

The tadpole of *Odontophrynus barrioi* Cei, Ruiz, and Beçak, 1982 (Anura: Odontophrynidae): a comparison with the other tadpoles of the genus

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Abstract. We describe the tadpole of *Odontophrynus barrioi* including external larval features, chondrocranial and cranial musculature, and compare it with the other species of the genus. Tadpoles of *O. barrioi* at stages 31–37 are about 52.46 mm long. The body is slightly depressed in lateral view and ovoid in dorsal view. Oral disc is emarginate laterally, anteroventral and small with a single row of marginal papillae, a single large dorsal gap, and labial tooth row formula 2(2)/3(1). Despite small interspecific variations, like different labial tooth row formulae, the general aspect of species is quite similar. Although poorly-known yet, the chondrocranium and cranial musculature display some variations within the genus.

Keywords. Chondrocranium, Cranial muscles, External morphology, Odontophrynidae, *Odontophrynus barrioi*, Tadpole.

INTRODUCTION

The genus *Odontophrynus* Reinhardt and Lütken (1862) is distributed in southern and eastern South America. It is composed of 11 species (Frost, 2014), that are divided into three species groups (Savage & Cei, 1965; Cei, 1987; Caramaschi, 1996; Amaro et al., 2009). The *O. occidentalis* Group includes *Odontophrynus barrioi* Cei, Ruiz, and Beçak, 1982, *O. occidentalis* (Berg, 1896), and *O. achalensis* Di Tada, Barla, Martori, and Cei, 1984. The species under study is associated with arid and semiarid environments of central and western Argentina in the Chaco Seco eco-region (Torrella and Adamoli, 2005). The *O. occidentalis* Group is characterized by possessing enlarged postorbital, temporal, and parotoid glands, and other

glands on the tibia (Savage and Cei, 1965). The adults of *O. barrioi* distinguish from the other species of the group by the following combination of characters: presence of irregularly arranged rounded dorsal glands; lack of a light vertebral stripe; presence of a great number of closely arranged post-orbital, temporal, and parotoid glands; absence of keratinous spines; presence of a well-developed gland between the eye and the maxilla; light brown background with dark brown spots; among others (for more details see Rosset et al., 2007). The tadpole of *O. barrioi* was described only synthetically by Cei et al. (1982) and compared in some morphometrical measurements with the tadpole of *O. occidentalis* by Cei and Crespo (1982).

The aim of this work is to provide a detailed description of the external larval features, chondrocranial and

cranial musculature of the tadpole of *Odontophrynus barrioi* and to compare these characteristics with the available information for other species of the genus.

MATERIALS AND METHODS

All specimens studied for the present work are housed at the amphibian collection of the Museo de La Plata (Buenos Aires, Argentina). *Odontophrynus barrioi* tadpoles were collected on 27 January 2011 in Las Tumanas stream (30°86'083"S, 67°32'628"W; 920 m a.s.l. – MLP 5690), La Mesada stream (30°99'132"S, 67°29'694"W; 784 m a.s.l. – MLP 5691), Astica stream (30°93'822"S, 67°34'055"W; 916 m a.s.l. – MLP 5692), and Agua de las Totoras (30°08'18"S, 67° 53'17.7"W; 1311 m a.s.l. – MLP 5693), Valle Fértil Department, San Juan, Argentina. The Valle Fértil Department is located in the Chaco Seco eco-region (Torrella and Adamolí, 2005). The vegetation of the area is diverse; predominantly tree species such as *Prosopis spp.* (Algarrobos), *Aspidosperma quebracho-blanco* (Quebracho blanco), *Ziziphus mistol* (Mistol) and shrub of *Larrea spp.* (Jarillas) are present, among others. The other anurans inhabiting in the area were tadpoles and adults of *Rhinella arenarum* (Bufonidae), *Leptodactylus latrans*, *L. bufonius* (Leptodactylidae), and *Phyllomedusa sauvagii* (Hylidae) (Sanabria and Quiroga, 2008). The average annual temperature is 17 °C, annual mean minimum is 10.2 °C and annual mean maximum 25.2 °C, with rainfall concentrated in summer, with an annual average of 225 mm (Cabrera, 1976).

The tadpoles were anesthetized (2.5 ml of 2% xylocaine and 2% lidocaine HCl, AstraZeneca Labs, Buenos Aires, Argentina) after capture and immediately fixed in 10% buffered formalin. Seven tadpoles of *Odontophrynus barrioi* (MLP 5694) were employed for the external morphology descriptions at Stages 31–37 (Gosner, 1960), also attaching morphological measurements at Stages 26–30 and 38–41. To clearly visualize oral disc papillae, it was stained with 1% of Giemsa solution, for 10 min. Three Stage 37–38 tadpoles of *O. barrioi* (MLP 5695) were double stained following the technique of Taylor and Van Dyke (1985) to study the chondrocranium and associated muscles. Muscles were observed before the clearing of specimens, after which the chondrocranium was studied. Measurements were taken under a Lancet stereomicroscope (10–40x) with an Essex digital caliper (accuracy 0.01 mm). Terminology follows Haas (1995), and d'Heursel and de Sá (1999) for chondrocranium; Alcalde and Rosset (2003) for chondrocranial measurements; Haas (2001) for mandibular muscles; Haas and Richards (1998) and Haas (2003) for hyobranchial muscles; Schlosser and Roth (1995) for innervations; Altig and McDiarmid (1999), Lannoo (1999), and Grenat et al. (2009) for external morphology; Altig and McDiarmid (1999) for oral disc morphology; and Altig and Johnston (1989) for tadpole ecomorphological types.

We measured 17 morphological variables: Total length (TL), Body length (BL), Tail length (TAL), Body height (BH), Maximum tail height (MTH), Tail muscle height (TMH), Dorsal fin height (DFH), Ventral fin height (VFH), Maximum body width (MBW), Body width at nares (BWN), Tail muscle width

(TMW), Eye diameter (ED), Interorbital distance (IOD), Internarial distance (IND), Eye-narial distance (END), Snout-narial distance (SND), Oral disc width (ODW). Measurements follow Lavilla and Scrocchi (1986), Altig and McDiarmid (1999), and Grenat et al. (2009). The morphological measurements are in millimeters (mm) and are reported as mean \pm standard error. The identification of the tadpole was based in the fact that *Odontophrynus barrioi* is the only species of this genus inhabiting at the Valle Fértil Department (San Juan, Argentina: see Rosset et al., 2007).

RESULTS

External morphology

Description: Tadpoles at stages 31–37 are 52.46 \pm 6.96 mm of TL. Body is slightly depressed in lateral view and ovoid in dorsal view (BH/MBW = 0.86 \pm 0.05), shorter than half of total length (BL/TL = 0.38 \pm 0.004). The snout is rounded in dorsal view, and abrupt and blunt in lateral view. The nostrils are dorsal, directed anterodorsally, scarcely visible laterally, and positioned closer to the eyes than the tip of the snout (SND/END = 1.49 \pm 0.13). The nostrils are elliptical, kidney-shaped, with a rounded and thin rim all around. Rounded eyes, small and in dorsal position, directed dorsolaterally, vis-

Table 1. Morphometric measurements (mm, Mean \pm SE) for tadpoles of *Odontophrynus barrioi*. 40 larvae at Stage: 26–30, 7 larvae at Stage 31–37 and 10 larvae at Stage 38–41 from Valle Fértil, San Juan, Argentina.

| Character | Mean \pm SE | | |
|---------------------------|------------------|------------------|------------------|
| | 26–30 | 31–37 | 38–41 |
| Total length TL | 32.21 \pm 4.17 | 52.46 \pm 6.96 | 76.76 \pm 7.64 |
| Body length BL | 12.65 \pm 1.61 | 20.15 \pm 2.95 | 28.85 \pm 2.80 |
| Tail length TAL | 20.40 \pm 3.23 | 34.12 \pm 3.92 | 48.10 \pm 5.35 |
| Body height BH | 5.69 \pm 1.03 | 9.12 \pm 2.32 | 13.52 \pm 2.58 |
| Maximum tail height MTH | 6.39 \pm 0.93 | 9.49 \pm 0.89 | 9.97 \pm 3.58 |
| Tail Muscle height TMH | 3.16 \pm 0.72 | 5.30 \pm 0.80 | 8.22 \pm 1.27 |
| Dorsal Fin height DFH | 2.90 \pm 0.50 | 4.52 \pm 0.58 | 8.08 \pm 0.67 |
| Ventral Fin height VFH | 2.65 \pm 0.58 | 4.36 \pm 0.52 | 6.50 \pm 1.44 |
| Maximum body width MBW | 6.77 \pm 1.04 | 11.24 \pm 1.72 | 17.48 \pm 4.89 |
| Body width at nares BWN | 4.92 \pm 0.88 | 7.35 \pm 1.84 | 11.55 \pm 2.62 |
| Tail muscle width TMW | 1.87 \pm 0.47 | 4.19 \pm 1.07 | 7.15 \pm 0.93 |
| Eye diameter ED | 1.28 \pm 0.23 | 2.03 \pm 0.31 | 2.60 \pm 0.32 |
| Interorbital distance IOD | 2.92 \pm 0.43 | 4.32 \pm 1.28 | 7.20 \pm 0.68 |
| Internarial distance IND | 1.54 \pm 0.23 | 2.15 \pm 0.51 | 2.47 \pm 0.38 |
| Eye-nares distance END | 1.87 \pm 0.36 | 2.98 \pm 0.61 | 4.40 \pm 0.39 |
| Snout-narial distance SND | 2.73 \pm 0.47 | 4.14 \pm 0.70 | 5.27 \pm 0.52 |
| Oral disc width ODW | 2.45 \pm 0.46 | 3.5 \pm 1.15 | 4.61 \pm 1.01 |

ible in dorsal and lateral views. The spiracle is single, short, sinistral, lateroventrally positioned, spiracle opening oval, posterodorsally directed and with the inner wall of the opercular tube absent, visible in lateral, dorsal and ventral views. Neuromasts of posterior supraorbital, supraorbital, infraorbital angular and posterior infraorbital are noticeable. The tail is large (TAL/TL = 0.65 ± 0.01), with its maximum tail height similar to the body height (MTH/BH = 1.19 ± 0.13) and its end portion rounded. Myomeres are more evident in the anterior portion of the tail, with the musculature almost reaching the tip of the tail. The dorsal fin height is slightly higher than ventral fin height (DFH/VFH = 1.16 ± 0.09) and originates at body-tail junction. The vent tube is medial, attached to ventral fin, opening dextrally.

Oral disc: The oral disc is anteroventral, small (OD/MBW = 0.37 ± 0.03), laterally emarginated with absent papillae in the emarginated edges (Fig. 1 D). It has a single row of marginal papillae, conical, with pointed tip, of variable sizes. A single large dorsal gap is present (approximately 85% of ODW), without ventral gap. Single or paired submarginal papillae are present in the supra- and infraangular zone, more common and numerous in the later. Labial teeth single, with one cusp, and posterior ridges curved. Labial tooth row formula 2(2)/3(1). Jaw sheaths keratinized, with upper jaw totally pigmented, and lower jaw pigmented on its upper half; serrated edges in both jaws; upper jaw sheath smooth arch-shaped with lateral processes and lower jaw sheath V-shaped.

Color in preservative: The body is black pale in the abdominal region and light brown in the anterior body region, with perinarial region darker. The ventral region is pale and transparent allowing the visualization of the

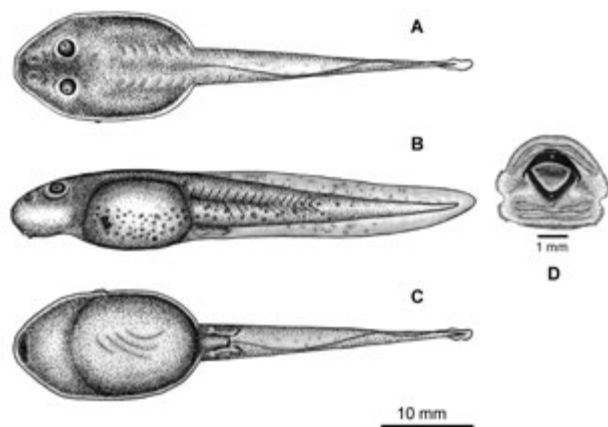


Fig. 1. External morphology of the tadpole of *Odontophrynus barrioi* at Stage 38 (MLPA-5695). (A) Dorsal, (B) Lateral, and (C) Ventral views (scale bar = 10 mm); (D) Oral disc (scale bar = 1 mm). Drawer: Gonzalez E.

visceral system. Tail musculature is yellow pale, slightly darker at the junction of the dorsal fin with the body, and it shows grouped chromatophores forming a dense reticulate. Fins are opalescent, in some cases finely reticulated and with irregular dark blotches.

Chondrocranium and cranial muscles

Neurocranium oval (width/length = 0.87) and depressed (height/width = 0.46), with greatest width at level of the arcus subocularis. The tetrapartite cartilago suprarostralis has the pars corpora medially joined by ligament (Fig. 2 D). A proximal bridge connects the pars corpora with the respective pars alaris at each side. The par alaris bears processus anterior dorsalis and processus posterior dorsalis. Spherical and small adrostral cartilages present. The cornu trabeculae diverges anterolaterally from the planum ethmoidale and comprises 27% of chondrocranial length. They are uniformly wide and bear a well-developed processus lateralis trabeculae. Both the lamina orbitonasalis and the septum nasi are present at the studied stages. The fenestra frontoparietalis is limited posteriorly by the tectum synoticum, laterally by the taenia tecti marginalis, and anteriorly by the taenia tecti ethmoidalis. The taenia tecti transversalis divides the fenestra in two parts, the frontal and parietal ones, being the later subdivided in left and right parietal fenestrae by the taenia tecti medialis. The cartilaginous lateral walls formed by the cartilagine orbitalis are open at level of the optic, metoptic, and trochlear foramina, and fisura prootica. At the studied stages, the basi cranii is completely closed. The capsula auditiva comprises 30% of the chondrocranial length and its anterior copula is slightly overlapped with the dorsum of the processus ascendens. The larval crista parotica with processus anterolateralis and posterolateralis well developed. The medial wall of the capsula auditiva is Alcian-blue negative and its openings could not be observed. The superior perilymphatic foramen opens in the posterior wall of the capsule. The operculum is present.

The palatoquadrate bears processus articularis quadrati, processus muscularis quadrati, commissura quadrato-cranialis anterior, commissura quadrato-orbitalis, long processus pseudopterygoideus, and processus ascendens. The processus ascendens meets the pila antotica just posterior to the oculomotor foramen (intermediate union) forming a straight angle with the cranial floor.

The lower jaw is composed by cartilagine infrarostales and cartilago meckeli. The later with processus retroarticularis, processus dorsomedialis and processus ventromedialis well developed. The commissura intramandibularis is Alcian-blue negative (Fig. 2D, E).

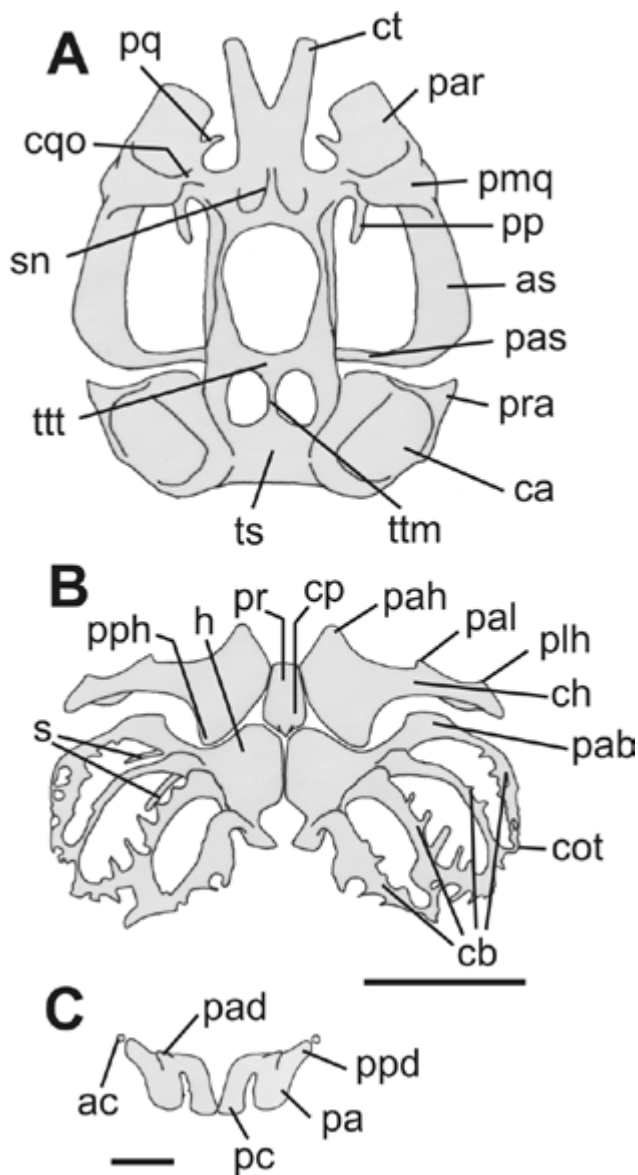


Fig. 2. Chondrocranium of *Odontophrynus barrioi* at stage 38. (A) Dorsal view, (B) Ventral view of hyobranchial apparatus (scale bar = 3 mm), (C) Frontal view of cartilago suprarostralis (scale bar = 1 mm). References: ac: adrostral cartilage, as: arcus subocularis, ca: capsula auditiva, cb: ceratobranchiales, ch: ceratohyale, cot: commissura terminalis, cp: copula posterior and processus urobranchialis, cqo: commissura quadrato-orbitalis, ct: cornua trabeculae, h: hypobranchiale, pa: pars alaris, pab: processus anterior branchialis, pad: processus anterior dorsalis, pah: processus anterior hyalis, pal: processus anterolateralis hyalis, par: processus articularis, pas: processus ascendens, pc: pars corporis, plh: processus lateralis hyalis, pmq: processus muscularis quadrati, pp: processus pseudopterygoideus, ppd: processus posterior dorsalis, pph: processus posterior hyalis, pq: processus quadrato-ethmoidalis, pr: pars reuniens, pra: processus anterolateralis, s: spiculae I–II, sn: septum nasi, tm: taenia tecti marginalis, ts: tectum synoticum, ttm: taenia tecti medialis, ttt: taenia tecti transversalis.

The hyobranchial apparatus lacks copula I. All ceratohyale processes (anterohyal lateral, anterohyal, postero-hyal and articular) are well developed. The ceratohyalia is medially joined by the pars reuniens. The copula II bears a short processus urobranchialis. The ceratobranchiales I, II, and IV are continuous to the planum hypobranchiale; the third joins the planum by a smooth connection. The commissura proximalis is absent in all ceratobranchiales and all them are distally joined by a double distal commissure. The processus branchialis is closed and the fourth spiculae are well developed. The exoccipital, frontoparietal, and parasphenoid are the only ossification centres present at the studied stages (not drawings in Fig. 2).

Respect to the cranial muscles, the ramus mandibularis of the nervus trigeminus runs laterally to all mm. levatorae mandibulae. In the Table 2 are detailed the origin and insertion of each muscle.

DISCUSSION

External morphology

The comparison of the larval external morphology of *Odontophrynus barrioi* with the available larval descriptions for other species of the genus allow us to propose the following tadpole characterization of *Odontophrynus* with small variations characteristic of each species: (1) small to medium sized tadpoles (TL = 30–75 mm, stages 31–39), (2) globose/ovoid in dorsal view and somewhat depressed or flattened below in lateral view, (3) rounded snout in dorsal view, (4) single and sinistral spiracle, directed dorsolaterally, (5) medial vent tube, (6) dorsal nostrils, (7) medium-sized tail, being always larger than 1/2 TL with robust musculature, (9) anteroventral oral disc, laterally emarginated (except in *O. cultripes* and *O. salvatori*), with a large dorsal gap and a single row of marginal papillae. Submarginal papillae occur in the species *O. barrioi*, *O. lavillai*, *O. cordobae*, and *O. maisuma* only, (10) the most common LTRF for the genus is 2(2)/3(1) (*O. barrioi*, *O. occidentalis*, *O. americanus*, *O. lavillai*, *O. cordobae*, *O. maisuma*, *O. cultripes*, and *O. salvatori*), but 2/3(1) (*O. maisuma* and *O. carvalhoi*), 2/3 (*O. maisuma*), and 2(2)/3 (*O. cultripes*) are also present (see Table 3), and (11) exotrophic, lentic and benthic tadpoles.

Regarding the *Odontophrynus occidentalis* Group to which *O. barrioi* belongs alongside *O. occidentalis* and *O. achalensis*, they are externally similar; the only difference that can be highlighted is that *O. barrioi* has the tip of the tail rounded contrary to *O. occidentalis* and *O. achalensis* in which the tip of the tail is acute. Selected external morphological characters of *Odontophrynus* tadpole

Table 2. Origin and insertion of the cranial muscles on tadpoles of *Odontophrynus barrioi* at Stages 37–38.

| Muscle | Origin | Insertion |
|--|--|--|
| <i>Nervus trigeminus (cranial nerve V), mandibular musculature</i> | | |
| Levator mandibulae internus | Processus ascendens | Cartilago meckeli |
| Levator mandibulae longus superficialis | Arcus subocularis | Cartilago meckeli |
| Levator mandibulae longus profundus | Arcus subocularis | Both muscles insert together in the pars alaris by a common tendon |
| Levator mandibulae externus profundus | Processus muscularis | |
| Levator mandibulae externus superficialis | Processus muscularis | Pars alaris |
| Levator mandibulae articularis | Processus muscularis | Cartilago meckeli |
| Levator mandibulae lateralis | Processus retroarticularis | Pars alaris |
| Submentalis | Cartilago infrastrotrale | Median raphe |
| Intermandibularis | Cartilago meckeli | Median raphe |
| Mandibulolabialis inferior | Cartilago meckeli | Oral disc |
| Mandibulolabialis superior | Absent | |
| <i>Nervus facialis, (cranial nerve VII), hyoid musculature</i> | | |
| Suspensoriohyoideus | Processus muscularis and arcus subocularis | Ceratohyale |
| Suspensorioangularis | Processus muscularis | Processus retroarticularis |
| Orbitohyoideus | Processus muscularis | Ceratohyale |
| Quadratoangularis | Anteroventral on palatoquadrate | Processus retroarticularis |
| Hyoangularis lateralis | Ceratohyale | Cartilago meckeli, retroarticular |
| Hyoangularis medialis | Absent | |
| Interhyoideus | Ceratohyale | Median raphe |
| Interhyoideus posterior | Ventral wall on branchial chamber | |
| Diaphragmatopraecordialis | Median endof m. interhyoideus posterior | Septum transversus |
| <i>Nervus glossopharyngeus (cranial nerve IX), branchial musculature</i> | | |
| Levator arcuum branchialium I | Arcus subocularis | Commissura terminalis I |
| Subarcualis rectus I | Dorsal head on ceratobranchiale I. Ventral heads on ceratobranchiales II and III | Ceratohyale |
| Constrictor branchialis I | Absent | |
| <i>Nervus vagus (cranial nerve X), branchial musculature</i> | | |
| Constrictor branchialis II | Ceratobranchiale II | Commissura terminalis I |
| Constrictor branchialis III | Ceratobranchiale II | Commissura terminalis II |
| Constrictor branchialis IV | Ceratobranchiale III | Commissura terminalis III |
| Diaphragmatobranchialis | Peritoneal wall | Commissura terminalis III |
| Levator arcuum branchialium II | Anterolateral on capsula auditiva and posterior arcus subocularis | Commissura terminalis II |
| Levator arcuum branchialium III | Posterolateral on capsula auditiva | Commissura terminalis III |
| Levator arcuum branchialium IV | Posteroventral on capsula auditiva | Ceratobranchiale IV |
| Subarcualis obliquus II | Ceratobranchiales II–III | Processus urobranchialis |
| Subarcualis rectus II–IV | Ceratobranchiale IV | Ceratobranchiale I |
| Tympanopharyngeus | M. levator arcuum branchialium IV | Pericardium |
| Dilatator laryngis | Posteroventral on capsula auditiva | Constrictor laryngis |
| Constrictor laryngis | Forms an annulus rounding the larynx | |
| Transversus ventralis IV | Absent | |
| <i>Nervus hypoglossus (spinal nerve II), hypobranchial musculature</i> | | |
| Geniohyoideus | Hypobranchial at level of ceratobranchiale III | Cartilago infarostrale |
| Rectus cervicis | Peritoneal wall | Ceratobranchiale III |

Table 3. Main morphological features of the tadpoles of *Odontophrynus*. Abbreviations: DG (dorsal gap), DV (dorsal view), LTRF (labial tooth row formula), LV (lateral view), S (sinistral), TOT (tip of tail). With asterisks (*) are marked the characters inferred from illustrations. (**) *O. salvatori* was transferred to *Proceratophrys*, should be remarked that possible this species also pertain to this genus, but provisionally is considered as a species of *Odontophrynus* not assigned to anygroup. The tadpole of *Odontophrynus monachus* was not included because it remains unknown (Caramaschi and Napoli, 2012).

| Species | Reference | Body Shape | Oral disc | LTRF | Spiracle | Vent Tube | Nostrils | Tail | Eyes |
|---------------------------|--|---|---------------------------------------|-------------------------------------|--------------------------------------|-------------------------|----------------------------|--------------------|--|
| <i>occidentalis</i> group | | | | | | | | | |
| <i>O. barrioi</i> | Present Study | Ovoid in DV, depressed in LV | Laterally emarginated, DG present | 2(2)/3(1) | S, opening posterodorsally directed | Medial, dextral opening | Dorsal, elliptical | Large, TOT rounded | Small, dorsal, directed dorsolaterally |
| <i>O. barrioi</i> | Cei et al. 1982; Cei and Crespo 1982; Cei 1987 | — | — | — | S, opening dorsolaterally directed | — | — | TOT rounded | — |
| <i>O. occidentalis</i> | Savage and Cei 1965; Cei 1980; Cei 1987 | Depressed in LV | Laterally emarginated, DG present | 2(2)/3(1) | S | Medial, dextral opening | Dorsal | Large, TOT rounded | Dorsal, directed upwards |
| <i>O. achalensis</i> | Di Tada et al. 1984; Cei 1987 | Short | Laterally emarginated, DG present* | 2(2)/3(1)* | S | — | Dorsal | Large, TOT acute | Dorsolaterally |
| <i>americanus</i> group | | | | | | | | | |
| <i>O. americanus</i> | Savage and Cei 1965; Cei 1980 | Ovoid in DV | Laterally emarginated, DG present | 2(2)/3(1) | S | Medial | Dorsal | Large, TOT acute | Dorsal, directed laterally |
| <i>O. lavillai</i> | Lavilla and Scrocchi 1991; Fabrezi and Vera 1997 | Ovoid in DV, depressed in LV | Laterally emarginated, DG present | 2(2)/3(1) | S | Medial, dextral opening | Dorsolaterally, elliptical | Large, TOT acute | Large, lateral |
| <i>O. cordobae</i> | Grenat et al. 2009 | Ovoid in DV, depressed in LV | Laterally emarginated, DG present | 2(2)/3(1) | S | Medial, dextral opening | Dorsal, elliptical | Large, TOT acute | Small, directed dorsolaterally |
| <i>O. maisuma</i> | Borteiro et al. 2010 | Ovoid in DV, depressed in LV | Laterally emarginated, DG present | 2(2)/3(1), 2/3(1) and 2/3 sometimes | S, opening posterodorsally directed | Medial, dextral opening | Dorsal, rounded | Large, TOT rounded | Large, dorsal, directed laterally |
| <i>cultripes</i> group | | | | | | | | | |
| <i>O. cultripes</i> | Savage and Cei 1965; Cei 1980 | Ovoid in DV, depressed in LV | Not laterally emarginated, DG present | 2(2)/3, 2(2)/3(1) | S, opening posterodorsally directed* | Medial, dextral opening | Dorsal | Large, TOT acute | Dorsal, directed laterally |
| <i>O. carvalhoi</i> | Caramaschi 1979 | Ovoid in DV, triangular elongated in LV | laterally emarginated, DG present | 2/3(1) | S | Medial, dextral opening | Dorsal | TOT acute | Large, dorsal, directed laterally |
| No group | | | | | | | | | |
| <i>O. salvatori</i> ** | Brandão and Batista 2000 | Ovoid in DV, depressed in LV | Not laterally emarginated, DG present | 2(2)/3(1) | S, opening posterodorsally directed | Medial, dextral opening | Dorsal, rounded | TOT rounded | Large, dorsal, directed laterally |

known to date are summarized in Table 3 complementing the table done by Do Nascimento et al. (2013).

Chondrocranium and cranial muscles

The cranial morphology of the *Odontophrynus occidentalis* Group is known only for *O. achalensis* (Haas, 1997; 2003). The chondrocranium of this species was illustrated and its cranial muscles and chondrocranial characters were described in the context of a broad phylogenetic analysis of anurans. In addition, only chondrocranial features (lacking muscle descriptions) are available for three species of the *O. americanus* Group (*O. americanus*, *O. lavillai*, *O. maisuma*; Fabrezi and Vera, 1997; Do Nascimento et al., 2013) and two species of the *O. cultripes* Group (*O. carvalhoi*, *O. cultripes*; Do Nascimento et al., 2013). The chondrocranial features were described for five species of *Proceratophrys* (Dos Santos Dias et al., 2013) but not for the other genus that composed Odontophrynidae (*Macrogenioglottus*). Do Nascimento et al. (2013) provided a chondrocranial characterization of *Odontophrynus* based on the following combination of characters: (1) tetrapartite suprarostrals cartilage, (2) processus lateralis trabeculae present, (3) crista parotica distinct, (4) processus pseudopterygoideus present, (5) low attachment of the processus ascendens, (6) commissural quadratoorbitalis present, (7) processus lateralis hyalis present, (8) tectum parietale present, (9) open processus branchialis, and (10) fourth spicule modified into a small plate. There is a notable variation in the character (1) of this characterization within *Odontophrynus* and *Proceratophrys*: although always tetrapartite, both corpora may be either free or distally joined by cartilage, the corpus – ala union may be absent, proximally present, or both proximally and distally present. The same condition of the characters 3, 4, 6, and 9 are present in species of *Proceratophrys* with available chondrocranial descriptions (see Dos Santos Dias et al., 2013), whereas the characters 2, 7, and 10 were not clearly described by Dos Santos Dias et al. (2013) for the *Proceratophrys* they studied. The characters 5 and 8 are variable within *Odontophrynus* since they have a different condition in *O. barrioi* (intermediate union of the processus ascendens and absence of tectum parietale at advanced stages of development). Furthermore, we have verified both characters in a sequence of larval stages of a tetraploid population of *O. americanus* (from Buenos Aires province, Argentina) housed at the Herpetological Collection of the Museo de La Plata (MLP. 5111). These specimens have an intermediate union of the processus ascendens and lack the tectum parietale (at least at stage 42) as we found here for *O. barrioi*. The fenestra frontoparietalis may be posteriorly closed by the formation of a tectum parietal (*O. achalensis*

at least at Stage 40); other condition is the presence of two fenestrae parietales limited by the tectum synoticum and the taenia tecti transversalis et medialis (*O. barrioi* at Stage 38); and the fenestra frontoparietalis remains widely opened by the existence of a tectum synoticum only (*O. americanus* and *O. lavillai* at Stages between 31–37). However, these features are clearly due to the heterochronic development observed at different developmental stages across the species. Finally, we wish to make a brief comment about the presence/absence of adrostral cartilages in the species of *Odontophrynus*. *Odontophrynus barrioi* is the unique species of the genus in which the adrostrals seem invariable present. In other species they may be either present or absent as in *O. americanus* (absent in the specimens studied by Do Nascimento et al., 2013; but present in those studied by Fabrezi and Vera, 1997) and *O. achalensis* (see Haas, 2003); or merely present as adrostral tissue mass (not chondrified, *O. carvalhoi*, *O. maisuma*).

The comparison of the cranial muscles of *O. achalensis* (Haas, 1997, 2003), with the muscles we described for *O. barrioi* shows a single variable feature between both species: the insertion site of the m. rectus cervicis (ceratobranchiale III in *O. barrioi*, ceratobranchiale III and IV in *O. achalensis*).

In summary, the external morphology of the tadpole of *Odontophrynus barrioi* is similar to the other species of the genus with small variations between them, and the internal larval features are controversial (e.g. morphology of the adrostral cartilages) to diagnose the species groups of *Odontophrynus*.

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REFERENCES

- Alcalde, L., Rosset, S.D. (2003): Descripción y comparación del condrocáneo en larvas de *Hyla raniceps* (Cope, 1862), *Scinax granulatus* (Peters, 1871) y *Scinax squalirostris* (A. Lutz, 1925) (Anura: Hylidae). Cuad. Herpetol. 17: 35-51.
- Altig, R., Johnston, G.F. (1989): Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. Herpetol. Monogr. 3: 81-109.

- Altig, R., McDiarmid, R.W. (1999): Body Plan: Development and Morphology. In: Tadpoles: The Biology of Anuran Larvae, pp. 24-51. McDiarmid, R.W., Altig, R., Eds., University of Chicago Press, Chicago.
- Amaro, R.C., Pavan, D., Rodrigues, M.T. (2009): On the generic identity of *Odontophrynus moratoi* Jim & Caramaschi, 1980 (Anura, Cycloramphidae). *Zootaxa* **2071**: 61-68.
- Borteiro, C., Kolenc, F., Pereyra, M.O., Rosset, S., Baldo, D. (2010): A diploid surrounded by polyploids: tadpole description, natural history and cytogenetics of *Odontophrynus maisuma* Rosset from Uruguay (Anura: Cycloramphidae). *Zootaxa*. **2611**: 1-15.
- Brandão, R.A., Batista, C.G. (2000): Descrição do girino de *Odontophrynus salvatori* (Anura, Leptodactylidae). *Iheringia, Ser. Zool.* **89**: 165-170.
- Cabrera, A.L. (1976): Regiones fitogeográficas de la República Argentina, Enciclopedia Argentina de Agricultura y Jardinería, Buenos Aires.
- Caramaschi, U. (1979): O Girino de *Odontophrynus carvalhoi* Savage & Cei, 1965 (Amphibia, Anura, Cera-
tophryidae). *Rev. Bras. Biol.* **39**: 1691-71.
- Caramaschi, U., Napoli, M.F. (2012): Taxonomic revision of the *Odontophrynus cultripes* species group, with description of a new related species (Anura, Cyclo-
ramphidae). *Zootaxa*. **3155**: 1-20.
- Cei, J.M. (1980): Amphibians of Argentina. *Monit. Zool. It. (NS), Monografie II, Italy*.
- Cei, J.M. (1987): Additional notes to "Amphibians of Argentina": an update, 1980-1986. *Monit. Zool. It., N.S., Monografia*, **21**: 209-272.
- Cei, J.M., Crespo, E.G. (1982): Differences in larval morphology of allopatric isolated populations of the *Odontophrynus occidentalis* Group from Western Argentina. *Arq. Mus. Bocage*. **1**: 335-340.
- Cei, J.M., Ruiz, I.R.G., Beçak, W. (1982): *Odontophrynus barrioi*, a new species of Anuran from Argentina. *J. Herpetol.* **16**: 97-102.
- d'Heursel, A., de Sá, R.O. (1999): Comparing the tadpoles of *Hyla geographica* and *Hyla semilineata*. *J. Herpetol.* **33**: 353-361.
- Di Tada, I.E., Barla, M.J., Martori, R.A., Cei, J.M. (1984): *Odontophrynus achalensis* una nueva especie de anfibio de la Pampa de Achala (Córdoba, Argentina). *Hist. Nat.* **17**: 149-155.
- Do Nascimento, F.A.C., Mott, T., Langone, J.A., Davis, C.A., de Sá, R.O. (2013): The genus *Odontophrynus* (Anura: Odontophryniidae): a larval perspective. *Zootaxa* **3700**: 140-158.
- Dos Santos Dias, P.H., Telles de Carvalho-E-Silva, M.D.P., Potsch de Carvalho-E-Silva, S. (2013): Larval chondrocranium morphology of five species of *Proceratophrys* Miranda Ribeiro (Amphibia; Anura; Odontophryniidae). *Zootaxa* **3683**: 427-438.
- Fabrezi, M., Vera R. (1997): Caracterización morfológica de larvas de anuros del Noroeste argentino. *Cuad. Herpetol.* **11**: 37-49.
- Frost, D.R. (2014): Amphibian Species of the World: an Online Reference, Version 5.6 (09 January 2013). American Museum of Natural History, New York, USA. Available from <http://research.amnh.org/vz/herpetology/amphibia/Amphibia/Anura/Odontophryniidae/Odontophrynus> (accesed 18 February 2014).
- Grenat, P.R., Zavala Gallo, L.M. Salas, N.E., Martino, A.L. (2009): The tadpole of *Odontophrynus cordobae* Martino & Sinsch, 2002 (Anura: Cycloramphidae) from central Argentina. *Zootaxa* **2151**: 66-68.
- Gosner, K.L. (1960): A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* **16**: 183-190.
- Haas, A. (1995): Cranial features of dendrobatid larvae (Amphibia: Anura: Dendrobatidae). *J. Herpetol.* **224**: 241-264.
- Haas, A. (1997): The larval hyobranchial apparatus of Discoglossoid frogs: Its structure and bearing on the systematics of the Anura (Amphibia : Anura). *J. Zool. Syst. Evol. Res.* **35**: 179-197.
- Haas, A. (2001): Mandibular arch musculature of anuran tadpoles, with comments on homologies of amphibian jaw muscles. *J. Herpetol.* **247**: 1-33.
- Haas, A. (2003): Phylogeny of frogs as inferred from primarily larval characters (Amphibia: Anura). *Cladistics* **19**: 23-89.
- Haas, A., Richards, S.J. (1998): Correlations of cranial morphology, ecology, and evolution in Australian suitorial tadpoles of the genera *Litoria* and *Nyctimystes* (Amphibia: Anura: Hylidae: Pelodyadinae). *J. Herpetol.* **238**: 109-141.
- Lannoo, M.J. (1999): Integration: Nervous and Sensory Systems. In: Tadpoles: The Biology of Anuran Larvae, pp. 149-169. Altig, R., McDiarmid, R.W., Eds., University of Chicago Press.
- Lavilla, E.O., Scrocchi, G.J. (1986): Morfometría larval de los géneros de Telmatobiinae (Anura: Leptodactylidae) de Argentina y Chile. *Physis* **44**: 39-43.
- Lavilla, E.O., Scrocchi, G.J. (1991): Aportes a la herpetofauna del Chaco argentino: II- Nuevos datos sobre *Odontophrynus lavillai* Cei, 1985 (Anura: Leptodactylidae). *Acta Zool. Lilloana*. **40**: 33-37.
- Rosset, S.D., Ferraro, D.P., Alcalde, L., Basso, N.G. (2007): A revision of *Odontophrynus barrioi* (Anura: Neobatrachia): Morphology, osteology, vocalizations, and geographic distribution. *S. Ame. J. Herpetol.* **2**: 97-106.

- Sanabria, E., Quiroga, L. (2008): Guía Sonora de los anfibios de San Juan. (CD-ROM) Versión Digital 1. ISBN 978-987-05-4623-8, San Juan, Argentina.
- Savage, J.M., Cei, J.M. (1965): A review of the Leptodactylid frog genus *Odontophrynus*. *Herpetologica* **21**: 178-195.
- Schlosser, G., Roth, G. (1995): Distribution of cranial and rostral nerves in tadpoles of the frog *Discoglossus pictus* (Discoglossidae). *J. Morphol.* **226**: 189-212.
- Taylor, W.R., Van Dyke, G.C. (1985): Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybiurn* **9**: 107-119.
- Torrella, A.T., Adamolí, J. (2005): Situación ambiental en la ecoregión del Chaco Seco. In: La situación ambiental de Argentina 2005, pp. 74-100. Brown, A., Ortiz, U., Acerbi, M., Corchera, J. Eds., Fundación Vida Silvestre, Buenos Aires, Argentina.

