

Description of the tadpole of *Cochranella resplendens* and redescription of the tadpole of *Hyalinobatrachium aureoguttatum* (Anura, Centrolenidae)

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Abstract

Description of the tadpole of *Cochranella resplendens* and redescription of the tadpole of *Hyalinobatrachium aureoguttatum* (Anura, Centrolenidae). The tadpole of *Cochranella resplendens* is described and that of *Hyalinobatrachium aureoguttatum* is redescribed; information on their ontogenetic variation also is included. *Cochranella resplendens* is characterized by having a non-emarginated oral apparatus and an upper jaw sheath nearly straight with a smooth arch in the middle. *Hyalinobatrachium aureoguttatum* has an emarginated oral apparatus with a characteristic M-shaped upper jaw sheath and bears few (1–5) submarginal papillae on the upper labium. Although the two species show few changes in the oral apparatus during their development (except for changes in Gosner Stages 24 and 42 in *C. resplendens* and 23–24 in *H. aureoguttatum*), there are major ontogenetic changes in size and coloration.

Keywords: Anura, Centrolenidae, larvae, ontogeny, Ecuador.

Resumen

Descripción del renacuajo de *Cochranella resplendens* y redescrípción del renacuajo de *Hyalinobatrachium aureoguttatum* (Anura, Centrolenidae). Se describe el renacuajo de *Cochranella resplendens* y se redescríbe el de *Hyalinobatrachium aureoguttatum*, incluyendo información sobre su variación ontogénica. *Cochranella resplendens* se caracteriza por tener un aparato oral sin inflexión intramarginal y un supraquerostoma casi recto, aunque ligeramente arqueado en la mitad. Por otro lado, *H. aureoguttatum* tiene un aparato oral con inflexión intramarginal; presenta un característico supraquerostoma en forma de “M” y pocas papilas intramarginales (1–5) en el labio superior. Ninguna de las dos especies mostró una variación significativa en el aparato oral durante su desarrollo (excepto en los estadios Gosner 24 y 42 en *C. resplendens* y 23–24 en *H. aureoguttatum*). Los cambios ontogénicos más evidentes fueron en el tamaño y la coloración.

Palabras claves: Anura, Centrolenidae, larva, ontogenia, Ecuador.

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Resumo

Descrição do girino de *Cochranella resplendens* e redescrição do girino de *Hyalinobatrachium aureoguttatum* (Anura, Centrolenidae). Descrevemos o girino de *Cochranella resplendens* e redescrivemos o girino de *Hyalinobatrachium aureoguttatum*, incluindo informação sobre sua variação ontogenética. *Cochranella resplendens* caracteriza-se por apresentar um aparato oral sem inflexão intramarginal e a porção superior do bico córneo quase reta, ainda que ligeiramente arqueado na porção mediana. Por outro lado, *H. aureoguttatum* possui aparato oral com inflexão intramarginal e apresenta a porção superior do bico córneo característica, em forma de “M”, e poucas papilas intramarginais (1–5) no lábio superior. Nenhuma das duas espécies mostrou uma variação significativa no aparato oral durante o desenvolvimento (exceto nos estágios 24 e 42 de Gosner em *C. resplendens* e 23–24 em *H. aureoguttatum*). As mudanças ontogenéticas mais evidentes estão relacionadas com o tamanho e a coloração.

Palavras-chave: Anura, Centrolenidae, larvas, ontogenia, Equador.

Introduction

Centrolenidae contains 150 species of glassfrogs (AmphibiaWeb 2009) that are distributed throughout the Neotropics, from Mexico to Bolivia (Guayasamin *et al.* 2009). Most of this diversity is concentrated in the northern Andes; such is the case for Ecuador, where 48 species have been reported so far (Coloma 2009).

Cochranella resplendens occurs in the Upper Amazon Basin in Ecuador, Peru, and southwestern Colombia (Lynch and Duellman 1973, Cisneros-Heredia 2008). This species seems to be rare, and only a handful of adult specimens are known; its tadpole has never been described. *Hyalinobatrachium aureoguttatum*, described by Barrera-Rodriguez and Ruiz-Carranza (1989) occurs on the western slopes of the Cordillera Occidental in Colombia (departments of Chocó, Antioquia, and Valle del Cauca), in Chocoan Ecuador (Esmeraldas Province), and in Panama (Darién Province, Frost 2009). Ibáñez *et al.* (1999) described the tadpole based on specimens from Serranía de Jungurudó, Panama.

Centrolenid tadpoles are exotrophic, lotic and burrower/fossorial. They correspond to Type-IV tadpole morphology as defined by Orton (1953), and the benthic ecomorphological

guild sensu Altig and Johnston (1989). Glassfrog tadpoles have a vermiform and depressed body, a long tail, and reduced fins; their coloration is reddish because of high skin vascularization, and the eyes are located dorsally on the head (McDiarmid and Altig 1999).

Larval descriptions are available for only 10 Ecuadorian centrolenids: *Centrolene geckoideum* (Rueda-Almonacid 1994), *Espadana prosoblepon* (Starrett 1960), *Hyalinobatrachium aureoguttatum* (Ibáñez *et al.* 1999), *H. fleischmanni* (Starrett 1960), *H. munozorum* (Duellman 1978), *H. valerioi* (Starrett 1960), *Teratohyla spinosa* (Starrett 1960), *T. pulverata* (Hoffman 2004), *T. midas* (Duellman 1978), and *Vitreorana oyampiensis* (Hero 1990). Most of these descriptions are based on individuals at early stages before the oral apparatus is fully developed. A potential consequence of limiting description to few developmental stages is that the ontogenetic variation of presumably relevant taxonomic traits is not reported (Rada *et al.* 2007). Here we describe for the first time the tadpole of *Cochranella resplendens*. We also redescribe the tadpole of an Ecuadorian population of *Hyalinobatrachium aureoguttatum*, previously described by Ibáñez *et al.* (1999). The two descriptions are based on larvae at different developmental stages.

Materials and Methods

Egg clutch collection: Hyalinobatrachium aureoguttatum

A clutch of 36 eggs (QCAZ 37752; Figure 1D) was collected at Estero Piedras (80°05'17.8" W, 0°42'18" N; 109 m) near Caimito-Tonchigue and Río Quingue, Provincia de Esmeraldas, Ecuador (Figure 2), on 25 August 2007 by Santiago R. Ron, Ítalo G. Tapia, and Leigh Marshal. The eggs were on the underside of a bush leaf along the stream; on the top of the same leaf, there was an adult male (QCAZ 42351) that was identified as the parent (Santiago R. Ron field notes, 25 August 2007) and that clearly corresponds to the species *H. aureoguttatum*. Another clutch of eggs (QCAZ 32072) was collected in a stream at Durango (78°37'26.6" W, 01°02'30.7" N; 243 m), Provincia de Esmeraldas, on 24 May 2006 by Italo G. Tapia, Luis A. Coloma and Diego Almeida-Reinoso. Four adults (QCAZ 32068–71) of *H. aureoguttatum* were near the egg clutch. Both localities are in primary Chococoan rain forest. The vegetation in this region corresponds to Evergreen Lowland Forest (Bosque Siempre Verde de Tierras Bajas, *sensu* Cerón *et al.* 1999). The annual rainfall in the region is 199–975 mm, and the mean annual temperature is 24.9°C (Hijmans *et al.* 2005).

Egg clutch collection: Cochranella resplendens

A clutch of 74 eggs (QCAZ 38088a–h, Figure 1C) in Stage 25 (*sensu* Gosner 1960) was collected at Río Napinaza (78°24'25.2" W, 02°55'36" S; 1100 m), 6.6 km N on the road from General Leonidas Plaza Gutiérrez (= Limón) to Macas, Provincia of Morona Santiago, Ecuador, on 07 June 2008 by Ítalo G. Tapia, Luis A. Coloma, Santiago R. Ron, and David Salazar-V. The creek and stream have been severely disturbed, but remains of natural vegetation can still be found. The stream is on the Amazonian

slopes of the Cordillera Oriental in the southern Ecuadorian Andes (Figure 2). The vegetation in this region corresponds to the Foothill Evergreen Forest (Bosque Siempreverde Piemontano, *sensu* Palacios *et al.* 1999). The annual rainfall in the region is 2588 mm, and the mean annual temperature is 21°C (Hijmans *et al.* 2005). The clutch of eggs was on the upper surface of a leaf of a bush along the Río Napinaza.

The eggs clutches of the two species were taken to the lab facilities of Centro de Investigación y Conservación de Anfibios (CICA) of Museo de Zoología of the Pontificia Universidad Católica del Ecuador (QCAZ), where they were raised (described below) and preserved at several stages of development. Original digital images cited in the text and a video file of the egg clutch of *H. aureoguttatum* are deposited at QCAZ and displayed at AmphibiaWeb Ecuador (<http://zoologia.puce.edu.ec/Anfibios.aspx>).

Laboratory rearing of eggs and tadpoles

The leaves (with the attached egg clutches) were attached to the top of a small plastic container that contained about 3 cm of filtered water. Once the eggs hatched, the larvae were transferred into a 50 x 30-cm aquarium, with about 7 cm of water; the water was replaced each 15 days. The water temperature was constant at 25°C. The tadpoles were fed daily with Super Alimento de Renacuajos (SAR: protein = 27%, humidity = 10.02%, fiber = 42.66%, and Carbohydrates = 48.28%), a product developed at CICA. Tadpoles in Stages 23–28 and 35 for *Hyalinobatrachium aureoguttatum* and Stages 24, 25, 27, 28, 36, 38 and 42 (*sensu* Gosner 1960) for *Cochranella resplendens* were preserved in buffered formalin (10% formaldehyde; Simmons 1987) for the description.

Description of the tadpoles

Tadpoles were staged following the methodology of Gosner (1960). For the general

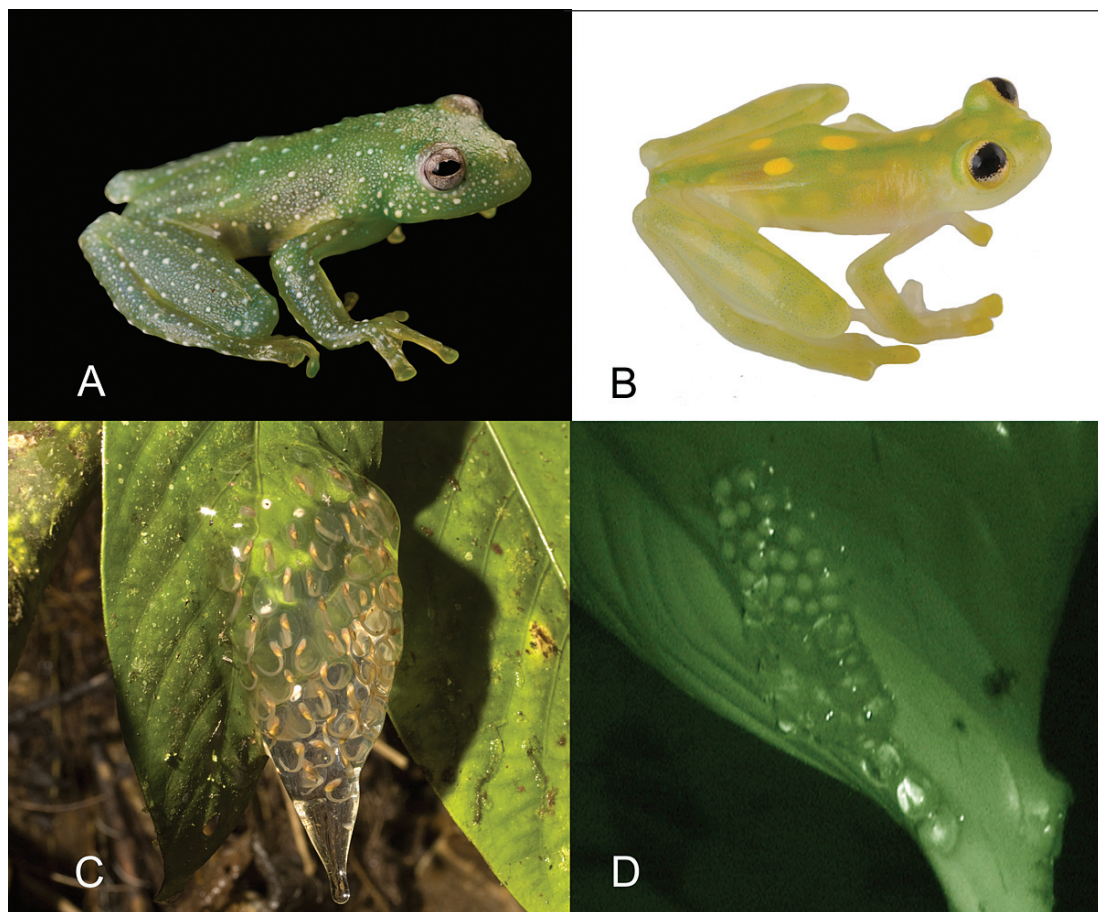


Figure 1 - Adults and clutch of eggs of the two species of glassfrogs described herein. (A) *Cochranella resplendens*, juvenile, SVL = 22.1 mm, QCAZ 38088 (photo QCAZ f5285); (B) *Hyalinobatrachium aureoguttatum*, undetermined sex, QCAZ 45365 (photo QCAZ 5284); (C) egg clutch of *C. resplendens*, QCAZ 38088 (photo QCAZ f5271); (D) egg clutch of *H. aureoguttatum*, QCAZ 37752 (photo QCAZ f5287). Photos by LAC.

description of the larvae of *Hyalinobatrachium aureoguttatum*, an individual in Stage 35 was selected, as recommended by Rada *et al.* (2007). The ontogenetic variation was documented using 15 tadpoles— 1 in Stage 23, 1 in Stage 24, 5 in Stage 25, 3 in Stage 26, 1 in Stage 27, 3 in Stage 28, and 1 in Stage 35.

The general description of the tadpole of *Cochranella resplendens* was based on an individual in Stage 36. The developmental variation was documented using 49 tadpoles—13

in Stage 24, 20 in Stage 25, 5 in Stage 27, 7 in Stage 28, 1 in Stage 31, 2 in Stage 38, and 1 in Stage 42.

The terminology for traits (body shape, tail shape, oral disc size etc.) used in the description was taken from Mijares-Urrutia (1998) and McDiarmid and Altig (1999). We measured the morphological characters suggested by Rada *et al.* (2007) and Castillo-Trenn (2004) with a Tresna digital caliper to the nearest ± 0.01 mm. The descriptions of

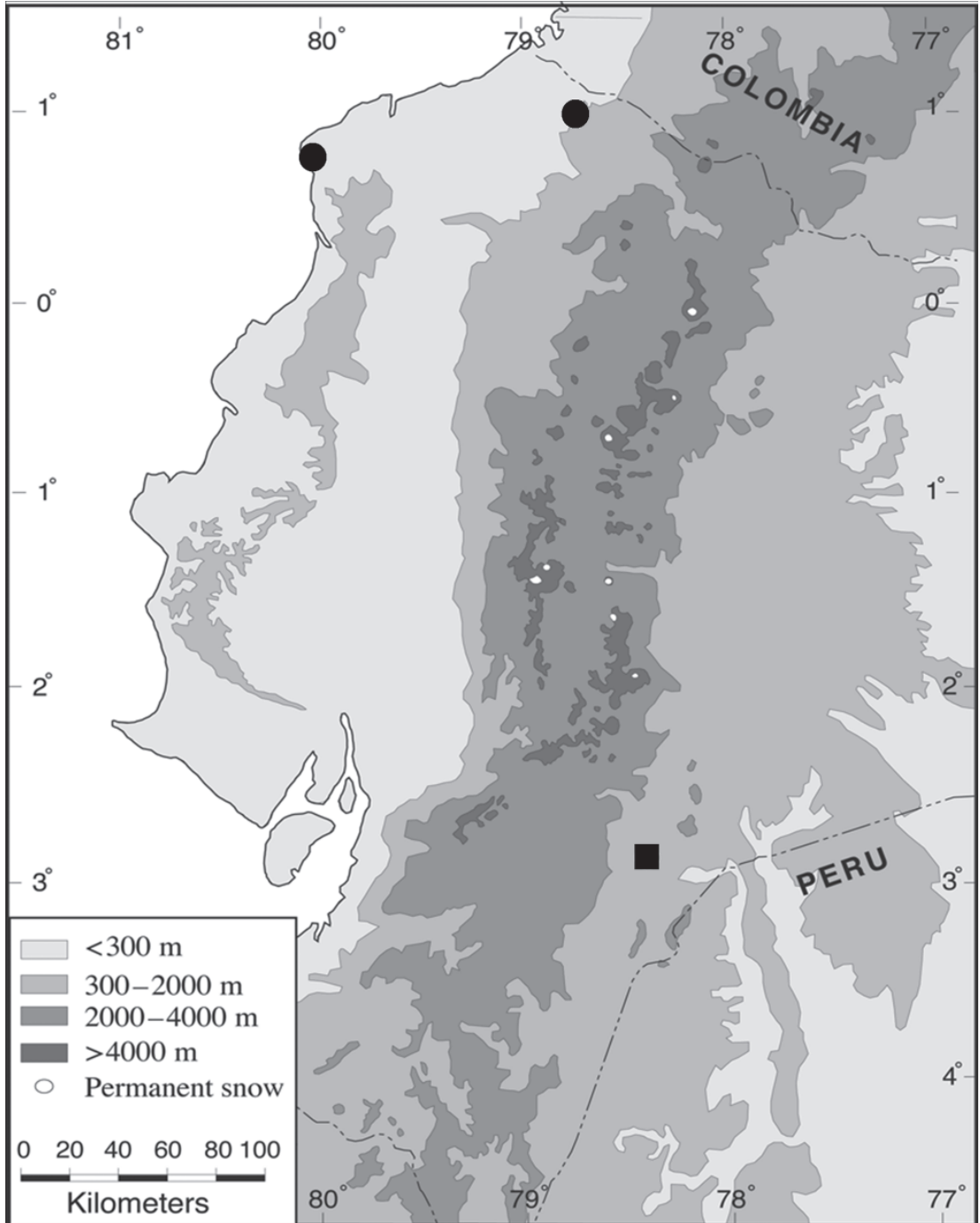


Figure 2. - Map of Ecuador showing localities of *Cochranella resplendens* (black square) and *Hyalinobatrachium aureoguttatum* (black circles).

the tadpoles were based in the 22 characters described below, but for the ontogenetic variation we only considered the 13 characters suggested by Rada *et al.* (2007).

Meristic characters were: (TL) total length = distance from tip of snout to tip of tail; (BL) = body length distance from tip of snout to beginning of caudal musculature; (TAL) tail length = distance from beginning of caudal musculature to tip of tail; (BW) body width = width of body at the level of spiracle; (BH) body height = height of the body behind the eyes; (IND) internarial distance = distance between centers of narial apertures; (NSD) nostril-snout distance = distance between center of nostril to tip of snout; (NED) nostril-eye distance = distance between center of nostril aperture to anterior edge of eye; (IOD) interorbital distance = distance between the internal border of the eyes; (SAD) spiracle aperture diameter; (SSD) spiracle-snout distance = distance between the tip of snout and posterior border of spiracle; (ESD) eye-snout distance = distance between tip of snout and anteriormost border of eye; (MTH) maximum tail height = height of tail, including the fins, where tail reaches its maximum height; (TMH) tail muscle height = height of caudal musculature at the beginning of the tail; (TMW) tail muscle width = width of muscle at the beginning of the tail; (DFH) dorsal fin height = maximum height of dorsal fin; (VFH) ventral fin height = maximum ventral fin height; (ODW) oral disc width = transverse diameter of oral disc; (UJW) upper jaw sheath width = upper jaw sheath transverse width, including lateral processes; (LJW) lower jaw sheath width; (VTL) vent tube length = distance between beginning of vent tube and its aperture; (VTW) vent tube width = transverse width of vent tube.

The oral apparatus of some specimens was stained with Methylene Blue to facilitate visualization of the structures. The taxonomy for glassfrogs follows the proposal by Guayasamin *et al.* (2009).

Results

Cochranella resplendens

Tadpole description (QCAZ 38088i, Stage 36, Figures 3A-B, 4A, 7C, Table 1)

Total Length: 34.8 mm; Body Length: 10.5 mm (30.2% of TL). Body elongate, oval-depressed (sensu Mijares-Urrutia 1998), wider (Body width: 4.8 mm) than high (Body height: 3.2 mm). Chondrocranial elements not visible. Snout rounded in dorsal and lateral views. Lateral-line system inconspicuous. Eyes dorsal, distance from eye to tip of snout: 2.9 mm; small narial apertures, opening: 1.7 mm from tip of snout, internarial distance: 1.8 mm; distance from narial opening to anterior edge of eye: 0.8 mm. Interorbital distance (1.2 mm) less than internarial distance. Short spiracle, single, sinistral, at the posterolateral region of the body; spiracular aperture with posterodorsal orientation; inner wall present as slight ridge (sensu McDiarmid and Altig 1999); aperture diameter: 0.7 mm; distance from tip of snout to spiracular opening: 7.6 mm, spiracle located at 72.4% of body length from tip of snout. Vent tube short and abdominal, free posteriorly, opening directed posteriorly; tube length: 0.4 mm, tube transverse width: 0.3 mm. Tail long (24.2 mm, 2.3 × BL) with subacute tip. Myotomes visible throughout entire length of tail; straight medial line visible separating dorsal and ventral myotomes. Tail muscle width: 2.2 mm; tail muscle height: 2.3 mm; maximum tail height: 4.0 mm; dorsal and ventral fin height: 1.1 mm. Dorsal fin originating at about midlength of tail; dorsal fin height almost uniform except for anterior and posterior ends. Ventral fin originating almost at base of the tail muscle and reaching its maximum height posterior to mid-length of tail.

Medium-sized oral disc transverse width: 2.5 mm (52% BW), not-emarginate (Figures 4A, 7C see labium without lateral inflections), anteroventral; 38 marginal and uniserial

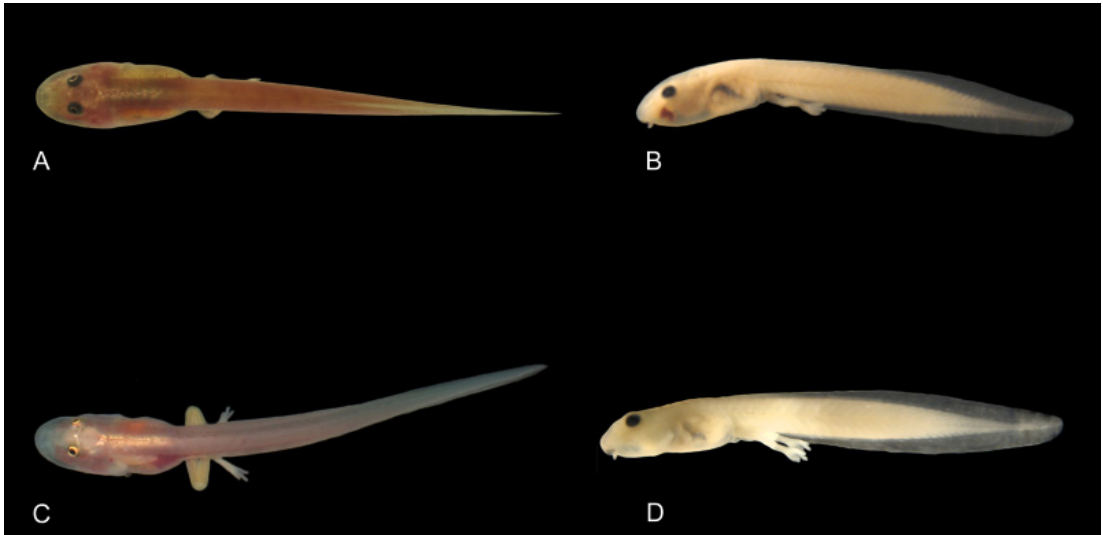


Figure 3 - Tadpoles of *Cochranella resplendens* and *Hyalinobatrachium aureoguttatum* in life and preservative. (A) *Cochranella resplendens* in life, dorsal view, Stage 36, QCAZ 38088i (photo QCAZ f5275); (B) *Cochranella resplendens* in preservative, lateral view, Stage 36, QCAZ 38088i (photo QCAZ f5277); (C) *Hyalinobatrachium aureoguttatum* in life, dorsal view, Stage 35, QCAZ 37752e (photo QCAZ f5283); (D) *Hyalinobatrachium aureoguttatum* in preservative, lateral view, Stage 35, QCAZ 37752e (photo QCAZ f5282). Photos in life by LAC.

papillae distributed around oral disc, mainly on the lower labium; upper labium with papillae only on lateral extremes. Papillae relatively large, acute. Lengths of lateral papillae ($n = 15$) 0.04–0.16 mm (mean = 0.10 ± 0.03), width 0.07–0.16 mm (mean = 0.09 ± 0.02); lengths of ventral papillae ($n = 23$) 0.02–0.16 mm (mean = 0.11 ± 0.03), width 0.07–0.18 mm (mean = 0.09 ± 0.03). Upper jaw sheath completely keratinized with serrated edge; nearly straight, with a smooth arch in middle. Lower jaw sheath keratinized, U-shaped and with serrated edge. Transverse width of upper jaw sheath including lateral processes: 0.96 mm (38.4% ODW); lower jaw sheath: 0.78 mm (31.2% ODW). Serrations broad-based, short, oriented straight medially. Labial tooth row formula 2(2)/3; tooth rows A-1 and P-3 less pigmented than other rows. Anterior and posterior tooth rows about equal in length and reaching extremes of the anterior and posterior

labia, respectively. Tooth row A-1 2.3 mm long, number of teeth = 208; tooth row A-2 interrupted medially located at the sides of upper jaw sheath, length of each side: 0.6 mm, number of teeth = 86; tooth row P-1 2.2 mm long, number of teeth = 154; tooth row P-2 2.1 mm long, number of teeth = 192; tooth row P-3 2.2 mm long, number of teeth 207.

Color in life (Figure 3A, Stage 36)

Based on a color digital photo (QCAZ f5275 of QCAZ 38088i) taken by LAC. Dorsally, the tadpole is mostly red, with some aggregations of iridophores that form an interorbital line and a middorsal band from behind the eyes to nearly the end of the body. Dorsally, the anteriormost part of the body is pale yellow. Laterally, the tadpole is translucent. The irises are mostly black with a yellow ring around the pupil.

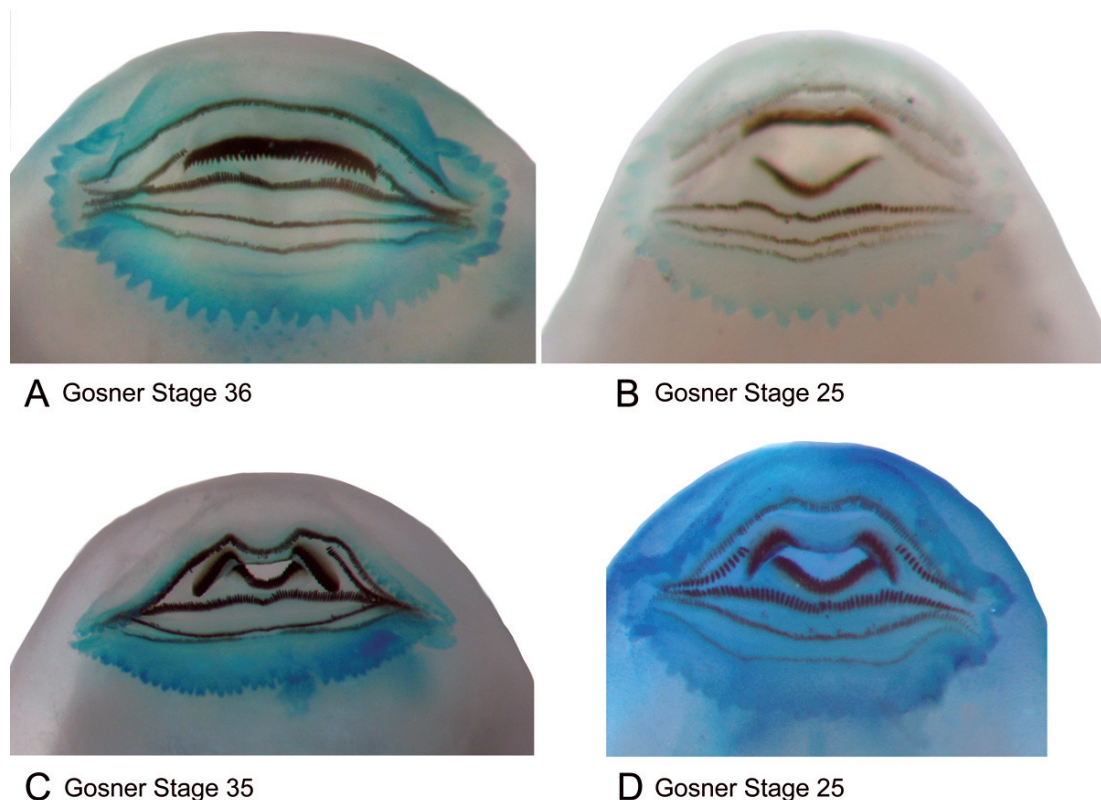


Figure 4 - Oral apparatus of *Cochranella resplendens* and *Hyalinobatrachium aureoguttatum*. (A) *C. resplendens*, QCAZ 38088i (photo QCAZ f5276); (B) *C. resplendens*, QCAZ 38088a (photo QCAZ f5273); (C) *H. aureoguttatum*, QCAZ 37752e (photo QCAZ f5281); (D) *H. aureoguttatum*, QCAZ 37752b (photo QCAZ f5280). The blue coloration is caused by the use of methylene blue to dye the papillae.

Color in preservative - buffered formalin (formaldehyde 10%), Stage 36

QCAZ 38088i. The tadpole is cream. Along the mid-dorsum, there is a light-brown coloration that extends dorsally throughout the length of the tail. The only evidence of the iridophores seen on the dorsum in life is a horizontal band behind the eyes. The belly and the sides of the body are translucent. The medial line of the tail is brown, but the color fades posteriorly.

Ontogenetic variation

Variation of 13 meristic characters of tadpoles in Stages 24–42 are given in Table 1. Individuals in Stage 24 still have some yolk (Figure 5A); the oral apparatus is not fully formed; none of the oral structures is keratinized; tooth ridges are present with no labial teeth, the upper jaw is not visible and the lower jaw is not completely developed; the papillae are small and with a rounded tip.

Table 1 - Dimensions in mm of the larvae of *Cochranella resplendens*, QCAZ 38088a-h, all fixed in the year 2008. Stages 24, 25, 27, 28: mean \pm standard deviation (first row), range (second row). Abbreviations: Total length (TL), Body length (BL), Tail length (TAL), Body width (BW), Body height (BH), Internarial distance (IND), Interorbital distance (IOD), Snout-spiracle distance (SSD), Eye-snout distance (ESD), Maximum tail height (MTH), Tail muscle height (TMH), Oral disc width (ODW), Vent tube length (VTL).

	Stage 24 <i>n</i> = 13	Stage 25 <i>n</i> = 20	Stage 27 <i>n</i> = 5	Stage 28 <i>n</i> = 7	Stage 31 <i>n</i> = 1	Stage 36 <i>n</i> = 1	Stage 38 <i>n</i> = 2	Stage 42 <i>n</i> = 1	
TL	10.2 \pm 0.25 9.7-10.5	14.1 \pm 2.5 11.8-19.5	21.6 \pm 3.01 18.9-25.8	26.1 \pm 2.58 23.2-29.4	-	34.8	38.2	35.0	37.3
BL	2.8 \pm 0.12 2.6-3.0	4.1 \pm 0.72 3.4-5.7	6.4 \pm 0.72 5.6-7.3	8.0 \pm 0.89 7.0-9.3	10.0	10.5	10.7	10.0	10.6
TAL	7.5 \pm 0.34 7.1-8.1	10.1 \pm 1.76 8.1-13.5	15.3 \pm 1.9 13.5-17.4	18.4 \pm 1.72 16.2-20.3	-	24.2	27.5	24.4	26.7
BW	1.3 \pm 0.1 1.1-1.4	1.9 \pm 0.3 1.5-2.5	2.9 \pm 0.39 2.5-3.5	3.6 \pm 0.52 2.9-4.5	4.7	4.8	5.3	4.8	4.1
BH	0.9 \pm 0.08 0.8-1.1	1.3 \pm 0.13 1.0-1.6	1.9 \pm 0.26 1.6-2.3	2.4 \pm 0.28 2.0-2.8	3.3	3.2	3.8	3.6	3.5
IND	0.7 \pm 0.07 0.6-0.8	0.8 \pm 0.15 0.7-1.2	1.2 \pm 0.18 1.1-1.5	1.4 \pm 0.14 1.3-1.7	1.8	1.8	2.4	1.4	1.1
IOD	0.7 \pm 0.04 0.7-0.8	0.8 \pm 0.06 0.7-0.9	1.0 \pm 0.05 0.9-1.0	1.1 \pm 0.08 1.0-1.2	1.1	1.2	1.1	1.1	1.4
SSD	- 2.6-4.1	3.1 \pm 0.49 4.2-5.3	4.6 \pm 0.52 4.8-6.4	5.6 \pm 0.56	7.5	7.6	8.1	7.3	-
ESD	0.9 \pm 0.08 0.8-1.0	1.4 \pm 0.2 1.2-1.8	2.0 \pm 0.19 1.8-2.3	2.4 \pm 0.26 1.9-2.7	3.3	2.9	3.3	3.0	2.6
MTH	1.3 \pm 0.11 1.0-1.4	1.6 \pm 0.23 1.3-2.0	2.4 \pm 0.36 2.1-2.8	3.0 \pm 0.3 2.7-3.4	-	4	4.0	3.9	3.6
TMH	0.8 \pm 0.04 0.8-0.9	1.0 \pm 0.15 0.7-1.3	1.4 \pm 0.16 1.2-1.6	1.8 \pm 0.24 1.5-2.1	2.6	2.3	2.3	2.0	1.9
ODW	0.7 \pm 0.03 0.7-0.8	1.2 \pm 0.24 0.9-1.6	1.8 \pm 0.22 1.6-2.1	2.2 \pm 0.18 1.9-2.4	2.5	2.5	2.6	2.6	2.4
VTL	-	0.4 \pm 0.07 0.2-0.5	0.5 \pm 0.13 0.3-0.6	0.5 \pm 0.12 0.3-0.6	0.7	0.4	-	-	-

There is a considerable change from Stage 24 to Stage 25, not only in total length (Table 1), but also in the oral apparatus. In Stage 25, the jaw sheaths and teeth are keratinized, but not fully pigmented; tooth row P-1 is the most pigmented (Figure 4B). Total length in Stage 27 increases considerably and the oral apparatus is completely formed, with all the structures perfectly pigmented. From this stage on, the oral apparatus does not change until Stage 42, at which time, the only structures left are part of the upper and lower jaw sheaths; the upper jaw sheath is still pigmented, whereas the lower jaw sheath has no pigmentation and it is more difficult to discern; tooth rows are present only as low ridges, except for tooth row A-1 where few teeth are still present. Size varies considerably until Stage 38; from Stage 38 to Stage 42 there is little increase in total length (Table 1). The number of papillae varies ontogenetically. In Stage 24 there are 13–18 papillae ($n = 7$). In Stage 25, the number of papillae is 26–32 ($n = 7$). In Stages 27 and 28 papillae vary from 30–37 ($n = 12$) and in Stages 31–42, the number of papillae is 39–41 ($n = 4$).

In early stages, the eyes are C-shaped in dorsal view (Figure 5A,B); they are not fully pigmented until Stage 36 when the eyes are round. The vent tube has no visible aperture in Stage 24; from Stages 27–36, its size does not vary. In Stages 38 and 42, the vent tube is no longer present. In Stage 24, the spiracle is not distinguishable and there is no aperture, in Stage 42 the spiracle is absent.

In preservative, tadpoles at early stages have brown pigments, which become diffuse at later stages. Individuals in Stage 24 bear abundant brown star-shaped marks on the dorsum of body and tail. The posterior midventer (where some yolk is present) is brown and, medially, there is a dark brown longitudinal band. The medial line of the tail (formed at the junction of dorsal and ventral myotomes) also bears star-shaped marks. Ventrally, along the tail, there are some brown dots. In Stages 25 and 27, the dorsum is

still brown, but the marks are not star-shaped; they are more diffuse. The brown on the venter is lighter and the brown band is not so obvious. In Stage 28, there is not much brown left on the venter and the brown on the dorsum is more diffuse and much lighter. Coloration in Stage 38 resembles that of Stage 36. Finally, in Stage 42, there is a light brown coloration only on the anterior part of the dorsum.

In life (Figure 5), the tadpole is overall reddish color, with gray pigments until Stage 38, when it becomes greenish colored. In Stage 42, the tadpole has a yellow-green coloration with white dots on the dorsum.

Hyalinobatrachium aureoguttatum

Tadpole description (QCAZ 37752e, Stage 35, Figures 3C-D, 4C, 7E, Table 2)

Total Length: 34.0 mm; Body Length: 10.4 mm (30.6% of TL). Body elongate, oval-depressed, wider (Body width: 4.5 mm) than high (Body height: 3.1 mm). Snout rounded in dorsal and lateral views. Lateral-line system inconspicuous. Medium-sized and dorsal eyes, separated from each other by a distance corresponding to the 22% of body width; distance from eyes to tip of snout: 2.6 mm. Interorbital distance: 1.0 mm. Very small narial apertures, openings: 1.8 mm from tip of snout, internarial distance: 1.5 mm; distance from narial opening to anterior edge of eye: 1.0 mm. Short spiracle, single, sinistral, at the posterolateral region of the body; spiracular aperture with posterodorsal orientation; inner wall free from body, tube length: 0.3 mm, tube width: 0.4 mm; aperture diameter: 0.4 mm; distance from tip of snout to spiracular opening: 7.0 mm; spiracle located at 67.3% of body length from tip of snout. Vent tube short and abdominal, free posteriorly, opening directed postero-ventrally; tube length: 1.0 mm, tube transverse width: 0.6 mm. Tail long (24.5 mm,

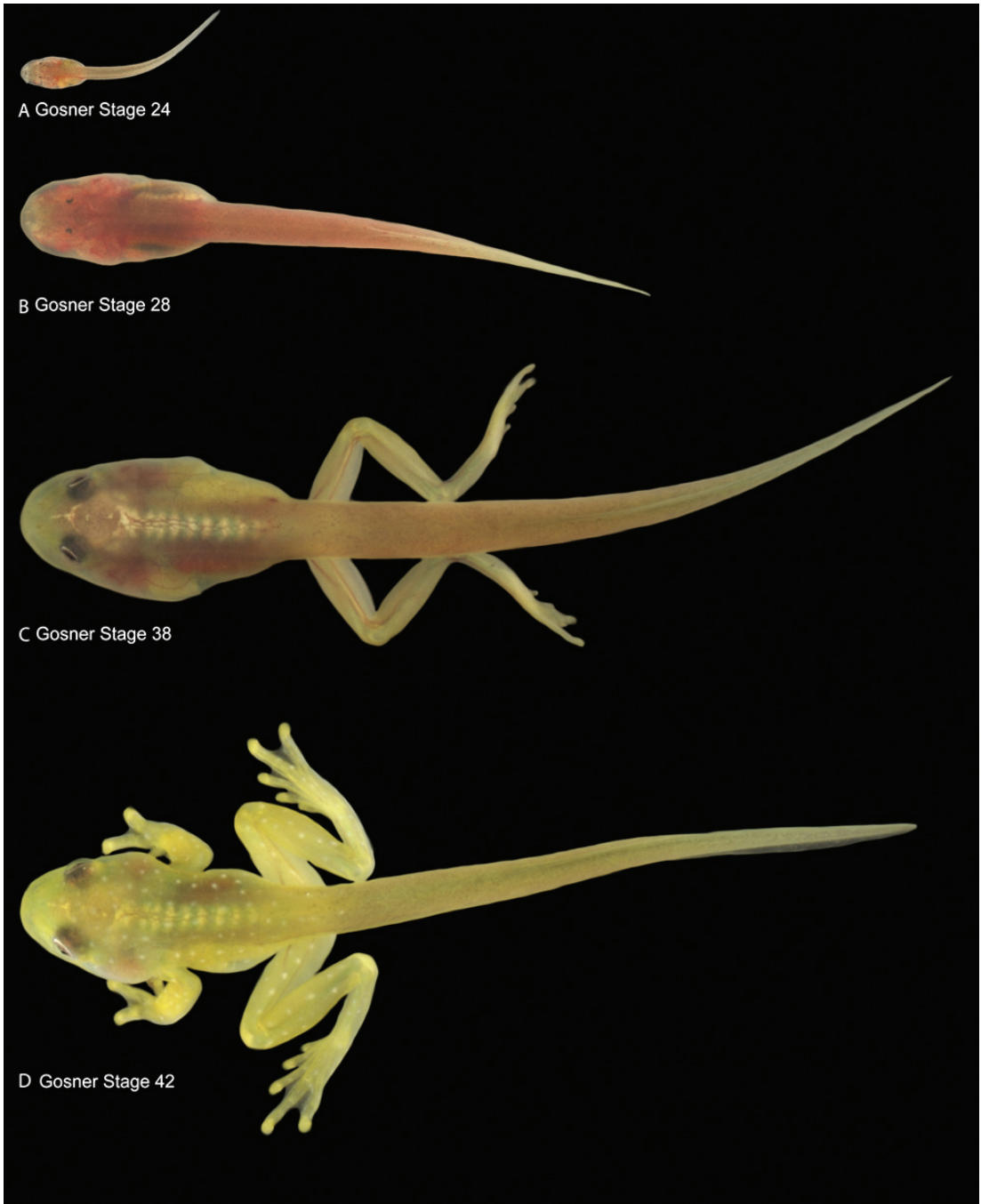


Figure 5 - Ontogenetic variation of the tadpoles of *Cochranella resplendens*. (A) QCAZ 38088a (photo QCAZ f5272); (B) QCAZ 38088c (photo QCAZ f5274); (C) QCAZ 38088k (photo QCAZ f5278); (D) QCAZ 38088m (photo QCAZ f5270). Relative size of tadpoles is approximate. Photos by LAC.

2.4 × BL) with subacute tip. Myotomes are visible throughout entire length of tail: straight medial line visible separating dorsal and ventral myotomes. Tail muscle width: 2.1 mm; tail muscle height: 2.3 mm; maximum tail height: 4.7 mm; dorsal fin height: 1.3 mm and ventral fin height: 1.4 mm. Dorsal and ventral fins originating at base of tail. Dorsal fin reaching its maximum height posterior to mid-length of tail; ventral fin reaching its maximum height at last quarter of tail.

Large oral disc, transverse width: 2.9 mm (65% of BW), emarginate and anteroventral, 101 marginal and uniserial papillae (ventral and lateral) distributed around oral disc; 4 submarginal papillae present on upper labium. Short and sub-acute papillae. Lengths of lateral papillae ($n = 39$) 0.02–0.09 mm (mean = 0.06 ± 0.01), width 0.02–0.11 mm (0.05 ± 0.02); lengths of ventral papillae ($n = 62$) 0.04–0.11 mm (mean = 0.07 ± 0.02), width 0.04–0.11 mm (mean = 0.06 ± 0.01). Upper jaw sheath “M” shaped, medial part thinner than lateral parts; serrated edge (serrations are broad-based and short, oriented straight and medially). Lower jaw sheath “U” shaped, with serrated edge (serrations at the sides of the “U” have same shape as the ones in upper jaw; serrations at the proximal region are more acute and narrower at their base). Transverse width of upper jaw sheath including lateral processes: 1.2 mm (representing 41.4% of ODW); lower jaw sheath: 0.7 mm (24.1% of ODW). Labial tooth row formula 2(2)/3. Anterior and posterior tooth rows long reaching extremes of the anterior and posterior labia, respectively. Tooth row A-1 “M” shaped, as upper jaw sheath, 2.2 mm long, number of teeth = 259; tooth row A-2 interrupted medially located at the sides of upper jaw sheath, length of each side: 0.7 mm, number of teeth = 110; tooth row P-1, 2.0 mm long, number of teeth = 158; tooth row P-2, 2.1 mm long, number of teeth = 206; tooth row P-3, 2.1 mm long, number of teeth = 206, teeth of this row shorter and lighter than those in other rows.

Color in life (Figure 3C, Stage 35)

Based on a color digital photo (QCAZ f5283 of QCAZ 37752e) taken by LAC. Dorsally, the anterior end of the body is gray; the rest of the body and the anterior half of the tail are red; the posterior half of the tail changes towards a gray coloration. Dorsally, there is an aggregation of iridophores that form an interorbital line, and a mid-band on the posterior part of the body. The irises are yellow. The posterior legs (not fully developed) are pale yellow.

Color in preservative - buffered formalin (formaldehyde 10%), Stage 35

QCAZ 37752e. The tadpole has a uniform cream color. The ventral, lateral and dorsolateral parts of the body are translucent. The only evidence of iridophores seen in life is a horizontal band behind the eyes. Dorsally, the tail has small black dots. Ventrally, the body has scarce small white dots.

Ontogenetic variation

Variation of 13 meristic characters of tadpoles in Stages 23–35 is given in Table 2. One individual in Stage 23 bears a large sac of yolk (length = 1.8 mm, 72% of body length); it does not have a developed spiracle and the vent tube is closed. The oral apparatus is not fully developed; jaw sheaths are slightly pigmented and they do not have the shape described in Stage 35. Only tooth rows A1 and P1 are present, the later has more teeth and pigmentation; the other tooth rows are visible as low ridges with no labial teeth. In Stage 24, the sac of yolk has almost disappeared. The spiracle is present and the vent tube is still closed. All the structures of the oral apparatus are present, except for tooth row P-3 that is visible as a ridge. Larvae of Stages 23–25 have black dots and marks along the body, dorsally and laterally (Figure 6A). Eyes are C-shaped because of the lack of pigmentation. In Stage

Table 2 - Dimensions in mm of the larvae of *Hyalinobatrachium aureoguttatum*; QCAZ 37752b-e, 32072. Stage 25: mean \pm standard deviation (first row), range (second row). Total length (TL), Body length (BL), Tail length (TAL), Body width (BW), Body height (BH), Internarial distance (IND), Interorbital distance (IOD), Snout-spiracle distance (SSD), Eye-snout distance (ESD), Maximum tail height (MTH), Tail muscle height (TMH), Oral disc width (ODW), Vent tube length (VTL).

	Stage 23 n = 1	Stage 24 n = 1	Stage 25 n = 5	Stage 26 n = 3	Stage 27 n = 1	Stage 28 n = 3	Stage 35 n = 2					
TL	8.3	11.9	11.4 \pm 1.04 (10.6-13.2)	20.3	17.1	21.4	25.2	29.8	33.1	34.9	38.5	34.0
BL	2.5	2.9	3.3 \pm 0.21 (3.1-3.6)	6.2	4.94	6.0	8.0	8.7	9.4	10.6	10.5	10.4
TAL	5.8	8.6	8.2 \pm 0.69 (7.6-9.3)	13.6	12.6	15.5	17.1	21.7	23.8	25.4	28.2	24.5
BW	1.0	1.2	1.5 \pm 0.20 (1.3-1.8)	3.2	2.6	2.5	3.0	4.1	4.4	4.9	5.6	4.5
BH	0.8	0.9	1.2 \pm 0.11 (1.0-1.3)	1.9	1.3	1.7	2.2	2.6	2.9	3.1	3.7	3.1
IND	-	0.8	0.7 \pm 0.05 (0.7-0.8)	1.4	1.1	1.2	1.4	1.6	1.8	1.8	1.6	1.5
IOD	0.5	0.6	0.7 \pm 0.05 (0.6-0.7)	1.1	0.9	0.9	1.0	1.3	1.3	1.4	1.2	1.0
SSD	-	2.3	2.6 \pm 0.24 (2.4-3.0)	5.0	3.9	4.4	5.4	6.0	6.8	7.3	7.7	7.0
ESD	0.7	1.0	1.1 \pm 0.14 (1.0-1.3)	2.2	1.8	2.0	2.3	2.4	3.1	2.6	3.0	2.6
MTH	0.9	1.6	1.5 \pm 0.17 (1.3-1.8)	3.1	2.3	2.9	3.3	4.2	4.8	4.9	5.4	4.7
TMH	0.6	0.9	1.1 \pm 0.44 (0.8-1.9)	1.7	1.3	1.5	1.7	2.6	3.1	2.9	2.8	2.3
ODW	0.7	0.9	1.1 \pm 0.10 (1.0-1.3)	2.6	1.8	1.9	2.3	3.0	3.0	3.2	3.3	2.9
VTL	-	-	0.3 \pm 0.09 (0.2-0.4)	0.7	0.5	0.7	1.0	0.8	0.9	0.8	1.0	1.0



Figure 6 - Ontogenetic variation of the tadpoles of *Hyalinobatrachium aureoguttatum*. (A) QCAZ 37752b (photo QCAZ f5279); (B) QCAZ 32072 (photo QCAZ f5286). Photos by LAC.

25, tooth row P-3 has almost no pigment and P-2 has slight pigmentation (Figure 4D). At Stage 26 there is a considerable increase in total length (Table 2), and the dark coloration has diminished; posterior tooth rows are slightly more pigmented. In Stage 27, coloration is very similar to that of Stage 26; eyes are still C-shaped (Figure 6B). In Stage 28, total length is twice the size of Stage 26, and dark coloration has totally disappeared, except for some black dots dorsally on the tail. The eyes and oral apparatus are totally pigmented. Finally, from Stage 28 to 35 there is not considerable change in size, coloration or oral disc morphology. At Stage 35, the vent tube is longer (Table 2) and the cloacal aperture is oriented postero-ventrally (not posteriorly as in previous stages). The number of marginal papillae varies considerably ontogenetically and among individuals in the same stage; the general tendency, however, is an increase in the number of papillae as the tadpoles develop. One individual in Stage 23 has 24 papillae; one in Stage 24 has 31 papillae;

individuals in Stage 25 have 30–51 papillae ($n = 5$); in Stage 26 there are 60, 77, 69 papillae ($n = 3$); in Stage 27 one individual has 87 papillae; and in Stage 28 there are 92–105 ($n = 3$). Some individuals bear few submarginal papillae on the upper labium; on Stage 26 one individual bears 1 submarginal papilla; in Stage 27, one individual has one and other has two submarginal papillae; finally, two individuals in Stage 28 have 4 submarginal papillae and one has 5 submarginal papillae.

Discussion

Some species of centrolenids, as well as other anurans, show variation in the morphology of the oral disc during development (Altig and Johnston 1989, Castillo-Trenn 2004, Rada *et al.* 2007). In the two species described herein, the primary changes of the oral apparatus between stages involve the numbers of papillae and tooth rows (Table 3). The shape of the oral disc does not change, and the number

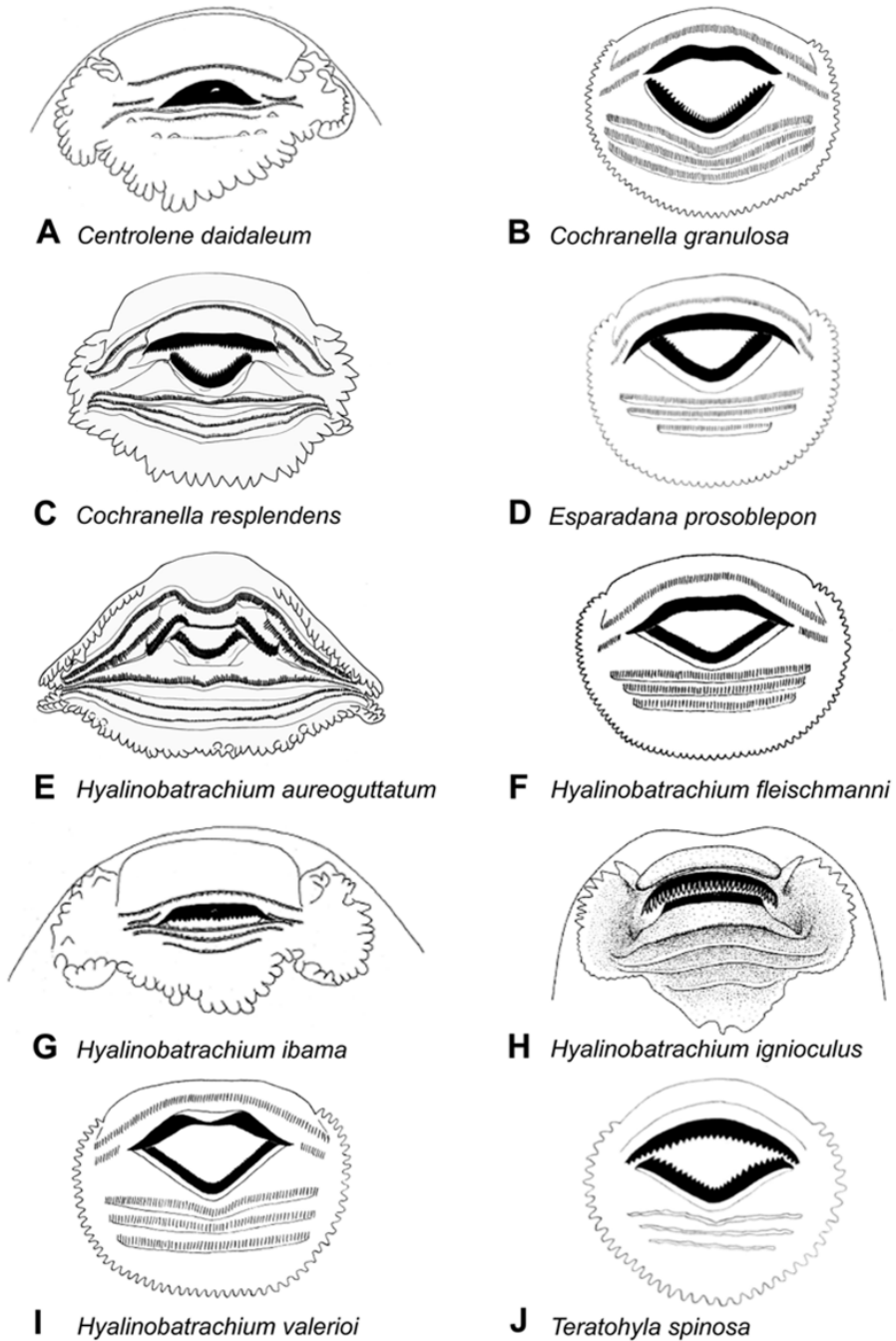


Figure 7 - Oral apparatus of different species of Centrolenidae. Compilation of figures from descriptions of tadpoles; for references see Table 3. *Cochranella granulosa* and *Hyalinobatrachium ibama* are in Stage 24, *Cochranella resplendens* in Stage 36, *Hyalinobatrachium ignioculus* in Stage 25, *Hyalinobatrachium aureoguttatum* in Stage 35. Gosner stages of the remaining species are not provided in the original descriptions.

Table 3 - Characteristics of the oral apparatus of tadpoles of different species of Centrolenidae.

Species	Gosner stage	Tooth row formula	Upper jaw sheath	Lower jaw sheath	Reference
<i>Centrolene andinum</i>	25	2(2)/2(1)	Straight with acute serrations	Inverted U-shaped with acute serrations	Mijares-Urrutia 1990
<i>Centrolene daidaleum</i> (Figure 7A)	24	0/0			Rada <i>et al.</i> 2007
	25	1/2-2/2			
	26-28	2/2			
	36	2/2	Curved with short well defined serrations.	U-shaped and serrated	
41	0/0				
<i>Cochranella granulosa</i> (Figure 7B)	-	2/3	Smooth arch in the middle, smooth edge.	U-shaped, serrations narrower in the middle of the jaw.	Starrett 1960
<i>Cochranella midas</i>	25	1/2	-	-	Duellman 1978
<i>Cochranella resplendens</i> (Figures 4A-B, 7C)	24	0/0	Not fully developed and not keratinized		This study
	25-38	2(2)/3	Nearly straight with smooth arch in the middle, serrated edge	U-shaped with a serrated edge	
	42	1/0 (Tooth row A1)	Lost pigmentation	Not pigmented, difficult to discern	
<i>Esparadana prosoblepon</i> (Figure 7D)	-	2/3	Curved, not serrated	U-shaped and serrated	Starrett 1960
<i>Hyalinobatrachium aureoguttatum</i> (Figures 4C-D, 7E)	23	1/1 (Tooth rows A1 and P1)	Not fully developed and not keratinized		This study
	24-35	2(2)/3	M-shaped, serrated edge	U-shaped, serrated edge	

Table 3 - Continued.

Species	Gosner stage	Tooth row formula	Upper jaw sheath	Lower jaw sheath	Reference
<i>Hyalinobatrachium colymbiphyllum</i>	25	2(2)2-3	Slightly curved with few pigmentation in the middle. Not serrated edge	–	Jaramillo <i>et al.</i> 1997
<i>Hyalinobatrachium fleischmanni</i> (Figure 7F)	–	2/3	Smoothly curved, without serrations	V-shaped with small uniform serrations	Starrett 1960
<i>Hyalinobatrachium ibama</i> (Figure 7G)	24	0/0		Slightly V-shaped with serrations.	Rada <i>et al.</i> 2007
	25	1/1-2/0-2/2-2/1-2/3			
	26	2/2-2/3			
	27-29	2/3			
	31	2/2			
	36	2/2	Thin and slightly arcuate with short, well defined serrations.	U-shaped and serrated	
	41	2/1			
	42	0/0			
<i>Hyalinobatrachium ignioculus</i> (Figure 7H)	25	0/3	Slightly arcuate; heavily serrated		Noonan & Bonett 2003
<i>Hyalinobatrachium muñozorum</i>	25	2/0	–	–	Duellman 1978
<i>Hyalinobatrachium valerioi</i> (Figure 7I)	–	2/3	Arcuate with a short V in the middle	V-shaped, with small equal serrations	Starrett 1960
<i>Teratohyla spinosa</i> (Figure 7J)	–	0/0	Slightly arcuate, with low and pointed serrations	Slightly V-shaped with long pointed serrations	Starrett 1960
<i>Teratohyla pulverata</i>	24	2/3	Smoothly curved, with pointed serrations	V-shaped and smooth edge	Hoffman 2004

of tooth rows is incomplete at early or late stages; Stages 24 (0/0) and 42 (1/0) in *C. resplendens* and Stages 23–24 (1/1) in *H. aureoguttatum*. Oral morphology is completely developed in Stages 27–38; therefore, tadpole descriptions based on early stages (i.e., before Stage 27) are likely to miss important traits such as total number and pigmentation of tooth rows, shape of jaw sheaths and papillae. Most tadpole descriptions are based on early stages and, therefore, are incomplete (Starret 1960, Duellman 1978, Ibañez *et al.* 1999, Noonan and Bonett 2003). Altig and Johnston (1989) describe the development and atrophy of tooth rows in tadpoles, but the order in which they appear or atrophy is known for few species. In *H. aureoguttatum* the first tooth rows to appear are A-1 and P-1 and the last is P-3. In *Cochranella resplendens*, tooth rows probably develop at earlier stages (before Stage 24), although pigmented tooth rows and jaw sheaths are not visible until Stage 25. After Stages 27 (*C. resplendens*) or 28 (*H. aureoguttatum*), there are no major changes in oral morphology. We lack individuals in stages later than 35 for *H. aureoguttatum* and in stages between 38 and 42 in *C. resplendens*; therefore, we cannot describe if there is a specific order in the atrophy of tooth rows.

The vent tube disappearance is variable between species. Gosner (1960) report that the vent tube disappears at Stage 41 or after it. Nevertheless, Fabrezi and Quinzio (2008) report variation in the stage where it disappears in some species of *Lepidobatrachus* and *Pseudis* (could be in Stage 37 to 43). Herein, it disappears in Stage 38 in *C. resplendens* and after Stage 35 in *H. aureoguttatum*, although the precise stage where it disappears in both species is unknown because of the lack of a series of individuals in all the Gosner Stages.

Ibañez *et al.* (1999) described the tadpole of *H. aureoguttatum* based on individuals in Stage 25. They differentiate these tadpoles from other centrolenid species based on the dorsal coloration pattern; nevertheless, this coloration


is characteristic only of tadpoles in early stages (before Stage 25); in Stage 26 the dark coloration diminishes considerably and by Stage 28 the tadpole lose almost all the dorsal pigmentation and is cream. Ibañez *et al.* (1999) also report a lack of pigmentation of tooth rows P-2 and P-3, feature present also in early stages. In Stage 26 tooth rows P-2 and P-3 are more pigmented and by Stage 28 the oral apparatus is completely pigmented. Serrations of the lower jaw sheath are described as low and uniformly distributed by Ibañez *et al.* (1999). Herein, we found that serrations are not equal throughout the jaw sheath; the ones on the sides are different from those distributed proximally.

McDiarmid and Altig (1999) compiled information of the genus *Cochranella* and *Hyalinobatrachium*; the characteristics observed in *C. resplendens* and *H. aureoguttatum* resemble those described for the two genera. The only difference in *C. resplendens* is that the oral disc is not emarginate, whereas McDiarmid and Altig (1999) report an emargination in the oral disc. Other two species, *Centrolene daidalea* and *Cochranella granulosa*, have a not-emarginated oral disc (Starret 1960, Rada *et al.* 2007). *Hyalinobatrachium aureoguttatum* has a distinctively M-shaped jaw sheath, whereas the compilation describes an upper jaw sheath with a smooth arch. McDiarmid and Altig (1999) compilation is useful and informative, although, tadpole descriptions are scarce and more studies are necessary to determine the general characteristics for different genera. The M-shaped upper jaw of *H. aureoguttatum* is a distinctive character that differentiates it from the other described glassfrogs species from Ecuador, which lack an arch or bear a smooth arch on the upper jaw (Starrett 1960, Duellman 1978, Hoffman 2004). The tooth-row formula is also a useful character to distinguish among tadpole species, although some ontogenetic variation is present; we summarize the information available for glassfrogs in Table 3.

Future studies should include a sampling of different developmental stages to document the

ontogenetic variation (Castillo-Trenn 2004, Rada *et al.* 2007). Moreover, it is important to produce homogeneous descriptions of tadpoles for a better comparison among them. McDiarmid and Altig (1999) and Mijares-Urrutia (1998) provide detailed description of tadpoles and appropriate criteria to define taxonomically relevant characters (body shape, oral disc shape, spiracle orientation, vent tube position etc.).

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