with sandy river beds. Other habitats include lentic systems such as lakes, lagoons or peat bogs. Curiously, in species from the *T. marmoratus* Group living in the more torrential streams of the western slopes flanking the Altiplano and Puna, e.g. *T. arequipensis* and *T. peruvianus*, the EPs are larger and consequently have lower densities ($< 10/mm^2$). The smaller EPs in *Telmatobius* occur in species of the *T. macrostomus* Group with a density of more than 100 EPs/mm^2. The species of this group are distributed in Junin lake (*T. macrostomus*) and its slow flowing tributaries (*T. brachydactylus*) as well as on both sides of the Cordillera Blanca, in Central Peru, in the relatively slow-flowing plateau streams of the upper Río Santa Valley (*T. mayoloi)* or in the Puna de Crusjircan (*T. carrillae*). These associations between nuptial pad morphology and habitat are not conclusive. A more detailed study of the nuptial pads, including the use of scanning electron microscopy to establish if there are also differences in the microstructure of the EPs, a more rigorous habitat characteriza-tion and behavioural observations need to be analysed to reach stronger conclusions. Nevertheless, this pattern is useful to focus future efforts and research.

Teeth

Two characters describing premaxillary and maxillary tooth morphology resulted in synapomorphies of *Telmatobius*: fang-like shape (16.1) and monocuspid distal end (17.0). These synapomorphies constitute a rare feature among anurans. In most anurans, teeth have a blunt or spatulate shape and their distal end is bicuspid (Lynch, 1971; Trueb, 1993). Fang-like teeth have been described in some taxa such as *Xenopus*, *Pipa carvalhoi*, *P. arrabali* (Cannatella and Trueb, 1988), *P. parva* (Fabrezi et al., 2014), *Bombina*, *Barbourula*, *Limnodynastes* (Cannatella, 1985), *Litoria australis* (as *Cyclorana australis*, Tyler, 1989), *Rheobatrachus* (Davies and Burton, 1982; Mahony et al., 1984), *Pixicephalus adspersus* (Sheil, 1999), *Callyptocephalella* (Muzzopappa and Báez, 2009) and Ceratophryinae (Lynch, 1971, 1982; Fabrezi, 2006). The monocuspid condition of teeth is even rarer than the fang-like shape. In anurans in general and among the species with fang-like teeth, the bicuspid condition is more common (e.g. *Bombina*, *Barbourula*, *Limnodynastes*, *Litoria*, *Rheobatrachus*, *Callyptocephalella*), although in some species, as occurs in *Telmatobius*, the fang-like teeth are at the same time monocuspid (e.g. Pipidae: Katow, 1979; Shaw, 1979; *Hemiphractus*: Shaw, 1989; Pixicephalidae: Sheil, 1999; Noble, 1931; *Leptopelis brevirostris*: Noble, 1931; Ceratophryidae: Fabrezi, 2006; Lynch, 1971, 1982). Among outgroup species this combination is observed only in Ceratophryidae but in these species the teeth are not pedicellate. The similarity in teeth morphology between Ceratophryidae and *Telmatobius* is noteworthy considering that they have been recovered as sister taxa in some recent phylogenetic hypotheses based on DNA sequences (Wiens et al., 2005; Correa et al., 2006; Grant et al., 2006; Blotto et al., 2013; Fouquet et al., 2013).

The presence/absence of teeth constitutes an old issue in *Telmatobius* taxonomic accounts (Peters, 1873; Vellard, 1951). In fact, this character, together with the morphology of the tongue, was proposed by Peters (1873) to distinguish the former genus *Batrachophrynus* (no teeth, reduced tongue) from *Telmatobius*. Recently, Aguilar and Valencia (2009), based on their phylogenetic hypothesis, placed *Batrachophrynus* in the synonymy of *Telmatobius* and this is corroborated in the present analysis. Other than former members of *Batrachophrynus* (*Telmatobius macrostomus* and *T. brachydactylus*), premaxillary and maxillary teeth are absent also in other species of *Telmatobius*, such as *T. dankoi* and *T. carrillae*.

Although the loss of teeth occurred in several anuran lineages, in some species of *Telmatobius* the lack of teeth is intraspecifically variable. *Telmatobius vilamensis* was described as edentate (Formas et al., 2003) but the presence of teeth has been observed in two specimens (KU 159839 and 159840). In the original description of *T. intermedius*, Vellard (1951) described its toothless condition but Lehr (2005) mentioned the presence of teeth in this species. This polymorphism constitutes an extremely rare case among anurans. The absence of premaxillary teeth when the maxillary teeth are still present is an even rarer condition with no precedent in Anura. This condition was reported for the first time by Wiens (1993) for *T. degener*, and subsequently by Formas et al. (2003) for *T. halli*. It is also surprising that this feature is polymorphic in some species, as I recorded this condition in one specimen of *T. thompsoni* (KU 218469) and in one specimen of *T. marmoratus* (KU 135903).

The loss of premaxillary and maxillary teeth has been interpreted in some cases as a consequence of heterochronic processes (Davies, 1989; Fabrezi, 2001b). In *Telmatobius oxycephalus*, the teeth develop at the end of metamorphosis along with vomer, neopalatine, plectrum and sphenethmoid (Barrionuevo, 2013). These "late" structures are missing, underdeveloped or reduced in some species of the genus. If we map characters describing some of these elements in the phylogenetic hypothesis of *Telmatobius* (see below), it is notable that the states representing immature configurations occur more frequently among the species of the *T. marmoratus* and *T. macrostomus* Groups.

Skull and development

Skeletal variation among species of *Telmatobius* is often very subtle. However, it is frequent, in adults of some species, the occurrence of skeletal elements resembling immature configurations. Within this variation are the relative position of frontoparietals and parasphenoid, and the morphology of vomers, neopalatines and sphenethmoid.

The anterior border of frontoparietals not reaching the level of planum antorbitale is a synapomorphy of *Telmatobius* (char. 4.1). During post-metamorphic growth and development of *T. oxycephalus*, the anterior borders of the frontoparietal change their relative position in relation to the planum antorbitale. In recently metamorphosed exemplars of this species, the anterior borders of frontoparietals are at the level of planum antorbitale, whereas in subadults and adults they are posterior to that level (Barrionuevo, 2013). The same pattern of post-metamorphic change occurs during the post-metamorphic growth of phylogenetically distant species (e.g. *Spea*: Banbury and Maglia, 2006; *Leptodactylus ocellatus*: Perotti, 2001; *L.*

bufonius: Vera and Ponssa, 2014). A similar pattern is evident on the ventral side of the skull regarding the relative position of the anterior border of the parasphenoid in relation to the planum antorbitale. Among adults of species of the *T. macrostomus* and *T. marmoratus* Groups, the condition that characterizes immature specimens of *T. oxycephalus* is more frequent (i.e. anterior border of frontoparietal and parasphenoid at the level of the planum antorbitale). Furthermore, the anterior border of frontoparietals reaching the planum antorbitale (char. 4.0) is a synapomorphy of the *T. marmoratus* Group (Fig. 4).

Vomers begin to ossify as small centres of ossification at stage 44 of Gosner (1960) in *Telmatobius oxycephalus* (Barrionuevo, 2013). After metamorphosis, the vomer begins to acquire its final configuration and vomerine teeth start to develop. In *T. oxycephalus*, the number of teeth per vomer increases from one or two in recently metamorphosed froglets to reach a maximum of nine in adults (more frequently from four to six at each vomer) (Barrionuevo, 2013). Vomers are well developed (20.0) in most species of the genus (Fig. 4) but they are reduced (20.1) or absent/vestigial (20.2) in the species of the *T. macrostomus* Group. Among the species of the *T. marmoratus* Group, the vomers are absent or vestigial (20.2) in *T. dankoi* and *T. vilamensis* whereas they are reduced (20.1) in some specimens of *T. arequipensis*, *T. culeus* and *T. peruvianus*. In the same way, the vomerine teeth are present (22.1) in the majority of the species but are absent (22.0) in the species of the *T. macrostomus* Group (except *T. mayoloi*, Fig. 4). Within the *T. marmoratus* group, vomerine teeth are absent in *T. huayra*, *T. dankoi* and *T. vilamensis* (Fig. 4), although in these last two species the vomer is absent or incipient. In some exemplars of species of this group such as *T. arequipensis*, *T. culeus*, *T. marmoratus*, *T. jelskii*, and *T. rubigo* the vomerine teeth are absent (Fig. 4). When the vomerine teeth are present, tooth number is also variable. Although each vomer can bear normally up to seven teeth, this number is smaller in some species, particularly among the species of the *T. marmoratus* Group, where normally there are no more than three teeth in each vomer.

Neopalatines begin to ossify after metamorphosis in *T. oxycephalus* and, at the beginning of its formation, these bones are thin and straight. Subsequently, during post-metamorphic growth, neopalatines become curved and boomerang shaped. Reduced neopalatines or neopalatines showing an early ontogenetic morphology (straight) are found, in general, among the species of the *T. macrostomus* and *T. marmoratus* Groups (char. 23.0, Fig. 4).

The sphenethmoid is the last element to ossify in *T. oxycephalus*. This bone is formed by bilateral centres of ossification that subsequently fuse dorsally and ventrally. Ossification of the ventral region of the
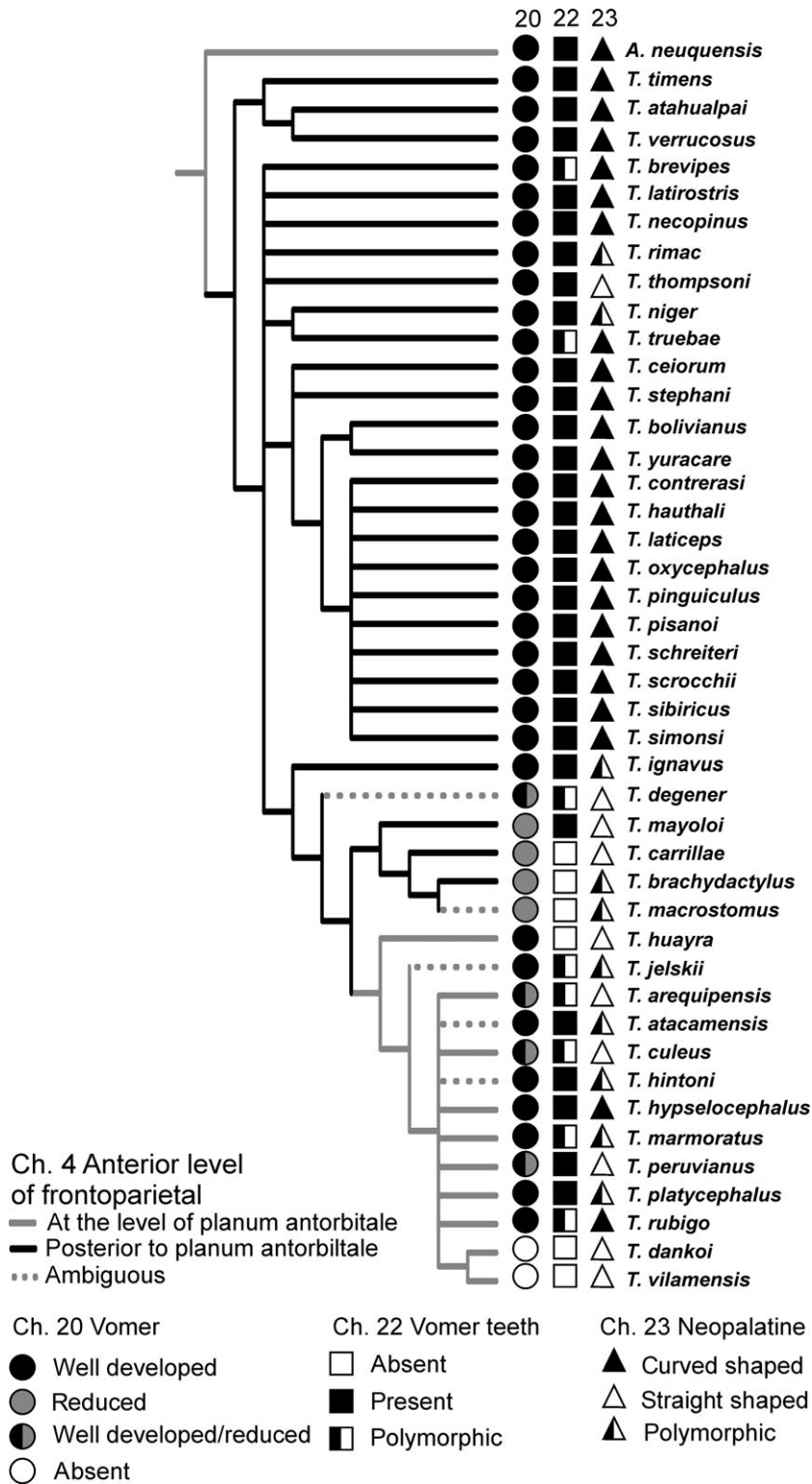
Fig. 4. Common mapping of character 4, describing the anterior level of frontoparietal, and taxonomic distribution of three osteological characters (chars. 20, 22 and 23) in the genus *Telmatobius*.

sphenethmoid progresses more slowly than that of the dorsal region. In three species of the *T. marmoratus* Group the sphenethmoid does not reach its final con-figuration and the two halves are not fused ventrally (*T. vilamensis*; polymorphic in *T. platycephalus* and *T. atacamensis*).

Form and function of the feeding apparatus: tongue, hyoid and mouth

A tongue largely attached anteriorly (around 70%) to the floor of the mouth is a synapomorphy of *Telmatobius*. This type of tongue is present among basal species including members of the *T. verrucosus* and *T. bolivianus* Groups. Figure 5 shows the common optimization over the consensus tree of the character describing the tongue (char. 64). A more attached tongue characterizes species belonging to the *T. marmoratus* Group. An even more attached tongue is characteristic of the species of the *T. macrostomus* Group.

The morphology of the tongue has important consequences for the mode of feeding because the vast majority of anurans use the tongue to capture their prey. Among frogs and toads, there are at least three basic mechanisms of tongue protraction: hydrostatic elongation, inertial elongation and mechanical pulling (Nishikawa, 2000). Hydrostatic elongation is restricted to Hemisotidae and Microhylidae and implies slow or rapid hydrostatic movements of the tongue. Inertial elongation implies a rapid tongue flip and is typical of Bufonidae, Ranidae, Leptodactylidae and Phyllomedusinae among others. The tongue in inertial elongators is free posteriorly and during feeding the prey is caught with the posterodorsal surface (the anteroventral surface of the tongue when it is flipped forward). Mechanical pulling, in turn, does not involve tongue flip but a short protraction and is common in Leiopelmatidae, Bombinatoridae, Discoglossidae and some Hylidae, among others. During protraction, the tongue is pulled upward and forward toward the symphysis (Nishikawa, 2000). As protraction of the tongue is short, normally the frog needs to lunge forward to catch the prey. In contrast to the inertial elongators, the tongue in mechanical pullers is more fleshy and it is attached to the floor of the mouth in a larger proportion.

Generally, underwater prey capture in anurans implies forelimb scooping and jaw prehension (O'Reilly et al., 2002). In the dense aquatic environment the tongue seems to have no role. Despite suction feeding being the most common way of underwater prey capture among aquatic vertebrates, in anurans it is extremely rare and has been described only in some members of Pipidae (Sokol, 1969; Lauder, 1985; Deban and Wake, 2000; Carreño and Nishikawa, 2010). Suction feeding implies the generation of rapid expansion of the bucco-pharyngeal cavity that decreases intraoral pressure. This drop of pressure generates suction flow carrying water into the mouth.

A suction force that is strong enough to maintain the position of the prey relative to the predator during the lunge (rather than pushing it away) is called compensatory suction (Van Damme and Aerts, 1997). For
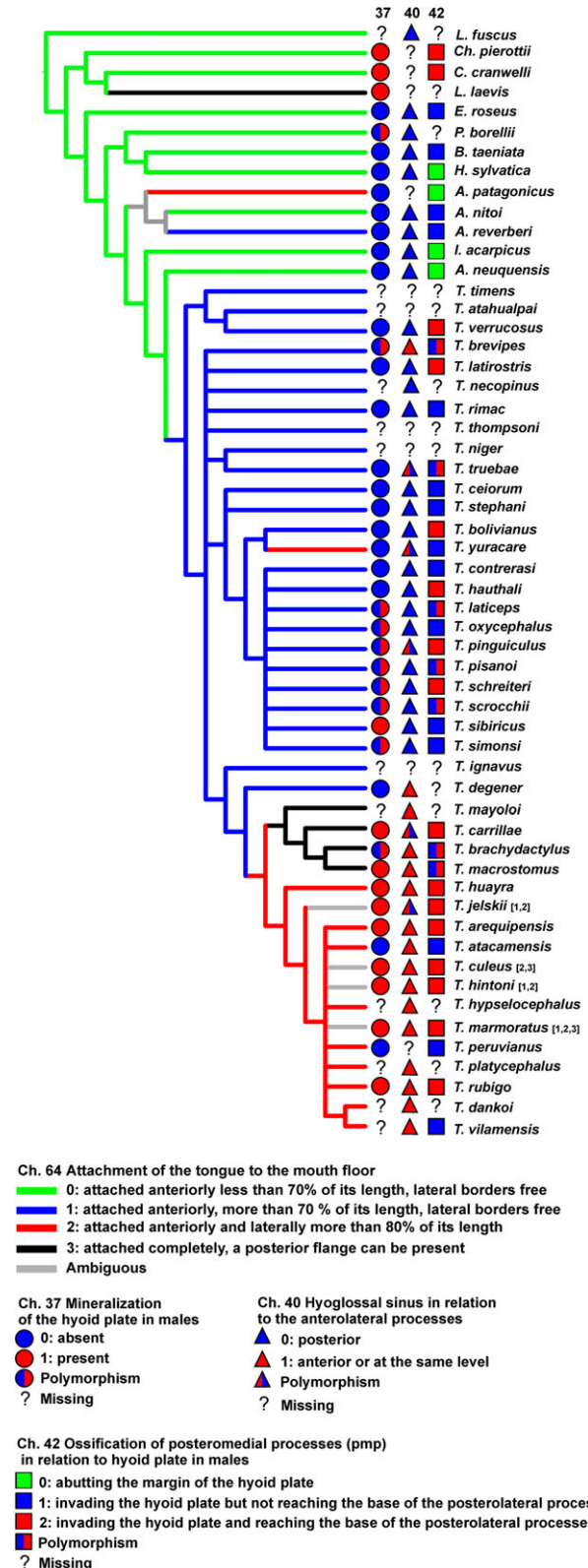

Fig. 5. Common mapping of character 64, describing the degree of attachment of the tongue to the floor of the mouth, and taxonomic distribution of three characters from the hyoid apparatus (chars. 37, 40 and 42) in the genus *Telmatobius* and outgroup.

the predator to seize the prey, compensatory suction must be complemented by scooping, ram feeding or jaw prehension. This was described for *Pipa* and *Xenopus* (Carreño and Nishikawa, 2010). When the suction force alone is sufficient to move the prey toward the mouth without the use of forelimbs it is called inertial suction (Van Damme and Aerts, 1997). This was described for *Hymenochirus* and *Pseudhymenochirus* (Sokol, 1969; Lauder, 1985; Deban and Wake, 2000; Carreño and Nishikawa, 2010).

Recently, observations during terrestrial feeding in *T. oxycephalus*, a member of the *T. bolivianus* Group, showed that it is a mechanical puller (Barrionuevo, 2016). This species has a short tongue protraction and lunges toward the prey flexing its head. *Telmatobius oxycephalus* is a semi-aquatic species and it is also able to capture prey underwater very efficiently by forearm scooping and jaw prehension, in the same way than other anurans that occasionally feed underwater (Barrionuevo, 2016).

Surprisingly, observations during underwater feeding in *T. rubigo*, a member of the *T. marmoratus* Group, showed that this species feeds by inertial suction (Barrionuevo, 2016). This species produces a rapid depression of the floor of the mouth that produces a flux of water inside the mouth carrying the prey. The forelimbs are not used for prey capture. This case constitutes the first record of inertial suction in non-pipid anurans.

In general, suction feeding has been associated with a particular morphology: (i) hyoid apparatus reinforced via mineralization or ossification of cartilage (Özeti and Wake, 1969; Deban and Wake, 2000; Nishikawa, 2000; Deban, 2003); (ii) tongue absent or reduced (Bramble and Wake, 1985; Miller and Larsen, 1989); and (iii) presence of labial lobes to occlude the gape laterally (Deban and Wake, 2000; Deban and Marks, 2002). Some of these morphological features are present in the compensatory suction feeders *Pipa* and *Xenopus* (lack of tongue, strong hyoid apparatus), whereas all these features together characterize the inertial suction feeders *Hymenochirus*, *Pseudhymenochirus* (Deban and Wake, 2000; Carreño and Nishikawa, 2010) and *Telmatobius rubigo* (Barrionuevo, 2016). The comparison of some morphological characters of *T. rubigo* (suction feeding) and *T. oxycephalus* (mechanical pulling in land, forelimb scooping in water) reveals two different morphological patterns in *Telmatobius* that are analysed herein in a phylogenetic context.

Hyoid apparatus. In *Telmatobius rubigo* the hyoid plate is mineralized whereas it is cartilaginous in *T. oxycephalus*, and ossification of the posteromedial processes invades the plate and reaches the base of the posterolateral processes (not reaching it in *T. oxycephalus*). The hyoglossal sinus is shallow, i.e. the posterior margin of the sinus is at the level of the anterolateral processes. In *T. oxycephalus* the hyoglossal sinus is deep, i.e. its posterior margin is posterior to the anterolateral processes (Barrionuevo, 2016).

The distribution of the characters describing mineralization/ossification of hyoid plate and posteromedial processes (chars. 37 and 42), and configuration of hyoglossal sinus (40) are shown in the consensus tree (Fig. 5). It is evident that in several species of *Telmatobius* there is a high level of mineralization or ossification of the hyoid plate. This is noteworthy if we consider that, in general, the hyoid plate is cartilaginous in anurans (Tyler, 1972; Trueb, 1973, 1993) and it is the condition found in species of the outgroup (Fig. 5) with the exception of the hyperossified Ceratophrynae. Moreover, *Telmatobius* shows a low level of ossification in the whole skeleton in relation to other anurans. Mineralization or ossifications in the hyoid plate occur in basal anurans (e.g. *Bombina*, *Barbourula* and *Ascaphus*). In these species there is a ventral ossification known as parahyoid bone (Cannatella, 1985) that is completely different from the endochondral ossification present in *Telmatobius*. Among Neobatrachia, a few species of *Litoria* (Tyler, 1972) show endochondral ossification. As commented above, the hyoid plate is also highly ossified among Ceratophryinae. In this case, this may be a consequence of the general hyper-ossification of the skeleton. By contrast, the low level of ossification in the skeleton of *Telmatobius* does not match the high level of mineralization/ossification in the hyoid plate present in several species. Even more curious is that within *Telmatobius* the species from the *T. macrostomus* and *T. marmoratus* Groups have a lower level of ossification or development of the skeleton (see above), and the hyoid plate is even more mineralized or ossified than in the other species of the genus (Fig. 5).

Tongue. In *Telmatobius rubigo* the tongue is small and flat, and around 90% of it is attached to the buccal floor, whereas in *T. oxycephalus* the tongue is larger and thicker and around 70% of it is attached to the buccal floor. The appearance of the anuran tongue is a result of the configuration of its constituent muscles and it is intimately related to the hyoid apparatus, which lies ventrally. In anurans in general, the tongue is formed by two muscles: the m. hyoglossus and the m. genioglossus. The m. hyoglossus originates in the ventral side of the posteromedial processes of the hyoid apparatus (Horton, 1982). The m. hyoglossus runs anteriorly and recurves dorsally at the level of the hyoglossal sinus and goes through the area limited by the sinus to enter the tongue. In *T. rubigo* just a few dorsal fibres of m. hyoglossus recurve dorsally, whereas the most of its fibres run anteriorly and insert on the tongue

superficially (i.e. ventrally). In this species, the size and the type of insertion of the m. hyoglossus implies with a smaller tongue and it is associated with a shallow sinus of the hyoid plate. By contrast, in *T. oxycephalus* most fibres of m. hyoglossus recurve dorsally and run through the area limited by the hyoglossal sinus and enter the tongue posteriorly. In this species, the size and the more posterior insertion of m. hyoglossal implies a larger tongue and it is associated with a deeper sinus. The distribution of the characters describing tongue and hyoglossal sinus in *Telmatobius* shows that this association is generally found within the genus (Fig. 5). A less developed tongue (more attached to the floor of the mouth, char. 64:2–3) is normally associated with a shallow sinus (char. 40:1). These states co-occur more frequently among species of the *T. macrostomus* and *T. marmoratus* Groups. By contrast, a more developed tongue (64:1) is normally associated with a deeper sinus (40:0) and represents the basal condition in the genus.

The m. genioglossus originates in the mandibular symphysis region (mentomeckelian bones and dentaries) and inserts into the tongue. In *T. rubigo*, the posterior fibres of m. genioglossus are superficial (i.e. ventral) and consequently their interdigitation with m. hyoglossus fibres is evident after removal of m. geniohyoideus. By contrast, in *T. oxycephalus* the posterior fibres of the m. genioglossus are deeper (i.e. dorsal) and their interdigitation with the m hyoglossus fibres is less evident (Barrionuevo, 2016).

Mouth and labial configuration. In *Telmatobius rubigo* the upper lips cover the lower lips laterally (not covering in *T. oxycephalus*); frontally, the lips form a notch (notch absent); the mandible is high in lateral view and low at the level of the symphysis (mandible low and uniform). The features present in *T. rubigo* are synapomorphies of the *T. marmoratus* Group: upper lips with a medial notch at mandibular symphysis (61.1), upper lips covering lower lips laterally (62.1) and lower jaw in lateral view high posteriorly but low anteriorly (63.1). The combination of these synapomorphies determines a configuration that could contribute during feeding to restrict the incoming flow of water to the anterior part of the mouth during a rapid depression of the floor of the mouth. This would make the suction force more effective. The configuration of the upper lip is analogous to the labial lobes of some salamanders (Deban, 2003) and *Hymenochirus* (O'Reilly et al., 2002; Dean, 2003). Along with reduction of the tongue and reinforcement of hyoid apparatus (see above), this mouth and labial configuration suggests that the mode of feeding of the species of the *T. marmoratus* Group would be inertial suction. Following the same

reasoning, the absence of these mouth and labial characters in the highly aquatic species of the *T. macrostomus* Group suggests that inertial suction would be absent. However, the extremely reduced tongue and a reinforced hyoid plate that characterize the species of this group suggest that they may feed underwater by compensatory suction. This type of suction requires complementary forelimb scooping, as occurs in *Pipa* and *Xenopus* (Carreño and Nishikawa, 2010). Curiously, in *T. macrostomus* the extremely long fingers parallels the long fingers of pipids.

In the species of the *T. marmoratus* Group the acquisition of this particular mouth configuration seems to be crucial to allow inertial suction. Drawing a parallel with Pipidae, the acquisition of labial lobes in the clade containing *Hymenochirus + Pseudohymenochirus* (Pyron and Wiens, 2011; Pyron, 2014) is related to the acquisition of inertial suction capability. Reduction of the tongue and reinforcement of the hyoid apparatus alone may be associated with compensatory suction. These characters are plesiomorphic in *Hymenochirus + Pseudohymenochirus* as well as in the species of *Telmatobius* of the *T. marmoratus* Group. This suggests that both groups of inertial suctorial frogs would have evolved from ancestors that fed by compensatory suction and that the labial lobes constitute a key acquisition for allowing inertial suction.

Conclusions

Telmatobius is a monophyletic genus that has evolved in relation to water ecosystems of the Andes and its precursor mountain ranges. The species groups recovered in the present phylogenetic hypothesis are congruent with previous hypotheses (Aguilar and Valencia, 2009; De la Riva et al., 2010). The taxonomic distribution of some osteological characters shows that the states resembling an immature morphological configuration are more common among species of the *T. marmoratus* and *T. macrostomus* Groups. This suggests that heterochronies in osteological development could explain part of the interspecific variation in the morphology of the skeleton. The species belonging to those two groups live at higher altitudes and are in general more aquatic than the remaining species living at lower altitudes. Furthermore, the occurrence of morphological characters associated with inertial suction feeding in the species of the *T. marmoratus* Group suggests that suction would have evolved in this highland aquatic group. It is noteworthy that this mode of underwater prey capture has no precedents in Neobatrachia, the group containing 96% of frogs and toads. The present analysis is the most comprehensive phylogenetic analysis of

Telmatobius to date and a total evidence analysis is the immediate next step.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Character matrix.

Appendix 1

Specimens examined

See abbreviations of museum collections in the main text.

Telmatobius arequipensis FMNH 68383-469, 68396 (DS), 34048, 34193, 34199, 34203, 40001-2; KU 162833-37, 162872-82; 162883-89, 162890, 164018 (DS), 164019, 164020, 194900-01, 194902-03, 214818-22, 164078; MCZ 1100; MHNSM 19474-75, 19491-95; *T. atacamensis* FML 03252 (3 paratypes), 04505 (28 specimens, 4 C&S), 20794-802, 20842-43; *T. atahualpai* KU182084-85; MHNSM 15976, 15978-79, 15984, unnumbered specimen; *T. bolivianus* CBF 1071 (C&S) 2061, 2063(C&S), 2072, 4124-25, 5377, 5379 (C&S), 5866, 5889; AMNH Field Series 15705, 15757, 15763; AMNH 165111-22; *T. brachydactylus* MHNSM 019, 023-26, 032; KU 139048-49, 181537-38, 217151, 215152 (C&S), 217153;FMNH 34212, 34215, 34220, 45146-84; MCZ 22883, 22901-9, 13402-6; ZFMK 66241 (C&S), 66242 (C&S); *T. brevipes* MHNSM 3740, 3742-44, 3749 (paratypes); KU 131684-89, 131690 (C&S), 181425-37, 181435 (C&S), 181486, 181489 (DS), 181857, 196611, 212412-46, 212447 (C&S), 212503, 212525, 215718, 221714; *T. carrillae* MHNSM 1528 (holotype), 3932-34 (paratypes), 6680, 6682-83; KU 204493, 214823-24, 214826-30; ZFMK 57263-65; *T. ceiorum* FML 01372 (holotype), 01373 (paratype), 01391 (4 specimens), FML 01543 (5 specimens), 01645 (6 specimens), 01768 (5 specimens), 02208 (7 specimens), 02629 (24 specimens, 4 C&S); KU 160845-47, 160848 (C&S); CM 65012-13; *T. contrerasi* FML 20813 (C&S), FML 20814-20; *T. culeus* CBF 0741, 1084, 1367, 4050 (C&S), 4052, 4057 (C&S); MHNSM 7769-70, 7768, 7777, 7785, 7699, 7793, 7808-09; AMNH 7479, 23455, 94281-315, 94261-80, 94252-60, 155086-92; KU 135849-60, 135861-63, 135864 (DS), 135865-75, 138743-45, 174961-63, 174964-71 (8 DS), 174973-77 (5 DS),174979-83 (5 DS), 183117-77, 185794; MCZ 1077-78, 1080; *T. dankoi* KU 291544 (DS); *T. degener* KU 218463, 218465 (DS), 218466 (C&S); *T. hauthali* FML 03264.9 (neotype), 03264.1 (paratopotype), 03264 (32 specimens), 03270 (14 specimens), 03315 (5 specimens C&S); *T. hintoni* AMNH 33968-9, 153623-39, FMNH 71796, 71798, 71800; MNCN 17361-63 (3 C&S), 43574-75; KU 160148-52, 160155-89, 160190 (DS), 160191 (DS), U160192, CM 4519; *T. huayra* CBF 1221 (holotype), 1222-3 (paratypes); MNCN 43567, 43568; *T. hypselocephalus* FML 03768 (holotype); 03767 (paratype), FML 03766 (6 paratypes), 04372 (C&S); *T. ignavus* MCZ 4093 (Holotype); KU 181438, 181440 (DS), 181441 (C&S), 181845, 181847, 219822; *T. jelskii* MHNSM 7748-52, 16769, 16773, 16851, 16864; AMNH 6736; FMNH 39683-91, 39693-97, 39703-12, 39714-17; KU 181453-72, 181835 (DS), 181850-51; MCZ 4797-800; ZFMK 66239 (C&S), 66240 (C&S), 71737-48, 71750-51; *T. laticeps* FML 0690 (4 specimens), 1498 (46 specimens), 1499 (4 specimens, C&S),

1541 (15 specimens), 2255 (holotype), 2418 (paratype), 2559 (2 specimens), 3960 (9 specimens), 3961 (7 specimens); KU 72879, 72879, 160885, 160886, 179743, 182837-40; MCZ 35365; CM 68428-29; *T. latirostris* MHNSM 3733-36, 3738 (paratypes); KU 212448-50, 212451 (C&S); *T. macrostomus* MHNSM 56-57, 69-72, 250, 252-53, 266, 372; FML 3690 (4 specimens); KU 98127 (DS), 173103-7, 181834(DS), 186840-1; AMNH 6737-8, 23454, 23565 (syntype); FMNH 34209 (DS); MCZ 4810 (DS), 4811 (DS), 4812, 4814, 15560, 22888, 134013, 134014, 134017, 134018, 134032, 134037; ZFMK 39266 (DS), 39267 (DS), 54193 (C&S), 54194 (C&S); *T. marmoratus* CBF 2165-66, 2167 (C&S), 3621, 3622 (C&S), 3624; MHNSM 10858-59, 10861-62, 10877-79, 10882-83, 10910, 10916-17, 10924, 12163, 12165, 12168, 12172, 12175, 12180, 12182 (topotypes); FML 2805, 2809 (8 specimens), 2817 (6 specimens), 3274 (14 specimens), 3275 (3 specimens), 3291 (9 specimens), 3537, 4521 (3 specimens)., 6663, 6675, 6679-80; CM 2634-35; KU 135903, 135904, 135911-65, 135966-69, 159837, 160012, 162913-57, 164021, 164022, 164023, 164079, 164080, 212453, 214832; AMNH 62678-9, 62680-87, 92703-12; FMNH 34071 (13 specimens), 34090 (20 specimens),34129, 34146 (70 specimens), 34214 (14 specimens), 40243 (9 specimens), 40244 (7 specimens), 40245 (4 specimens), 40245 (2 specimens, C&S); MCZ 1096, 26230-32, 65001-3, 65004-5, 65007-14, 85378-80; ZFMK 39766-69; *T. mayoloi* MHNSM 20479-80, 20483, 20488; KU 220842, ZFMK 57259 (paratype); *T. necopinus* KU 212481, 212482, 212484 (C&S); *T. niger* AMNH 13968; FMNH 73354 (paratype), KU 131779, 131795 (DS), 131796 (DS), 166237, 166295 (DS), 178234, 202271, 202672-78, 202661, 202963, 218348, 218349, 218350; MCZ 3037 (Holotype) MCZ 3038-40 (paratypes); *T. oxycephalus* FML 0225 (Holotype), 1369, 1589 (9specimens), 1590 (4 specimens), 1734 (5 specimens), 1758 (14 specimens), 2020 (2 specimens), 2071, 2095 (7 specimens), 2242, 2536 (8specimens), 2861 (3 specimens), 2867 (9 specimens, 4 C&S), 2883, 3836 (3 specimens C&S), 20806-12, 20880-82, FML SB 019 (C&S); KU128875-79, 128880 (DS); CM 65006-7; *T. peruvianus* FMNH 6390, 6394-96, 6397 (C&S), 6400; KU 159838, 162075, 162113 (DS), 162114 (DS), 162115; MCZ 15824-5; ZFMK 24912, 24913; *T. pinguiculus* FML 03910 (holotype),03920 (paratype),03921 (7 paratypes), 04373 (2 specimens C&S), 20846-57, 20859-72; FML SB 187 (C&S), 208, 208 (C&S), 253; *T. pisanoi* FML 2419 (13 specimens), 2421 (28 specimens), 2442 (holotype), 2443 (paratype), 2963 (22 specimens, 2 C&S, 2 DS), 3269 (24 specimens, 4 C&S), 20844-45; MCZ 17737-40; *T. platycephalus* FML 3763 (holotype), 3764 -65 (paratypes), 3769 (paratype), 3789 (8 specimens), 3790 (paratype), 4371 (C&S); FML SB 82 (C&S); MLP DB 4730; *T. rimac* MHNSM 20493, 20496-98; FMNH 34224 (paratype); KU 181852-3; ZFMK 57261 (C&S), 57262 (C&S); *T. rubigo* FML 2602 (10 specimens), 2812 (3 specimens), 2813 (6 specimens), 2814 (6 specimens), 2818 (7 specimens), 3293 (2 specimens), 3621, 4391 (4 specimens), 4517 (4 specimens), 20827, 20828 (holotype), 20829 (paratype, C&S), 20830-5 (paratypes); MACN 39092-94 (paratypes); MLP DB3457-9, 3576-8, 3614-16, 3621-22, 3648, 4710, 4755-6, 4760, 4765-66, 4812; CM 65008-9; *T. schreiteri* FML 0216 (holotype), 1976 (27 specimens), 1977 (27 specimens, 4 C&S); CM 65010-11, 147873-76; *T. scrocchii* FML 1515 (97 specimens, 7 C&S), 3532 (holotype), 5772 (9 specimens); FML SB 107; *T. sibiricus* MNCN 17364 (C&S), 17365 (C&S), 43257-58; ZFMK 70315 (paratype); *T. simonsi* AMNH 165224-5; CBF 2122, 2124. 3050, 3081 (C&S), 3082 (C&S); KU 160130-38, 160140; MCZ 17495-97; MNCN 17366 (C&S), 23833, 43251; ZFMK 67117, 69922, 69923; *T. stephani* FML 1594 (14 specimens), 1743 (holotype), 1744 (paratype), 2765 (11 specimens, 4 C&S); KU 206702-3; *T. thompsoni* KU218468 (DS); *T. timens* AMNH 153099; KU 139038, 139042-47, 162893-912, 164081 (DS), 164082 (DS); *T. truebae* MHNSM 6185, 12366-70; KU 181492-535, 181528, 181536, 181855, 212454, 212464 (C&S), 212465-76, 212477 (C&S), 212478 (C&S), 212479 (C&S), 212480 (C&S); *T. verrucosus* CBF 1571, 1675, 2765 (C&S), 3227, 5372 (C&S), 5881-82; AMNH 24377, 24378-9, 24380-3, 165123-31; MNCN 43540, 43544; *T. vilamensis* KU 159839-40; *T. yuracare* CBF 1355-54; MNCN 16645

(C&S), 16646 (C&S); ZFMK 60185, 66990; CM 4230, 4232; *Alsodes neuquensis* MACN 37845, 37851, 37853, 37919-20, 37928-29., 37930 (C&S) 37951 (C&S); MLP 2872-94; *Atelognathus nitoi* CENAI 4621 (holotype), 6876, 6878-81, 6882 (C&S), 6883, 7263 (C&S); KU 203319; *Atelognathus patagonicus* MACN 37903, 37907-8; CENAI 1070 (C&S); KU 160522 (C&S), 203321 (C&S), 203324 (C&S), 203326 (C&S); *Atelognathus reverberii* CENAI 36, 38-40; MACN 33937 (C&S), 33938, 33939-40; *Batrachyla taeniata* CENAI 3371, 4059-60, 6864, 6865 (C&S), 6866 (C&S); KU 161473 (C&S), 161496 (C&S); *Ceratophrys cranwelli* FML 3635 (9 specimens), 5473 (DS), 5474 (DS),5476 (DS); *Chacophrys pierottii* FML 1019 (3 specimens, C&S), 3640, 9012 (C&S), 9269-70; *Eupsophus roseus* MACN 37972, 37974, 37976 (C&S), 37977-78, 37980, 37979 (C&S), 37981; *Hylorina sylvatica* CENAI 1869, 1873-77; FML 3918(C&S), 3919 (4 specimens); *Insuetophrynus acarpicus* CENAI 3697 (holotype), 6896 (C&S) 6897, 6899, 6906, 6908 (C&S), 6911; KU 203352 (C&S); *Lepidobatrachus laevis* FML 13703 (DS), 13709 (DS); MACN 43103-22; *Pleurodema borellii* FML 4404 (C&S), 7912-19; FML SB 168 (C&S); *Leptodactylus fuscus* FML 11941 (C&S), 11943 (C&S), 16015-21.

Appendix 2

Phylogenetic characters

Continuous characters (0-1). 0 Number of vomerine teeth in each vomer

1 Density of epidermal papillae (EP) of the nuptial pad in Finger II (EP/mm^2).

Discrete characters (2–96)

Cranium—2 Size and shape of nasals (Fig. 6): (0) large, quadrangular; (1) medium-sized, claviform or triangular; (2) small, claviform or triangular. In his work on "Telmatobinae", Lynch (1978) defined two states to describe the size of nasals: state 0, large and in broad median contact and state 1, small and tenuously in median contact. In state 0, he included *Atelognathus*, *Telmatobius brachydactylus* and *T. macrostomus* (as *Batrachophrynus brachydactylus* and *B. macrostomus*), and in state 1 *Alsodes*, *Batrachyla*, *Eupsophus*, *Hylorina*, *Insuetophrynus* and the remaining species of *Telmatobius*. In the figures of *Atelognathus* presented by Lynch (1978), as well as in specimens of *Atelognathus* examined herein, the condition "broad median contact" has not been confirmed. The broad median contact is polymorphic in *Telmatobius macrostomus*, whereas in *T. brachydactylus* the nasals are separated in the specimens examined. The nasals of *T. macrostomus* and *T. brachydactylus* are more similar in size and shape to the nasals of the other species of *Telmatobius* and are, consequently, included in state (1). The nasals of *T. atahualpai*, *T. dankoi*, *T. timens*, *T. verrucosus* and *T. vilamensis* are much reduced in relation to the other species of the genus, and are included in a new state (2).

3 Relation of frontoparietals in the parietal region: (0) frontoparietals not fused in parietal region; (1) frontoparietals fused in parietal region. The fusion of frontoparietals is not common among anurans. In some species of *Telmatobius* the paired frontoparietals are fused medially in the parietal region, i.e. from the level of the taenia tecti transversalis to the level of tectum synoticum. To codify this character we need to be careful because in some species the fusion of each separate frontoparietal with the underlying neurocranium can drive us to misinterpret it as a real fusion between frontoparietals (De la Riva et al., 2012). The frontoparietals fused posteriorly was previously proposed as a putative synapomorphy of *Telmatobius* (Wiens, 1993).
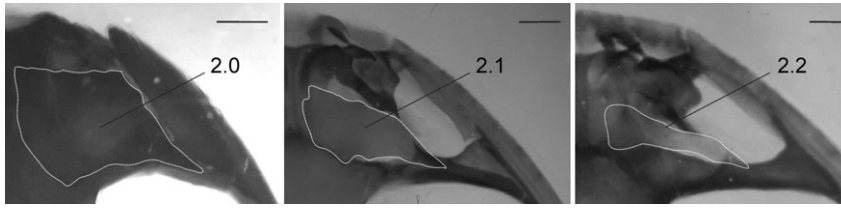
Fig. 6. Dorsal view of the right half of nasal region of (from left to right) *Atelognathus reverberii* (MACN 33937), *Telmatobius oxycephalus* (FML 2867-2) and *T. verrucosus* (CBF 5372); scale bars = 1 mm.

4 Anterior end of frontoparietals (Fig. 7): (0) at the level of planum antorbitale; (1) posterior to the level of planum antorbitale.

5 Level of exposure of the frontoparietal fenestra (Fig. 7; modified from Scott, 2005, char. 69). I consider the relative width of frontoparietals anterior to the taenia tecti transversalis in relation to the width of the frontoparietal fenestra: (0) frontoparietals narrower than the fenestra; (1) frontoparietals equal or slightly wider than the fenestra; (2) frontoparietals in contact or jointed to each other, no frontoparietal fenestra. Additive.

6 Orientation of alary process of premaxillary in lateral view, measured in relation to the horizontal axis (modified from Scott, 2005; char. 78; from Pramuk, 2006; char. 26; from Grant et al., 2006, char 131): (0) directed posterodorsally, angle less than 60°; (1) directed dorsally, angle between 60° and 80°; (2) directed anterodorsally, angle approximately 90° or more. Additive.

7 Orientation of alary process of premaxillary in frontal view (Fig. 8; modified from Ponssa, 2008, char. 32): (0) not divergent, the distal tip of alary process (dorsal) at the same level as the base; (1) divergent, the distal tip of alary process (dorsal) is directed laterally.

8 Width of the base of the alary process of premaxillary in relation to its distal end in frontal view (Fig. 8) (modified from Ponssa,

2008, char. 35): (0) base narrower than or equal to the distal (dorsal) end; (1) Base wider than the distal (dorsal) end.

9 Premaxillaries in frontal view (Fig. 8): (0) not flexed; (1) flexed, forming an arch. Several species of *Telmatobius* have a notch in the symphysis of the upper lip at the level of the premaxillaries, but this character is independent of the character described here. In most cases, the labial notch is the result of the configuration of the soft tissue of the upper lips without modification of the premaxillaries (the premaxillaries are not arched in species with a notch in the upper lip). In other cases, as in *T. culeus* and *T. dankoi*, the labial notch is formed by soft tissue but also by the arched premaxillaries. In *T. hintoni*, *T. jelskii*, *T. marmoratus* and *T. peruvianus* the labial notch is present and the premaxillaries flexion is polymorphic.

10 Squamosal process of pars facialis of maxillary (Lynch, 1971): (0) absent; (1) present.

11 Posterior end of maxillary in relation to the central part of pterygoid (the base of the three rami): (0) at the level or posterior to the central part of pterygoid; (1) anterior to the central part of pterygoid.

12 Pterygoid process of maxillary (Lynch, 1978): (0) absent; (1) present. The pterygoid process is formed as a result of the posterior
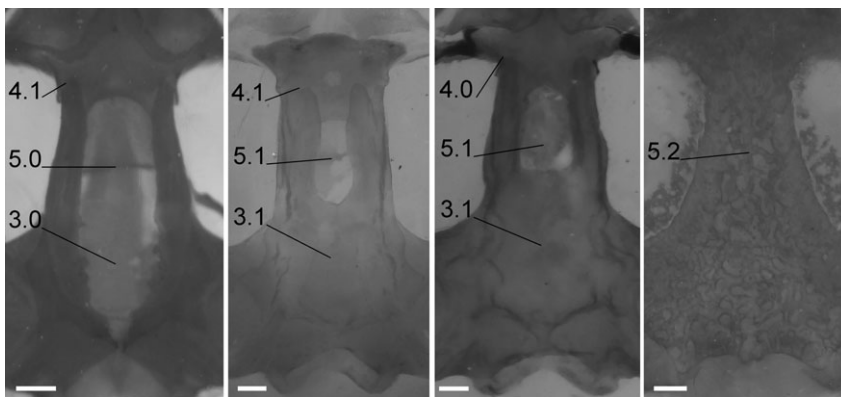

Fig. 7. Dorsal view of frontoparietals of (from left to right) *Atelognathus nitoi* (CENAI 6882), *Telmatobius laticeps* (FML1499-4), *T. marmoratus* (CBF 3622) and *Chacophrys pierottii* (FML 9012); scale bars = 1 mm.
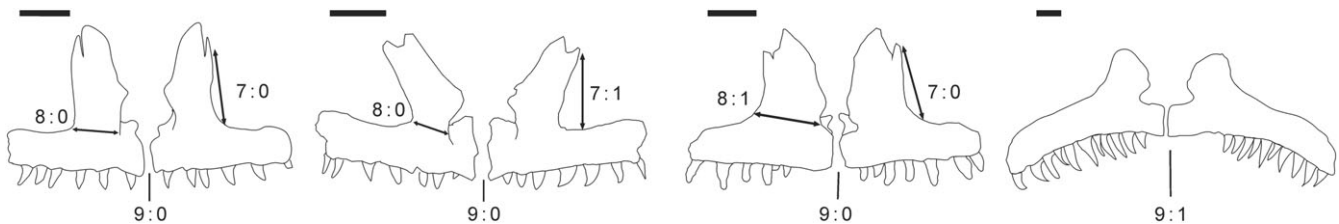

Fig. 8. Frontal view of premaxillaries of (from left to right) *Telmatobius simonsi* (CBF 3082), *T. oxycephalus* (FML 2867-1), *T. atacamensis* (FML 4505) and *T. culeus* (KU 135864); scale bars = 1 mm.

widening of the pars palatina of maxillary in its articulation with the pterygoid. This character was used by Lynch (1978), who noted their presence in *Eupsophus* and *Batrachyla* and its absence in the other studied genera (including *Alsodes*, *Atelognathus*, *Hylorina*, *Insuetophrynus* and *Telmatobius*).

13 Premaxillary teeth (modified from Aguilar and Valencia, 2009): (0) present; (1) absent.

14 Maxillary teeth (modified from Aguilar and Valencia, 2009): (0) present; (1) absent.

15 Condition of maxillary and premaxillary teeth (Lynch, 1971; Fig. 9): (0) pedicellate; (1) not pedicellate.

16 Shape of maxillary and premaxillary teeth (Lynch, 1971; Fig. 9): (0) blunt or spatulate teeth; (1) fang-like teeth.

17 Distal tip of maxillary and premaxillary teeth (Fabrezi, 2006; char.12; Fig. 9): (0) monocuspid; (1) bicuspid.

18 Anterior portion (=pars jugalis) of quadratojugal (modified from Clarke, 2007, char. 19): (0) well developed, exceeding the level of the central part of pterygoid; (1) moderate, can reach but not exceed the level of the central part of pterygoid; (2) vestigial. Additive.

19 Relation of the quadratojugal and maxillary (Grant et al., 2006, char. 133): (0) quadratojugal and maxillary not fused; (1) quadratojugal and maxillary fused.

20 Vomer (Lynch, 1971; Fig. 10): (0) well developed; (1) reduced, pre and postchoanal processes absent; (2) vestigial or absent.

21 Anterior process of the vomer (modified from Clarke, 1981, char. 10): (0) reaching the level of the union premaxillary–maxillary; (1) not reaching the level of the union premaxillary–maxillary.

22 Vomerine teeth (Aguilar and Valencia, 2009; Fig. 10): (0) absent; (1) present.

23 Shape of the neopalatine (Fig. 11): (0) straight; (1) curved or boomerang-shaped.

24 Anterior process of neopalatine (Lynch, 1978): (0) absent; (1) present. The anterior process of neopalatine is an osseous eminence of the medial region of the neopalatine. Lynch (1978) described this process in *Atelognathus*.

25 Medial end of neopalatine: (0) not reaching the level of the internal border of the orbit; (1) reaching and overpassing the level of the internal border of the orbit.

26 Lateral end of neopalatine: (0) not reaching the pars palatina of maxillary; (1) reaching the pars palatina of maxillary.

27 Length of the cultriform process of parasphenoid (modified from Baez and Trueb, 1997; char. 29; Ponssa, 2008; char 58; Lynch, 1978; char. 10; Fig. 11): (0) short, not reaching the level of planum antorbitale; (1) long, reaching the level of planum antorbitale.
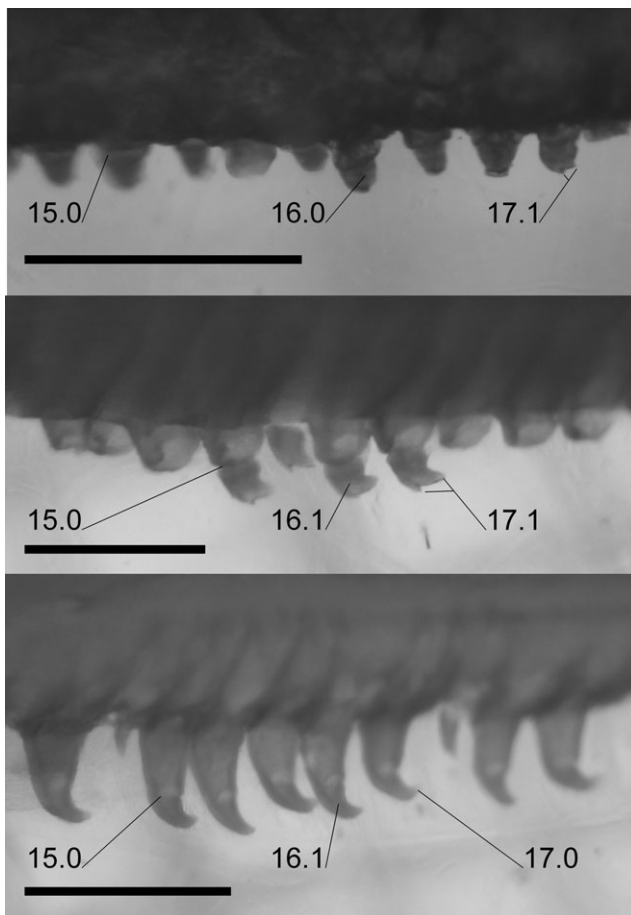

Fig. 9. Maxillary teeth of *Atelognathus nitoi* (CENAI 7263, top), *Insuetophrynus acarpicus* (CENAI 6908, middle) and *Telmatobius oxycephalus* (FML2867-2, bottom); scale bars = 1 mm.
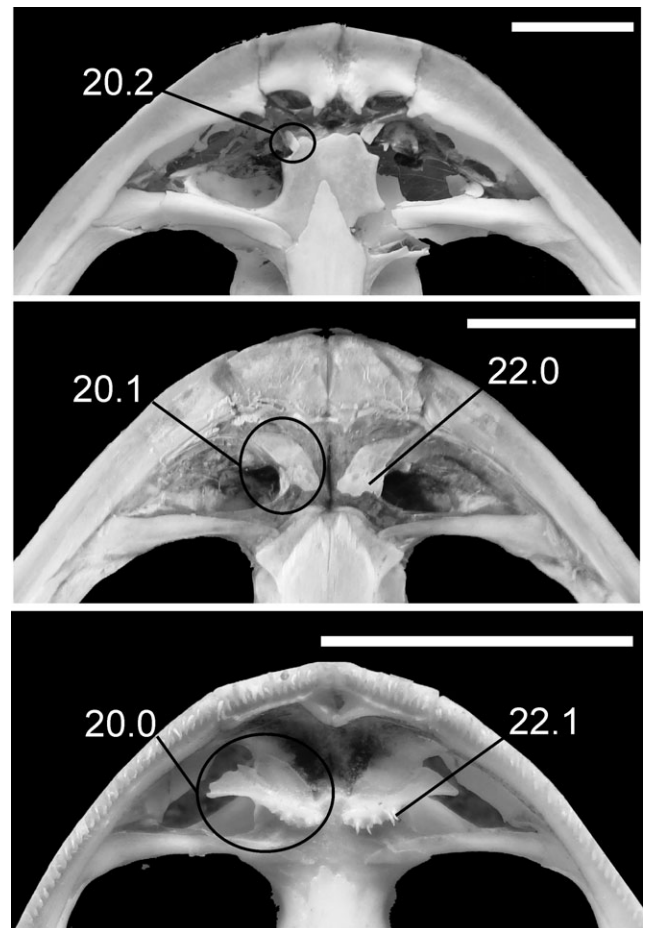

Fig. 10. Ventral view of the anterior region of the skull of *T. macrostomus* (KU 98127, top; FMNH 34209 middle) and *T. brevipes* (KU 181489, bottom); scale bars = 10 mm.

28 Anterior ramus of pterygoid (Fig. 11): (0) robust, width more or less uniform; (1) gracile, becoming thinner anteriorly.

29 Length of anterior ramus of pterygoid (modified from Clarke, 1981, char. 13): (0) short, not reaching the level of neopalatines; (1) long, reaching the level of neopalatines.

30 Contact between zygomatic ramus of squamosal and maxillary (Lynch, 1971; Heyer, 1975; char. 25; Fabrezi, 2006, char. 11): (0) not in contact; (1) in contact.

31 Otic ramus of squamosal (Lynch, 1978): (0) short or incipient, not expanded distally; (1) well developed, expanded distally.

32 Sphenethmoid in ventral view (modified from Wiens et al., 2005; char. 31): (0) fused; (1) not fused.

33 Coronoid process of angulosplenial (modified from Baez and Trueb, 1997, char. 34): (0) developed, conspicuous; (1) vestigial, inconspicuous.

34 Coronoid process in relation to the lower jaw articular surface: (0) reaching the level of the lower jaw articular surface; (1) anterior to the level of the lower jaw articular surface.

35 Odontoids of the lower jaw (Lynch, 1971; Fabrezi, 2006, char. 23): (0) absent; (1) present.

36 Relation between dentary and angulosplenial (Wild, 1997): (0) not fused; (1) fused or suture obscured.

Hyolaryngeal apparatus

37 Mineralization and ossification in central and anterolateral regions of the hyoid plate in males (Fig. 12): (0) absent; (1) present.

38 Dorsal dermal ossification over the hyoid plate (modified from Fabrezi, 2006; char. 80; Fabrezi and Lobo, 2009): (0) absent; (1) present.

39 Anterolateral processes of the hyoid plate (Lynch, 1971; Wiens et al., 2005; char. 44; Fabrezi, 2006; Clarke, 2007, char. 2): (0) present; (1) absent.

40 Hyoglossal sinus in relation to the anterolateral processes of the hyoid plate (modified from Scott, 2005; char. 88; Fig. 12): (0) posterior to the level of the anterolateral processes; (1) anterior or at the same level of the anterolateral processes

41 Position of the sinus laryngeus (*sensu* Roček, 1981; Fig. 12) with respect to the contact of the posterior border of the base of posterolateral process with the hyoid plate: (0) Sinus laryngeus posterior to the base of posterolateral processes; (1) Sinus laryngeus at the same level as the base of the posterolateral processes.

42 Ossification of posteromedial processes in relation to hyoid plate in males (modified from Fabrezi, 2006; char. 29; Fig. 12): (0) abutting the margin of the hyoid plate; (1) invading the hyoid plate but not reaching the base of the posterolateral processes; (2) invading the hyoid plate and reaching the base of the posterolateral processes. Additive.

Vertebral column—43 Relationship of the atlas with presacral vertebra II (Lynch, 1973): (0) not fused; (1) fused.

Pectoral girdle—44 Shape of the sternum (Lynch, 1971; Fig. 13): (0) plate-like; (1) style.

45 Proportions of the plate-like sternum (Fig. 13): (0) wider than long or as wide as long; (1) longer than wide.

46 Distal (posterior) margin of sternum (Heyer, 1975; Lynch, 1978; Wiens et al., 2005; char. 69; Fig. 13): (0) medial notch present; (1) medial notch absent.

47 Contact between clavicle and scapula in males (Baez and Trueb, 1997, char. 44): (0) sindesmosis; (1) sinostosis.

48 Contact between clavicle and scapula in females (Baez and Trueb, 1997, char. 44): (0) sindesmosis; (1) sinostosis.

49 Crest in the anterior margin of the scapula (modified from Sanchiz et al., 2002; Fig. 14): (0) absent; (1) present.
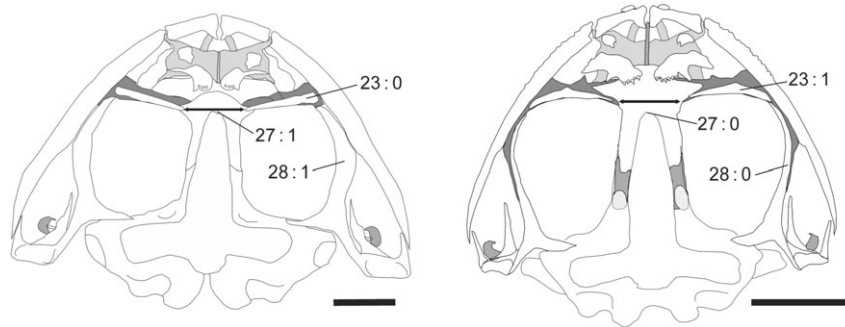

Fig. 11. Ventral view of the skull of *Telmatobius atacamensis* (FML 4505-1, left) and *T. oxycephalus* (2867-2, right); scale bars = 5 mm.
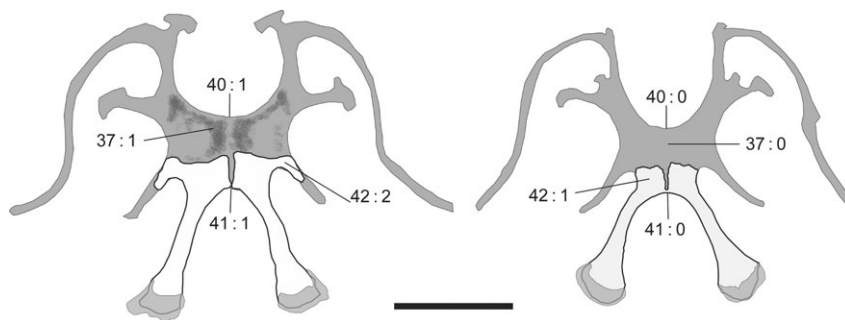

Fig. 12. Ventral view of hyoid apparatus of *Telmatobius rubigo* (FML 20829, left) and *T. oxycephalus* (FML 2867-2, right); scale bars = 5 mm.
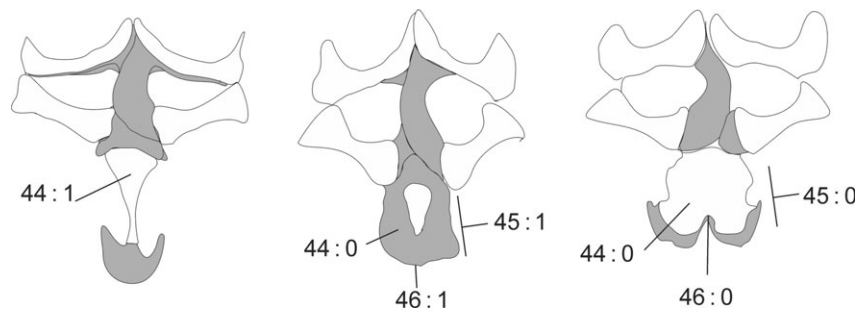
Fig. 13. Ventral view of pectoral girdle of (from left to right) *Leptodactylus fuscus* (FML11941), *Telmatobius timens* (KU164081) and *T. oxycephalus* (FML2867-1).

50 Cleithrum (Trueb, 1973; Wiens et al., 2005, char. 71): (0) bifurcated; (1) not bifurcated.

Forelimb—51 Humeral spine in males (Noble, 1924; Wiens et al., 2005; char. 92): (0) absent; (1) present. The humeral spine is formed by a hypertrophied crista ventralis. In *Telmatobius*, the occurrence of the humeral spine it was considered to occur only in *T. bolivianus*, *T. mendelsoni* and *T. yuracare* (Parker, 1940a; De la Riva, 1994b, 2005; De la Riva et al., 2012).

52 Crista medialis and crista lateralis (Gaupp, 1896) in the humerus of males (Lynch, 1971, 1978): (0) absent or poorly developed; (1) well developed.

53 Metacarpal II in males (modified from Wiens et al., 2005, char. 81): (0) metacarpal II similar to metacarpals III, IV and V; (1) metacarpal II more developed than metacarpal III, IV and V.

54 Bony knob in the medial margin of metacarpal II in males (modified from Liem, 1970, char. 26): (0) absent; (1) present.

55 Bony knob in the lateral margin of the metacarpal V (modified from Liem, 1970, char. 26): (0) absent; (1) present.

56 Distal end of terminal phalanges (modified from Liem, 1970; char. 27; Lynch, 1971): (0) knobbed; (1) T-shaped; (2) pointed.

57 Number of elements in the prepollex (modified from Scott, 2005; char. 112; and from Fabrezi, 2006, char. 66): (0) a proximal element and one distal element; (1) a proximal element and two distal elements; (2) a proximal element and three distal elements; (3) a proximal element and four distal elements; (4) a proximal element and five distal elements.

Hindlimb—58 Number of the elements of the prehallux (modified from Fabrezi, 2006, char. 59): (0) a proximal element and one distal element; (1) a proximal element and two distal element; (2) a proximal element and three distal elements.

External morphology—59 Orange pigmentation in the ventral skin of thighs: (0) present; (1) absent. This character only can be codified in living specimens, and therefore the information for species that have not been observed in the field or for which no pictures were available has been codified from the literature as follows: *T. hauthali* (Koslowsky, 1895; Laurent and Lavilla, 1986); *T. ceiorum*, *T. schreiteri*, *T. laticeps* (as *T. hauthali*), *T. stephani* (Cei, 1980); *T. scrocchii* (Laurent and Lavilla, 1986); *T. hypselocephalus*, *T. platycephalus* (Lavilla and Laurent, 1988); *T. bolivianus*, *T. culeus*, *T. huayra*, *T. marmoratus*, *T. simonsi*, *T. verrucosus*, *T. yuracare* (De la Riva, 2005); *Telmatobius brevipes*, *T. truebae*, *T. latirostris* (Wiens, 1993), *T. mayoloi* (Salas and Sinsch, 1996), *T. brachydactylus*, *T. carrillae*, *T. jelskii*, *T. macrostomus* (Lehr, 2005); *Hylorina*
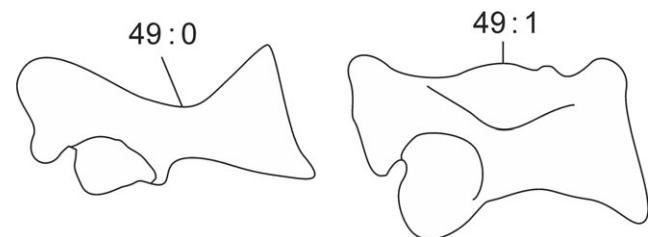

Fig. 14. Ventral view of scapula of *Telmatobius truebae* (KU181536, left) and *T. laticeps* (FML1499-1, right).

sylvatica, *Batrachyla taeniata*, *Atelognathus nitoi*, *Eupsophus roseus* (Úbeda, 1998), *Atelognathus reverberii* (Cei, 1969).

60 Tympanic membrane (modified from Heyer, 1975; char 2; and from Scott, 2005, char. 144): (0) present; (1) absent.

61 Labial medial notch at upper mandibular symphysis (Aguilar and Valencia (2009): (0) absent; (1) present. This character is independent of character 7 (premaxillaries in frontal view). In most cases, the labial notch is the result of the configuration of the soft tissue of the upper lips without modification of the premaxillaries.

62 Upper lips (Boulenger, 1882): (0) not overhanging lower lips laterally; (1) overhanging lower lips laterally (see figure 10 in Barrionuevo, 2016).

63 Lower jaw in lateral view: (0) low, uniform depth; (1) higher posteriorly, lower anteriorly (see figure 11 in Barrionuevo, 2016).

64 Attachment of the tongue to the floor of the mouth (modified from Aguilar and Valencia, 2009): (0) attached anteriorly less than 70% of its length, lateral borders free; (1) attached anteriorly more than 70% of its length, lateral borders free; (2) attached anteriorly and laterally more than 80% of its length; (3) attached anteriorly and laterally completely, a posterior flange can be present. Additive (see states 1 and 2 in figure 6 in Barrionuevo, 2016).

65 Keratinized spicules on the skin (modified from Grant et al., 2006, char. 0): (0) absent; (1) present.

66 Keratinized spicules on the loreal region: (0) present; (1) absent. This character is independent of character 71 and 72 because they do not necessarily co-occur

67 Keratinized spicules on the palmar surface: (0) absent; (1) present. This character is independent of character 70 and 72 because they do not necessarily co-occur

68 Keratinized spicules on the plantar surface (Ponssa, 2008, char. 6): (0) absent; (1) present. This character is independent of character 70 and 71 because they do not necessarily co-occur

69 Nuptial pad on the fingers of males (modified from Heyer, 1975; char 3; Grant et al., 2006, char. 23): (0) absent; (1) present.
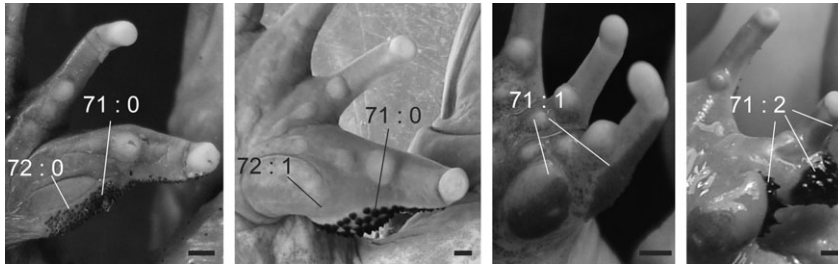
Fig. 15. Dorsal view of the thumb and nuptial pad of (from left to right) *Telmatobius rubigo* (FML20828), *T. truebae* (KU181528), *Pleurodema borellii* (FML7912) and *Insuetophrynus acarpicus* (CENAI 3697); scale bars = 1 mm.

70 Position of the nuptial pad in males (Lynch, 1978; modified from Aguilar and Valencia, 2009, char. 1): (0) finger II; (1) fingers II and III; (2) fingers II, III and IV. Additive.

71 Nuptial pad of finger II (Fig. 15): (0) one single nuptial pad; (1) one single pad in the thumb and one separated pad on the inner metacarpal tubercle; (2) two pads in the thumb and one pad at the base of the inner metacarpal tubercle.

72 Relation of the nuptial pad on finger II and the inner metacarpal tubercle (modified from Aguilar and Valencia, 2009, char. 2): (0) in contact; (1) not in contact.

73 Keratinized spicules on the pectoral region in sexually mature males (Lynch, 1971, 1978; Fig. 15): (0) absent; (1) present.

74 Disposition of the keratinized spicules on the pectoral region (Lynch, 1978, char 19): (0) evenly distributed, not forming discrete patch; (1) forming two discrete patch.

75 Forearm of adult males (De la Riva, 2005): (0) normal; (1) hypertrophied.

76 Dermal fringes in the fingers (modified from Aguilar and Valencia, 2009, char. 3): (0) absent; (1) incipient; (2) well developed. Additive.

77 Tarsal fold (Grant et al., 2006, char 28): (0) absent; (1) present.

Musculature—78 Extension of the posterior slip of the m. depressor mandibulae in relation to m. dorsalis scapulae: (0) not covering significantly the m. dorsalis scapulae; (1) covering significantly or completely the m. dorsalis scapulae (see figure 9 in Barrionuevo, 2016).

Skin histology—Histological characters of the skin of *Alsodes neuquensis*, *Atelognathus nitoi*, *At. patagonicus, At. reverberii*, *Batrachyla taeniata*, *Ceratophrys cranwelli*, *Chacophrys pierottii*, *Eupsophus roseus*, *Hylorina sylvatica*, *Insuetophrynus acarpicus*, *Lepidobatrachus llanensis*, *Telmatobius atacamensis*, *T. bolivianus, T. ceiorum*, *T. culeus*, *T. hauthali*, *T. laticeps*, *T. marmoratus*, *T. oxycephalus, T. pinguiculus, T. pisanoi, T. platycephalus, T. rubigo, T. schreiteri, T. scrocchii, T. simonsi, T. stephani* and *T. verrucosus* were based directly on histological slides. *Telmatobius brachydactylus*, *T. carrillae*, *T. jelskii*, *T. macrostomus*, *T. mayoloi*, *T. rimac*, *Leptodactylus fuscus* and *Pleurodema borellii* were codified from the literature (Sinsch et al., 2005; Sinsch and Lehr, 2010; García et al., 2011; Ferraro et al., 2013).

79 Serous glands of small granules (Type I, Sinsch et al., 2005): (0) absent; (1) present.

80 Serous glands of large granules (Type II, Sinsch et al., 2005): (0) absent; (1) present.

81 Eberth–Kastschenko (E-K) layer (Elkan, 1968, 1976): (0) absent; (1) present.

Cytogenetics—Cytogenetic characters were codified directly from karyotypes of *Telmatobius marmoratus*, *T. oxycephalus*, *T. pisanoi*, *T. pinguiculus*, *T. platycephalus* and *T. rubigo*. The following taxa were codified from the literature: *Telmatobius laticeps* (Barbieri, 1954), *T. ceiorum*, *T. stephani* (Morescalchi, 1973), *T. carrillae*, *T. arequipensis*, *T. jelskii*, *T. rimac*, *T. marmoratus*, *T. brachydactylus*, *T. macrostomus* (Córdova and Descailleaux, 2005), *Eupsophus roseus* (Iturra and Veloso, 1989), *Alsodes neuquensis* (Blotto et al., 2013), *Batrachyla taeniata*, *Hylorina sylvatica*, *Insuetophrynus acarpicus* (Barrio and Rinaldi de Chieri, 1971), *Pleurodema borellii* (as *P. cinerea*, Barrio and Rinaldi de Chieri, 1970a), *Leptodactylus fuscus* (Bogart, 1974; Silva et al., 2000), *Chacophrys pierottii* and *Ceratophrys cranwelli* (as diploid form of *Ceratophrys ornata*, Barrio and Rinaldi de Chieri, 1970b)

82 Diploid number: (0) $2n = 22$; (1) $2n = 24$; (2) $2n = 26$; (3) $2n = 30$.

External larval morphology—The condition of external larval characters from *Telmatobius arequipensis*, *T. atacamensis*, *T. ceiorum*, *T. culeus*, *T. hauthali*, *T. jelskii*, *T. macrostomus*, *T. marmoratus*, *T. oxycephalus*, *T. peruvianus*, *T. rimac*, *T. stephani*, *Alsodes neuquensis*, *Atelognathus patagonicus*, *At. reverberii*, *Batrachyla taeniata*, *Eupsophus roseus*, *Hylorina sylvatica* and *Insuetophrynus acarpicus* was codified from Lavilla (1983). The following taxa were codified from other sources as follows: *Leptodactylus fuscus* and *Pleurodema borellii* (Altig and Johnston, 1986), *Telmatobius yuracare* (De la Riva, 1994b), *T. simonsi* (De la Riva and Harvey, 2003), *Chacophrys pierottii* (Wild, 1999; Quinzio et al., 2006), *Atelognathus nitoi* (Úbeda, 1998), *T. brevipes* and *T. truebae* (Wiens, 1993), *Ceratophrys cranwelli* (Lavilla and Fabrezi, 1992; Vera Candioti (2005), *Lepidobatrachus laevis* (Wassersug and Heyer, 1988; Ziermann et al., 2013), and *Hylorina sylvatica* (Cárdenas-Rojas et al., 2007).

83 Oral disc modified into oral sucker (Lavilla and De la Riva, 1993; Aguilar et al., 2007): (0) absent; (1) present.

84 Condition of the lateral margins of oral disc (Aguilar and Valencia, 2009): (0) not emarginated; (1) emarginated.

85 Marginal papillae of the oral disc (Aguilar and Valencia, 2009): (0) interrupted by rostral gap; (1) continuous.

86 Submarginal papillae in the oral angle region (modified from Aguilar and Valencia, 2009): (0) absent but may be present in the supra- or infra-angular region; (1) present.

87 Submarginal papillae in the mental region of the oral disc (Lavilla, 1983; Aguilar and Valencia, 2009): (0) absent; (1) present, disposed in line. This character was used by Lavilla (1985, 1988) to divide the genus *Telmatobius* in the "Meridional" —Southern— group (present) and the "Septentrional"—Northern (absent). Lavilla (1985) included *T. atacamensis* in the "Meridional" group but here it is considered having state (0). The direct examination of the larvae

of this species shows that some specimens have isolated mental papillae but not forming a line.

88 Number of rows of submarginal papillae in the mental region of the oral disc: (0) one; (1) two or three.

89 Upper labial tooth rows (modified from Wiens et al., 2005, char. 121): (0) 2 labial tooth rows; (1) 3 labial tooth rows; (2) 7 labial tooth rows.

90 Lower labial tooth rows (modified from Wiens et al., 2005, char. 122): (0) 2 tooth rows; (1) 3 tooth rows; (2) 4 tooth rows; (3) 6 tooth rows; (4) 8 tooth rows.

91 Medial gap in the second upper labial tooth row (modified from Wiens et al., 2005, char. 123): (0) present; (1) absent.

92 Position of the spiracle (Lavilla, 1983): (0) lateral; (1) abdominal.

93 Proctodeal tube (Lavilla, 1983): (0) medial; (1) dextral.

94 External canal on the nostrils (Lavilla, 1983): (0) external canal absent; (1) external canal present.

Chondrocranium—The conditions of chondrocranium characters were codified from literature as follows: *T. atacamensis*, *T. ceiorum*, *T. laticeps*, *T. oxycephalus*, *T. pinguiculus*, *T. pisanoi*, *T. schreiteri*, *T. scrocchii* and *T. stephani* (Vera Candioti, 2008); *Alsodes neuquensis*, *T. arequipensis*, *T. atahualpai*, *T. brachydactylus*, *T. brevipes*, *T. carrillae*, *T. culeus*, *T. jelskii*, *T. latirostris*, *T. macrostomus*, *T. marmoratus*, *T. mayoloi*, *T. peruvianus*, *T. rimac* and *T. truebae* (Aguilar and Valencia, 2009), *Ceratophrys cranwelli* (Lavilla and Fabrezi, 1992), *Chacophrys pierottii* (Wild, 1999), *Lepidobatrachus laevis* (Ziermann et al., 2013), *Eupsophus roseus* (Vera Candioti, 2005), *Hylorina sylvatica* (Cárdenas-Rojas et al., 2007) and *Insuetophrynus acarpicus* (Rabanal and Formas, 2009).

95 Corpus of the suprarostral (Aguilar and Valencia, 2009): (0) separated; (1) fused.

96 Quadrato-orbital commissure (Aguilar and Valencia, 2009): (0) absent; (1) present.