

Osteology and Postmetamorphic Development of *Telmatobius oxycephalus* (Anura: Telmatobiidae) with an Analysis of Skeletal Variation in the Genus

J. Sebastián Barrionuevo*

CONICET, División Herpetología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina and Instituto de Herpetología, Fundación Miguel Lillo, San Miguel de Tucumán, Argentina

ABSTRACT The osteological diversity among species of *Telmatobius* has been considered conservative. Nonetheless, the degree of ossification of several features varies both intraspecifically and interspecifically. Herein, intraspecific osteological variation and postmetamorphic ontogenetic changes in osteological features are described in *Telmatobius oxycephalus*. These data are compared with published descriptions of congeners. There is a considerable intraspecific osteological variation in *T. oxycephalus*, with cranial characters varying polymorphically, and the hyoid and postcranial characters being sexually dimorphic. This intraspecific variation is expressed by subtle differences in the degree of ossification or mineralization. Interspecific variation also can be described in terms of differential development of osteological features; these differences are more obvious than intraspecifically variable characters. The adult skeletons of several species of *Telmatobius* resemble the morphology observed in early stages of postmetamorphic development of *T. oxycephalus*. This is especially evident in the neopalatines, parasphenoid, sphenethmoid, exoccipitals, prootics, vomers, nasals, and plectra. These results suggest that within the conservative osteological architecture of *Telmatobius*, the variation observed is the result of heterochronic changes during the ossification process. *J. Morphol.* 274:73–96, 2013. © 2012 Wiley Periodicals, Inc.

KEY WORDS: *Telmatobius oxycephalus*; osteology; postmetamorphic development

INTRODUCTION

Aquatic frogs of the genus *Telmatobius* occur in the Andes from Ecuador to Argentina; they inhabit some of the highest elevation aquatic habitats, including deglaciated ponds in Peru at 5,200 m (Seimon et al., 2006). At present, the genus comprises 60 species, but its phylogenetic relationships are only partially resolved, because of the restriction of taxon sampling to species from Peru (Aguilar and Pacheco, 2005; Córdova and Descailleaux, 2005; Sinsch et al., 2005; Aguilar and Valencia, 2009) or Bolivia (De la Riva et al., 2010).

Our knowledge of the osteology of species of *Telmatobius* is variable, ranging from detailed descriptions to simple mentions of few osteological characters (e.g., Peters, 1873; Holmgren, 1933; Vellard, 1951; Lynch, 1971, 1978; Andersen, 1978;

Trueb, 1979; Jaslow et al., 1988; Lobo Gaviola, 1988; Wiens, 1993; De la Riva, 1994a; Lavilla and Ergueta Sandoval, 1995; Lavilla and Ergueta Sandoval, 1999; Formas et al., 1999, 2003, 2006; Fabrezi, 2001; Benavides et al., 2002; Cuevas and Formas, 2002; Sinsch et al., 2005; Barrionuevo and Baldo, 2009). Some of these works have implied or in some cases have stated explicitly that there is little osteological diversity among species of *Telmatobius* (e.g., Lobo Gaviola, 1988; Sinsch et al., 2005). In addition, the latter authors reported wide intraspecific variation in osteological characters. Lobo Gaviola (1988) commented that much of the osteological variation in *Telmatobius* involves different degrees of ossification of the skeleton, which may result from shifts in the relative timing or rates of the ossification process known as heterochronic changes. The role of heterochrony in the generation of phenotypic change among closely related species has been suggested for several taxa (e.g., Stephenson, 1960, 1965; Tyler et al., 1981; Trueb and Alberch 1985; Davies, 1989; Yeh, 2002; Fabrezi, 2006), but it has not been explored in *Telmatobius*.

The study of the skeleton and its development in *Telmatobius oxycephalus* may help to elucidate the morphological diversification of *Telmatobius*. Accordingly, the goals of this study are to 1) describe the osteology based on several specimens of *T. oxycephalus*; 2) detect polymorphic and sexu-

Contract grant sponsor: ANPCyT PICT; Grant numbers: 2006/223 and 2010/1740; Contract grant sponsor: CIUNT-UNT; Grant number: 26/G315; Contract grant sponsors: PIP-CONICET 5780 and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

*Correspondence to: J. Sebastián Barrionuevo, División Herpetología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Av. Ángel Gallardo 470—C1405DJR, Buenos Aires, Argentina. E-mail: sbarrionuevo@macn.gov.ar

Received 31 May 2012; Revised 3 August 2012; Accepted 12 August 2012

Published online 1 October 2012 in Wiley Online Library (wileyonlinelibrary.com) DOI: 10.1002/jmor.20079

ally dimorphic characters; 3) describe postmetamorphic osteological maturation; and 4) compare the results with published descriptions of other species of *Telmatobius*. The description of the developmental progress of each bone will help to document the degree of development of each element in adult congeners. This is an initial step in the identification of developmental patterns to understand the role of heterochrony in the morphological evolution of *Telmatobius*.

MATERIALS AND METHODS

Seventeen postmetamorphic specimens ranging from recently metamorphosed individuals to adult males and females were examined. Snout-vent lengths (SVL) were measured with digital calipers (Appendix A). The age of the specimens was not established; they were ordered by size (SVL) and sorted into five categories: 1) recently metamorphosed specimens, termed postmetamorphs (three specimens, 20–23 mm); 2) Stage-I juveniles (two specimens, 25–29 mm); 3) Stage-II juveniles (two specimens, 32–36 mm); 4) subadults (two specimens, 38–41 mm); and 5) adults (eight specimens, >41 mm). One specimen at the end of metamorphosis (Stage 44 of Gosner, 1960) was included in the series. The specimens were cleared and double-stained for cartilage and bone following the protocol of Wassersug (1976). All specimens are from Fundación Miguel Lillo Herpetological Collection (FML) or were collected in the field. Osteological terminology follows that of Trueb (1973, 1993); Fabrezi (1992, 1993) for carpus and tarsus; and Maglia et al. (2007) for nasal capsules.

The interspecific comparison with species of Argentina, Chile, and southern Bolivia was based on published osteological descriptions (see Appendix B) of *T. hypselocephalus* and *T. platycephalus* (Lavilla and Laurent, 1988); *T. ceiorum*, *T. laticeps*, and *T. pisanoi*, (Lobo Gaviola, 1988); *T. huayra* (Lavilla and Ergueta Sandoval, 1995); *T. dankoi* (Formas et al., 1999); *T. frontieriensis* (Benavides et al., 2002); *T. philippii* (Cuevas and Formas, 2002); *T. vilamensis* (Formas et al., 2003); *T. sibiricus* and *T. simonsi* (De la Riva and Harvey, 2003); *T. chusmisensis* (Formas et al., 2006); and *T. rubigo* (Barrionuevo and Baldo, 2009). In addition to the published data, material from *T. ceiorum*, *T. pisanoi*, *T. laticeps*, *T. platycephalus*, *T. hypselocephalus*, and *T. rubigo* was examined (Appendix A).

RESULTS

Cranium

The cranium of *Telmatobius oxycephalus* (Figs. 1 and 2) is slightly wider than long (width/length = 1.16, range = 1.06–1.29, $N = 5$). In dorsal view, the snout is rounded anteriorly. The skull is lightly built, with the rostral region being poorly ossified or mineralized. The length of the orbit is half of the total length of the skull.

Endocranium

Nasal capsules. These cartilages (Fig. 3) together with the bony septomaxillae support the nasal sacs and the nasolacrimal duct. The septum nasi is the common medial wall of the nasal capsules; dorsally, the tectum nasi forms a roof and ventrally, the solum nasi floors each capsule. Superior and inferior prenasal cartilages support the premaxillae, whereas crista subnasalis and processus

triangularis (Fig. 3) support maxillae. Dorsal and ventral coverage is provided by the nasals and vomers, respectively.

The most evident developmental changes in the nasal capsules during postmetamorphic growth are related with the increasing ossification of the sphenethmoid that involves septum, solum, and tectum nasi. The septomaxillae are already present in Stage 44.

Sphenethmoid. Dorsally, the anterior margin of the sphenethmoid reaches the nasals in some specimens (FML 2867-I, 2867-IV, 3836-I, and FML SB 019); likewise, the anterolateral ossification of the sphenethmoid involves part of the planum antorbitale (Fig. 1). The margin of orbitonasal foramen is complete in bone. Anteromedially, the sphenethmoid forms the ossified nasal septum. The degree of this ossification varies. In some adults of both sexes (e.g., FML 2867-I, 3836-I, and 3836-II), the sphenethmoid involves approximately the posterior half of the septum nasi, whereas in others (e.g., FML 2867-II, 2867-III, and 3836-III), this ossification involves only the posterior third of the septum. Ventrally, the sphenethmoid involves solum nasi at the level of the vomers (Fig. 2) except in two specimens (FML 2867-III and 3836-III). The extension of posterior margins of the sphenethmoid is variable. In lateral view in most individuals, the sphenethmoid does not reach the border of the optic foramen, but in some (e.g., FML 2867-I), it reaches the anterior border of the foramen. Intraspecific variation of this bone is summarized in Tables 1 and 2.

The sphenethmoid is not yet present in Stage 44 or in the postmetamorphs (Figs. 1 and 2). In Stage-I Juveniles, bilateral centers of ossification are present on either side of the anteromedial wall of the braincase in the orbital cartilage. In Stage-II juveniles, the ossification has progressed dorsally, but the contralateral halves of the bone are not fused (Figs. 1 and 2); ossification of the ventral region of the sphenethmoid progresses more slowly than in the dorsal region. In the subadult female, the dorsal halves of the sphenethmoid are completely fused, but ventrally, they are only partially fused. In the subadult male, the sphenethmoid is fused dorsally and ventrally, forming a complete ring. In subadults, the anterior margin of the sphenethmoid is rounded. The posterior margin is concave in dorsal view and does not reach as far posteriorly as in the adults. In lateral view, the posterior margin of sphenethmoid is midway between the anterior margin of optic foramen and the planum antorbitale. Ontogenetic variation of this and other bones is summarized in Tables 3 and 4.

Exoccipitals. These bones are fused to each other dorsally (Fig. 1) and ventrally (Fig. 2), delimiting the foramen magnum. The shape of foramen magnum varies from subtriangular to rounded or

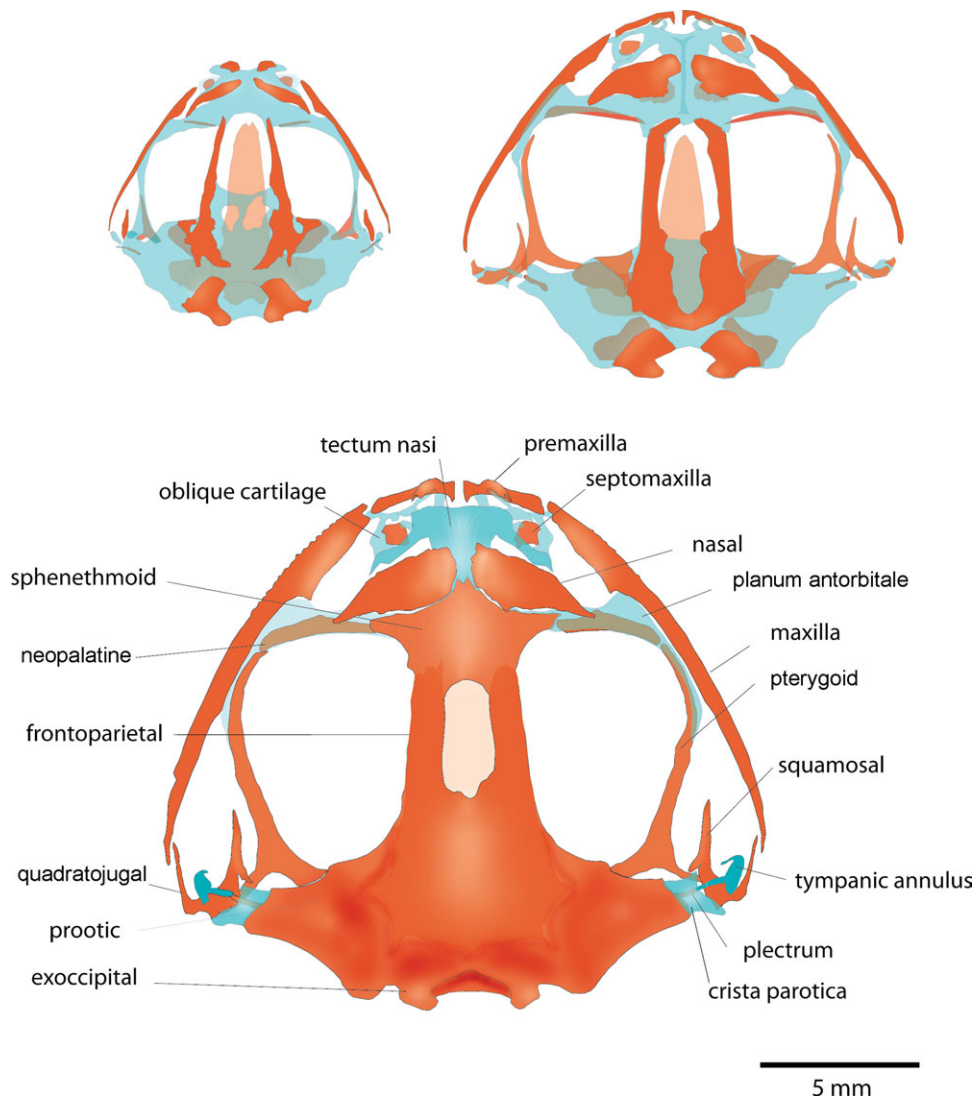


Fig. 1. Dorsal view of the cranium of *T. oxycephalus* at different postmetamorphic stages. Upper left: a postmetamorph of 21.9 mm SVL (FML SB 102). Upper right: a Stage-II juvenile of 35.44 mm (FML SB 24). Below: an adult male (FML 2867-II). Cartilage shown in blue and bone in red.

rhomboidal. The occipital condyles are located at the ventrolateral margin of the foramen magnum; the intercondylar distance is less than the length of the longest axis of each condyle (longest axis of condyle/intercondylar distance: 1.20–1.53). There is no evident intraspecific variation in the morphology of exoccipitals.

The condyles and parts of the exoccipital are ossified almost completely by Stage 44; however, traces of cartilage remain in the condyles. The progressive ossification of the exoccipitals can be described with respect to their topographic relationship with the parasphenoid, which changes less dramatically during postmetamorphic development. In Stage 44, the exoccipitals are not in contact with the parasphenoid. In postmetamorphs and in Stage-I juveniles, the margins of the exocci-

pitals are in contact with the parasphenoid alae, and in Stage-II juveniles, the margins of exoccipitals underlie the parasphenoid alae. In the subadult male, the exoccipitals are in contact ventrally with the prootics (not in contact in the subadult female), and synchondrotically united to each other ventrally. In Stage 44, the dorsal parts of the exoccipitals are widely separated from each other and from the posterior borders of the frontoparietals. This degree of development does not change significantly until subadults. In this stage, exoccipitals are synchondrotically united to each other dorsomedially, overlapped by the frontoparietals, and narrowly separated from the prootics.

Prootics. Except for the cartilaginous crista parotica on each side, the paired prootics are completely ossified in adults. Dorsally, the prootics

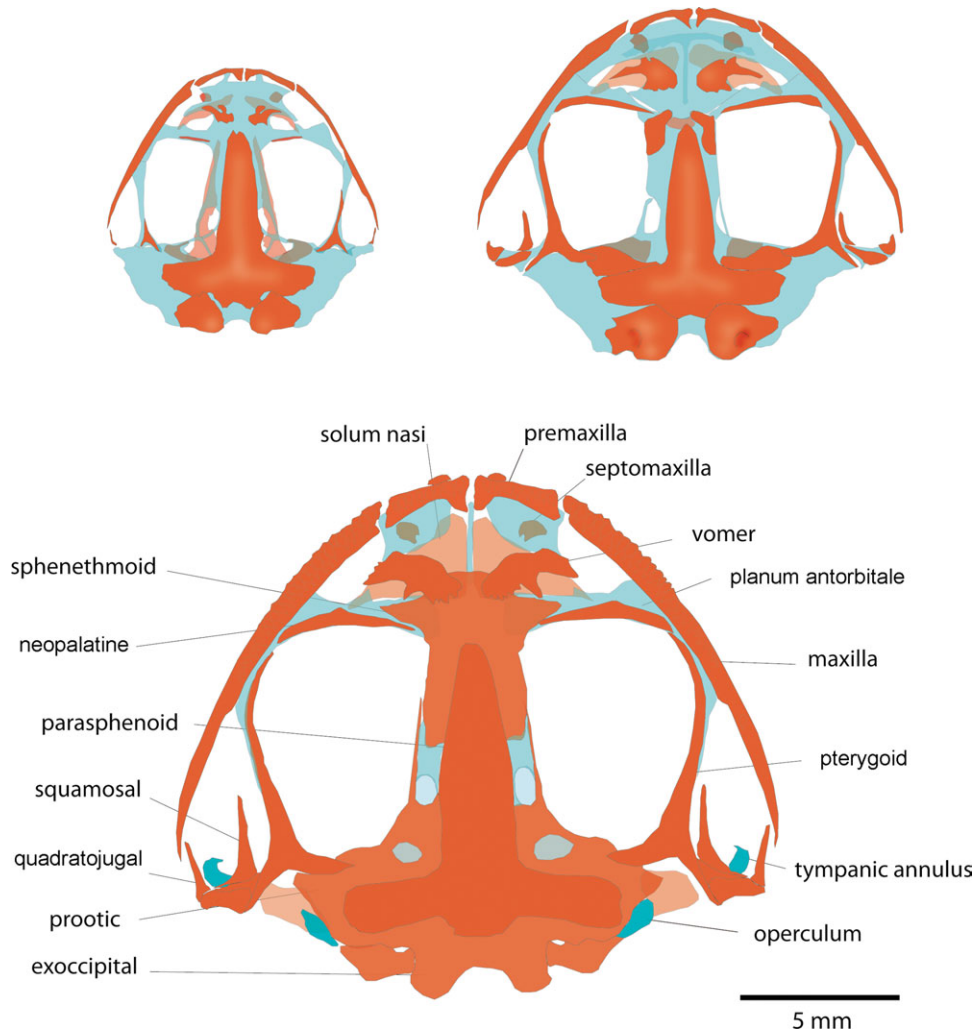


Fig. 2. Ventral view of the cranium of *T. oxycephalus* at different postmetamorphic stages. Upper left: a postmetamorph of 21.9 mm SVL (FML SB 102). Upper right: a Stage-I juvenile of 35.44 mm (FML SB 24). Below: an adult male (FML 2867-II). Cartilage shown in blue and bone in red.

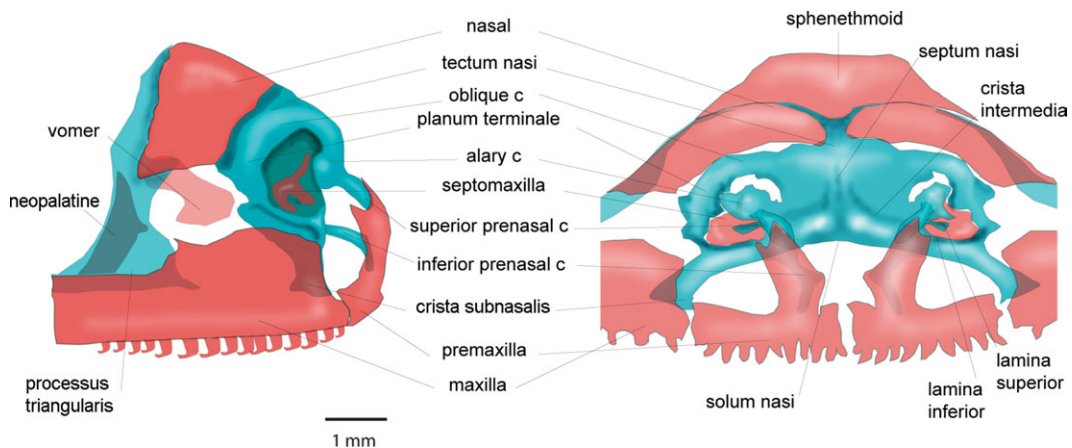


Fig. 3. Lateral (left) and frontal (right) view of nasal capsules of *T. oxycephalus* (FML 2867-II). Abbreviation: c = cartilage. Cartilage shown in blue and bone in red.

TABLE 1. *Intraspecific variation in cranial characters of T. oxycephalus*

	FML 2867-I, male	FML 2867-II, male	FML 3836-II, male	FML 3836-III, male	FML SB19, male	FML 2867-III, female	FML 2867-IV, female	FML 3836-I, female
Frontoparietals in the parietal region	Fused	Fused	Fused	Fused	Fused	Fused	Sutured	Sutured
Extension of the frontoparietal fontanelle to the parietal region	No	No	No	No	No	Yes	Yes	Yes
Relation of nasals with sphenethmoid	Overlapped	In contact	In contact	In contact	Overlapped	In contact	Overlapped	Overlapped
Relation of vomer with sphenethmoid	Overlapped	In contact	In contact	Not in contact	In contact	Not in contact	In contact	In contact
Margin of parasphenoid in relation to otic capsule	Not visible	Not visible	Not visible	Not visible	Not visible	Visible	Visible	Visible
Maximum n° of teeth in each vomer	4	4	6	5	4	6	6	9
Anterior process of quadratojugal	Long	Short	Short	Short	Long	Long	Short	Long
Shape of foramen magnum	Rhomboidal	Rhomboidal	Subtriangular	Rounded	Rounded	Rounded	Rhomboidal	Subtriangular
Coronoid process reaches the articular region	No	No	No	No	No	Yes	No	No
Anterior process of the hyal	Present	?	?	?	Present	Present	Absent	?
Mineralization of the distal cartilage of posteromedial processes	Yes	?	?	?	Yes	No	No	?
Base of the posteromedial process	Invading hyoid plate	Invading hyoid plate	?	?	Invading hyoid plate	Abuts the border of hyoid plate	Abuts the border of hyoid plate	?

Dark gray cells indicate sexual dimorphism.

TABLE 2. *Intraspecific variation in postcranial characters of T. oxycephalus*

	FML 2867-I, male	FML 2867-II, male	FML 3836-II, male	FML 3836-III, male	FML SB19, male	FML 2867-III, female	FML 2867-IV, female	FML 3836-I, female
Anterior border of scapula	Concave	Straight	Straight	Straight	Convex	Concave	Concave	Straight
Scapula and clavicle	Fused	Fused	Fused	Fused	Fused	Sutured	Sutured	Fused
Ossification of sternum	Ossified completely	Ossified completely	Ossified completely	Ossified completely	Ossified completely	Ossified proximally	Ossified proximally	Ossified completely
Sternum notch	Pronounced	Pronounced	Pronounced	Pronounced	Weak	Pronounced	Weak	Weak
Omosternum	Mineralized proximally	Mineralized proximally	?	?	Mineralized proximally	Completely cartilaginous	Completely cartilaginous	?
Lateral and medial crest in the humerus	Present	Present	Present	Present	Present	Absent	Absent	Absent
Osseous tubercle in the inner margin of metacarpal I	Present	?	?	?	Present	Absent	Absent	?
N° of elements of the prepollex	6	?	?	4	5	5	5	?
N° of mineralized/ossified elements of the prepollex	4	?	?	4	2	2	2	?
Ilium-ischium	Fused	Fused	Fused	Fused	Fused	Sutured	Fused	Fused
Cartilaginous part of acetabulum	Less than the half	Less than the half	Less than the half	More than the half	Completely ossified	More than the half	Less than the half	Less than the half
N° of mineralized/ossified elements of the prehallux	3	1	?	?	2	1	2	?

Dark gray cells indicate sexual dimorphism.

TABLE 3. Ontogenetic variation in cranial characters during postmetamorphic growth of *T. oxycephalus*

	Stage 44	Postmetamorph	Stage-I juvenile	Stage-II juvenile	Subadult	Adult
Cultriform process reaching level of neopalatines	Yes	Yes	Yes	No	No	No
Medial contact between exoccipitals	Widely separated	Widely separated	Widely separated	Widely separated	Separated	Fused
Frontoparietals (fp) in the parietal region	Separated	Separated	Separated	Fused in tectum synoticum, parietal fontanelle large	Fused in tectum synoticum, parietal fontanelle small	Completely ossified, parietal fontanelle absent
Anterior end of fp reaching anterior margin of orbit	Yes	Yes	Yes	Yes	No	no
Relation of prootics with exoccipitals	Widely separated	Widely separated	Widely separated	Widely separated	Synchondrosis	Synostosis
Mx and pmx teeth	Teeth buds in premaxilla, no teeth in maxilla	Premaxilla toothed, teeth buds in maxilla	Teeth not well developed in the posterior region of maxilla	Teeth not well developed in the posterior region of maxilla	Teeth not well developed in the posterior region of maxilla	Teeth well developed in all the maxilla
Vomer	Two centers of ossification	Centers of ossification in contact, there is a notch between them	Centers of ossification in contact, there is a notch between them	Single bone, notch absent	Complete bone	Complete bone
N° of teeth in each vomer	0	1-2	3-5	4	4	4-9
Nasals	Small	Large	Large	Large	Large	Large
Neopalatine	Pi and pm not ossified	Straight	Slightly curved	Curved	Curved	Curved
Plectrum: pars interna (pi) and pars media plectri (pm)	Pi and pm not ossified	Pi not ossified, pm poorly ossified	Pi not ossified, Pm ossified	Pi not ossified, pm ossified	Pi slightly ossified, pm ossified	Pi and pm ossified, pi reaching operculum
Sphenethmoid	Cartilaginous	Two halves	Two halves	Two halves	Incomplete ring ventrally (female), complete ring (male)	Complete ring, more ossified
Hyoid plate	Cartilaginous	Cartilaginous	Cartilaginous	Cartilaginous	Slightly mineralized	Mineralized
Base of posteromedial processes of hyoid	Not invading plate	Not invading plate	Not invading plate	Not invading plate	Not invading plate (female), invading a small portion (male)	Not invading plate (females), invading plate (males)
Distal tip of posteromedial processes	Cartilaginous	Cartilaginous	Cartilaginous	Cartilaginous	Cartilaginous (female), mineralized (male)	Mineralized (males), cartilaginous (females)

Dark gray indicates immature morphology; light gray indicates transitional state to adult morphology.

TABLE 4. Ontogenetic variation in postcranial characters during postmetamorphic growth of *T. oxycephalus*

	Stage 44	Postmetamorph	Stage-I juvenile	Stage-II juvenile	Subadult	Adult
Sternum	Cartilaginous	Cartilaginous	Cartilaginous	Cartilaginous	Slightly mineralized (female), mineralized (male)	Ossified
Base of omosternum	Cartilaginous	Cartilaginous	Cartilaginous	Cartilaginous	Cartilaginous (female), mineralized (male)	Mineralized (males), cartilaginous (females)
Procoracoid and epicoracoid	Cartilaginous	Cartilaginous	Cartilaginous	Cartilaginous	Slightly mineralized	Slightly mineralized (females), mineralized (males)
Union of scapula and clavicle	Separated by cartilage	Separated by cartilage	Separated by cartilage	Separated by cartilage	Sutured	Fused in most specimens
Anterior margin of scapula	Concave	Concave	Concave	Concave	Straight	Straight or concave
Pubis	Cartilaginous	Cartilaginous	Cartilaginous	Cartilaginous	Slightly mineralized	Ossified
Carpus	Cartilaginous	Cartilaginous	Some elements ossified	Some elements ossified	(female) completely ossified (male)	Ossified
Prepollex	Cartilaginous	Cartilaginous	Cartilaginous	Cartilaginous	At least one element ossified	Till four elements ossified in males and two in females
Tarsus	Cartilaginous	Cartilaginous	Cartilaginous	Cartilaginous	Some elements ossified	Ossified
Prehallux	Cartilaginous	Cartilaginous	Cartilaginous	Cartilaginous	At least one element mineralized	Till three ossified elements in males, none in females

Dark gray indicates immature morphology; light gray indicates transitional state to adult morphology.

have conspicuous anterior epiotic eminences (Fig. 1). The bones are synostotically united to the exoccipitals at the posterior epiotic eminences and are overlapped dorsally by the frontoparietals at the level of the medial union of anterior and posterior epiotic eminences. There is no evident intraspecific variation in the morphology of prootics.

In Stage 44, each prootic is present as a ventral ossification that is isolated from other osseous structures. The anteroventral part of the prootic reaches the anterior border of parasphenoid ala in postmetamorphs. In Stage-I and II juveniles, prootic ossification underlies the parasphenoid. In the subadult male, the prootics articulate with the exoccipitals via a ventral osseous bridge (not in contact in the subadult female). Dorsally, the ossification of prootic is evident in Stage-I juveniles as a small ossification along the anteromedial margin of the anterior epiotic eminences. In Stage-II juveniles, dorsal ossification has progressed slightly to the anterolateral margin of the anterior eminence. In subadults, the prootics are almost completely ossified and each is overlapped by the frontoparietal at the level of the medial union of anterior and posterior epiotic eminences. The prootics are synchondrotically united to exoccipitals at the posterior epiotic eminences. In the subadult male, the anterior epiotic eminences are ossified, whereas in the subadult female, these remain cartilaginous.

Quadrate. The quadrate is flanked medially by the pterygoid, laterally by the quadratojugal, and dorsally by the ventral ramus of the squamosal. In *T. oxycephalus*, the quadrate is spool shaped in ventral view; the medial surface is larger than the lateral. Its articular face is concave.

In Stage 44 and in postmetamorphs, the quadrate has not begun to mineralize/ossify. In Stage-I and II juveniles, one quarter of the lateral part of the quadrate is mineralized/ossified. In subadults, the lateral half of the quadrate is mineralized/ossified, whereas the medial portion is completely cartilaginous.

Middle ear. The middle ear comprises two skeletal structures of endochondral origin: the plectrum and the operculum. The plectrum (= stapes or columella) is composed of three parts, that is, pars interna, pars media, and pars externa plectri. The pars interna plectri (or footplate) occludes part of the fenestra ovalis. It bears a posterior groove that accommodates the anterior border of the operculum. The pars media plectri is a straight, osseous shaft bridging the pars interna medially and the pars externa laterally. It has a slight dorsal orientation and narrows as it reaches the pars externa. The pars externa plectri is a cartilaginous structure, the lateral surface of which is adjacent to the tym-

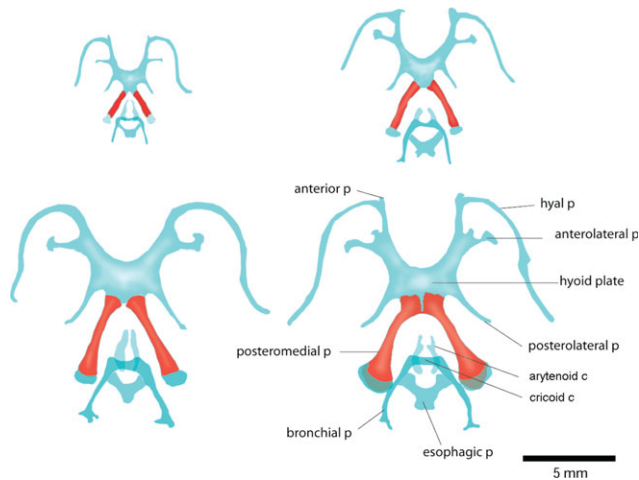


Fig. 4. Ventral view of the hyolaryngeal complex of *T. oxycephalus* at different postmetamorphic stages. Upper left: a post-metamorph of 22.38 mm SVL (MLP DB3620). Upper right: a Stage-II juvenile of 35.44 mm (FML SB 24). Lower left: an adult female (FML 03836-IV). Lower right: an adult male (FML 2867-II). Abbreviations: c = cartilage; p = process. Cartilage shown in blue and bone in red.

panic skin and is nearly perpendicular to the pars media plectri. There is a very thin processus ascendens plectri that probably connects the pars externa with the crista parotica and tympanic annulus; however, the contact of processus ascendens could not be observed. The tympanic annulus is a cartilaginous, sickle-shaped structure that lies ventral to the pars media plectri; it is incompletely developed (10–50%) and, therefore, does not describe a complete annulus. In one specimen, the annulus is absent; it is unclear whether it is completely absent or it was lost during the clearing-and-staining process. The oval cartilaginous operculum has a low crest for the attachment of the opercular muscle.

The plectrum is not ossified in Stage 44, but the midportion of pars media is ossified in postmetamorphs. In these specimens, the tympanic annulus is crescent shaped, with the concavity oriented dorsally as it is in the adults. In Stage-I and II juveniles, ossification of the pars media is more extensive medially and laterally. The pars interna is partially ossified in subadults, but at this stage, the ossified portion is not in contact with the operculum and the pars media plectri is thin. The operculum is well formed in the earlier postmetamorphic stages and has the same shape as in the adult.

Hyolaryngeal complex. The hyoid plate is wider than long and it is slightly mineralized around the bases of its posteromedial processes (Fig. 4). In one male FML 2867-I, the mineralization extends to the bases of the anterolateral processes. In one female (FML 2867-IV), the plate is completely cartilaginous. The hyalia are long and sinuous, and each one has an anterior process (not

evident in FML 2867-IV). The anterolateral processes are expanded distally. The posterolateral processes are straight, divergent from the midline, not expanded distally, and longer than anterolateral processes. The posteromedial processes are long and ossified; the distal ends are completely cartilaginous in females but mineralized in males. In males, the base of the posteromedial process invades the hyoid plate and in one individual (FML 2867-II), the bases are in contact to each other. None of these states is present in the females.

The arytenoids are well developed. The cricoid ring has two well-developed bronchial processes that are distally bifurcate. Dorsally, the ring has an esophagic process that can be wide or narrow; this variation is not sexually dimorphic.

In Stage 44, the posteromedial processes of the hyoid plate are ossified. In postmetamorphs and in Stage-I juveniles, these processes contact the hyoid plate via cartilaginous stalks and the distal ends of these processes are completely cartilaginous. In Stage-II juveniles, the posteromedial processes are in contact with the posterior margin of the hyoid plate. The plate has no trace of mineralization. In the subadult female, a slight trace of mineralization lies in the proximal region of the posteromedial processes. In the subadult male, these processes invade a small portion of the plate that is mineralized around this region.

Exocranium

Nasals. The nasals are triangular, and in some specimens, the anterior margin is convex. In any case, these bones have irregular borders. The medial margins either converge anteriorly or parallel one another, with the amount of medial separation varying. The maxillary process of the nasal is either sharp or blunt.

In Stage 44 and in the postmetamorphs, the nasals are narrow and anteriorly convergent. In those stages, the nasals are very close to the premaxillae, maxillae, and septomaxillae (Fig. 1). During later development, nasal ossification becomes more extensive posteriorly and the bone soon acquires the adult triangular shape. Conversely, however, as a result of the growth of the nasal region, the nasals are separated more broadly from the premaxillae, maxillae, and septomaxillae (Fig. 1).

Frontoparietals. The paired frontoparietals are fused with one another medially in the parietal region (from the level of the taenia tecti transversalis to the level of tectum synoticum) of most of the specimens (Fig. 1). The degree of fusion between the frontoparietals varies. In some specimens, the frontoparietals are fused all along the parietal portion, but in others, this fusion is only limited far posteriorly, to the level of the tectum

synoticum. In some females (e.g., FML 2867-IV and FML 3836-I), these bones are not fused, and there is a suture between them at the level of the tectum synoticum. In those specimens with the frontoparietals not fused, the completely ossified/mineralized endocranial roof is evident. The frontoparietals are narrow in the frontal region (anterior to taenia tecti transversalis), and its anterior ends lay far posterior to the level of the anterior limit of the orbit.

In Stage 44 and in postmetamorphs, the frontoparietals are represented by two, irregularly shaped strips of bone (Fig. 1), which are narrow anteriorly and broad posteriorly. These bones extend from the tectum synoticum to the level of planum antorbitale anteriorly. In Stage-I juveniles, each frontoparietal is expanded medially; in addition, it is ossified posterolaterally in the parietal region and extends along the anteromedial margin of the anterior epiotic eminence. In Stage-II juveniles, the frontoparietals fused to each other at the level of the tectum synoticum (Fig. 1). The posterior part of the bone from the taenia tecti transversalis backwards is wider than the anterior portion, delimiting a narrower fontanelle than the one present in the frontal region. In subadults, the frontoparietal fusion remains limited to a narrow posterior area at the level of tectum synoticum, but its medial margins are closer than in Stage-II juveniles. In the subadults, unlike previous stages, the anterior end of the frontoparietals is not reaching the level of the anterior margin of orbit. Laterally and posteriorly, frontoparietals contact prootics and exoccipitals, respectively. In adults, the fusion of frontoparietals progresses and includes the complete fusion between the two frontoparietals in the parietal region in some specimens.

Vomers. Each vomer is well developed, with a dentigerous process and a laminar anterior region that bears a prechoanal and postchoanal ramus. Dentigerous processes typically bear four to six pedicellate fanglike teeth, although one female has nine teeth (FML 2867-IV). Bilateral differences may exist in the number of teeth. The prechoanal ramus is well developed, with a broad base and a sharp distal tip. The postchoanal ramus is smaller than the prechoanal ramus; it is posterolaterally oriented, forming an acute angle with the prechoanal ramus.

In Stage 44, two centers of ossification are evident; the posterior center gives rise to the dentigerous process and the anterior one to the choanal rami. In postmetamorphs, there is a notch between the anterior region and the dentigerous process, and the prechoanal and postchoanal rami are well developed. There are one or two incipient teeth. In Stage-I juveniles, a deep notch persists, but there are three to five better developed teeth on each vomer. In Stage-II juveniles, the bone expands

between the anterior part of vomer and the dentigerous process; however, it should be noted that evidence of the notch can persist in subadults, although it is absent in the adults.

Neopalatine. The neopalatines are long and arcuate (Fig. 2). The medial tip tapers gradually and lies ventral to the sphenethmoid, but it does not reach the tip of the cultriform process of the parasphenoid. Laterally, the neopalatine overlaps the pars palatina of the maxilla.

In Stage 44, the neopalatines are absent. In postmetamorphs, these bones are thin, straight strips (Fig. 2). The bone does not reach the maxilla laterally or the incipient sphenethmoid, medially. In Stage-I juveniles, the neopalatine has begun to acquire a curved shape but still fail to reach the level of maxilla and sphenethmoid. In Stage-II juveniles, the neopalatine resembles that of adults.

Parasphenoid. The cultriform process of this dermal element has a blunt tip at a level slightly posterior to that of the neopalatines (Fig. 2). The posterolateral alae have a slight posterolateral orientation and the lateral margins do not contact the ventral border of the fenestra ovalis. In males, the limits of the posterior margin of parasphenoid and the limits of the lateral margin of alae are not distinguishable from the underlying otic capsule.

The parasphenoid is well formed in Stage 44 and does not undergo significant modification during postmetamorphic growth, except for the anterior extent of the cultriform process. In Stage 44, as well as in postmetamorphs and Stage-I juveniles (Fig. 2), the anterior tip of the cultriform process reaches the level of neopalatines; however, in older stages and usually in adults, the neopalatines are anterior to the cultriform process.

Pterygoids. This pair of triradiate bones is well developed but slender. The long anterior ramus extends medial to the maxilla and reaches the level of neopalatines. The posterior ramus adjoins the pars articularis of palatoquadrate and the medial ramus abuts the prootic along the anteroventral margin of the otic capsule. The medial margins of anterior and medial rami describe a curve from the maxilla to the otic capsule, whereas the lateral margins of the anterior and posterior rami configure a sinusoid curve between the maxilla and palatoquadrate.

In Stage 44, the pterygoid is represented by a center of ossification that invests the medial part of the palatoquadrate. In postmetamorphs, the three rami are present and subsequent variation during the postmetamorphic development involves the lengthening of the rami. In Stage-I juveniles, the medial ramus does not reach the otic capsule and the anterior ramus does not reach the level of neopalatines. The posterior ramus invests the pars articularis of the palatoquadrate and almost has achieved its adult shape. In Stage-II juveniles, the medial ramus abuts the otic capsule. The

ossification of anterior ramus progresses throughout postmetamorphic development and reaches the level of neopalatines only in adults.

Squamosals. The slender zygomatic ramus of the squamosal is acuminate and longer than the otic ramus. The otic ramus does not bear an otic plate and, in some specimens, this ramus is reduced. The ventral ramus invests the lateral surface of the palatoquadrate. In lateral view, this ramus describes an angle of 55–60° with the horizontal axis of the skull.

In Stage 44, only the ventral ramus of the squamosal is ossified. In postmetamorphs, the three rami are developed, and they do not change substantially in length in Stage-I and II juveniles. The zygomatic ramus is longer and wider in subadults. In Stage 44, the ventral ramus is nearly perpendicular to the maxilla in lateral aspect; in postmetamorphs, it is inclined anteriorly at about 75°. In Stage-I and II juveniles, the angles are 70° and 65°, respectively, and in subadults, the adult condition is achieved with an angle between 55° and 60°.

Premaxillae and maxillae. The pars dentalis of each premaxilla bears between 9 and 11 fanglike teeth. In frontal view, the basal parts of the alary processes converge medially, whereas the distal (dorsal) parts diverge from one another (Fig. 3). The distal tip of the alary process is bifurcate and the anterior surface is convex and curved in lateral profile (Fig. 3). The pars palatina of the premaxilla is a narrow lingual ledge of the pars dentalis; it is expanded in its lateral end, but it narrows gradually at the level of the lateral border of the alary process. In its medial end the pars palatina expands onto a triangular palatine process. In lateral view, the maxillae are straight and attenuate posteriorly. The pars dentalis of the maxilla bears 28–30 fanglike, pedicellate teeth. The pars palatina is a narrow, lingual shelf similar to the pars palatina of the premaxilla; it extends along the maxilla from the posterior union of the pterygoid with the maxilla to the anterior end of the maxilla at its articulation with the premaxilla. The laminar pars facialis projects dorsally from the pars dentalis in the region of the rostrum. The pars facialis is low and the dorsal edge is straight. In some specimens, the posterodorsal edge of pars facialis forms a preorbital process.

The premaxillae have acquired its adult shape by the end of metamorphosis, but the maxillae undergo significant changes during postmetamorphic development. In Stage 44, the maxillae are short and barely extend posterior to the orbits, but these bones lengthen during postmetamorphic growth. In postmetamorphs, the posterior end of the maxilla scarcely reaches the anterior end of the quadratojugal, but the pars facialis is well developed. In Stage-I juveniles, the maxillae have the same relative length as in the adults. In Stage 44, there are a few incipient teeth in the premaxil-

lae but not in the maxillae. In postmetamorphs, premaxillary teeth are well formed and the maxillary teeth are incipient in the maxilla anterior to the region of the planum antorbitale. In Stage-I juveniles, the anterior maxillary teeth are well developed but the ones posterior to the planum antorbitale are incipient. The posterior teeth are well developed in the adults.

Quadratojugals. The posterior part of the quadratojugal is expanded to form a cup-shaped structure that is synostotically united to the lateral margin of the quadrate bone. The anterior process is slender and acuminate and better developed in some specimens (e.g., FML 2867-II, 3836-I) than others, in which it is short (e.g., FML 2867-IV).

In postmetamorphs, only the anterior region of the quadratojugal is ossified and it is needle shaped. In Stage-I juveniles, the posterior region is ossified, but the anterior end is separate from the end of the maxilla. In Stage-II juveniles, the state of quadratojugal resembles that of the adults, although it is more gracile. In later stages, the quadratojugal becomes progressively more robust.

Mandible. The dentary extends along approximately two-thirds the length of the mandible. The angulosplenic invests Meckel's cartilage posteromedially and medially, and extends anteriorly over about three quarters the entire length of the lower jaw. The coronoid process of the angulosplenic is well developed. In most individuals, this process is distinct from the articular region of the bone, but in some (e.g., FML 2867-II and 2867-III), the process extends posteriorly reaching the articular region.

In Stage 44 and in postmetamorphs, the angulosplenials and the dentaries are slender, and most of Meckel's cartilage is exposed. The coronoid process of the angulosplenic is low and the mentomeckelian bone is not formed. In Stage-I juveniles, the coronoid process is more developed and the articular region has begun to ossify. The mentomeckelian bone has begun to form in the medial side of infrarostral cartilages that are fused to Meckel's cartilage. The ossification of the mentomeckelian continues during subsequent postmetamorphic growth. Aside from an overall increase in size, the dentary does not undergo significant changes during postmetamorphic development.

Vertebral Column

The presacral region is composed of eight procoelous vertebrae. The neural arches are well ossified and do not overlap each other (nonimbricate vertebrae) leaving a broad space between the neural arch of each vertebra and exposing the spinal cord dorsally (Fig. 5). The neural arches of the first five vertebrae bear neural spines; that of the atlas may reach the Presacral II. Some traces of cartilage are present in the neural spine of each of the first four

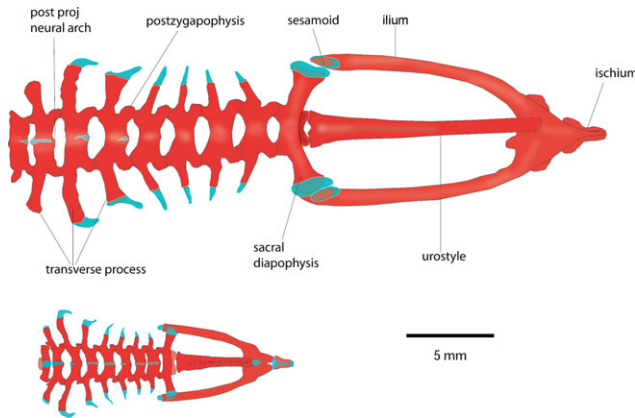


Fig. 5. Dorsal view of the vertebral column and pelvic girdle of *T. oxycephalus*. Top: an adult male (FML 2867-II). Below: a postmetamorph of 21.9 mm SVL (FML SB 102). Abbreviation: post proj = posterior projection. Cartilage shown in blue and bone in red.

vertebrae. Transverse processes of Presacrals II–IV are expanded distally (along a longitudinal axis). The ends of the transverse process of Presacrals III and IV are cartilaginous and are deflected posteriorly, whereas the cartilaginous ends of transverse processes of the posterior presacrals are straight. The transverse process of Presacral II has a small cartilaginous tip. The relative lengths of the transverse processes are: III > II = IV > V = VI = VII = VIII. The orientations of the larger transverse processes with respect to the longitudinal axis of the column vary greatly. In some specimens, the processes of Presacral II are anteriorly inclined; those of III are perpendicular and those of IV are posteriorly oriented (FML 2867-I, 2867-III, and FML SB 19). In other specimens, the processes of Presacral III are anteriorly oriented. In a female (FML 2867-IV), the processes of Presacrals II and III are anteriorly oriented and those of Presacral IV are perpendicular. The sacral diapophyses are moderately expanded and have a slight dorsal inclination. The distal margins of these diapophyses are cartilaginous, and a sesamoid articulates with the ilium. The dorsal ridge of the urostyle extends nearly one-third the length of the urostyle.

In Stage 44 and in postmetamorphs, the midline of neural arches is cartilaginous, as are the junctions of the neural arches with the centra. The distal ends of the transverse processes of all presacral vertebrae are cartilaginous. The most anterior three to five centra are completely ossified around the notochord, whereas the posterior centra are not ossified ventrally. In Stage-I juveniles, the neural arches of the posterior vertebrae are more ossified than those of the anterior ones vertebrae. All presacral centra are ossified ventrally. In Stage-II juveniles, the midline of the neural arches is completely ossified, except for Presacrals I and II.

The junction of neural arches with the centrum is ossified in all but in the first three presacrals. The vertebral centra are completely ossified. In subadults, the neural arches are completely ossified but retain some traces of cartilage at the midline. The midline of neural arches projects backward as a neural spine in Presacrals II–IV. The distal ends of the transverse processes of Presacral II are ossified. The postmetamorphic ossifications of the centra and the neural arches follow two different sequences. Centra ossify in an antero-posterior sequence, whereas the neural arch ossified in a postero-anterior sequence.

In Stage 44 and in postmetamorphs, the neural arch of the sacrum is ossified, but there are traces of cartilage at midline. The sacral centrum has begun to ossify bilaterally. In Stage-I juveniles, there is no trace of cartilage in the lamina. The sacral centrum is ossified bilaterally and in one specimen is ossified ventrally. In Stage-II juveniles, the centrum is completely ossified. In subadults, the sacrum has the adult state, although the sesamoids between sacral diapophyses and ilia are cartilaginous. The sacral diapophyses do not undergo significant changes during postmetamorphic growth.

In Stage 44, the ventral hypochord and the dorsal coccyx are ossified. In postmetamorphs, these structures are fused but the sutures between them are evident. The hypochord constitutes the body of the urostyle, whereas the coccyx forms the dorsal ridge. During subsequent postmetamorphic growth, the relation of the length of the ridge and the body of the urostyle varies. In Stages I and II juveniles, the ridge length extends over about half the length of the urostyle, whereas in subadults and adults, it extends over only about one-third the length of the urostyle.

Pectoral Girdle

The pectoral girdle is arciferal (Fig. 6). The omosternum has an expanded distal (anterior)

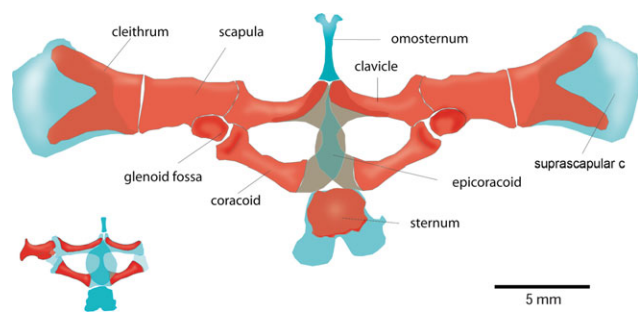


Fig. 6. Ventral view of the pectoral girdle of *T. oxycephalus*. Top: an adult male (FML 2867-II). Lower left: a postmetamorph of 22.38 mm SVL (MLP DB3620). Cartilage shown in blue and bone in red.

end. It is completely cartilaginous in females, but slightly mineralized proximally in males. The procoracoids and epicoracoids are extensively and strongly mineralized in males, but mineralization is slight in females. The sternum is rectangular and it is broader than long. The distal (posterior) margin of the sternum is notched. Most of the sternum is ossified in males; however, in FML 3836-III, the ossification only extends to the base of the notched region. In females, only the proximal (anterior) portion of the sternum is ossified, except in the female FML 3836-I, in which the sternum is extensively ossified as in the males. The anterior margin of the scapula in males is slightly convex (FML SB 19) or straight (FML 2867-II, 3836-II, and 3836-III), and in one individual (FML 2867-I), it is concave. In females, the anterior border of scapula is straight (FML 3836-I) or concave (FML 2867-III and 2867-IV). In all males and in one female (FML 3836-I), the clavicle is synostotically united to the scapula, and in the remaining females, they are united syndesmotically. The bifurcated cleithrum invests the ventral side and the anterior border of the suprascapula. The cartilaginous suprascapula is heavily mineralized in the males, whereas in the females, it is diffusely mineralized.

In Stage 44, as well as in postmetamorphs and Stage-I and II juveniles, the epicoracoids and procoracoids are completely cartilaginous. In subadults, these cartilages are slightly mineralized. The sternum is cartilaginous even in the subadult female, although some incipient mineralization is present. In the subadult male, the sternum is extensively mineralized. The omosternum is completely cartilaginous in all immature stages except in the male subadult, in which it is slightly mineralized proximally as in the adult males. The clavicle and the scapula are separated by cartilage, and the anterior margin of the scapula is concave in Stage 44, in postmetamorphs, and in Stage-I and II juveniles. In subadults of both sexes, the clavicle and the scapula are united by a suture (may be fused in adults), and the anterior margin of scapula is straight.

Forelimbs

The male humerus is robust and flattened, with well-developed ventral (=anteroproximal), lateral, and medial crests (Fig. 7). The female humerus is lightly built, lacking lateral and medial crests and having only a poorly developed ventral crest. The radius and ulna are fused completely to form radio-ulna. A sulcus is evident from the midlength of this bone to the distal end.

The carpus is composed of five elements: ulnare, distal carpal 5-4-3, element Y, distal carpal 2, and the radiale. Metacarpals V-III articulate with distal carpal 5-4-3, and metacarpal II articulates with

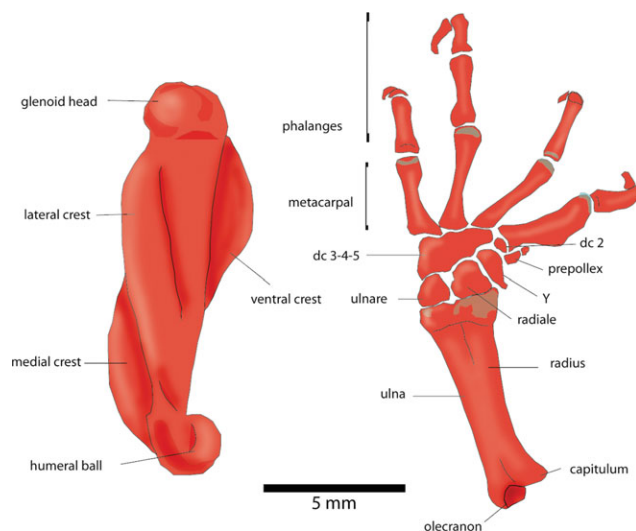


Fig. 7. Lateral view of right humerus (left) and dorsal view of left hand (right) of an adult male *T. oxycephalus* (FML 2867-II). Abbreviations: dc = distal carpal; Y = element Y. Cartilage shown in blue and bone in red.

distal carpal 2. In males, metacarpal II is hypertrophied and bears a ridge on its medial side. The phalangeal formula of the hand is 2-2-3-3. The terminal phalanges are knobbed. The prepollex is composed of six and five elements in males and females, respectively. The first proximal element is the largest and similar in size to distal carpal 2. In males, the first four proximal elements are ossified and the distal ones are cartilaginous. In females, only the first two proximal elements are ossified. A cartilaginous palmar sesamoid is evident ventral to distal carpal 5-4-3.

In Stage 44, as well as in postmetamorphs and Stage-I and II juveniles, the proximal and the distal epiphyses of the humerus and radio-ulna are cartilaginous. The humeral ventral crest is cartilaginous and poorly developed. In subadults, the epiphyses are ossified but traces of cartilage remain. The ventral crest of the humerus is more developed in this stage, but has not attained the development that is evident in the adults. In Stage 44 and in postmetamorphs, all carpal elements are cartilaginous. In Stage-I and II juveniles, distal carpal 5-4-3 has begun to ossify laterally. In the subadult female, it is almost completely ossified, with the exception of its medial end. Element Y is nearly completely ossified too, but distal carpal 2 is completely cartilaginous. In the subadult male, all carpal elements are ossified. All prepollical elements are cartilaginous in Stage 44 as well as in postmetamorphs and Stage-I and II juveniles. In the subadult male, the first three proximal elements are ossified, whereas in the subadult female, only the first proximal element is ossified.

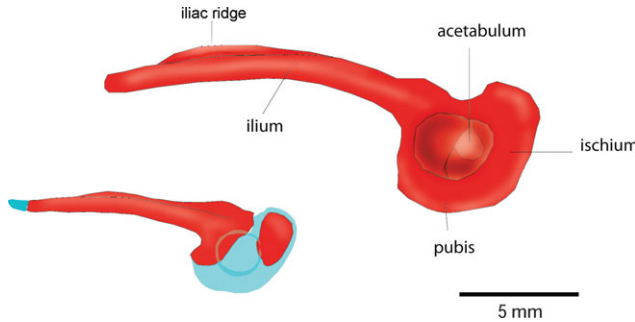


Fig. 8. Lateral view of pelvic girdle of *T. oxycephalus*. Top: an adult male (FML 2867-II). Below: a Stage-II juvenile of 35.44 mm (FML SB 24). Cartilage shown in blue and bone in red.

Pelvic Girdle

The ilia bear a dorsal, longitudinal ridge that extends over nearly 80% the length of the shaft (Figs. 5 and 8). The ilia are synostotically fused to each other at the proximal ilial corpus, where a dorsolateral iliac protuberance is evident. The ischia are synostotically fused to each other and bear an interischiadic crest dorsally. In all specimens examined, the ilia and ischia are also fused to each other, except for one female (FML 2867-III) in which a suture is evident between the bones. The pubis forms the ventral portion of the acetabulum. It is completely ossified in both sexes, but in females, a slight rim of cartilage is evident along its ventral border. The ossified pubis is synostotically fused with the ischium and ilium. In most specimens, the ischium, ilium, and pubis fail to meet in the central part of the acetabulum; thus, there is a cartilaginous region in the acetabular depression that is less than the half the size of the acetabulum. In FML 2867-III and FML 3836-III, these elements occupy more than the half of the acetabulum, whereas in the male specimen FML SB 016, the acetabulum is fully ossified because of the complete fusion of ischium, ilium, and pubis.

In all immature stages, the pubis is cartilaginous but it is slightly mineralized in subadults. Ilium and ischium are united synchondrotically even in subadults. More than the half of the acetabulum is not ossified in all immature specimens.

Hind Limbs

The femur is sigmoid-shaped and its proximal and distal epiphyses are completely ossified (Fig. 9). The tibiofibula is approximately as long as the femur. The distal and proximal epiphyses of tibiofibula are similar in size. There are five tarsal elements: the fibulare, tibiale, distal tarsal 3-2, distal tarsal 1, element Y, and the prehallux. The tibiale and fibulare are elongate, widely separated elements that are fused at the proximal and distal

ends. Distal tarsal 3-2 articulates principally with metatarsal III and partially with metatarsals II and IV, distal tarsal 1, and the union of tibiale and fibulare. Metatarsal IV and V articulate directly with fibulare. Distal tarsal 1 articulates with element Y, distal tarsal 3-2, metatarsals I and II, and the union between the tibiale and fibulare. Element Y articulates with the proximal element of the prehallux, distal tarsal 1, tibiale, and metatarsal I. The prehallux is formed by a proximal single element and a series of distal elements that vary in number and nature between sexes. The proximal element is the largest element. In males, the proximal element is ossified but with some traces of cartilage, and there are three or four distal elements. In the adult male FML 2867-II, all distal elements are cartilaginous, whereas in others (FML 2867-I and FML SB 019), the first two distal elements are ossified. In addition to the proximal element, there are two completely cartilaginous distal elements in females. The phalangeal formula is 2-2-3-4-3.

As in the long bones of the forelimb, the femur and the tibiofibula have cartilaginous epiphyses in

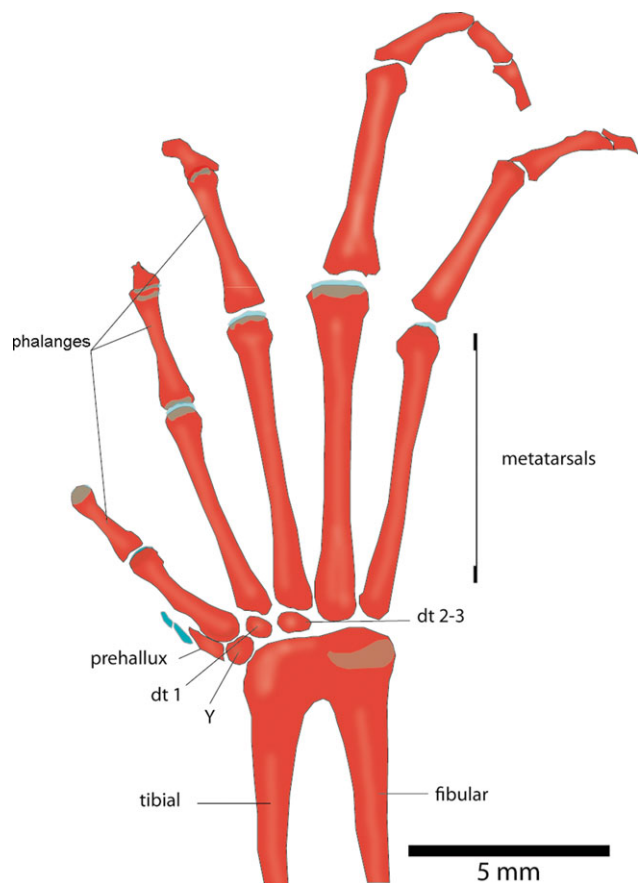


Fig. 9. Dorsal view of right foot of an adult male of *T. oxycephalus* (FML 2867-II). Abbreviations: dt = distal tarsal; Y = element Y. Cartilage shown in blue and bone in red.

Stage 44, in postmetamorphs, and in Stage-I and II juveniles. In subadults, the epiphyses are ossified, although they retain traces of cartilage. In all immature stages except subadults the tarsal elements are completely cartilaginous. They begin to ossify in subadults. In this stage, distal tarsal 3-2 is almost completely ossified, whereas distal tarsal 1 and element Y are partially ossified. In immature specimens, all elements of prehallux are cartilaginous except in subadults, in which the proximal element has begun to mineralize.

Interspecific Osteological Variation in the Genus *Telmatobius*

The comparison of the osteology of *T. oxycephalus* with published data of congeners shows that *T. oxycephalus* resembles *T. ceiorum*, *pisanoi*, and *laticeps* (Lobo Gaviola, 1988), and *sibiricus* and *simonsi* (De la Riva and Harvey, 2003). The differences among these species are subtle and are the same as differences found intraspecifically in *T. oxycephalus*, *ceiorum*, *laticeps*, and *pisanoi*. The most evident variation in these species involves the extension of sphenethmoid with respect to the nasals and vomers. The frontoparietals are fused to each other in all these taxa, except in *T. oxycephalus* and *T. ceiorum*, in which frontoparietal fusion is polymorphic (i.e., fused/not fused). The fusion of the parasphenoid with the prootics and exoccipitals is sexually dimorphic in *oxycephalus* and *laticeps*, with the margins of the parasphenoid being visible in females, not visible in males. In other species (*ceiorum*, *pisanoi*), this character varies polymorphically. Other intraspecific differences, not expressed within specimens of *oxycephalus*, are the ossification of epiotic eminences, which can show some traces of cartilage in some specimens of *pisanoi*, or in the fusion of the exoccipitals in the ventral margin of foramen magnum, that are not completely fused in some specimens of *pisanoi* and *ceiorum*.

There is another group of species of *Telmatobius* characterized by osteological variation that exceed the subtle variation described above. These species occur in the Puna region of Argentina (*hypselocephalus*, *platycephalus*, and *rubigo*), Chile (*chusmisensis*, *dankoi*, *fronteriensis*, *philippii*, and *vilamensis*), and Southern Bolivia (*huayra*). The variation is summarized in Tables 5 and 6, and it is based on text and figures of published descriptions and on observations of additional material (see Appendix A and B). This interspecific diversity involves the extension of the cultriform process of the parasphenoid and the morphology of sphenethmoid, exoccipitals, prootics, vomers, nasals, neopalatines, and plectra. In many cases, osteological characters of these species resemble the juvenile or subadult morphology of *T. oxycephalus*. These characters are analyzed in detail below.

Parasphenoid. In *Telmatobius philippii*, *platycephalus*, *rubigo*, and *vilamensis*, the anterior tip of the cultriform process of the parasphenoid lies at the level of the neopalatines. This state resembles that of immature *T. oxycephalus*, whereas in the adults, the tip of the cultriform process lies far posterior to the level of the neopalatines. In *T. chusmisensis* and *fronteriensis*, the anterior tip of the cultriform process approximates, but does not reach, the level of neopalatines. The changes in the relative positions of these bones seem to be related with the rostro-caudal growth of the skull. Apparently, the rostro-caudal growth is not correlated with a concomitant growth of the parasphenoid, which undergoes few changes in shape during postmetamorphic growth. The same topological changes of the neopalatines with respect to the parasphenoid during postmetamorphic growth are evident between juvenile and adult *Leptodactylus chaquensis* (Perotti, 2001).

Exoccipitals. These bones are less variable ontogenetically than the prootics, because at the end of metamorphosis, the condyles are almost completely ossified. The most noteworthy interspecific differences are the dorsomedial and ventromedial unions of the exoccipitals at the margin of foramen magnum. In *T. chusmisensis*, and *vilamensis*, the paired exoccipitals are not fused; they are widely separated from each other, as is the case of Stage-II juveniles of *T. oxycephalus*. In *T. philippii* and *T. platycephalus*, the exoccipitals are closer one another but unfused; the bones are separated by a wide band of cartilage, as is the case of subadult *T. oxycephalus*. As described above, the relation of exoccipitals can be intraspecifically variable in *T. pisanoi* and *T. ceiorum*. In these species, the exoccipitals are fused to each other, as in adult *T. oxycephalus*, or are separated by a suture.

Frontoparietals. Fusion of these bones in the parietal region varies, ranging from a thin, osseous bridge at the level of tectum synoticum (*Telmatobius chusmisensis*, and *T. vilamensis*, resembling juvenile *T. oxycephalus*) to fusion over the entire parietal region (*dankoi*, *fronteriensis*, *huayra*, and adult *oxycephalus*). Between these two extremes, there are several intermediate states (e.g., *T. philippii* and *T. platycephalus*). The anterior extent of frontoparietals also varies. In *T. huayra*, *philippii*, and *platycephalus*, the anterior end of frontoparietals lies at the level of the anterior margin of orbit, as in Stage-II juveniles of *T. oxycephalus*. In the other species, the frontoparietals are shorter, with the anterior margins lying posterior to the anterior margin of orbit. As discussed in the variation of the parasphenoid, relative length of the frontoparietal seems to be related to the rostro-caudal growth of skull.

Prootics. In *Telmatobius chusmisensis*, *philippii*, *platycephalus*, and *vilamensis*, the prootics are not completely ossified and not united with the

TABLE 5. Interspecific diversity in cranial characters

	<i>T. oxycephalus</i>	<i>T. chusmisensis</i>	<i>T. dankoi</i>	<i>T. frontierensis</i>	<i>T. huayra</i>	<i>T. hypselocephalus</i>	<i>T. philippii</i>	<i>T. platycephalus</i>	<i>T. rubigo</i>	<i>T. vilamensis</i>
Cultriform process reaching level of neopalatines	No	No (f,t), but it is close	No (f,t)	No (f,t), but it is close	Yes (f)	No	Yes (f,t)	Yes	Yes	No (f)
Medial contact between exoccipitals	Fused	Widely separated (f)	Fused (f,t)	Fused (f,t)	Fused (f,t)	Fused	Separated (f)	Separated	Fused	Widely separated (f)
Frontoparietals (fp), parietal region	Fused entirely	Fused in tectum synoticum	Fused entirely	Fused entirely	Fused entirely	Fused entirely	Fused in half of parietal region	Fused in half of parietal region	Fused entirely	Fused in tectum synoticum
Anterior end of fp reaching anterior margin of orbit	No	No	No	No	Yes	No	Yes	Yes	No	No
Prootic	Completely ossified	Not completely ossified (f,t)	Completely ossified (f,t)	Completely ossified (f,t)	Completely ossified (f,t)	Completely ossified	Poorly ossified (f,t)	Poorly ossified	Completely ossified	Poorly ossified (f,t)
Relation of prootics with exoccipitals	Fused	Not in contact (f,t)	Fused (f,t)	Fused (f,t)	Fused (f,t)	Fused	Not in contact (f,t)	Not in contact	Fused	Not in contact (f)
Mx and pmx teeth	Present	Present (f,t)	Absent (f,t)	Present (f,t)	Present (f,t)	Present	Present (f,t)	Present	Present	Absent (f,t)
Vomer	Present	Reduced (f,t)	Absent (f,t)	Present (f,t)	Present (f,t)	Present	Present (f,t)	Present	Present	Absent (f,t)
N° of teeth in each vomer	4-9	0-2 (f,t)	—	2-3 (f)	0 (f,t)	1	0-1 (f,t)	3-4	0-3	—
Nasals	Developed	Developed (f,t)	Reduced (f,t)	Developed (f,t)	Developed (f,t)	Developed	Developed (f,t)	Developed	Developed	Reduced (f,t)
Neopalatine	Curved	Straight (f,t)	Reduced (f,t)	Straight and thin (f,t)	Reduced (f,t)	Curved	Almost straight (t), curved (f)	Straight	Straight	Reduced (f,t)
Pletrum: pars interna (pi) and pars media plectri (pm)	Pi and pm ossified, pi reaching operculum	Reduced (not specified) or absent (t)	Pi and pm not ossified (f,t)	Pi and pm not ossified (f,t)	Pi and pm not ossified (t)	Pi slightly ossified not reaching operculum, pm ossified	Pi and pm not ossified (f,t)	Pi not ossified, pm ossified	Pi slightly ossified not reaching operculum, pm ossified	Pi and pm not ossified (t)
Sphenethmoid	Complete ring	Complete ring (f)	Complete ring (f,t)	Complete ring (f,t)	Complete ring (f,t)	Complete ring	Complete ring (f,t)	Incomplete ring ventrally	Complete ring	Two halves (f)
Hyoid plate	Mineralized	Cartilaginous (f)	Cartilaginous (f,t)	Cartilaginous (f,t)	Mineralized (f,t)	Isolated ossifications	Cartilaginous (f,t)	Cartilaginous	Mineralized	Cartilaginous (f)
Base of postero-medial processes	Invading plate (males), not invading plate (females)	Not invading plate (f)	Not invading plate (f)	Not invading plate (f)	Fused and invading plate (f,t)	Slightly invading plate	Not invading plate (f,t)	Not invading plate.	Invading plate	Not invading plate (f)
Distal tip of postero-medial processes	Mineralized (males), cartilaginous (females)	cartilaginous (f, t)	Cartilaginous (f,t)	Cartilaginous (t)	Distal tips cartilaginous (f,t)	Cartilaginous	Cartilaginous (f, t)	Cartilaginous	Mineralized	Cartilaginous (f)

The letters indicate if the character states were taken from figures (f), text (t), or both of the literature. When it is not specified, the original material was studied. Dark gray indicates hypo-ossified or underdeveloped characters; light gray indicates transitional states to completely ossified or developed characters.

TABLE 6. *Interspecific diversity in postcranial characters*

	<i>T. oxycephalus</i>	<i>T. chusmisensis</i>	<i>T. dankoi</i>	<i>T. frontierensis</i>	<i>T. huayra</i>	<i>T. hypselocephalus</i>	<i>T. philippii</i>	<i>T. platycephalus</i>	<i>T. rubigo</i>	<i>T. vilamensis</i>
Sternum	Ossified	Poorly mineralized (f,t)	Cartilaginous	Ossified (f)	Ossified (f,t)	Ossified	Mineralized (f,t)	Cartilaginous	Ossified	Ossified (f,t)
Base of omosternum	Mineralized (males), cartilaginous (females)	Cartilaginous (f)	Cartilaginous (f)	Cartilaginous (f)	Mineralized (f,t)	Cartilaginous	Cartilaginous (f)	Cartilaginous	Mineralized	Mineralized (f, base and distal tip) (f,t)
Procoracoid and epicoracoid	Extensively mineralized (males), slightly mineralized (females)	Mineralized (f)	Mineralized (f)	Mineralized	Mineralized (f,t)	Mineralized	Cartilaginous (f)	Slightly mineralized	Mineralized	Cartilaginous (f,t)
Union of scapula and clavicle	Fused in most specimens	Not fused (f)	Not fused (f)	Fused (f,t)	Fused	Fused	Not fused (f,t)	Not fused	Fused	Not fused (f)
Anterior margin of scapula	Straight or concave	Straight (f)	Concave (f)	Concave (f)	?	?	Concave (f)	Concave	Straight	Concave (f)
Pubis	Ossified	Cartilaginous (t)	“Strongly mineralized” (t)	“Well mineralized” (t)	Ossified (t)	Ossified	“Scarce mineralization” (t)	Cartilaginous	Ossified	“Slightly ossified” (t)
Carpus	Ossified	Cartilaginous (f,t)	Ossified (f,t)	Ossified (f)	Ossified (f,t)	Ossified	Ossified (f,t)	Not completely ossified	Ossified	Ossified (f,t)
Prepollex	Four elements ossified (males), two (females)	Cartilaginous	Two ossified elements (f)	Two ossified elements (f,t)	Three ossified elements (f,t)	Two ossified elements	One ossified element (f,t)	Cartilaginous	Four ossified elements	Two ossified elements (f,t)
Tarsus	Ossified	Cartilaginous (f,t)	Ossified (f,t)	Ossified (f)	Ossified (f)	Ossified	Partially ossified (f)	Cartilaginous	Ossified	Ossified (f,t)
Prehallux	Three ossified elements (males), 0 (females)	Cartilaginous (f,t)	Three ossified elements (f,t)	One ossified element (t)	One ossified element (f,t)	One ossified element	One mineralized element (f)	Cartilaginous	Two ossified elements	One ossified element (f)

The letters indicate if the character states were taken from figures (f), text (t), or both in the literature. When it is not specified, the original material was studied. Dark gray indicates hypo-ossified or underdeveloped characters; light gray indicates transitional states to completely ossified or developed characters.

exoccipitals. The ossification of prootics in *philippii*, *platycephalus*, and *vilamensis* resembles that of Stage-II juveniles *T. oxycephalus*. The state observed in *T. chusmisensis* is more developed and resembles that of subadult *T. oxycephalus*, although less ossified. The intraspecific variation in the development of the prootics as was described in *T. ceiorum* and *T. pisanoi* is subtle and involves the persistence of traces of cartilage in the posterior epiotic eminences (the union of prootic and exoccipitals).

Premaxillary and maxillary teeth. *Telmatobius dankoi* and *T. vilamensis* are edentate. There are no equivalent stages in the postmetamorphic stages analyzed of *T. oxycephalus*, because in the less-developed specimen (Stage 44), the maxilla is edentate but there are incipient teeth in the premaxilla.

Nasals. These bones are reduced only in *T. dankoi* and *T. vilamensis*, in which the morphology resembles the nasals of Stage-44 and postmetamorphs of *T. oxycephalus*.

Vomers. *Telmatobius dankoi* and *T. vilamensis* lack vomers, and the bones are much reduced in *T. chusmisensis*, with remnants of the anterior region and reduced prechoanal and postchoanal processes. Although the vomers appear at Stage 44 in *T. oxycephalus*, in postmetamorphs, they almost have acquired the adult form. There is variation in the number of vomerine teeth. In *T. fronteriensis*, there are two or three rudimentary teeth as in postmetamorphs of *T. oxycephalus*. In other species, there are fewer teeth than in *T. oxycephalus*, as follow: *T. huayra* (no teeth), *philippii* (0–1), *chusmisensis* (0–2), *rubigo* (0–3), and *hypselocephalus* (1). In *T. platycephalus*, the maximum number of vomerine teeth recorded is four. In *T. oxycephalus*, the number of teeth increases during the postmetamorphic growth from one or two to reach a maximum of nine in each vomer.

Neopalatines. In *Telmatobius chusmisensis*, *fronteriensis*, *platycephalus*, and *rubigo* are straight as in early postmetamorphic stages of *T. oxycephalus*. In adult *T. oxycephalus*, the neopalatines are curved or boomerang shaped. In *T. dankoi*, *huayra*, and *vilamensis*, the neopalatines are reduced, with the medial ends separated from the sphenethmoid.

Middle ear. In *Telmatobius dankoi*, *fronteriensis*, *huayra*, *philippii*, and *vilamensis*, the plectrum is absent. In *T. platycephalus* and *T. hypselocephalus*, the pars interna plectri is not ossified and the pars media is slender, as it is in young *T. oxycephalus*. In *T. chusmisensis*, the plectrum is present, reduced, or absent. The plectrum originates from a cartilaginous primordium (the future pars interna plectri) that covers the anterior portion of the fenestra ovalis. From this primordium, a cartilaginous stylus develops laterally (the future pars media plectri) and comes into contact with the skin that

eventually will form the tympanic membrane through a developing pars externa plectri (Hetherington, 1987; Smirnov, 1991). The first part of the plectrum to ossify in *T. oxycephalus* is the pars media, early in postmetamorphic development. Wiens (1993) described the variation in plectrum morphology in species of *Telmatobius* from northern Peru. He pointed out that a striking intraspecific variation exists that is not recorded in any other group of anurans. In some cases, the variation is bilateral in the same individual. Wiens (1993) described the absence of pars media but did not mention the absence of the pars interna, as was recorded in some highland species mentioned above. The lack of ossification of the plectrum or the lack of ossification of pars interna plectri in highland species matches with the development of plectrum observed in *T. oxycephalus* (the ossification of pars media precedes the ossification of pars interna).

Sphenethmoid. In *Telmatobius vilamensis*, the sphenethmoid is represented by bilateral ossifications on the anterior part of the braincase; this resembles the developmental state present in Stage-II juveniles of *T. oxycephalus*. In *T. platycephalus*, the sphenethmoid is incomplete ventrally as in subadult *T. oxycephalus*. In other species (*T. chusmisensis* and *T. philippii*), it is poorly ossified, as evidenced by the state of the anterior dorsal margin of sphenethmoid, which resembles that of subadult *T. oxycephalus*. The variation found in *T. chusmisensis* and *T. philippii* is comparable to the intraspecific variation recorded in *oxycephalus*, *ceiorum*, *laticeps*, and *pisanoi*.

Hyoid apparatus. The hyoid plate has mineralized areas in *Telmatobius huayra*, *hypselocephalus*, and *rubigo*. In these species, the bases of the posteromedial processes invade the plate as in the adult male *T. oxycephalus*. In *T. chusmisensis*, *dankoi*, *fronteriensis*, *philippii*, *platycephalus*, and *vilamensis*, the plates are cartilaginous and the posteromedial processes do not invade the plate as is the case in the immature stages and in adult female *T. oxycephalus*.

The degree of ossification of postcranial structures in some Puna species (Table 6) is not correlated with the degree of ossification of cranial characters. This is the case of species that show hypo-ossified or immature cranial elements and at the same time show well-ossified postcranial elements (e.g., *T. dankoi* or *T. vilamensis*).

Sternum. Ossified extensively in *Telmatobius vilamensis*, *huayra*, *hypselocephalus*, and *rubigo*. In *T. fronteriensis*, the sternum is ossified proximally (anteriorly). In *T. philippii* and *T. chusmisensis*, the sternum is mineralized proximally and in *T. platycephalus* and *T. dankoi*, it is cartilaginous. The beginning of mineralization/ossification of sternum and mineralization of the base of omosternum takes place late, during postmetamorphic growth in *T. oxycephalus*.

Clavicle and scapula. These elements are fused to one another in *T. fronteriensis*, *hypselocephalus*, *huayra*, and *rubigo*, as in adult *T. oxycephalus*. In the rest of the Puna species compared here, the elements articulate with one another. The anterior border of the scapula is concave in *T. dankoi*, *fronteriensis*, *philippii*, *platycephalus*, and *vilamensis*. In *T. chusmisensis* and *T. rubigo*, the scapula is straight as it is in subadult and adult *T. oxycephalus*.

Pubis. This element is ossified or strongly mineralized in *T. dankoi*, *fronteriensis*, *huayra*, *hypselocephalus*, and *rubigo*. In *T. vilamensis* and *T. philippii*, the pubis is slightly mineralized. In the description of the pubis of *T. vilamensis* (Formas et al., 2003), it is possible that the authors erroneously used "slightly ossified" instead of "slightly mineralized," because the poor mineralization of the pubis is clear in their figure. In *T. chusmisensis* and *T. platycephalus*, the pubis is completely cartilaginous. Mineralization of pubis occurs late during the postmetamorphic growth of *T. oxycephalus* at the subadult stage.

Carpus. The carpal elements are ossified in all the species analyzed here except in *Telmatobius platycephalus* (partially ossified) and *T. chusmisensis* (cartilaginous). In these species, all the prepollical elements are also cartilaginous. There are one or two ossified elements in the prepollices of *T. dankoi*, *fronteriensis*, *hypselocephalus*, *philippii*, and *vilamensis*, three in *T. huayra*, and four in *T. rubigo* as in adult male *T. oxycephalus*.

Tarsus. The distal tarsal elements and the prehallux are completely cartilaginous in *Telmatobius chusmisensis* and *T. platycephalus*. In *T. philippii*, only distal tarsals 3-2 and distal tarsal 1 are completely ossified, whereas element Y is partially ossified. In the remaining species, the tarsus is ossified completely. For *T. dankoi*, Formas et al. (1999) described a configuration of the tarsus different than it was described for all species of *Telmatobius*; in Figure 5-E of Formas et al. (1999: 436), distal tarsal 3-2 is fused with distal tarsal 1, whereas in the other species, distal tarsal 1 is free. In *T. philippii*, there is only one mineralized element of the prehallux. In *T. fronteriensis*, *huayra*, *hypselocephalus*, and *vilamensis*, there is one ossified element in the prehallux, there are two in *T. rubigo*, and three in *T. dankoi*. In the osteological description of *T. fronteriensis* (Benavides et al., 2002) and *T. vilamensis* (Formas et al., 2003), it is probable that the authors have misidentified element Y as the proximal element of the prehallux. If so, the prehallux would have just one ossified element, instead of two, as the authors proposed.

DISCUSSION

This study reveals a differential distribution of characters with sexual (dimorphic) and intraspe-

cific (polymorphic) variation in *T. oxycephalus*. Cranial characters, with the exception of the hyoid, tend to vary polymorphically, whereas the hyoid and postcranial skeletons tend to vary sexually. The most remarkable polymorphic cranial variation in *T. oxycephalus* involves the development of sphenethmoid and the relation of frontoparietals to one another (Table 1). The visibility of the suture of the parasphenoid with the otic capsules and the degree of mineralization and ossification of the hyoid plate vary dimorphically. Among the sexually dimorphic postcranial characters are the mineralization of the omosternum and the development of the humeral crests, metacarpal II, and the prepollex (Table 2). Polymorphic postcranial characters include features of the girdles and prehallux (Table 2). Several workers (e.g., Parker, 1940; Vellard, 1951; Trueb, 1979; De la Riva, 2005) commented on the extraordinary polymorphism of external characters in *Telmatobius*. Sinsch et al. (2005) claimed the high degree of polymorphism of osteological characters in *Telmatobius* and questioned the value of osteological characters in systematic studies. In fact, the latter authors only analyzed one male and one female, and for that reason, it is possible that they were dealing with sexually dimorphic characters. In any case, these authors do not describe this presumed, polymorphic variation. To date, the only detailed account of osteological variation is the work of Lobo Gaviola (1988), who analyzed three species of the genus (*laticeps*, *pisanoi*, and *ceiorum*). With slight differences, the intraspecific variation reported by Lobo Gaviola (1988) is comparable with the intraspecific variation recorded in *T. oxycephalus*.

Here, it was assumed that the different sizes of specimens of *T. oxycephalus* in the postmetamorphic series are correlated with age, but this assumption needs to be tested using skeletochronology. Nonetheless, there is a positive correlation between the degree of ossification and the size of specimens examined. During postmetamorphic growth (from a froglet about 20.0 mm SVL to an adult frog of 50 mm or more), osteological structures complete their development at different stages (Table 3). Several elements begin to ossify in premetamorphic or metamorphic stages and do not undergo substantial changes in shape during postmetamorphic growth in *T. oxycephalus*. Included are the septomaxillae, premaxilla, maxilla, squamosal, quadratojugal, and pterygoid. These elements have acquired their final form before or immediately after the beginning of postmetamorphic life, and are well formed in the postmetamorphs (~20–23 mm SVL). Along with the postmetamorphic elements, there are other premetamorphic and metamorphic elements that undergo significant changes during postmetamorphic growth. Independently of time of onset, these elements complete their development at different

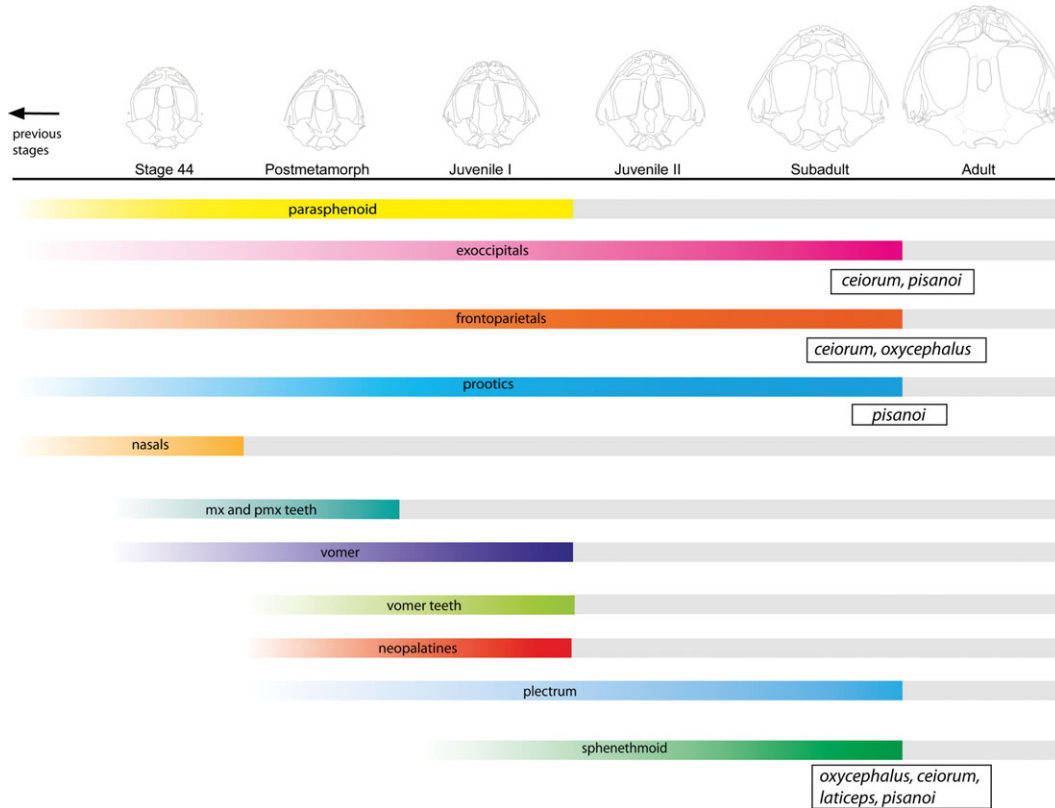


Fig. 10. Color bars represent morphological change of different cranial bones during the postmetamorphic development of *T. oxycephalus*. Gray bars indicate the stage at which the adult or final form is achieved. Below each bar, boxes include the species whose adult morphology (for each particular bone) shows polymorphism. This polymorphism involves subtle differences in ossification. This variation is similar to the variation found between subadult and adult stages of *T. oxycephalus*.

postmetamorphic stages (Fig. 10). Some elements attain their final form or state early during the postmetamorphic growth: parasphenoid (premetamorphic onset), nasals (metamorphic onset), premaxillary and maxillary teeth, vomer, vomerine teeth, neopalatines, and mentomeckelian (postmetamorphic onset). Other elements attain its final state late: exoccipitals and frontoparietals (premetamorphic onset), prootics (metamorphic onset), sphenethmoid, and plectrum (postmetamorphic onset).

Postcranially, the main elements of the vertebrae and the pectoral and pelvic girdles are formed by Stage 44, although they continue to ossify during postmetamorphic growth. Epicoracoids, procoracoids, omosternum, sternum, and pubis, and the junction of ilium and ischium begin to ossify/mineralize during postmetamorphic growth. Likewise, the epiphyses of the long bones of the limbs (humerus, radio-ulna, femur, and tibio-fibula) are completely ossified only in the adults (45–55 mm SVL). Among carpal elements, distal carpal 5-3 begins to ossify early, whereas the prepollex and distal tarsal elements (including the prehallux) ossify at the end of postmetamorphic growth (Table 4).

In *Telmatobius*, intraspecific and interspecific variation involves different degrees of development

in the skeleton. In most cases, there is a clear distinction between these two levels of variation. Intraspecific variation includes subtle differences in the development of structures. Usually, structures that vary intraspecifically attain their final state late, during the subadult to adult transition (Fig. 10; e.g., the anterior ossification of sphenethmoid, the mineralization of epiotic eminences). Conversely, interspecific variation usually involves elements that attain their final state early, during postmetamorphic growth (Fig. 11; e.g., the parasphenoid and frontoparietals in relation to planum antorbitale, the neopalatines, and teeth). Some bones show variation at both levels. For example, the sphenethmoid has a wide intraspecific variation in *T. oxycephalus*, *ceiorum*, *laticeps*, and *pisanoi*. This variation is related with the degree of anterior ossification that usually is described with reference to the nasals and vomers. The anterior region of sphenethmoid ossifies late, in the transition from subadult to adult in *T. oxycephalus*, and even during adult growth. Interspecific variation in the sphenethmoid is evident in the state recorded in two Puna species, in which this bone still consists of two ossifications centers (*T. vilamensis*) or it is not fused ventrally (*T. platycephalus*).

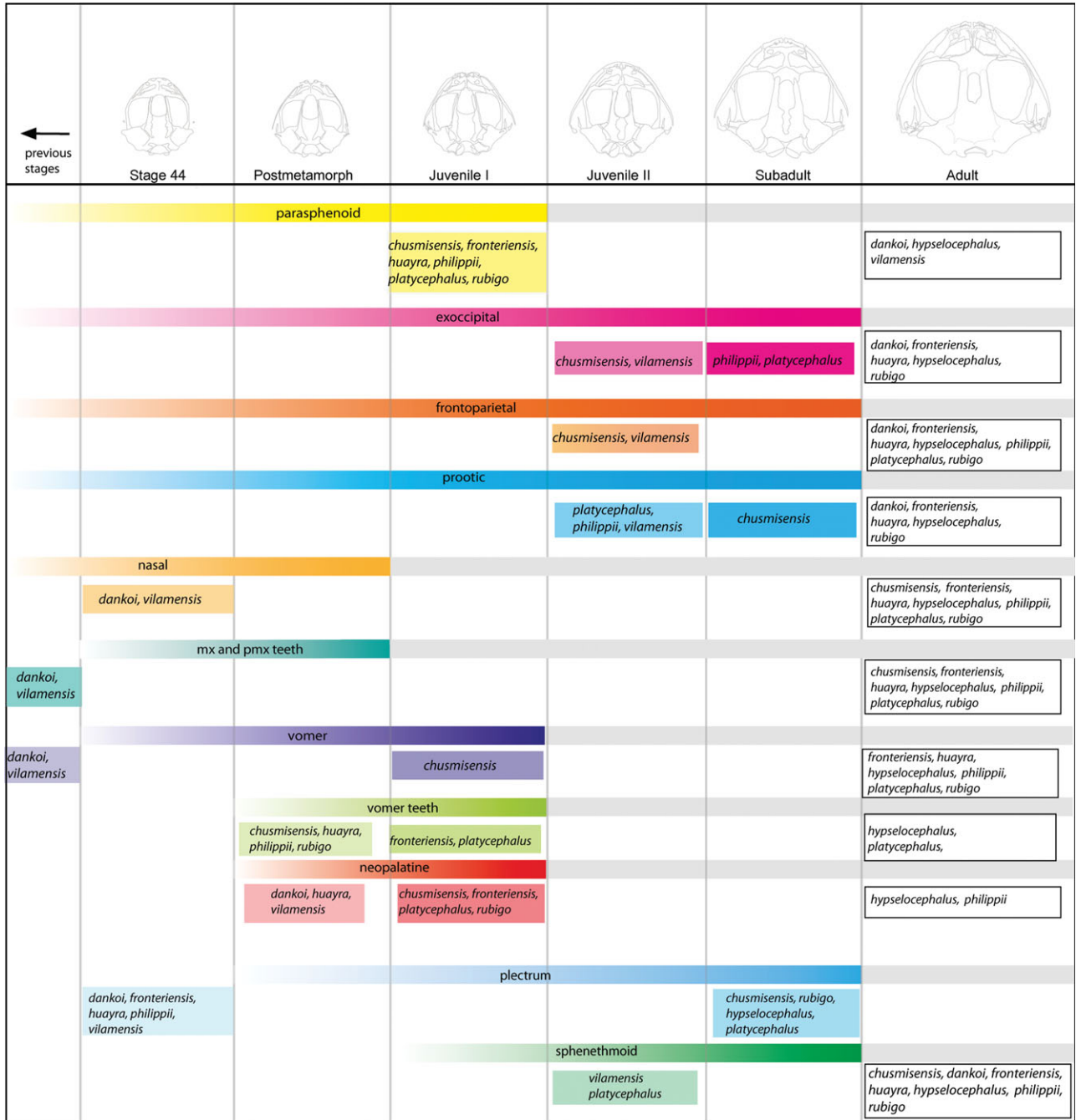


Fig. 11. Color bars represent morphological change of different cranial bones during the postmetamorphic development of *T. oxycephalus*. Gray bars indicate the stage at which the adult or final form is achieved. Below each bar, color boxes include the species whose adult morphology (for each particular bone) is similar to the corresponding immature morphology recorded during the development of *T. oxycephalus*. White boxes include species whose adult morphology (for each particular bone) is similar to the adult morphology of *T. oxycephalus*.

lus), as in the first stages of postmetamorphic growth of *T. oxycephalus*.

Based on osteological characters, and the habitat and distributions of the species of *Telmatobius* considered here, the frogs can be sorted into two groups: (1) A forest and inter-Andean group: *T.*

ceiorum, *laticeps*, *oxycephalus*, *pisanoi*, *sibiricus*, and *simonsi*; and (2) a high Andean or Puna group: *T. platycephalus*, *hypselocephalus*, *dankoi*, *vilamensis*, *fronteriensis*, *philippii*, *chusmisensis*, *rubigo*, and *huayra*. In general, the forest and inter-Andean species seem to be semiaquatic, that

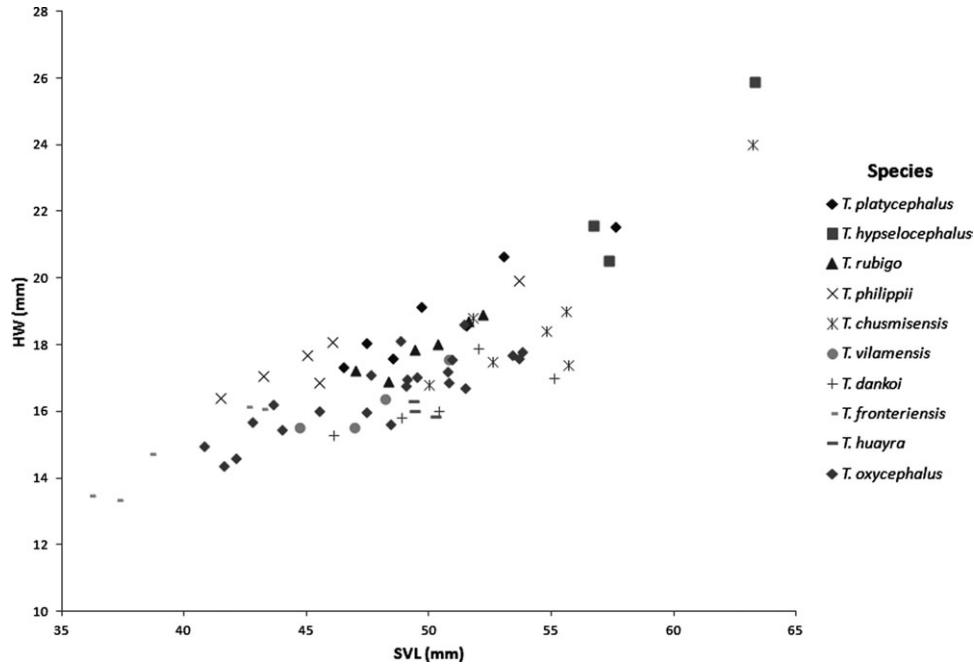


Fig. 12. Scatter diagram showing total size (SVL) versus head width (HW) of *Telmatobius* species studied herein.

is, they can be found outside the streams (Laurent, 1970, 1973; De la Riva, 1994b). The high Andean or Puna species seem to be exclusively aquatic; they always are found in the water and their diet consists exclusively of aquatic prey (Formas et al., 2005). Osteologically, the forest and inter-Andean species resemble each other, and variation is restricted to subtle differences in mineralization or ossification. In contrast, the variation among mem-

bers of the Puna group is more evident and involves major differences in the degrees of mineralization/ossification and in the topological relationships among some bones. At the same time, Puna species differ from forest and inter-Andean species in having a lower degree of ossification/mineralization, and in other characters that resemble immature morphology of *T. oxycephalus*. In a phylogenetic analysis of Bolivian species

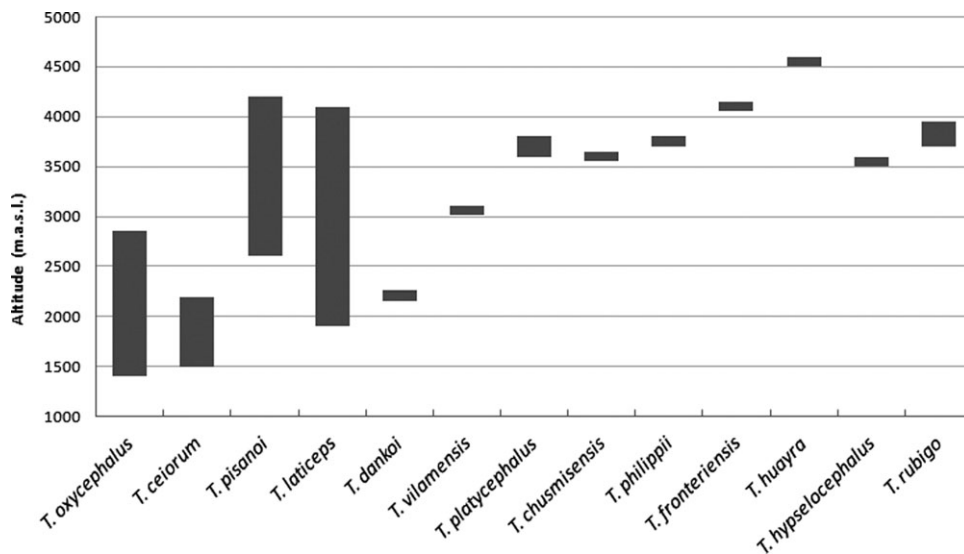


Fig. 13. Altitudinal distributions of *Telmatobius* species studied herein.

based on 12S and 16S mtDNA sequences (De la Riva et al., 2010), the Puna species form a monophyletic clade (named the *T. marmoratus* Group). This group is nested within a large clade of forest and inter-Andean Bolivian species. With the exception of *T. huayra*, no other Puna species described herein were included in the analysis of De la Riva et al. (2010). However, based on external morphology, it is probable that these species belong to the monophyletic *T. marmoratus* clade defined by De la Riva et al. (2010).

The presence of a hypo-ossified skeleton or the occurrence of immature characters has been associated with a smaller body size (Trueb and Alberch, 1985; Yeh, 2002; Maglia et al., 2007). A comparison of body size (Fig. 12) shows that such association is not evident among the species analyzed here. The total body size of Puna species ranges from the small *T. fronteriensis* (up to 43.2 mm SVL) to a relatively large *chusmisensis* (up to 63.2 mm SVL). Most Puna species share the same range in body size as *T. oxycephalus* or are even larger (*T. chusmisensis*, *hypselocephalus*, and *platycephalus*). Even more, the small *fronteriensis* shows a more ossified skeleton than the large *chusmisensis*.

Another issue that emerges when the degree of ossification is analyzed is the effect of environmental conditions. It is known, experimentally, that froglets emerging from low-temperature treatments are less ossified than those emerging from higher temperature environments (Gomez-Mestre et al., 2010). The effect of temperature is especially relevant in *Telmatobius* because of the wide altitudinal range of the genus. However, among the species analyzed here, those with the lowest degree of ossification or those showing immature characters (e.g., *T. dankoi*, *vilamensis*) do not occur in the highest (and coldest) environments (Fig. 13).

Interspecific variation in *Telmatobius* is extremely scarce in some cases (e.g., among forest and inter-Andean species). The paucity of osteological diversity has led to some authors to question the value of osteological characters for systematic purposes (Sinsch et al., 2005). The comprehensive osteological study presented herein shows that, within this conservative framework, several osteological characters distinguish Puna species from other species of the genus. In general, several osteological characters of Puna species resemble the morphology characterizing early postmetamorphic stages of *T. oxycephalus*, a member of the forest and inter-Andean species group. Although it seems evident that osteological variation among the species groups considered here could arise through heterochronic processes, the direction of these developmental processes (peramorphic or paedomorphic), as well as its evolutionary implications, cannot be established without a comprehensive phylogenetic framework. Within this frame-

work, the study of additional species and series of development, including larval stages, is essential to understand the morphological evolution of *Telmatobius* and the relationship of morphological patterns with highland habitats.

ACKNOWLEDGMENTS

The author is grateful to L. Trueb and M. Fabrezi for making valuable suggestions on the manuscript and to J. Faivovich for revising an early version. The author thanks S. Kretzschmar, M. Cánepa, and especially E. Lavilla (FML) for providing specimens and working space, and to D. Baldo for providing additional specimens (MLP DB).

LITERATURE CITED

- Aguilar C, Pacheco V. 2005. Contribución de la morfología bucofaríngea larval a la filogenia de *Batrachophrynus* y *Telmatobius* (Anura: Leptodactylidae). *Monografías de Herpetología* 7:219–238.
- Aguilar C, Valencia N. 2009. Relaciones filogenéticas entre telmatobiinidos (Anura, Ceratophryidae, Telmatobiinae) de los Andes centrales basado en la morfología de los estados larval y adultos. *Revista Peruana de Biología* 16:43–50.
- Andersen ML. 1978. The comparative myology and osteology of the carpus and tarsus of selected anurans [Ph.D. dissertation]. University of Kansas, Lawrence, Kansas. 235 p.
- Barrionuevo JS, Baldo D. 2009. A new species of *Telmatobius* (Anura, Ceratophryidae) from Northern Jujuy Province, Argentina. *Zootaxa* 2030:1–20.
- Benavides E, Ortiz JC, Formas JR. 2002. A new species of *Telmatobius* (Anura: Leptodactylidae) from Northern Chile. *Herpetologica* 58:210–220.
- Córdova JH, Descailleaux J. 2005. El análisis cladístico preliminar de los cariotipos de cinco especies de *Telmatobius* y dos de *Batrachophrynus* (Amphibia: Leptodactylidae: Telmatobiinae) no apoya su separación genérica. *Monografías de Herpetología* 7:187–217.
- Cuevas C, Formas JR. 2002. *Telmatobius philippii*, una nueva especie de rana acuática de Ollagüe, norte de Chile (Leptodactylidae). *Revista Chilena de Historia Natural* 75:245–258.
- Davies M. 1989. Ontogeny of bone and the role of heterochrony in the Myobatrachine Genera *Uperoleia*, *Crinia*, and *Pseudophryne* (Anura: Leptodactylidae: Myobatrachinae). *J Morphol* 200:269–300.
- De la Riva I. 1994a. A new aquatic frog of the genus *Telmatobius* (Anura: Leptodactylidae) from Bolivian cloud forests. *Herpetologica* 50:38–45.
- De la Riva I. 1994b. Description of a new species of *Telmatobius* from Bolivia (Amphibia: Anura: Leptodactylidae). *Graellsia* 50:161–164.
- De la Riva I, Harvey MB. 2003. A new species of *Telmatobius* from Bolivia and a redescription of *T. simonsi* Parker, 1940 (Amphibia: Anura: Leptodactylidae). *Herpetologica* 59:127–142.
- De la Riva I. 2005. Bolivian frogs of the genus *Telmatobius* (Anura: Leptodactylidae): Synopsis, taxonomic comments, and description of a new species. *Monografías de Herpetología* 7:65–101.
- De la Riva I, García-París M, Parra-Olea G. 2010. Systematics of Bolivian frogs of the genus *Telmatobius* (Anura, Ceratophryidae) based on mtDNA sequences. *Syst Biodivers* 8:49–61.
- Dingerkus G, Uhler LD. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technol* 52:229–232.
- Fabrezi M. 1992. El carpo de los Anuros. *Alytes* 10:1–29.

- Fabrezi M. 1993. The anuran tarsus. *Alytes* 11:47–63.
- Fabrezi M. 2001. A survey of prepollex and prehallux variation in anuran limbs. *Zool J Linn Soc* 131:227–248.
- Fabrezi M. 2006. Morphological evolution of the Ceratophryinae (Anura, Neobatrachia). *J Zool Syst Evol Res* 44:153–166.
- Formas JR, Northland I, Capetillo J, Núñez JJ, Cuevas CC, Brieva L. 1999. *Telmatobius dankoi*, una nueva especie de rana acuática del norte de Chile (Leptodactylidae). *Rev Chil Hist Nat* 72:427–445.
- Formas JR, Benavides E, Cuevas C. 2003. A new species of *Telmatobius* (Anura: Leptodactylidae) from Río Vilama, northern Chile, and the redescription of *T. halli* Noble. *Herpetologica* 59:253–270.
- Formas JR, Veloso A, Ortiz JC. 2005. Sinopsis de los *Telmatobius* de Chile. *Monografías de Herpetología* 7:103–114.
- Formas JR, Cuevas C, Núñez JJ. 2006. A new species of *Telmatobius* (Anura, Leptodactylidae) from Northern Chile. *Herpetologica* 62:173–183.
- Gomez-Mestre I, Saccoccio VL, Iijima T, Collins EM, Rosenthal GG, Warkentin KM. 2010. The shape of things to come: linking developmental plasticity to postmetamorphic morphology in anurans. *J Evol Biol* 23:1364–1373.
- Gosner KL. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183–190.
- Hetherington TE. 1987. Timing of development of the middle ear of Anura (Amphibia). *Zoomorphology* 106:289–300.
- Holmgren N. 1933. On the origin of the tetrapod limb. *Acta Zool (Stockh)* 14:185–295.
- Hollister G. 1934. Clearing and dyeing fish for bone study. *Zoologica* 12:89–101.
- Jaslow AP, Hetherington TE, Lombard RE. 1988. Structure and function of the amphibian middle ear. In: Fritzsche B, editor. *The Evolution of the Amphibian Auditory System*. New York: Wiley. pp 69–91.
- Laurent RF. 1970. Dos nuevas especies argentinas del género *Telmatobius* (Anura: Leptodactylidae). *Acta Zool Lilloana* 25:207–226.
- Laurent RF. 1973. Nuevos datos sobre el género *Telmatobius* en el Noroeste Argentino, con la descripción de una nueva especie de la Sierra del Manchao. *Acta Zool Lilloana* 30:163–187.
- Lavilla EO, Ergueta Sandoval P. 1995. Una nueva especie de *Telmatobius* (Anura: Leptodactylidae) de la Ceja de Montaña de La Paz (Bolivia). *Alytes* 13:45–51.
- Lavilla EO, Ergueta Sandoval P. 1999. A new Bolivian species of the genus *Telmatobius* (Anura: Leptodactylidae) with humeral spine. *Amphibia-Reptilia* 20:55–64.
- Lavilla EO, Laurent RF. 1988. Deux nouvelles espèces du genre *Telmatobius* (Anura: Leptodactylidae) en provenance de El Moreno (Province de Jujuy, Argentina). *Alytes* 7:77–89.
- Lobo Gaviola FJ. 1988. Osteología comparada de tres especies de *Telmatobius* (Anura: Leptodactylidae) de la Provincia de Tucumán (Argentina) [dissertation]. Universidad Nacional de Tucumán, Tucumán, Argentina.
- Lynch JD. 1971. Evolutionary relationships, osteology, and zoogeography of Leptodactyloid frogs. *Misc Publ Mus Nat Hist Univ Kansas* 53:1–238.
- Lynch JD. 1978. A re-assessment of the Telmatobiine leptodactylid frogs of Patagonia. *Occas Pap Mus Nat Hist Univ Kansas* 72:1–57.
- Maglia AM, Pugener LA, Mueller JM. 2007. Skeletal morphology and adult ontogeny of *Acris crepitans* (Anura: Hylidae): A case of miniaturization in frogs. *J Morphol* 268:193–282.
- Parker HW. 1940. Percy Sladen trust expedition to lake Titicaca under the leadership of Mr. H. Cary Gilson, M.A.-XII-Amphibia. *Trans Linn Soc Lond* 3:203–216.
- Perotti MG. 2001. Skeletal development of Leptodactylus chaquensis (Anura: Leptodactylidae). *Herpetologica* 57:318–335.
- Peters W. 1873. Über neue oder weniger bekannte Gattungen und Arten von Batrachiern. *Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin* 1873:411–418.
- Seimon TA, Seimon A, Daszak P, Halloy SRP, Schloegel LM, Aguilar CA, Sowell P, Hyatt AD, Konecky B, Simmons JE. 2006. Upward range extension of Andean anurans and chytridiomycosis to extreme elevations in response to tropical deglaciation. *Glob Change Biol* 13:288–299.
- Simmons JE. 1986. A method of preparation of anuran osteological material. In: Waddington J, Rudkin JM, editors. *Proceedings of Workshop on care and maintenance of Natural History collections*. Life Sciences Misc Publ. Royal Ontario Mus 37–39.
- Sinsch U, Hein K, Glump B. 2005. Reassessment of central Peruvian Telmatobiinae (genera *Batrachophrynus* and *Telmatobius*): Osteology, palmar morphology and skin histology. *Monografías de Herpetología* 7:239–260.
- Smirnov SV. 1991. The anuran middle ear: Development heterochronies and adult morphology diversification. *Belg J Zool* 121:99–110.
- Song J, Parenti LR. 1995. Clearing and staining whole fish specimens for simultaneous demonstration of bone, cartilage, and nerves. *Copeia* 1995:114–118.
- Stephenson EM. 1960. The skeletal characters of *Leiopelma hamiltoni* McCulloch, with particular reference to the effects of heterochrony on the genus. *Trans R Soc New Zealand* 88:473–488.
- Stephenson NG. 1965. Heterochronous changes among Australian Leptodactylid frogs. *Proc Zool Soc Lond* 144:339–350.
- Trueb L. 1973. Bones, frogs, and evolution. In: Vial JL, editor. *Evolutionary Biology of Anurans: Contemporary Research on Major Problems*. Columbia: University of Missouri Press. pp 65–132.
- Trueb L. 1979. Leptodactylid frogs of the genus *Telmatobius* in Ecuador with the description of a new species. *Copeia* 1979:714–733.
- Trueb L. 1993. Patterns of cranial diversity in Lissamphibia. In: Hanken J, Hall BK, editors. *The skull: Patterns of structural diversity (vol II)*. Chicago: The University of Chicago Press. pp 255–343.
- Trueb L, Alberch P. 1985. Miniaturization and the anuran skull: A case study of heterochrony. In: Duncker HR, Fleischer G, editors. *Vertebrate Morphology. Fortschritte der Zoologie, Band 30*. Stuttgart, NY: Gustav Fischer Verlag. pp 113–121.
- Tyler MJ, Davies MM, Martin AA. 1981. Australian frogs of the leptodactylid genus *Uperoleia* Gray. *Aust J Zool* 79:1–64.
- Vellard J. 1951. Estudios sobre batracios andinos I: El grupo *Telmatobius* y formas afines. *Memorias del Museo de Historia Natural Javier Prado* 1:1–89.
- Wassersug RJ. 1976. A procedure for differential staining of cartilage and bone in whole formalin-fixed vertebrates. *Stain Technol* 51:131–134.
- Wiens JJ. 1993. Systematics of the leptodactylid frog genus *Telmatobius* in the Andes of Northern Peru. *Occas Pap Mus Nat Hist Univ Kansas* 162:1–76.
- Yeh J. 2002. The evolution of development: Two portraits of skull ossification in Pipoid frogs. *Evolution* 56:2484–2498.

APPENDIX A Specimens Examined

Abbreviations for Institutions are: Fundación Miguel Lillo, Tucumán, Argentina (FML), J. S. Barrionuevo field numbers housed at Fundación Miguel Lillo (FML SB); D. Baldo field numbers housed at Museo de La Plata (MLP DB). In parenthesis, is expressed the postmetamorphic stage and SVL in millimeters as well as if are cleared-and-stained (CS).

Telmatobius oxycephalus.—**ARGENTINA:**
JUJUY: DEPARTAMENTO LEDESMA: Quebrada Río Jordán, Parque Nacional Calilegua, FML 03836-I

(adult female, CS), 3836-II, and 3836-III (adult males, CS); DEPARTAMENTO VALLE GRANDE: Río Jordán (1500 m a.s.l.), FML 2867-I, 2867-II (adult males, CS), 2867-III, and 2867-IV (adult females, CS); El Duraznillo, cerca de Calilegua, FML 1589 (nine adult specimens for SVL measurements), FML 1592 (Stage 44), Quebrada Agua del Tigre, FML 2861 (two adult specimens for SVL measurements); DEPARTAMENTO TILCARA: Río Huasamayo, Garganta del Diablo, FML SB 101 (postmetamorph, 22.6, CS), 102 (postmetamorph, 21.86 mm, CS), 031 (Stage-I juvenile, 28.66 mm, CS), 024 (Stage-II juvenile, 35.44 mm, CS), 029 (Stage-II juvenile, 32.8 mm, CS), 021 (subadult male, 40.8 mm SVL, CS), 023 (subadult female, 38.5 mm, CS), 019 (adult male, CS), 016 (adult specimen for SVL measurements), 018–20 (adult specimens for SVL measurements), MLP DB 3620 (postmetamorph, 22.38 mm, CS), 3619 (Stage-I juvenile, 28.66 mm, CS); DEPARTAMENTO MANUEL BELGRANO: El Duraznito, 8 km from Tiraxi, FML 1758 (five adult specimens for SVL measurements).

Telmatobius ceiorum.—**ARGENTINA: TUCUMÁN:** DEPARTAMENTO TAFÍ VIEJO: Alto de la Perdiz, Cabra Horco, road to Peñas Azules (2300 m a.s.l.), FML 02629 (four CS specimens).

Telmatobius hypselocephalus.—**ARGENTINA: JUJUY:** DEPARTAMENTO TUMBAYA: El Moreno, (3500 m a.s.l.), FML 04372 (CS).

Telmatobius laticeps.—**ARGENTINA: TUCUMÁN:** DEPARTAMENTO TAFÍ DEL VALLE: El Infiernillo, FML 1499 (four CS specimens).

Telmatobius pisanoi.—**ARGENTINA: TUCUMÁN:** DEPARTAMENTO TAFÍ DEL VALLE: Quebrada de Los Cardones, Ruta Provincial N 307, Km 98; FML 03269 (four CS specimens).

Telmatobius platycephalus.—**ARGENTINA: JUJUY:** DEPARTAMENTO TUMBAYA: El Angosto, 6 km S El Moreno (3600 m a.s.l.), FML 04371 (CS).

APPENDIX B

Summary of specimens studied and methods used in the published osteological descriptions of species of *Telmatobius*. Abbreviations for Institutions are: Fundación Miguel Lillo, Tucumán, Argentina (FML); Instituto de Zoología de la Universidad Austral, Valdivia, Chile (IZUA); Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN); Colección Boliviana de Fauna, La Paz, Bolivia (CBF); Museo de Zoología de la Universidad de Concepción, Chile (MZUC).

	Material	Method of preparation
<i>T. chusmisensis</i>	Five adult specimens, sex not specified (IZUA 3395–96, 3398–99, 3402)	Song and Parenti (1995)
<i>T. ceiorum</i>	Four adult females (FML 2629, 4348), three adult males (FML 2629)	Wassersug (1976), Simmons (1986)
<i>T. dankoi</i>	Two adult specimens, sex not specified (IZUA 2112)	Hollister (1934)
<i>T. fronteriensis</i>	Two adult females (MZUC 25095; MZUC 25103)	Hollister (1934)
<i>T. huayra</i>	One adult male (CBF 1224)	Wassersug (1976)
<i>T. hypselocephalus</i>	One adult female (FML 4372)	Wassersug (1976)
<i>T. laticeps</i>	Six adult females (FML 1499, 3956, 4385), four males (FML 1499, 3959)	Wassersug (1976), Simmons (1986)
<i>T. philippii</i>	Three specimens, sex not specified (IZUA 3193, 3194, 3195)	Dingerkus and Uhler (1977)
<i>T. pisanoi</i>	Five adult females (FML 3269, 3973), five adult males (FML 3269, 3969, 3979)	Wassersug (1976), Simmons (1986)
<i>T. platycephalus</i>	One adult female (FML 4371)	Wassersug (1976)
<i>T. rubigo</i>	One adult male (FML 20829)	Wassersug (1976)
<i>T. sibiricus</i>	One adult female (MNCN 17364), one adult male (MNCN 17365)	Dingerkus and Uhler (1977)
<i>T. simonsi</i>	One adult male (MNCN 17366)	Dingerkus and Uhler (1977)
<i>T. vilamensis</i>	Three adult males (IZUA 3146), one adult female (IZUA 3224)	Hollister (1934), Song and Parenti (1995)