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Chondrocranium and visceral skeleton of *Atelopus tricolor* and *Atelophryniscus chrysophorus* tadpoles (Anura, Bufonidae)

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Abstract. *Atelopus tricolor* and *Atelophryniscus chrysophorus* have gastromyzophorous tadpoles. Aside from specific differences, the larval chondrocrania and visceral skeletons show several shared character states, including an almost quadrangular, open chondrocranium, cornua trabeculae with expanded tips, cartilago suprarostralis as a single element, a posteriorly projected arcus subocularis quadrati, a closed muscular tunnel, and a simplified branchial basket, with only three pairs of ceratobranchiales. They are compared with diverse character states of suctorial larvae considering them as causally related to the stream life adaptations.

Resumen. *Atelopus tricolor* y *Atelophryniscus chrysophorus* poseen larvas gastromizóforas. Dejando de lado las diferencias específicas, los condrocráneos y esqueletos hiobranquiales larvales comparten diversos estados de carácter, incluyendo el condrocráneo cuadrangular y abierto, los cuernos trabeculares con extremos expandidos, el cartílago suprarostral como elemento único, el arco subocular proyectado hacia atrás, el túnel muscular cerrado y la cestilla branquial simplificada, con sólo tres pares de ceratobranquiales. Algunos de estos estados de carácter son comparados con aquellos de larvas suctoras considerados como causalmente relacionados a los hábitats torrentícolas, para una mejor comprensión de de la vida en ambientes de corriente rápida.

Introduction

The concept of gastromyzophorous larvae (first used by Inger, 1966) describes anuran tadpoles that inhabit fast flowing waters and have several morphological characteristics causally correlated to this kind of environment. They include the presence of a well developed abdominal sucker, an expanded and papillated oral disk, low caudal fins, normally terminating beyond the body and massive caudal muscles (Altig and Johnston, 1989; McDiarmid and Altig, 1999; Altig and McDiarmid, 1999).

Gastromyzophory has evolved independently in diverse anuran lineages, such as Ranidae (*Amolops* spp., *Huia* spp., *Meristogenys* spp., *Rana* sp. (part.)) (Inger, 1966; Kuramoto et al., 1984; Yang, 1991) and Bufonidae (*Ansonia* sp. (part), *Atelopus* spp., *Atelophryniscus*

sp., *Bufo* sp. (part)) (Starrett, 1967; Duellman and Lynch, 1969; Mebs, 1980; Lescure, 1981; Gray and Cannatella, 1985; Lynch, 1986; Gascon, 1989; Lindquist and Hetherington, 1988; McCranie et al., 1989; Cadle and Altig, 1991; Inger, 1992; Lavilla et al., 1997). Although the mentioned papers deal with diverse morphological aspects of gastromyzophorous larvae, little is known about their chondrocranial anatomy (Haas and Richards, 1998; Cannatella, 1999).

Herein, we describe the larval chondrocranial anatomy of two species of gastromyzophorous bufonids, the neotropical *Atelopus tricolor* and *Atelophryniscus chrysophorus*. Although it is not possible yet to establish if the shared characters in both taxa are due to environmental constraints or to common ancestry, they will be used for comparison with those of suctorial tadpoles (Haas and Richards, 1998), for a better understanding of anuran tadpole adaptations to life in fast flowing waters.

Material and Methods

Tadpoles of *Atelopus tricolor*, Boulenger, 1902, and *Atelophryniscus chrysophorus* McCranie, Wilson and Williams, 1989, were deposited at the herpetological collection of the National Museum of Natural History, Smithsonian Institution (USNM). They were preserved in 10%, neutral-buffered formalin, and staged according Gosner (1960) table. Tadpoles were cleared and double stained for bone and cartilage using alizarin red S and alcian blue, respectively (Dingerkus and Uhler, 1977).

Specimens examined are as follows:

Atelophryniscus chrysophorus. USNM 304978. Honduras, Atlántida, Cordillera de Nombre de Dios, south slope of Cerro Búfalo, Quebrada de Oro; 780 m. 15°38′S-86°47′W. 1 ind., stage 31 of Gosner (1960).

Atelopus tricolor. USNM 346226. Perú, Cuzco, Paucartambo. 68 km (by road) of Puente Unión on Río Tachila (= Bosque de las Nubes), km 150 on Paucartambo-Atalaya Road. 13°04′S-71°34′W. 1 ind., stage 33 of Gosner (1960).

Atelopus tricolor. USNM 346227. Perú, Cuzco, Paucartambo. 68 km (by road) of Puente Unión on Río Tachila (= Bosque de las Nubes), km 150 on Paucartambo-Atalaya Road. 13°04′S-71°34′W. 1 ind., stage 33 of Gosner (1960).

Atelopus tricolor. USNM 346228. Perú, Cuzco, Paucartambo. 55 km (by road) of Quebrada Morro Leguia (km 137 on Paucartambo-Atalaya Road). 13°07′S-71°34′W. 1 ind., stage 33 Gosner (1960).

Atelopus tricolor. USNM 346981. Perú, Cuzco, Paucartambo. 55 km (by road) of Quebrada Morro Leguia (km 137 on Paucartambo-Atalaya Road). 13°07′S-71°34′W. 1 ind., stage 33 Gosner (1960).

Chondrocranial terminology is a synthesis of that of De Sá (1988) and Haas (1995). Observations and illustrations were made using a Wild MC3 stereomicroscope with the aid of a camera lucida attachment.

Results

Chondrocranium of Atelopus tricolor *(fig. 1)*

At stage 33, the chondrocranium is nearly as long as wide, depressed, and mostly open dorsally. Each cartilago suprarostralis has the pars corporis and the pars alaris fused. Furthermore, the two corpora are medially fused, forming a thin, almost cylindrical cartilaginous bar perpendicular to the longitudinal axis of the chondrocranium. The partes alares, at both sides, are laminar and complex; their external margins have four distinct processes, the p. lateralis, p. ventrolateralis, and a strongly developed p. posterodorsalis. The p. posterodorsalis has a strong projection, directed backwards, that may represent the processus dorsalis posterior reported in other tadpoles. Overall, the cartilago suprarostralis represents about 56% of the chondrocranial width and lies posterior to the free anterior tips of the cornua trabeculae.
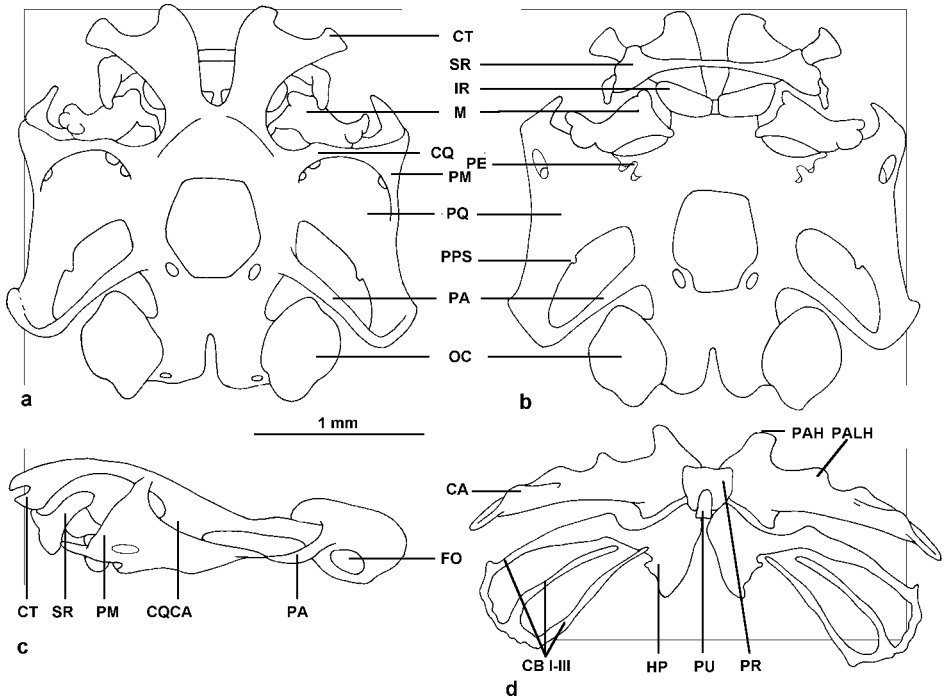

Figure 1. Chondrocraniu m and hyobranchial skeleton of *Atelopus tricolor* at stage 33 (USNM 346226). a) Dorsal view. b) Ventral view. c) Lateral view. d) Hyobranchial apparatus (ventral view). CA: condylus articularis; CB 1-3: ceratobrachial e 1-3; CQ: commissura quadratoorbitalis; CQCA: commissura quaratocraneali s anterior; CT: cornua trabeculae; FO: fenestra ovalis; HP: planum hypobranchiale; IR: cartilago infrarostrales; M: cartilago Meckeli; OC: otic capsule; PA: processus ascendens; PAH: processus anterior hyalis; PALH: processus antero-lateralis hyalis; PE: processus ethmoidalis; PM: processus muscularis; PPS: processus pseudopterygoideus; PQ: palatoquadratum ; PR: pars reuniens; PU: processus urobranchialis; SR: cartilago suprarostralis. Bar represents 1 mm.

The cornua trabeculae represent 27% of the chondrocranial length and they are free from each other along their length. The anterior margin of each cornu is widely expanded (2.8 times their basal width); it shows a wide and relatively deep, semicircular terminal notch, and bears a cartilaginous connection with the cartilago suprarostralis (fig. 2a). Because structures in the ethmoidal region are not yet differentiated (no septum nasi, tectum nasi, or lamina orbitonasalis are at stage 33), the cornua trabeculae are continuous with, and diverge from, the basicranial floor.

The cartilago orbitalis is not yet formed and the trabeculae cranii are strongly chondrified. The center of the basicranial floor is occupied by a large basicranial fenestra (corresponding to 27% of the chondrocranial length), and the two foramina carotica primaria are clearly visible at the posterolateral edges of the fenestra. The foramina craniopalatina are not observable, and they are probably included in the fenestra.

Dorsally, the otic capsules appear rhomboid and they have a posterior constriction on their external margin; they correspond to about 29% of chondrocranium length. A large fenestra ovalis (almost half the length of the capsule) is present, and the operculum is not yet developed. The otic capsules are fused to the basicranial floor, and this represents the only attachment to the neurocranium, due to the lack of larval processus oticus, processus basalis, taeniae tecti marginales, occipital arch, and tectum synoticum. Furthermore, the otic capsules lack a crista parotica.

The processus ascendens of the palatoquadrate is continuous with the posterior tip of the arcus subocularis; their junction occurs at about the mid-level of the otic capsule. The processus ascendens is oriented anteriorly, forming an approximately 45° angle with the main chondrocranial axis, forming a low suspensorium (Sokol, 1981).

The arcus subocularis is narrow posteriorly and widens anteriorly; its external edge is straight and almost parallel to the main axis of the chondrocranium. It is inclined in such a way that in cross section its inner margin lies below the level of the outer margin. Close to the confluence of the palatoquadrate and the processus ascendens there is a
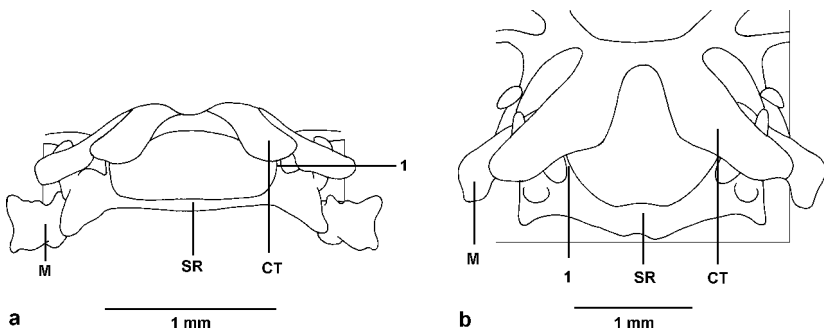

Figure 2. Anterior view of the chondrocranium of a) *Atelopus tricolor* (USNM 346226; stage 33) and b) *Atelophryniscus chrysophorus* (USNM 304978; stage 31). References as in fig. 1. (1) indicates the area of fusion of the cartilago suprarostralis with the cornua trabeculae. Bar represents 1 mm.

small, subtriangular projection, directed outwards and anteriorly. The subocular fenestra is displaced backwards, proportionally short (about 29% of chondrocranial length), and placed obliquely, following orientation of the processus ascendens.

The quadratum portion of palatoquadratum is complex. The commisura quadratocranealis anterior is wide and broadly continuous with the arcus subocularis. The palatoquadrate is dorsally concave along its length. On the anterior margin of the commissura quadratocranialis anterior, close to its attachment to the neurocranium, there is a laminar and triangular processus quadratoethmoidalis. Whereas, the processus pseudopterygoideus is scarcely visible on its posterior margin.

The processus muscularis is triangular and continuous with a cartilaginous bar (the commissura quadratoorbitalis), that fuses with the basicranial floor immediately anterior to the commissura quadratocranialis anterior. These three elements form a closed muscular tunnel. In lateral view, at the base of the processus muscularis there is a well developed foramen (its longer axis about 12% of the chondrcranial length). A cartilaginous bridge extends between the anterolateral tip of the processus muscularis and the pars articularis quadrati, forming the anterodorsal borders of the foramen. The anterolateral tip of the pars articularis quadrati has a triangular, finger-like and well-developed process (16% of the cranial length), directed anteriorly and medially.

The cartilago Meckeli is wide, flat, curved (S), and bears three well developed processes. The posterior end bears a rounded p. retroarticularis that articulates with the anterior tip of the pars articularis quadrati. The anterior tip has two processes, the p. dorsoventralis and the well developed, triangular, and dorsally projected p. dorsomedialis.

The cartilagines infrarostrales are paired, oblong, and wider laterally than medially. The commissura intramandibularis is ligamentous, while the copula intermandibularis consists of connective tissue with traces of chondrification, mostly close to the anterior edge.

Hyobranchial skeleton (fig. 1d)

Copula I (basihyale) is not visible as a discrete element. The ceratohyale is strongly chondrified and bears the typical five processes. The p. anterioris is proportionally wide; it curves anteriorly and outwards; the pp. lateralis, medialis and hyoquadratum are of similar size, subtriangular and blunt, whereas the p. posterioris is laminar and triangular.

The pars reuniens and Copula II (basibranchiale) are scarcely chondrified and consist of connective tissue with scattered chondrocytes. In contrast, the processus urobranchialis is well chondrified and subquadrangular in shape. The plana hypobranchiales are almost rhomboidal and show no peculiar characters.

There are only three pairs of ceratobranchialia. Ceratobranchiale I is the most completely developed and the only one continuous with the planum hypobranchiale. Ceratobranchialia II and III are thin and smooth. They are not connected by a secondary bridge and are free from the planum hypobranchiale. The ceratobranchialia are connected poste-

riorly by the commissurae terminales that show a small, anteriorly and upwardly directed projection at the level of Ceratobranchiale I. No spicula are evident.

Chondrocranium of Atelophryniscus chrysophoru s *(fig. 3)*

The chondrocranium of *Atelophryniscus chrysophorus* at stage 31 is wider than long, depressed and mostly open dorsally. Each cartilago suprarostralis has the pars corporis and the pars alaris fused. Furthermore, the two corpora are medially fused, forming a single, massive suprarostral element perpendicular to the longitudinal axis of the chondrocranium. In frontal view, the cartilago suprarostralis has two dorsolateral clefts that serve as points of articulation with the anterior tips of the cornua trabeculae. Medially, the cartilago suprarostralis consists of a transverse bar that curves posteriorly, giving it a strong convex contour anteriorly. The medial component of the cartilago suprarostralis connects to the ventral side of the cornua trabeculae through thin and cartilaginous projections (fig. 2b). The tip of the cartilago suprarostralis projects posteriorly, into strong and subcylindrical processes, forming a 90° angle. Although there are no clear limits, these posterolateral processes probably correspond to the pars alaris. Close to the posterior tips of the cartilago suprarostralis, adrostral chondrifications are visible as two small and elliptical cartilages.
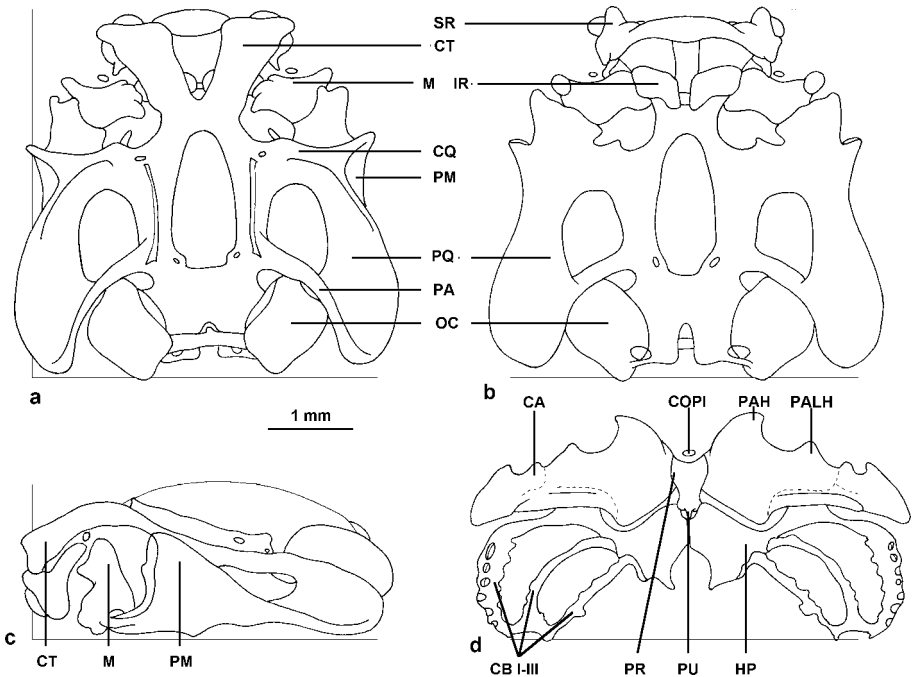

Figure 3. Chondrocranium and hyobranchia l skeleton of *Atelophryniscu s chrysophorus* at stage 31 (USNM 346226). a) Dorsal view. b) Ventral view. c) Lateral view. d) Hyobranchia l apparatu s (ventral view). Reference s as in fig. 1. Bar represent s 1 mm.

The cornua trabeculae are 25% of the chondrocranial length and are independent of each other along their length. The anterior margin of each cornu is widely expanded (about twice their basal width); each cornu is smoothly and ventrally curved throughout its length. A small projection on the ventral and outer margin of each cornu may represent the processus lateralis. At the ethmoidal region, the only differentiated structure is a small, rectangular projection for the insertion of the outer meninges (no septum nasi, tectum nasi or lamina orbitonasalis are developed at stage 31). The cornua trabeculae are continuous with, and diverge from, the basicranial floor.

The weakly developed cartilagines orbitales are mostly evident posteriorly. Two foramina are visible on their posterior half, the foramen opticum and the foramen oculomotorium. In addition, the foramen prooticum is visible and opens dorsally, due to the incomplete development of the taenia tecti marginalis. The center of the basicranial floor is occupied by a large (about 35% of chondrocranial length) fenestra basicranealis, covered by a thin sheet of weakly AB+ tissue. The foramina carotica primaria are clearly visible at the posterolateral edges of the fenestra, whereas the usually anterior foramina craniopalatina are not observable (probably included in the fenestra).

Dorsally, the otic capsules appear rhomboid and correspond to about 28% of chondrocranial length. A large fenestra ovalis, occupying almost half of the capsule's length, is present; the operculum is not yet developed. The otic capsules are fused to the basicranial floor; they connect to each other dorsally by a thin tectum synoticum that bears a short taenia tectum medialis. Other structures, such as the larval processus oticus, taenia tecti marginalis, and crista parotica are absent.

The processus ascendens of the palatoquadrate is continuous with the posterior tip of the subocular. It is oriented anteriorly, forming an approximately 45° angle with the main chondrocranial axis. It fuses with the trabeculae cranii below foramen oculomotorium, forming a low suspensorium condition (Sokol, 1981).

The arcus subocularis is narrow anteriorly and wide posteriorly. The posterior tip of the arcus subocularis extends back, almost reaching the posterior margin of the otic capsules, beyond the level of the occipital condyles. The fenestra subocularis is displaced backwards; relatively short (about 24% of chondrocranial length), and oriented obliquely, following orientation of the processus ascendens.

The anterior end of the palatoquadratum has a distinct and robust pars articularis quadrati, which articulates with the cartilago Meckeli. The processus muscularis is triangular and continuous with a cartilaginous bar, the commissura quadratoorbitalis. The later fuses with the commissura quadratocranealis anterior at the basis of the sharp and triangular processus quadratoethmoidalis. The muscular tunnel is closed and a processus pseudopterygoideus is absent. A small processus ventralis is evident from the anterolateral base of the p. muscularis.

Each cartilago Meckeli is wide, curved (S) and contorted. The proximal edge is rounded and bears a rounded processus retroarticularis that articulates with the anterior tip of the pars articularis quadrati. The anterior tip has a p. dorsoventralis and a p. dorsomedialis.

The commissura intramandibularis is formed by a weakly chondrified ligament, and runs from the medial process of the cartilago Meckeli to the respective cartilago infrarostrale.

The cartilagines infrarostrales are paired, semilunar and connected medially to form a semicircular ring. The cartilagines infrarostrales attach to each other through a thin, cartilaginous commissura intermandibularis.

Hyobranchial skeleton (fig. 3d)

A small, almost oval, and well chondrified Copula I (basihyale) is present. The ceratohyale is strongly chondrified and bears the typical five processes. The processus anterior and the p. posterior are the most prominent ones; the p. hyoquadratum is well developed, and the pp. medialis and lateralis are the smallest and about equal in size.

The pars reuniens is better chondrified than the Copula II (basibranchiale), and bears a wide and short processus urobranchialis. The plana hypobranchiales are the least chondrified elements of the visceral complex and show no peculiar traits.

There are only three pairs of ceratobranchialia. Ceratobranchiale I is the most completely developed and the only one continuous with the planum hypobranchiale; it possesses a pierced outer margin. Ceratobranchialia II and III are less developed. They are not connected by a secondary bridge, but they have spicula-like projections that connect to the planum hypobranchiale. The ceratobranchialia are connected to each other posteriorly by well-developed commissurae terminales.

Discussion

Among anurans, several morphotypes (guilds sensu Altig and Johnston, 1989) evolved in relation to fast flowing water environments. Members of two of these categories, suctorial and gastromyzophorous, inhabit the microhabitats with the fastest current speeds. It is logical to suppose that they will show peculiar anatomical specialization.

The characteristics of the external morphology of the species considered here have been previously reported (*Atelopus tricolor*, Lavilla et al., 1997; *Atelophryniscus chrysophorus*, McCranie et al., 1989). On the other hand the chondrocranial anatomy of generalized, pond-type bufonid larvae was described by Sedra (1950) and Sedra and Michael (1958).

Six of the characters shared by *Atelopus tricolor* and *Atelophryniscus chrysophorus* larvae are used for comparison between gastromyzophorous and suctorial tadpoles (table 1). They follow those considered as causally linked to highly specialized habits among suctorial tadpoles (Haas and Richards, 1998: 133-134), plus those derived from the hyobranchial skeleton. Our samples consisted of prometamorphic tadpoles in early stages (31 and 33 of Gosner, 1960); consequently, lacking structures are quoted as not recorded, to avoid the confusion between absence (not present in any stage) and not yet developed (not present in earlier stages).

Table 1. Comparison of suctorial and gastromyzophorou s tadpoles. Information on suctorial tadpole s based on Haas and Richards (1998).

Character	Suctorial tadpoles	Gastromyzophorou s tadpoles
Cornua trabeculae	Very wide anteriorly and fused along most of their length in some taxa	Very wide anteriorly; independen t from each other in all their length
Lower jaw	Robust	Well developed, but never as massive as drawn for suctorial tadpoles (figs. 3-4 in Haas and Richards, 1998)
Cartilago suprarostralis (=cartilago labialis supe-rior)	Components robust and partially or fully fused	All component s always fused in a sin-gle structure; pars corpori s proportion-ally thin
Maximum width of the skull	At the jaw articulation	Skull almost uniformly wide; outer margins of arco suboculari s subparal-lel to axial axis
Palatoquadrate	Robust. Attached to the chondrocra-nium by broad commisura quadra-tocranealis anterior, larval processu s oticus, processus ascenden s (thin or absent in some) and larval processu s basalis	Robust. Attached to the chondrocra-nium by a broad commisura quadra-tocranealis anterior, the commissura quadrato orbitalis and the processu s ascendens. Larval processus oticus and processus basalis not recorded
Processus ventralis	At the anterolateral base of the p. mus-cularis palatoquadrat i	Not recorded
Ceratobranchiale IV	Present	Absent
Planum hypobranchial e	Fused	Independent
Spicula	Present	Absent

Overall, the chondrocrania of the gastromyzophorou s larvae appear to be weaker than those of suctorial larvae. In fact, they are flat, open structures, in which the cornua trabeculae are not joined each other and the palatoquadratum has no direct cartilaginous connections with the otic capsules. Furthermore, the otic capsules are attached to the neurocranium only by means of the chondrocranial floor (pars parachordalis). This posterior weakness of the neurocranium is compensated by a massive structure of the commissura quadratocranialis anterior and the commisura quadratoorbitalis, that forms the dorsal roof of the muscular tunnel.

The weaker condition of the chondrocranium of the gastromyzophorou s tadpoles could be functionally related to the presence of a well developed belly sucker, which is mostly responsible for the adhesion to the substrate. Among suctorial forms, the widely expanded oral disk and its related musculature, along with the strongly developed skeletal support, are the structures involved in attachment (Gradwell, 1971; Altig and Brodie, 1972; Wake, 1993).

The branchial baskets of gastromyzophorou s taxa are weakly developed and with areas of poor chondrification. In whole mounted, cleared and stained *Atelopus* and

Atelophryniscus larvae only three pairs of simple ceratobranchialia are visible. This seems to be unique among anurans. However, in cross sections of *Atelopus* larvae, a very small 4th ceratobranchial can be found (Haas, per. com.). Here again, the supplementary adhesion that is provided by the belly sucker could explain the almost complete reduction of one ceratobranchial. Then, in gastromyzophorous larvae, negative pressure produced by the buccal pump complex could be lower than in suctorial tadpoles.

The extreme reduction of one ceratobranchial, to the effect of having only three pairs of chondrified ceratobranchialia needs further comments. This character state can be considered either as a convergence produced by the life in fast running waters in these two taxa or could be taken as a synapomorphy uniting them. Because all other known rheophilous tadpoles have four pairs of chondrified ceratobanchialia, we could possibly discard the convergence argument. Therefore, the existence of a recent common ancestor of *Atelopus* and *Atelophryniscus* (and maybe for those *Bufo* with gastromyzophorous tadpoles, like *B. veraguensis*) should be considered. However, this question must be addressed in the context of a robust phylogenetic hypothesis for the family Bufonidae, which is currently lacking (Graybeal, 1997).

Besides the characters shared between *Atelopus* and *Atelophryniscus*, the two larvae show some important differences. Particularly, the chondrocranium of *Atelopus tricolor* exhibits several unique traits. Among them, the pars alaris of the cartilago suprarostralis is complex; the cornua trabeculae have a distinct notch in their free and expanded ends; the subocular fenestra is reduced in size and displaced posteriorly; a distinct foramen is found at the base of the muscular process; and a well-developed, finger-like, process extends from the anterolateral margin of the pars articularis quadrati. The latter process is in opposite direction to the processus ventralis reported by Haas and Richards (1998) in *Hyla armata*, *Litoria nannotis*, *L. rheocola*, *Nyctimystes dayi* and *Boophis* sp. In addition, the hyobranchial apparatus of *Atelopus* lacks copula I (basihyale) and spicula.

On the other hand, the chondrocranium of *Atelopus tricolor* is unique by the posterior extreme extension of the arcus subocularis of the palatoquadrate, that lies at the level of the posterior margin of the otic capsules, beyond the level of the occipital condyles.

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