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Complementary diagnosis of the genus *Insuetophrynus* (Anura, Cycloramphidae) based on larval characters

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Abstract

The external and internal characteristics of the tadpoles of *Insuetophrynus acarpicus* are compared with other members of the family Cycloramphidae and used to complement the generic diagnosis previously based solely on adult morphological characteristics. The redescription includes larval external morphology, internal buccal features examined by SEM, and description of the chondrocranium and hyobranchial apparatus.

Key words: Chondrocranium, hyobranchial apparatus, internal buccal anatomy, larval morphology, systematics

Introduction

The external and internal morphology of tadpoles have been successfully used to improve generic diagnosis and to infer phylogenetic relationships among anurans (Larson & de Sá 1998; Haas 1995, 2001, 2003; Maglia *et al*. 2001; Púgener *et al*. 2003; Grosjean *et al*. 2004). Among the members of the Cycloramphidae family, typical examples of generic diagnosis improved with the addition of larval traits are frogs of the genera *Thoropa* [tooth row formula 2(1–2)/3(1); some parts of the lateral margins of the abdominal wall expanded as a free flap (Lynch 1971)] and *Eupsophus* [tooth row formula 2(2)/2, endotrophy; (Formas 1989)]. *Insuetophrynus acarpicus* Barrio (Cycloramphidae, Frost 2009) is a monotypic frog endemic to the *Nothofagus* forests of temperate southern Chile [Mehuín (39º26'S, 73º13'W) Valdivia province (Díaz & Valencia 1985)] and it is considered to be a critically endangered species (IUCN 2007) mainly due to low population abundances and its extremely narrow distribution (Díaz-Páez & Ortiz 2003). The generic diagnosis of *Insuetophrynus* given by Barrio (1970) was supported by three adult characters; two from the osteology (firmisternal pectoral girdle and carpal elements without ossification) and one from the external morphology (males with two bilateral rounded blank patches of keratinous spines). Lynch (1978) proposed that the unique traits of *Insuetophrynus* are the very small sternum and the functionally firmisternal pectoral girdle.

Lavilla (1988) used external traits of the tadpoles *Insuetophrynus* (oral disc, spiracle position, level of the nostrils aperture, and proctodeal tube) to diagnose the genus among frogs of the subfamily Telmatobiinae (*sensu* Lynch 1978). Formas *et al.* (1980) described the external morphology of *I. acarpicus* tadpoles based on 16 specimens (IZUA 538, 1817; stages 25 to 43). In order to improve the generic diagnosis of *Insuetophrynus*, in this paper the tadpoles are redescribed, including new external morphological characteristics, internal oral features, chondrocranium, and hyobranchial apparatus. Some larval characters are useful in the generic diagnosis of *Insuetophrynus* and also could be considered as a baseline in intergeneric comparisons among tadpoles of the family Cycloramphidae [*Alsodes*, *Crossodactylus*, *Cycloramphus*, *Eupsophus*, *Hylorina*, *Insuetophrynus*, *Limnomedusa*, *Macrogenioglottus*, *Odontophrynus*, *Proceratophrys*, *Rhinoderma*, *Thoropa*, and *Zachaenus* (Frost *et al.* 2009)].

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Material and methods

All specimens used in this study were collected at the type locality (Mehuín, Provincia de Valdivia, southern Chile), in three different times: seven larvae (IZUA 1815, Instituto de Zoología Universidad Austral de Chile) used in the previous descriptions (Formas *et al.*1980), seven larvae (IZUA 3743) collected on February 2006) and five larvae (CHFR 061, Felipe Rabanal, personal collection) captured on 27 November 2007.

Most of the tadpoles were fixed in 10% buffered commercial formaldehyde solution, but some were reared in the laboratory to verify species identification. Tadpoles were staged following Gosner table of normal development (Gosner 1960). Description is based on seven specimens (stages 26, 27 and 30; from lots IZUA 1815 and 3743) and the illustrated tadpole is at Gosner stage 30 (IZUA 1815). Eight measurements were taken with a dial caliper (to the nearest 0.1 mm) following Altig & McDiarmid (1999): total length, body length, tail length, maximum tail height, tail muscle height, tail muscle width, internarial distance, and interorbital distance. Morphometric data of 19 specimens (stages 25–43) are given as mean ± standard deviation.

Three tadpoles at stages 26, 30, and 35 (IZUA 3743) were dissected for observation of the internal buccal anatomy with scanning electronic microscopy (SEM), following the methodology described by Larson *et al.* (2003). Buccal cavity features were examined and photographed using scanning electron microscope (Leo-420) connected to a computer. Terminology follows Wassersug (1976) and Wassersug & Heyer (1988).

Chondrocrania were cleared and double stained with Alcian Blue and Alizarin Red (Song & Parenti 1995). Chondrocranial and hyobranchial anatomy was analysed with a stereomicroscope and drawings were made with a camera lucida. Chondrocranial anatomy description was based on the examination of four larvae (IZUA 3743) at Gosner stages 31, 32, and 34. Terminology follows Larson & de Sá (1998) and D'Heursel & de Sá (1999). The overall description and illustrations were based on tadpoles at stage 30 (IZUA 1815, 3743).

Results

The tadpole of Insuetophrynus acarpicus

In lateral view the body is robust and slightly compressed (Fig. 1A); dorsally ovoid (Fig. 1B). The total length is 44.0 ± 3.1 mm (stage 26) and the tail length is 1.7 times the body length; tail width is 1.8 times the interorbital distance. The nostrils are oval and not protruding, surrounded by a thin cutaneous marginal brown fringe which is anterolaterally located. The nostrils are closer to the eye than to the tip of the snout. The internarial distance is 72% of the interorbital distance. The tip of the snout is gently flattened. The pupil is circular and the eyes are anterolaterally situated, approximately 0.5 times the internarial distance. The interorbital distance is 1.5 times the internarial distance. The ventral oral disc is not emarginated (Fig. 1C), its maximum width is approximately equivalent to the internarial distance; a single row of short marginal papillae surround the oral disc, the rostral gap is present and the mental gap and intramarginal (*sensu* Lavilla 1988) papillae are absent. The lower jaw sheath is "U-shaped". The upper and lower jaw sheath are thin, with weak, minute (range 1.1–1.8 µm in height and 2.2–2.7µm in width) keratinized serrations with rounded tips (about 5–6 per 100µm) (Fig. 2D). The labial tooth row formula is 2(2)/2(1–2). The scarcely curved keratodonts present their heads poorly differentiated and the cups are absent (Fig. 2C). The spiracle is sinistral, short (63% of internarial distance), posterolaterally directed at an approximately 60° regarding the main axis of the body. The spiracular tube is not free, the inner wall is attached to the body; its tip is not raised and the diameter of the spiracular aperture corresponds to 50% of the eye diameter (Fig. 1A). The vent tube has a dextro-ventral ovoid aperture (Fig. 1D), representing approximately 67% of the internarial distance; its posterior border is continuous with the ventral margin of the tail fin. The low dorsal fin does not extend beyond the tail-body junction. The ventral fin originates at the posterior margin of vent. The maximum tail height locates at the posterior third of the tail, and it is about 32% of the tail length. The tip of the tail is rounded. A conspicuous lateral line system is observed. In life, the myomeres and fins present light-brown irregular spots, the dorsal surface of the body has greenish tonalities. In formaldehyde solution tadpoles are grey and the belly is transparent. The tadpole measurements are shown in table 1.

TABLE 1. Morphometric data (mean ± SD) of the tadpoles of *Insuetophrynus acarpicus* (all data in mm).

Stage	n	Total length	Body length	Tail length	Maximum tail height	Tail muscle height	Tail muscle width	Internarial distance	Interorbital distance
25	4	40.0 ± 3.9	14.7 ± 2.1	25.3 ± 2.6	7.3 ± 0.9	5.2 ± 0.4	5.1 ± 0.9	2.9 ± 0.3	4.3 ± 0.3
26	9	45.1 ± 3.1	17.1 ± 1.7	27.9 ± 2.5	8.7 ± 0.6	5.4 ± 0.7	5.4 ± 1.2	2.8 ± 0.5	4.6 ± 0.5
27	1	56.1	20.1	36.0	9.7	5.9	6.7	3.3	5.5
28	1	54.2	19.2	35.1	11.6	7.0	7.2	3.6	6.3
31	2	56.5 ± 2.4	19.3 ± 2.9	37.3 ± 0.6	10.3 ± 0.4	7.1 ± 0.7	5.8 ± 0.2	3.4	5.5 ± 0.5
32	1	59.1	22.3	36.8	11.0	7.6	6.9	3.8	5.8
43	1	51.9	17.3	34.6	7.8	5.65	5.2	2.7	5.9

Internal buccal anatomy

Internal buccal anatomy description is based on three tadpoles at stages 26, 30, and 35.

Buccal roof. The buccal roof (Fig. 2A) is oval-shaped, 1.6 times larger than wide. The prenarial arena has two pairs of single, short and blunt papillae. The nares, approximately 4 times longer than wide, are oriented at about 45° regarding the main axis of the oral cavity; narial valves are well developed (Fig. 2A), and the thin anterior rims bear 2–3 low and blunt papillae. The postnarial arena shows ten single, pointed papillae located close to the median ridge. The median ridge is a short, wide structure extending ventrally from the buccal roof and its margin has nine pointed papillae. Lateral ridge papillae place at the level of the median ridge; they are well-developed, large, flat and bear 7–8 long acute branches. The buccal roof arena is inverted heart-shaped, defined by 28–30 blunt and short papillae on each side; its anteromedial region bears 14–16 pointed papillae; the posterolateral area is covered by numerous pustulations (35.0 ± 3.2 µm width; 33.5 ± 3.3µm height). The glandular region is poorly defined, with some scattered secretory pits. The dorsal velum has two continuous rows of well developed papillae; the anterior row presents 14–16 large papillae per side and the posterior row 6–8 shorter papillae per side.

Buccal floor. The buccal floor (Fig 2B) is rectangular-shaped. There are two infralabial papillae; their tips are bifurcate. Five lingual papillae project dorsally from the tongue anlage at the anteromedial region of the buccal floor. The more conspicuous structures are one pair of large, palp-like papillae, medial to buccal pockets; other BFA papillae are absent. Buccal pockets are deep, long (50% of the buccal floor arena), and obliquely oriented, approximately 45° of the main axis of the body. The ventral velum is well-developed and bilobed. It is covered by a wide band (3.5 times wider than long) of numerous short pustulations (100–140; 5–8/100 µm²); its posterior margin has 16–18 long, conical papillae per side.

Chondrocranium

At stage 31 and 32 the chondrocranium is completely cartilaginous, whereas at stage 34 the ossification of the parasphenoid is marked (Fig. 3B). The chondrocranium is elongated (Fig. 3A, B). Its greatest width (at the level of the palatoquadrates) corresponds to 74% of the total length, while the greatest depth (at the level of the cornua trabeculae) to about 26% of the total length (Fig. 3C).

Neurocranium

Ethmoidal region. The paired cartilago suprarostralis support the upper jaw sheath. The cartilago suprarostralis includes two cartilages on each side; the pars alaris, slightly triangular, and the pars corporis, a medial slender bar. The partes are fused distally and proximately between them, leaving an ovoid opening in the central area (Fig. 3E). Additionally, the pars corporis of each side are also ventromedially fused, through a continuous and narrow sheet of cartilage (Fig. 3E). The adrosal cartilage lies dorsolateral to the tip of the processus dorsalis, posterior of the pars alaris. The cornua trabeculae originate from the planum trabeculare anticum and represent approximately 32% of the total chondrocranial length; they diverge and curve ventrally. They have a developed processus lateralis trabeculae.

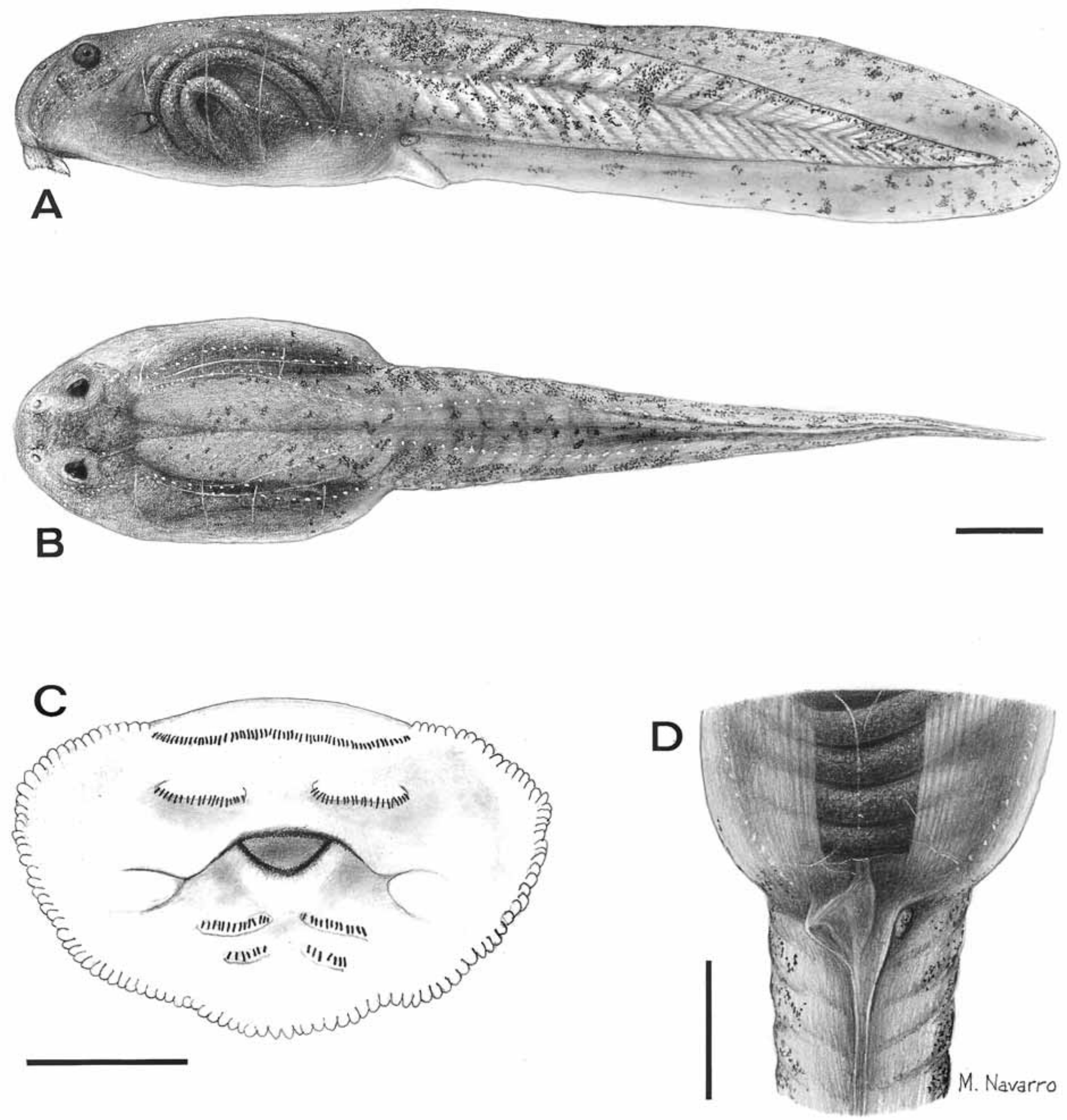

FIGURE 1. Tadpole of *Insuetophrynus acarpicus* (Stage 30) (A) Lateral view, (B) dorsal view, (C) oral disc, (D) ventral view. Bar A, B, D = 5 mm; C = 2 mm.

Orbitotemporal region. The lateral walls of the braincase are formed by the cartilage orbitalis, which connects posterodorsally to the otic capsule. These connections form the dorsal margin of the foramen prooticum, a wide and elongated foramen located between the anterior edge of the otic capsule and the posterior margin of the cartilage orbitalis. Two other ovoid small foramina, similar in size, are visible in the posteroventral portion of the cartilage orbitalis; the smaller foramen is the foramen opticum, whereas the posterior is the foramen oculomotorium. The fenestra frontoparietalis is ovoid and represents approximately 29% of the total chondrocranial length (Fig. 3A). It is bordered anteriorly by the planum ethmoidale, laterally by the taeniae tecti marginales, and posteriorly by the tectum synoticum. In these stages (31, 32, 34), the fenestra frontoparietalis divides into an anterior frontal and two posterior parietal fenestrae (Fig. 3A). This subdivision occurs by the growth of the taenia tecti transversalis from the taeniae tecti marginales, and the elongation of the taenia tecti medialis anteriorly from the medial portion of the tectum synoticum. The planum intertrabeculae form the floor of the braincase and it is perforated by the foramen caroticum primarium.

Occipital region. The tectum synoticum bridges the two rhomboid otic capsule, and forms the dorsal roof of the foramen magnum (Fig. 3A). Each archus occipitalis is continuous with the tectum synoticum dorsally and the planum basale ventrally forming the foramen magnum and the foramen jugulare. The otic capsule are 28% of the total chondrocranial length. Beneath the crista parotica a large fenestra ovalis (approximately 50% of the otic capsule length) is found (Fig. 3B, C). The foramina jugulare are approximately one third of the fenestra ovalis length. In these stages the foramen perilymphaticum was not observed.

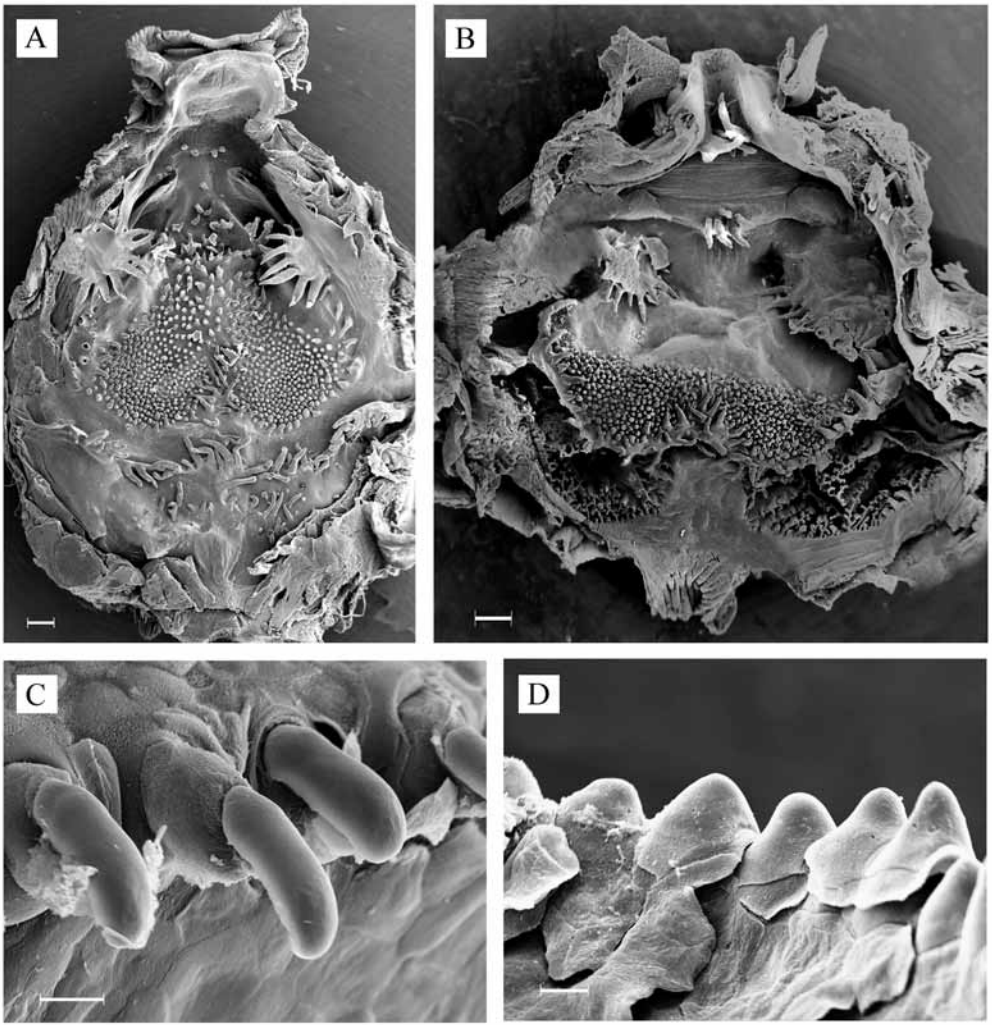

FIGURE 2. Roof (A) and floor (B) of the buccal cavity of *Insuetophrynus acarpicus* (Stage 30). Labial teeth: Stage 32 (C). Upper jaw sheath: Stage 34 (D). Bar = A, B = 30 µm; C, D = 10 µm.

Visceral components

Palatoquadrate. The palatoquadrate attaches to the lateral walls of the braincase anteriorly by the commissura quadratocranialis anterior and posteriorly by the processus ascendens. The narrow commissura quadratocranialis anterior extends between the palatoquadrate and the floor of the neurocranium. It bears a well-developed, triangular processus quadratoethmoidalis on its anterior margin. The low processus antorbitalis and the processus muscularis quadrati are connected by the ligamenti tecti superius et inferius which is not dorsally visible. In lateral view the processus muscularis quadrati is triangular-shaped (Fig. 3C)

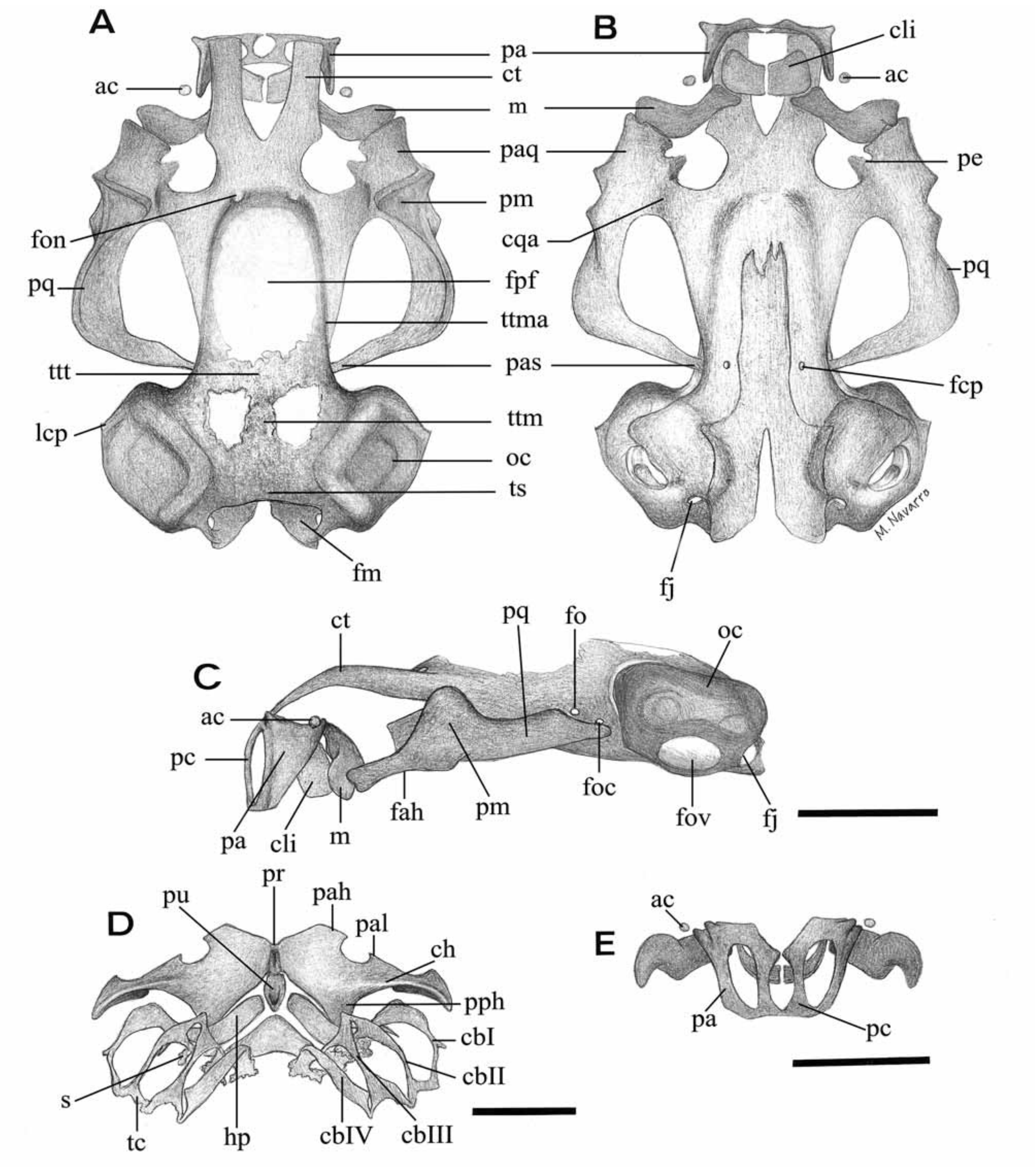

FIGURE 3. Chondrocranium and hyobranchial apparatus of *Insuetophrynus acarpicus* (Stage 32). (A) dorsal view, (B) ventral view, (C) lateral view, (D) hyobranchial apparatus, (E) cartilago suprarostralis. Abbreviations: ac = adrosal cartilage, cb I–IV = ceratobranchials I–IV, ch = ceratohyal, cli = cartilago labialis inferior, cqa = commissural quadratocranialis anterior, ct = cornua trabeculae, fah = facies articularis hyalis, fcp = foramen caroticum primarium, fon = foramen orbitonasal, fj = foramen jugulare, fm = foramen magnum, fo = foramen opticum, foc = foramen oculotomotorium, fov = fenestra ovalis, fpf = fenestra frontoparietalis, hp = planum hypobranchiale, lcp = larval crista parotica, m = cartilago Meckeli, oc = otic capsule, pa = pars alaris, pc= pars corporis, pah = processus anterior hyalis, pal = processus anterolateralis hyalis, paq = pars articularis quadrati, pas = processus ascendes, pm = processus muscularis quadrati, pph = processus posterior hyalis, pq = palatoquadrate, pe = processus ethmoidalis, pr = pars reuniens, pu = processus urobranchialis, s = spiculum, tc = commissura terminalis, ts = tectum synoticum, ttm = taenia tecti medialis, ttma = taenia tecti marginalis, ttt = taenia tecti transversalis. Bar = 2 mm.

and its rounded tip is located at the end of the septum nasi, not reaching the dorsal surface of chondrocranium (Fig. 3C). In dorsal view (Fig.3A) it is medially inclined. Below the processus muscularis quadrati, there is a notch, the facies articularis quadrati, which constitutes the point of articulation with the ceratohyal. Posteriorly, the palatoquadrate attaches to the orbital cartilage via the processus ascendens, which is a narrow, rod-like cartilage connecting the posteromedial margin of palatoquadrate to the region of the pila antotica of the orbital cartilage. The processus ascendens forms an angle of about 45–48° with the main axis of the chondrocranium; it attaches below the posterior margin of the foramen oculomotorium ("low" condition, Sokol 1981; Fig. 3A, B).

Cartilago Meckeli and cartilago labialis inferior. The cartilago Meckeli together with the cartilages labiales inferiores form the lower jaw (Fig.3 B). The short and stout cartilago Meckeli is slightly sigmoid in shape, transversely oriented, placed ventral to the cornua trabeculae. The cartilago Meckeli articulates anteriorly with the posterior margin of the cartilago labialis inferior and posteriorly with the pars articularis quadrati. The cartilago Meckeli has three processes: the processus dorsomedialis, projecting dorsally towards the cornua trabeculae; the processus retroarticularis, which curves posteriorly and ventrally to articulate with the pars articularis quadrati; and the processus ventromedialis, the anterior processus that articulates with the cartilago labialis inferior. The cartilago labialis inferior provides support to the lower jaw sheath; each cartilage is nearly rectangular-shaped, 1.4 times wider than long, and curved (Fig. 3B).

Hyobranchial morphology. The anterior margin of the ceratohyale bears two anterior processes, the processus anterior hyalis and the processus anterolateralis hyalis, both similar in size, with pointed tips. The posterior margin of the ceratohyal presents a pointed and well-developed processus posterior hyalis. Medially, the ceratohylia are connected by a well-chondrified pars reuniens. The pars reuniens is continuous with the basibranchial which possesses a well-defined processus urobranchialis. The almost rectangular plana hypobranchialia, about 2.5 times longer than wide, remain independent from each other. The plana hypobranchialia are continuous with the first and fourth ceratobranchialia. The ceratobranchialia are connected posteriorly by the commissurae terminales. The first three ceratobranchialia bear a spiculum, which projects dorsally from their proximal ends.

Ecology

According to Formas *et al*. (1980) and Díaz & Valencia (1985), the tadpoles of *Insuetophrynus acarpicus* are typical inhabitants of a coastal fast running stream in a wooded (*Aextoxicum punctatum*) ravine at the type locality (Mehuín). Vegetation in the stream bank includes predominantly *Luzuriaga radicans*, *Blechnum blechnoides*, *Hipopterigium* sp., *Chusquea quila*, *Lophosoria quadripinnata*, *Hymenophyllum plicatum* and *H. caudiculatum*. During February 2005, 2006, and November 2007, the ravine was visited and different extents of human disturbance were observed. The most remarkable is the cutting of the largest trees (*A. punctatum*) that shaded the stream. In spite of this, apparently the original stream remains without changes. On February 2006 and November 2007, 12 tadpoles were collected under stones in muddy areas close to the stream bank with slow current; they were never seen swimming in the current, but they moved rapidly in the mud, seeking shelter between the stones. In one tadpole (stage 28), the digestive tract (gut length index 18.8; Heyer 1973) was filled with unidentified organic material and many inorganic particles (irregular in shape, maximum size range from 0.1 to 0.3 mm, light brown in color). In order to observe their mode of feeding, tadpoles of *Insuetophrynus* were kept in an aquarium (18° C). During nine days (three times/day) one of us (F. Rabanal) observed the tadpoles protruding the ventral mouth and sucking the mud deposited on the bottom of the aquarium.

Discussion

The tadpoles of *Insuetophrynus acarpicus* belong to the morphological type IV tadpole of Orton (1953) and they present typical characteristics related to the lotic benthic habitat: depressed body, low fins rounded tip, dorsal fin originating at the dorsal tail-body junction and ventral oral disc (Altig & Johnston 1989). The present analysis agrees with the previous descriptions (Formas *et al.* 1980); however we added characteristics not reported before (fusion of the inner wall of the spiracle to the body wall, the wide vent tube with dextro-ventral aperture and posterior continuous border with the ventral margin of the tail and jaw sheaths thin and poorly keratinized). In *I. acarpicus* the buccal floor arena is rectangular whereas in *Alsodes*, *Limnomedusa*, *Proceratophrys*, and *Odontophrynus* is broad and "U-shaped", in *Macrogenioglotus* is ovoid-triangular and narrow, and in *Hylorina* is elongated (Wassersug & Heyer 1988; Formas & Brieva 2004; Cárdenas-Rojas *et al.* 2007). The buccal roof arena of *I. acarpicus* is unique by been heart-shaped.

The cartilage labiales superiores of *I. acarpicus* are distinguishable from those of *Alsodes* (Formas & Brieva 2004), *Eupsophus* (Vera-Candioti *et al*. 2005); Cárdenas-Rojas *et al.* 2007), *Limnomedusa* (Turner 1999) and *Rhinoderma* (Lavilla 1987) by having the pars alaris and pars corpora fused dorsal and ventrally.

If we take into consideration that the oral disc is ventrally positioned, the weak and blunt serrations on the upper and lower sheath, the scarce keratodonts with their blunt tips, the fusion of the proximal and distal parts of the pars alaris and pars corporis of the cartilago suprarostralis, and the ventromedially fusion of their pars corpora, we hypothesize that those characters are associated with the suctorial mode of feeding.

According to the new morphological features of the tadpoles here described (i.e. external morphology, chondrocranium and buccal internal features) and osteological characters considered by Lynch (1978) the genus *Insuetophrynus* can be diagnosed in the following way: (1) sternum small and firmisternal pectoral girdle; (2) oral disc ventral and not emarginated; (3) intramarginal papillae absent; (4) teeth row formula 2(2)/2(1–2); (5) smooth and scarcely curved keratodonts with blunt distal tips; (6) jaw sheaths poorly keratinized; (7) ventral velum covered by a wide band of numerous pustulations; (8) ventral velum covered by a wide band of numerous postulations and long marginal papillae; (9) continous dorsal velum with two rows of well-developed five lingual papillae; (10) tetrapartite cartilago suprarostralis, with pars alaris and pars corpora fused dorsal and ventrally.

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