Morphology and feeding in tadpoles of *Ceratophrys cranwelli* (Anura: Leptodactylidae)

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Abstract

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This paper provides data on the skeleton, musculature, buccal apparatus, buccopharyngeal cavity and diet of *Ceratophrys cranwelli* tadpoles, and attempts to contribute to the knowledge of relations between morphology and ecology in anuran larvae. Both in morphological characters and feeding habits, these tadpoles are very similar to other species within the genus. They possess many of the structural features usually found in predaceous tadpoles: strong, keratinized jaw sheaths and keratodonts, reduced buccal papillation, high values of in-lever arm proportion and buccal floor area, well-developed ceratohyals, and hypertrophied jaw muscles. Food sources consist of other tadpoles, microcrustaceans, larvae of insects, plant fragments, as well as rotifers and microalgae. As facultative carnivores, they are likely to play an important role in regulating the aquatic communities of the ephemeral ponds where they develop.

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Introduction

The genus *Ceratophrys* includes seven species from forest and non-forest areas in South America. Lynch (1982) summarized the relations within the genus. *Ceratophrys cranwelli* was first described by Barrio (1980) and is distributed from the Chacoan region of Argentina to Bolivia, Brazil and Paraguay, with an altitudinal range up to 700 m above sea level. Notes on the external morphology and behaviour of the tadpoles appear in the study by Cei (1980). Aspects of internal morphology of *Ceratophrys* larvae have been studied in four species: *C. cornuta*, *C. cranwelli*, *C. ornata* and *C. aurita* (Wassersug and Heyer 1988; Lavilla and Fabrezi 1992; Fabrezi and García 1994; Wild 1997; Palavecino 1999; Haas 2003). Although tadpoles of all these species are known to be predaceous, there is no exhaustive record of their feeding habits. Several researchers have attempted to correlate morphological characters with ecology and behaviour in tadpoles (e.g. Noble 1929; Wassersug 1980; Satel and Wassersug 1981; Altig and Johnston 1989; Haas and Richards 1998; Hall *et al.* 2002; Alcalde and Rosset 2003; Vera Candioti and Haas 2004; Vera Candioti *et al.* 2004). Their results show that in some cases it is possible to find external and internal traits that are associated with particular feeding habits, microhabitats, etc.

It would seem interesting, then, to address a complete description of the morphological traits and feeding habits of *Ceratophrys cranwelli* tadpoles, given their role as predators and regulators of pond assemblages. This paper provides baseline data on the skeleton, musculature, buccal apparatus, buccopharyngeal cavity and diet, with descriptions being supplemented by behavioural observations. This paper is also an attempt to contribute to the knowledge of relations between morphological and ecological features in anuran larvae.

Materials and Methods

Two groups of tadpoles of *C. cranwelli* from Las Lajitas (Anta, Salta Province; collected in January 1996 and December 2003) were studied. Larvae were preserved in 10% formalin and staged according to Gosner (1960).

Tadpoles of the first group (*n* = 9, all Stage 33) were used for morphological study of the chondrocranium, musculature, buccal apparatus and buccopharyngeal cavity. Five larvae were prepared according to Wassersug's clearing and staining protocol (Wassersug 1976a). For muscle observation, three
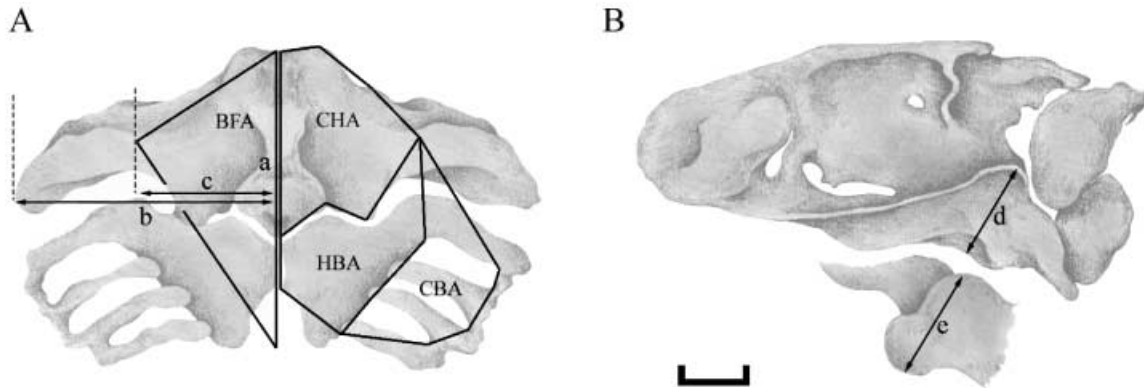
Fig. 1—Measurements of the hyobranchial apparatus in —**A**. ventral and —**B**. lateral view. a, length of the ceratohyal and the hypobranchial plate; b, width of ceratohyal; c, distance between the condylus articularis and the middle line; d, height of the muscular process; e, height of the ceratohyal at the palatoquadrate, at the point of articulation; BFA, area of the buccal floor; CBA, area of the ceratobranchials; CHA, area of the ceratohyal; HBA, area of the hypobranchial plate. Scale bar 1 mm.

specimens were removed before the digestion step of the clearing and staining procedure (Lavilla, personal communication), and then stained with a solution of Lugol's iodine (Bock and Shear 1972). The remaining four larvae were used for studying the buccal apparatus and buccopharyngeal cavity. Oral discs and buccal roofs and floors were exposed and stained with methylene blue, following Wassersug's technique (Wassersug 1976b). One sample of an oral disc and buccal cavity was prepared for scanning electron microscopy, following the protocol of Echeverría (Echeverría 1997). Observations and micrographs were made with a JEOL 35 CF scanning electron microscope.

All dissections and illustrations were made using a stereomicroscope equipped with a camera lucida. Some measurements were taken from the drawings of the hyobranchial apparatus, using IMAGE TOOL 1.28 software (Fig. 1). Measurements were employed to calculate the in-lever arm proportion (taken as the projected width of the lateral portion of the ceratohyal over the total width of the ceratohyal, b–c/b), buccal floor, ceratohyal, hypobranchial and ceratobranchial areas, and buccal volume, according to Wassersug and Hoff (1979) and Haas and Richards (1998). The areas can only be approximated because the method uses flat planes to measure surfaces that are not exactly flat surfaces, especially in the case of the branchial basket. In this work, however, this would be a minor problem, because the ceratobranchials of *C. cranwelli* are almost straight bars. The muscles interhyoideus (ih) and orbitohyoideus (oh) were dry-weighed (after drying at 56°C for 5 days, using a scale with precision = 0.0005 g) to calculate the ih : oh ratio and evaluate the pumping mechanism. The muscles mentioned above intervene in raising and lowering the buccal floor, respectively. According to Satel and Wassersug (1981), microphagous suspension feeders generally have large buccal floor elevator muscles (ih) compared to the buccal floor depressors (oh), giving a high ih : oh value, whereas macro-

phagous exhibit larger depressor muscles, and thus a low ih : oh value.

Tadpoles of the second group (*n* = 13, Stages 35–39) were used for trophic analysis. The whole digestive tracts of 10 larvae were removed and their contents were extracted and diluted in a 3 : 1 (water : erythrosine) solution. Three aliquots were quantified, and the number of organisms per millilitre of solution was calculated. Each food item was measured with a micrometric ocular to analyse the size distribution of food particles. The use of numerical frequencies to indicate the contribution of each item to the total gut content overemphasizes the importance of small particles present in large numbers. To correct this, volumes can be used. They are estimated from linear dimensions, taking as a reference the geometric shape each food item most closely resembles (Hyslop 1980). Therefore, the percentage values in the Results section represent the volume accumulated by the particles of each size range. Some tadpoles of the second group (*n* = 3, Stages 38–39) were kept alive in the laboratory, starved for 48 hours, and then given *Pleurodema borelli* tadpoles to visualize prey capture mode.

The terminology for descriptions of cartilages and muscles follows that of Haas (2003), and oral disc and buccal cavity nomenclature is that of Altig and McDiarmid (1999). Intact individuals from the same original series are preserved as voucher specimens (FML15842. Herpetological Collection of Fundación Miguel Lillo).

Results

Chondrocranium and hyobranchial apparatus (*n* = 5, Stage 33)

The cartilaginous skeleton of *C. cranwelli* tadpoles was described by Lavilla and Fabrezi (1992). Figure 2 shows the chondrocranium and hyobranchial apparatus of the larvae considered in this paper; the only differences with Lavilla and Fabrezi's
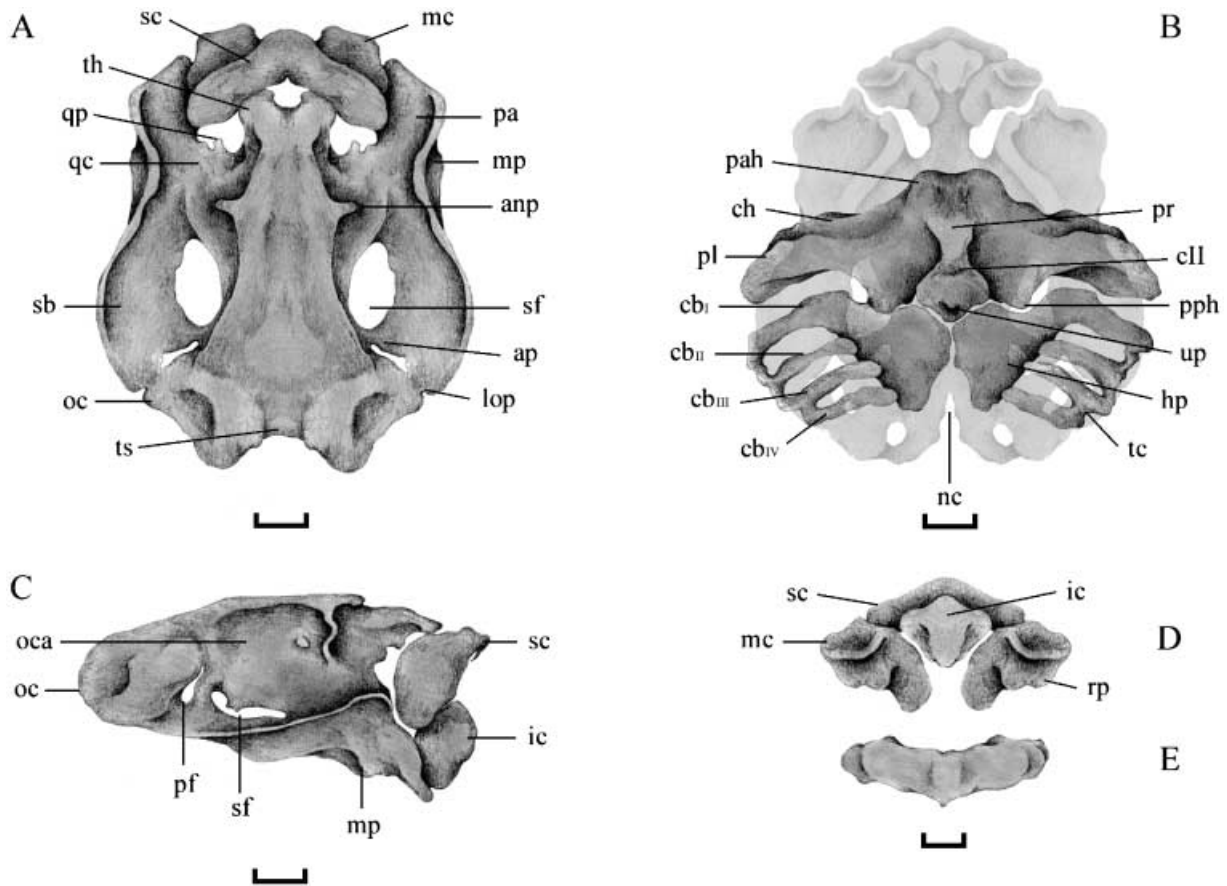
Fig. 2—*Ceratophrys cranwelli* Stage 33. Chondrocranium and hyobranchial apparatus. —**A**. Chondrocranium, dorsal view. —**B**. Hyobranchial apparatus, ventral view. —**C**. Chondrocranium, lateral view. —**D**. Detail of mandibles, ventral view. —**E**. Detail of suprarostral cartilage, frontal view. anp, antorbital process; ap, ascending process; $cb_{(I-IV)}$, ceratobranchial; ch, ceratohyal; cII, copula II; hp, hypobranchial plate; ic, infrarostral cartilage; lop, larval otic process; mc, Meckel's cartilage; mp, muscular process; nc, notochordal canal; oc, otic capsule; oca; orbital cartilage; pa, pars articularis; pah, processus anterior hyalis; pf, pro-otic foramen; pl, processus lateralis; pph, processus posterior hyalis; pr, *pars reuniens*; qc, quadratocranial commissure; qp, quadratoethmoid process; rp, retroarticular process; sb, subocular bar; sc, suprarostral cartilage; sf, subocular fenestra; tc, terminal commissure; th, trabecular horn; ts, tectum synoticum; up, urobranchial process. Scale bars 1 mm.

tadpoles are the absence of lateral projections on the cerato-branchials and the complete chondrification of the chondro-cranial roof. Measurements taken from the hyobranchial apparatus are: in-lever arm proportion, 0.51; buccal floor area, 4.56 mm^2; area of the ceratobranchials (relative to the total hyobranchial apparatus area), 0.29%; area of the ceratohyal, 0.39%; area of the hypobranchial plate, 0.32%; and buccal volume, 13.19 mm^3.

Musculature (n = 4, Stage 33)

Part of the musculature (mandibular and hyoid muscles) was described by Palavecino (1999).

Table 1 and Figure 3 show the origin and insertion of man-dibular, hyoid and branchial muscles of the larvae considered in this paper. Unlike the observations in tadpoles by Palave-

cino, the m. levator mandibulae longus superficialis inserts on Meckel's cartilage, and the m. suspensoriohyoideus is absent. The value of the ih : oh ratio was 0.25.

Buccal apparatus and buccopharyngeal cavity (n = 5, Stage 33)

The oral disc is circular with small indentations in the commissures. It has very well-developed protruding lips with conical papillae sparsely dispersed (Figs 4A,B and 5A). The suprarostrodont is thin, U-shaped and well keratinized, with short, pointed serrations. Serrations have an average width of 14 μm, and distance between them is approximately 10 μm (Fig. 5B). Serration density is 27/mm. The infrarostrodont is well-developed, wider than the suprarostrodont. Serrations are similar, short and pointed (Fig. 5C), but denser because of the shorter distance between them (55/mm; 5 μm). The

Table 1 Musculature of *Ceratophrys cranwelli* Stage 33

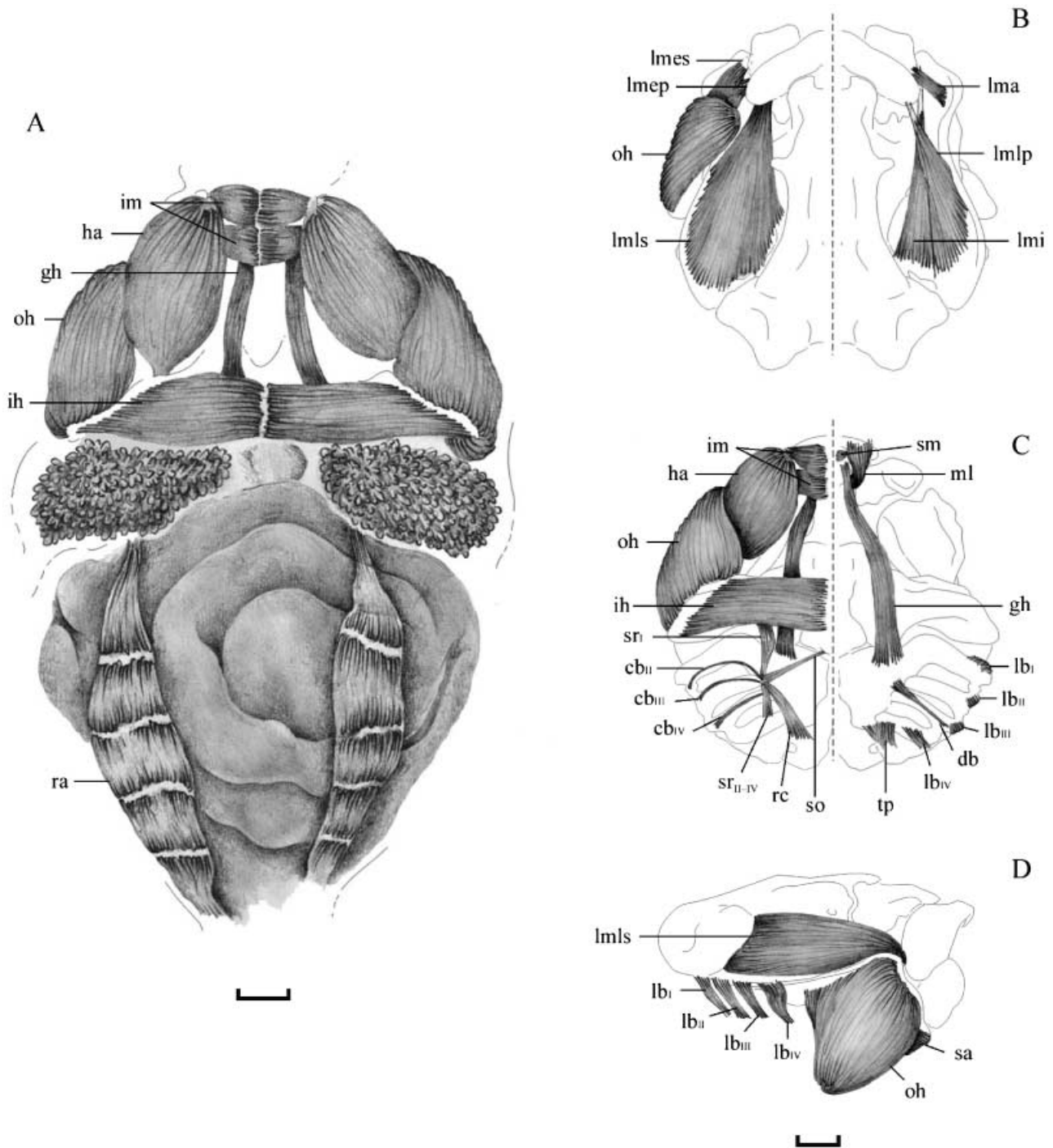| Muscle	Origin	Insertion	Comment
Mandibulolabialis	medial edge of Meckel's cartilage	lower lip of the oral disc	cylindrical and compact
Submentalis	medial region of the ventral face of infrarostral cartilages	short and without aponeurosis	
Intermandibularis	lateral edge of Meckel's cartilage	aponeurosis media	short and well-developed; two slips: anterior, semicircular shape; posterior, more developed and rectangular shape
Levator mandibulae longus superficialis	posteroexternal border of the subocular bar and ascending process	mediodorsal region of Meckel's cartilage	very well-developed
Levator mandibulae longus profundus	external border of the subocular bar	lateral edge of suprarostral cartilage	its origin occupies half the area of m. l. m. l. superficialis
Levator mandibulae externus superficialis	medial inferior face of the muscular process	lower lip of the oral disc, next to the commissure	distinction is not clear, because only one slip arises from the medial face of muscular process; a small group of fibers diverges only distally and inserts on the suprarostral cartilage; the ramus V_3 of trigeminal nerve is dorsal to both muscles
Levator mandibulae externus profundus	medial inferior face of the muscular process	lateral edge of the suprarostral cartilage	
Levator mandibulae internus	ventral surface of the ascendant process and otic capsule	distal edge of Meckel's cartilage	insertion is through a well-developed tendon, which is more than half the muscle length
Levator mandibulae articularis	medial face of muscular process	lateral edge of Meckel's cartilage	short and well-developed
Orbitohyoideus	muscular process	ventral face of the edge of ceratohyal	very well-developed
Suspensorioangularis	inferior region of the descending border of the muscular process	retroarticular process of Meckel's cartilage	fibers occupy less than half the lateral face of the process
Hyoangularis	dorsal face of the edge of the ceratohyal	retroarticular process of Meckel's cartilage	very well-developed
Interhyoideus	ventral face of the edge of ceratohyal	aponeurosis media	very well-developed
Geniohyoideus	posteroventral surface of infrarostral cartilages	hypobranchial plate	
Levator arcuum branchialium I	lateral margin of the subocular bar	ceratobranchial I	
Levator arcuum branchialium II	larval otic process	terminal commissure II	
Levator arcuum branchialium III	larval otic process	terminal commissure III	
Levator arcuum branchialium IV	posterolateral part of the otic capsule	ceratobranchial IV	
Constrictor branchialis II	branchial process II	terminal commissure I	
Constrictor branchialis III	branchial process II	terminal commissure II	
Constrictor branchialis IV	branchial process III	terminal commissure III	
Subarcualis rectus I	lateral base of processus posterior hyalis	branchial process II	
Subarcualis rectus II–IV	branchial process II	ventral proximal region of ceratobranchial IV	
Subarcualis obliquus	urobranchial process	branchial process II	
Tympanopharyngeus	ventral proximal region of ceratobranquial IV and posterior region of hypobranchial plate	otic capsule	
Diaphragmatobranchialis	peritoneum	distal region of ceratobranchial III	
Rectus cervicis	peritoneum	branchial process II and III	
Rectus abdominis	pelvic griddle	peritoneum, posterior to gills	

Fig. 3—*Ceratophrys cranwelli* Stage 33. Musculature. —**A**. Ventral view, complete. —**B**. Dorsal view. —**C**. Ventral view, organs removed. —**D**. Lateral view. $cb_{(II-IV)}$, constrictor branchialis; db, diaphragmatobranchialis; gh, geniohyoideus; ha, hyoangularis; ih, interhyoideus; im, intermandibularis; lma, levator mandibulae articularis; $lb_{(I-IV)}$, levator arcuum branchialium; lmep, levator mandibulae externus profundus; lmes, levator mandibulae externus superficialis; lmi, levator mandibulae internus; lmlp, levator mandibulae longus profundus; lmls, levator mandibulae longus superficialis; ml, mandibulolabialis; oh, orbitohyoideus; ra, rectus abdominis; rc, rectus cervicis; sa, suspensorioangularis; so, subarcualis obliquus; sm, submentalis; sr_I, subarcualis rectus I; sr_{II-IV}, subarcualis rectus II–IV; tp, tympanopharyngeus. Scale bars 1 mm.
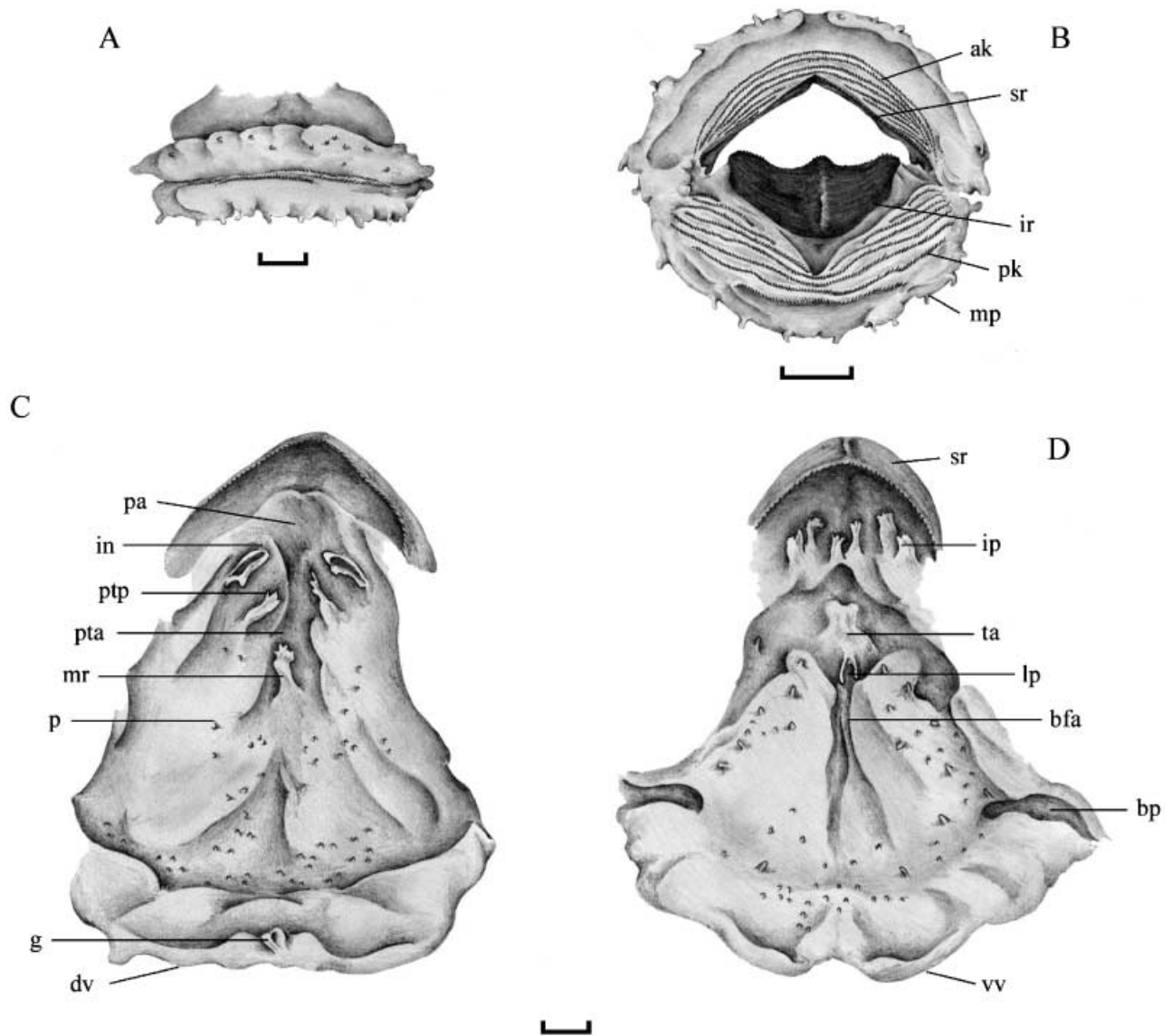
Fig. 4—*Ceratophrys cranwelli* Stage 33. Buccal apparatus and buccopharyngeal cavity. —**A**. Oral disc, relaxed, frontal view. —**B**. Oral disc, open, frontal view. —**C**. Buccal roof. —**D**. Buccal floor. ak, anterior rows of keratodonts; bfa, buccal floor arena; bp, buccal pocket; dv, dorsal velum; g, glotis; in, internal nares; ip, infralabial papillae; ir, infrarostrodont; lp, lingual papillae; mp, marginal papillae; mr, median ridge; p, pustulation; pa, prenarial arena; pk, posterior rows of keratodonts; pta, postnarial arena; ptp, postnarial papillae; sr, suprarostrodont; ta, tongue anlage; vv, ventral velum. Scale bars 1 mm.

keratodonts are arranged in eight anterior and eight posterior rows. The eight rows next to the rostrodonts are discontinuous, with gaps that increase their length towards the rostrodonts. The length of the rows then decreases towards the rostrodonts, with the exception of the two most posterior rows of the inferior lip, which are, respectively, three-quarters and one-half shorter than the immediately anterior. The keratodonts have a short, cylindrical base, slightly wider than the head, which is conical with a sharp or round tip

(Fig. 5D,E). The distance between contiguous teeth is 5 µm, making a tooth density of 95/mm.

The buccal roof is triangular and scarcely pigmented (Fig. 4C). The internal nares are elongated and obliquely disposed; the nasal valve is well-developed. Posteriorly, there is a pair of tall, laminar and trifurcate postnarial papillae. The median ridge is tall and thin and has an irregular margin. The lateral ridge papillae are absent. The buccal roof arena is not defined, because of the lack of papillae; it has only a few
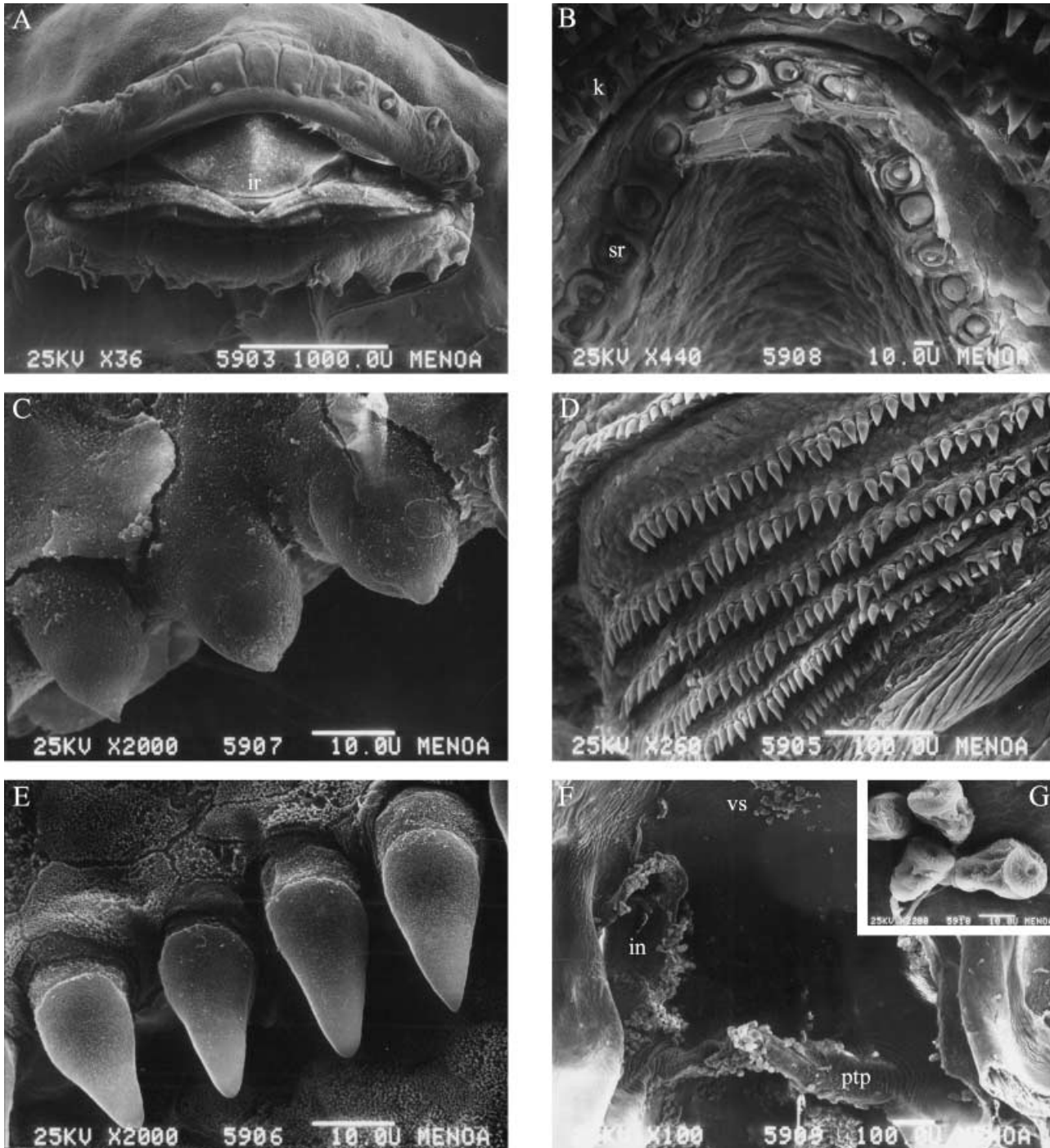
Fig. 5—*Ceratophrys cranwelli* Stage 33. Buccal apparatus and buccopharyngeal cavity, SEM micrographs. —**A**. Oral disc, relaxed, frontal view. —**B**. Suprarostrodont, inferior view. —**C**. Detail of infrarostrodont. —**D**. Posterior rows of keratodonts. —**E**. Detail of keratodonts. —**F**. Detail of internal nares. —**G**. Detail of *Vorticella* sp. in, internal nares; ir, infrarostodont; k, keratodont; ptp, postnarial papillae; sr, suprarostrodont; vs, *Vorticella* sp. group. Scale bars appear in each micrograph.

pustules. Conspicuous groups of peritrich ciliates of the genus *Vorticella* are fixed on the papillae, the internal nares and the arena (Fig. 5F,G). Finally, there is a glandular epithelium on the dorsal velum.

The buccal floor is triangular (Fig. 4D). Anteriorly, there are three pairs of tall and multifid infralabial papillae. The tongue anlage has a pair of lingual papillae. The buccal floor arena has scarce, short, conical papillae that are restricted to the lateral and posterior region. Pustules are scattered among the buccal floor papillae and on the central area of the ventral velum. The glandular epithelium is present.

Diet (n = 7, Stages 35–37)

Volumetrically, the predominant food items found in the gut are the Volvocaceae, insect remnants and crustaceans. All the other items accumulate only 2% of the total. The more represented sizes are those > 1.5 mm (29%) (Tables 2 and 3).

Table 2 Food items in gut contents of *Ceratophrys cranwelli* tadpoles; values represent averages from seven specimens, Stages 35–37

Food item	%
Volvocaceae	47.05
Insects	30.94
Crustaceans	19.76
Oligochaetes	0.79
Rotifers	0.45
Vegetal remnants	0.37
Nematods	0.32
Desmideaceae	0.22
Euglenoids	0.13
Shell-bearing amoebas	0.06
Diatoms	0.03

Table 3 Distribution of food items sizes in gut contents of *Ceratophrys cranwelli* tadpoles; values represent averages from seven specimens, Stages 35–37

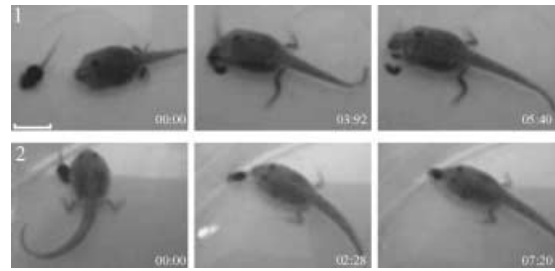| Sizes (mm)	%
< 0.1	0.32
0.1–0.2	0.76
0.2–0.3	1.77
0.3–0.4	1.59
0.4–0.5	4.27
0.5–0.6	5.98
0.6–0.7	6.15
0.7–0.8	5.74
0.8–0.9	2.02
1.0–1.1	12.82
1.1–1.2	0.43
1.2–1.3	11.54
1.3–1.4	0
1.4–1.5	4.06
> 1.5	29.90

Fig. 6—Two sequences of *Ceratophrys cranwelli* (Stage 39) capturing *Pleurodema borelli* tadpoles. Time is in seconds. Scale bar 1 cm.

All the *Pleurodema* tadpoles offered to the starved *C. cranwelli* were eaten within approximately 1 h. Small prey are pursued and engulfed whole, and larger ones are grabbed at any part of the body, either tail, head or side, and swallowed piecemeal (Fig. 6).

All the tadpoles examined were parasitized by intestinal Cestodes, probably *Ophiotaenia* because of their unarmed scolex with four suckers and cosmopolitan distribution.

Discussion

The chondrocranium and part of the musculature of *Ceratophrys cranwelli* tadpoles were previously described for larvae in equivalent stages and different environments. The only differences observed in the tadpoles studied by Lavilla and Fabrezi (1992) are the presence of lateral projections on the ceratobranchials and the incomplete chondrification of the chondrocranial roof. This could be accounted for by individual variation in developmental timing, or simply intraspecific morphological variation. Regarding the muscles of the larvae analysed by Palavecino (1999), some differences have been noted. This author described a m. levator mandibulae longus superficialis inserting on the jaw sheaths, named a new muscle of the intermandibular group (the intermandibularis medio superficialis, referred to as anterior slip of the intermandibularis in this paper), and reported the presence of the m. suspensoriohyoideus. Regarding this latter, the m. suspensoriohyoideus can be easily confounded with the most posterior and inner fibres of the m. orbitohyoideus; the earlier report could probably be attributable to this. Additionally, Haas (2003) revised *C. ornata* tadpoles and did not find the muscle, considering thus its absence to be a synapomorphy of Ceratophryinae.

Ceratophrys cranwelli tadpoles share several characters with the cogeneric species previously studied. The chondrocranium is almost identical to that of *C. cornuta* in that it has a robust construction, very short trabecular horns, strong jaw cartilages, and a completely cartilaginous chondrocranium roof (Wild 1997). For musculature, tadpoles of *C. ornata* (Haas 2003) exhibit similar traits, except the location of the ramus V_3 of the trigeminal nerve, between both mm. levator mandibulae externus, the presence of the m. l.m. lateralis,

and the configuration of the m. subcualis rectus I, with two slips. In *C. cranwelli*, the ramus V_3 of the trigeminal nerve runs dorsally to both the mm. l. m. externus, the m. l. l. lateralis is absent, and the m. subcualis rectus I has only one slip. The absence of m. l. m. lateralis can be accounted for by ontogenetic differences among the larvae analysed (*C. ornata*, Stage 38). Finally, in contrast with Carr and Altig (1991), who mentioned the absence of the m. mandibulolabialis in *C. ornata*, Haas (2003) did find this muscle, with the configuration similar to that described here for *C. cranwelli*. The similarities among the species within the genus also include the buccal apparatus and buccopharyngeal cavity. Wassersug and Heyer (1988) studied *C. aurita* tadpoles, and the characteristics closely resemble those of *C. cranwelli*: oral disc with well-keratinized jaw-sheaths, labial row tooth formula ≥ 7/8, three infralabial papillae, two lingual papillae, lateral ridge papillae absent, and scarce papillation on buccal roof and floor. Lastly, the references to larvae of different species of the genus reported without exception a carnivorous diet (Duellman 1978; Cei 1980; Wassersug and Heyer 1988).

The most used classification of ecological guilds of tadpoles is the one proposed by Altig and Johnston (1989), modified by McDiarmid and Altig (1999), which links external characters with types of feeding mechanisms and use of microhabitat across various species. *Ceratophrys* tadpoles belong to the lentic carnivore guild, which also includes tadpoles of *Leptodactylus pentadactylus* (e.g., Heyer *et al.* 1975), *Hymenochirus boettgeri* (e.g., Deban and Olson 2003), *Spea* spp. (e.g., Bragg 1962; 1964), and *Lepidobatrachus* spp. (Ruibal and Thomas 1988; Wassersug and Heyer 1988). Within this guild, there is some variability regarding detection, capture, manipulation, etc. of prey. Thus, several species target their prey visually, others by using a lateral-line system; some of them pursue and capture their prey in groups, others individually; some engulf the prey whole, others bite and tear them to pieces. Furthermore, some species are obligate carnivores, whereas others change their diets facultatively in response to availability in the environment.

Besides external morphology, several researchers have inquired into the relation between internal structure and ecology, linking anatomical features to specific ecological habits. Particularly, the works of Wassersug and Hoff (1979) and Satel and Wassersug (1981) provide useful tools for the association of skeletal and muscular characters with feeding mechanisms. According to these authors, macrophagous carnivorous tadpoles possess characters tending to achieve a great suction force inside the buccal cavity (like the carnivorous larvae studied in these papers: *Anotheca spinosa*, *Ceratophrys aurita*, *Hymenochirus boettgeri*, *Scaphiopus* spp.), Values of in-lever arm proportion and buccal floor area of *C. cranwelli* tadpoles indicate a macrophagous diet. Furthermore, all these tadpoles show enlargement of the area of the ceratohyals. The same occurs in suctorial (Haas and Richards 1998) and macrophagous larvae such as *Hyla nana* and *H. microcephala* (Vera Candioti *et al.* 2004; Vera Candioti and

Haas 2004). The ih : oh ratio is low, similar to that expected from comparison with macrophages (*C. cranwelli* = 0.25; $\bar{x}$ macrophages = 0.26; *C. aurita* = 0.29, Satel and Wassersug 1981). To discard the effect of size or developmental stage on the ratio, I measured also the muscles of an available specimen at Stage 39. The ih : oh ratio was 0.26. Although this result is preliminary, it indicates that a comparison among species at different stages is not misleading. Likewise, the species studied by Satel and Wassersug (1981) show slight or non-existent allometric changes in ih : oh values. The similarity between ih : oh values obtained with different methodologies (cross-sectional area and dry weight) indicates that both procedures are reliable.

Larson and Reilly (2003) studied the participation of several muscles in gill irrigation and feeding mechanisms. These authors argue that the m. levator mandibulae longus superficialis is only active during feeding and hyperexpiration, and provokes a forceful closing of the mouth. In *Ceratophrys cranwelli*, the well-developed muscles of the levator mandibulae complex, in addition to the robust jaw sheaths, would supply the force needed to bite and tear large prey apart. The same could be inferred regarding the m. intermandibularis. This muscle is highly developed, even divided into two well-distinguishable slips, and it is supposed to cause the jaw sheaths to meet more closely during feeding (Gradwell 1972).

Altig and Johnston (1989) mentioned features of the buccal apparatus which correlate with a carnivorous diet, such as terminal position of the mouth and strongly keratinized jaw sheaths and keratodonts. These authors mention two instances of the functional implications of the structure of keratodont rows: cusped, highly dense teeth (115/mm), vs. non-cusped, sparse teeth (39/mm). They predict that species belonging to the second group would be able to forage on thicker, less dense substrates and remove a larger amount per feeding stroke than the species of the first group. *Ceratophrys cranwelli* keratodonts are spike-like, without cusps, very numerous but spaced out (tooth density = 95/mm; inter-tooth distance = 5 μm), and their function possibly resembles that of the Species of the second group. Similar sharply pointed keratodonts have been described in macrophagous tadpoles of *Leptobrachium* (Inger 1986) and *Spea bombifrons* (Altig and McDiarmid 1999).

With regard to prey capture, the opening of the mouth and the presence of forceful, well-keratinized sheaths limit the size of the particle to be ingested and allow it to be torn apart. This differentiates *Ceratophrys* from *Lepidobatrachus* or *Hymenochirus* larvae, which necessarily engulf their prey whole because of their lack of strong biting and cutting structures. This is also related to buccal cavity volume, which allows housing of large prey. The high values calculated for *C. cranwelli* tadpoles coincide with those recorded for other carnivores of comparable snout–vent length (*C. cranwelli* snout to vent length $\bar{x}$ = 18.32 mm, Wassersug and Hoff 1979).

Reduction of buccal sieving structures is also associated with macrophagous and carnivorous diets. One can find

reduction or even absence of papillae, ridges and secretory pits in tadpoles such as *Anotheca spinosa*, species of the *Hyla microcephala* group, *Hymenochirus boettgeri* and *Lepidobatrachus* spp. (Wassersug 1980; Wassersug and Heyer 1988; Vera Candioti *et al.* 2004; personal observation).

Heyer *et al.* (1975) studied *Leptodactylus pentadactylus*, and argue that predatory tadpoles are likely to appear in small, ephemeral aquatic situations. In fact, tadpoles for the present paper (the second group) were collected in a small roadside pool, and furthermore, this was the only species of tadpole in it. In such conditions, facultative carnivores are supposed to develop because their ecological plasticity would allow them to survive once they have consumed a particular type of resource. An extreme example of this situation is found in the genus *Spea*, some of whose species develop carnivorous morphs whose diet and also morphology change depending on environmental conditions (Bragg 1956; Bragg and Bragg 1959; Acker and Larsen 1979; Hall and Larsen 1998; Hall *et al.* 2002). *Ceratophrys cranwelli* larvae, besides eating other tadpoles, feed on microalgae, crustaceans, insects, rotifers, tracheoid plant fragments, and even carcasses of dead tadpoles. The presence of the small-size items (e.g., diatoms, euglenoids) could also be the result of passive entrance with respiratory inflows.

It is noteworthy that tadpoles of both groups (collected in the same environment but 8 years apart) showed *Vorticella* sp. on the buccal cavity roof. Heterotrich ciliates are reported as being commensals of tadpoles (Alford 1999 and references therein), and Echeverría (personal communication) found *Vorticella* spp. inside the buccal cavity of *Leptodactylus gracilis* tadpoles. The association between these peritrichs and tadpoles has yet to be discussed.

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