

RESEARCH ARTICLE OPEN ACCESS

Suction Feeding in *Dendropsophus cerradensis* Tadpoles: New Behavioral Observations and Morphological Traits in a Member of the *D. microcephalus* Group (Anura, Hylidae)

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Received: 20 August 2024 | **Revised:** 14 April 2025 | **Accepted:** 18 April 2025

Funding: FAPEMIG: 13580; CAPES: 88887.892985/2023-00, 8887.468027/2019-00; MSCA: 101030742.

Keywords: Anura | evolution | feeding behavior | macrophagy | protractile oral tube

ABSTRACT

We present, for the first time, the suction feeding behavior of the tadpole of *Dendropsophus cerradensis* (Hylidae, Dendropsophini), along with a detailed description of its external morphology, buccopharyngeal cavity, and musculoskeletal system. The tadpole exhibits a depressed body, anteriorly positioned nostrils, a modified oral disc (completely covered by external folds), and a low tail, resembling other members of the *D. microcephalus* group. The buccopharyngeal cavity is reduced in features, with internal nares positioned at an acute angle and covered by prenarial papillae, exclusive for this species. Muscle insertion patterns are generally consistent with other Dendropsophini tadpoles, except for the insertion of the m. levator mandibulae longus profundus on Meckel's cartilage. The feeding behavior is characterized by the use of an oral tube that protrudes exclusively during predation. This mechanism may be associated with robust mandibular and hyoid musculature, as well as a modified cranial structure—including a unique suprarostal element, quadrangular muscular processes, robust ceratohyals, and a reduced branchial basket in the hyobranchial skeleton—which enables fast suction movements. This study presents a previously unknown aspect of the protractile oral tube and feeding behavior of the *D. microcephalus* group, providing new insights into the morphology and feeding behavior of the group.

1 | Introduction

Tadpoles, the larval stage of anurans, are a diverse and abundant component of freshwater ecosystems (e.g., Inger et al. 1986; Ranvestel et al. 2004; Whiles et al. 2006). In the aquatic environment, tadpoles consume as much energy as

possible to develop until a complex metamorphosis (Alford and Harris 1988). They acquire nutrients through various strategies, from different food sources, including algae, plant material, pollen, aquatic invertebrates (both eggs and larvae), and even other tadpoles (Kupferberg 1997; Crump 1990; 1992; Altig 2007; Kloh et al. 2019).

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Tadpoles are known to exhibit diverse behavioral feeding strategies. Scraping species use keratinized structures, such as jaw sheaths and labial teeth, in a sequential and coordinated way to scrape off debris (Venesky et al. 2010). Carnivorous species can tear apart their prey using keratinized jaw sheaths before swallowing (Vera-Candioti 2005), while macrophagous species ingest whole items by suction (Deban and Olson 2002).

Dendropsophus is the most diverse hyloid genus, with 105 recognized species assigned to eight species groups (Faivovich et al. 2005; Orrico et al. 2021; Whitcher et al. 2025; Frost 2025). The *Dendropsophus microcephalus* group currently comprises 35 species (Orrico et al. 2021; Nakamura et al. 2025). This group was first defined to accommodate species whose tadpoles had xiphicercal tails and a terminal oral disc, lacking teeth and labial papillae (Duellman 1970). The tadpoles are classified in macrophagous ecomorphological guild, characterized by an LTRF 0/0 or 0/1; presence of jaw sheaths; presence of a small, terminal oral disc with few or no marginal papillae (Altig and Johnston 1989).

The modified oral disc of *Dendropsophus microcephalus* group has been described in various ways in the literature, but is consistently characterized by the absence of labial teeth and/or marginal papillae. Initially, Bokermann (1963) described it as a U-shaped suction cup in *D. nanus*. Later, Lavilla (1990) identified it as a retractable U-shaped suctorial tube. Other descriptions did not mention the structure or described it simply as a small, ventral oral disc, as in *D. microcephalus* (Cruz and Dias 1990) and *D. sturdae* (Carvalho-e-Silva et al. 2003). Vera-Candioti et al. (2004) referred to it as a suctorial tube. The most recent description of *D. branneri* highlighted the U-shaped structure (De Abreu et al. 2015). Kaplan (2017), based on histological sections, provided a detailed description of the structure in *D. microcephalus*, *D. rhodopeplus*, and *D. mathiassoni*.

The protrusion of the oral disc in the *D. microcephalus* group has been widely discussed in the literature. Lavilla (1990) was the first to recognize the retractability of the oral disc. Vera-Candioti et al. (2004) discussed how the musculoskeletal system could function in the suction feeding in *D. nanus* and later suggested a protrusion function (Vera-Candioti 2007). Although Kaplan (2017) rejected the idea of oral disc extension and retraction due to the turgid lower labium, he acknowledged the possibility of tube projection if the external fold could be retracted.

Previous analyses of gut content support the macrophagous diet in tadpoles of the *D. microcephalus* group. Wassersug and Rosenberg (1979) found abundant, large vegetal material in the guts of *D. phlebodes* and *D. microcephalus*. Subsequently, whole oligochaetes were described as the main food item, followed by smaller algae, in *D. microcephalus* and *D. nanus* (Vera-Candioti et al. 2004; Vera-Candioti 2007). While these species may show a preference for oligochaetes, data from Wassersug and Rosenberg (1979) also suggest flexibility in their diet.

The internal morphology—including a large buccal volume, reduced gill filters, and the absence of secretory epithelium in *Dendropsophus microcephalus* (Wassersug and Hoff 1979)—also supports the inclusion of tadpoles from *Dendropsophus microcephalus* group in the macrophagous ecomorphological guild. Moreover, the musculoskeletal system is known for *Dendropsophus*

nanus and *D. microcephalus* (Vera-Candioti 2007), and buccopharyngeal cavity has been described for *D. nanus*, *D. microcephalus*, and *D. phlebodes* (Wassersug 1980; Vera-Candioti 2007). The body musculature is robust (i.e., hyoid and mandibular muscles), the larval cranium is narrow, the branchial basket and buccopharyngeal features are highly reduced, and the ceratohyals are robust (Wassersug 1980; Vera-Candioti 2007), all features associated with the ingestion of large items.

Dendropsophus cerradensis (Napoli and Caramaschi 1998) is a small treefrog of *Dendropsophus microcephalus* group (Faivovich et al. 2005; Orrico et al. 2021; Whitcher et al. 2025). Despite some fragmented information available about its tadpole, a formal description remains absent (see Alves-Ferreira et al. 2021), and its internal morphological features are unknown. Here, we present an analysis of the external morphology, buccopharyngeal cavity, and musculoskeletal system, and describe the suction feeding behavior of *Dendropsophus cerradensis* tadpoles. Additionally, we discuss the feeding behavior of this species, comparing it to other macrophagous tadpoles to provide insights into the suction feeding mechanisms in *Dendropsophus microcephalus* group.

2 | Material and Methods

2.1 | Sampling

We collected tadpoles and adults at Refúgio Estadual da Vida Silvestre Libélulas da Serra de São José (21°06'52.7"S; 44°12'13.7"W), in the municipality of Tiradentes, and tadpoles at Parque Nacional da Serra da Canastra (20°09'56.4"S 46°41'15.7"W), in the municipality of São Roque de Minas, both located in Minas Gerais state, southeastern Brazil, in open areas within the Cerrado domain (Figure 1; additional information in the Supporting Information). We euthanized the tadpoles and adults with 5% lidocaine and fixed them in 10% formalin. Tadpoles were preserved in formalin, while adults were stored in 70% ethanol. Additionally, we preserved one tadpole from each lot in absolute ethanol for molecular identification. We deposited the lot and specimen in the Tadpole and Adult Collection (UFMG-GIR and UFMG-AMP) of Centro de Coleções Taxonômicas of the Universidade Federal de University of Minas Gerais (CCT-UFMG) and Amphibia-tadpoles Collection of Universidade Estadual Júlio de Mesquita, campus São José do Rio Preto (DZSJRP-Amphibia-tadpoles; Table S1). Taxonomic identification of both tadpoles and adults was confirmed through mitochondrial molecular markers (Supporting Information).

2.2 | Tadpole Description

External morphology descriptions, measurements and proportions were based on nine tadpoles at stages 28–32 (sensu Gosner 1960; Table S1). We followed Altig and McDiarmid (1999) and Altig (2007) for morphology terminology. We took 24 measurements to the nearest 0.1 mm from photos following Altig and McDiarmid (1999), Grosjean (2005), Lavilla and Scrocchi (1986), Pinheiro et al. (2012), and Lins et al. (2018) (Supporting Information). We followed Pezzuti et al. (2021) for standardization of character and character states and Schlosser

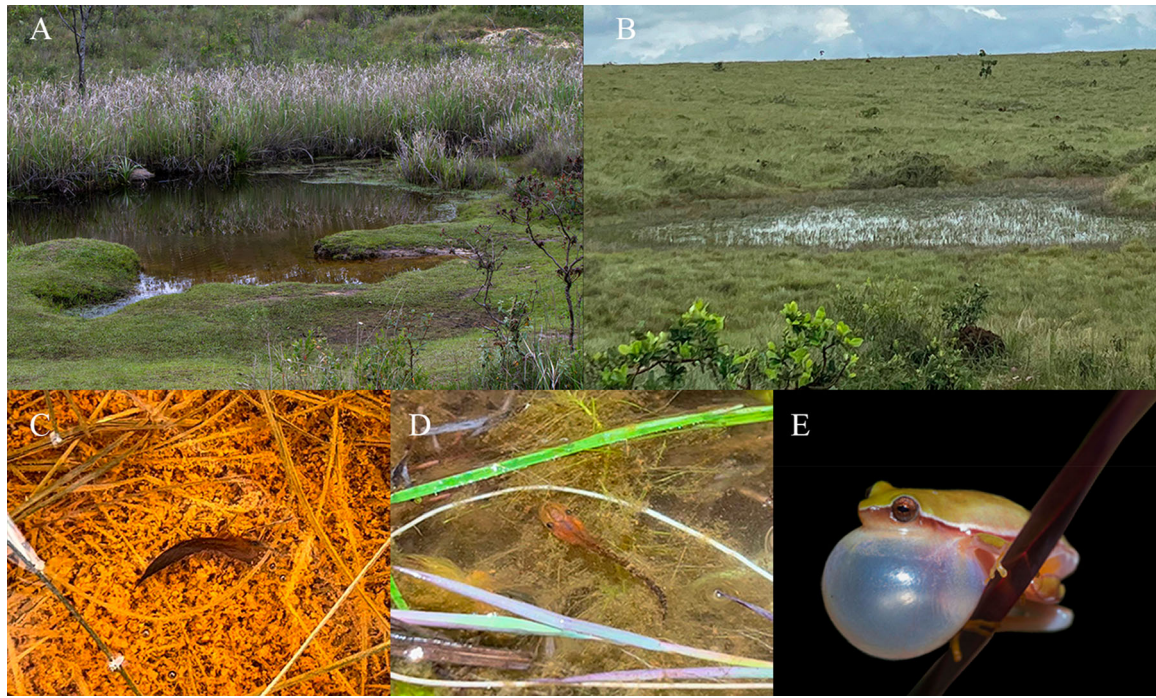


FIGURE 1 | Natural habitat of tadpoles of *Dendropsophus cerradensis* at (A) Serra de São José (Tiradentes, MG) and (B) Serra da Canastra (São Roque de Minas, MG). (C, D) Tadpoles in microhabitats between hydrophytic vegetation and (E) an adult individual from Serra da Canastra, MG.

(2002a, 2002b) for lateral line terminology. We obtained standardized photographs of lateral, dorsal, and ventral views of specimens using an adjustable platform to support tadpoles immersed in water (Schacht and McBrayer 2009). Regarding morphometric analysis, we used TpsUtil 1.78 (Rohlf 2019) for image compilation, TpsDig 2.31 (Rohlf 2017) for measurements, and ImageJ Version 1.50b (Schneider et al. 2012) for angle measurement.

Five tadpole specimens were used for histological analyses. The animals were fixed in buffered formalin solution, dehydrated in a gradual ethanol series, diaphanized in xylol, embedded in paraffin Histosec (Merck) in a Leica Enclosed System (TP1020, Leica Biosystems), and then sectioned at a thickness of 6–8 micrometers using an automatic rotary microtome. For the photomicrographic documentation, sections of 6 micrometers were employed. The tadpoles were embedded to obtain sagittal sections of the animals. After deparaffinization and rehydration, the histological sections were stained using the hematoxylin-eosin technique. The slides were photographed using a light photomicroscope (Olympus BX60). The images were digitized using the Image-Pro Plus 6.1 software (Media Cybernetics, Silver Spring, MD). Digital images were processed with Adobe Photoshop and Adobe Illustrator. We followed Altig and McDiarmid (1999), Altig (2007), and Kaplan (2017) for morphology terminology.

We dissected two individuals (stages 32 and 37, Table S1) according to Wassersug (1976a) to expose the buccopharyngeal cavity and subjected them to the protocol of Dias and Anganoy-Criollo (2024) for scanning electron microscopy (SEM). We followed Wassersug (1976a) for descriptive terminology. For the study of the larval cranium and musculoskeletal system, we processed two individuals (stages 31–32) according to the protocol of Wassersug (1976b) for clearing and double staining; we

interrupted the procedure after the Alcian Blue step and manually dissected them for the study of larval muscles. After observations and illustrations, we finished the clearing protocol. We followed Vera-Candioti et al. (2024) for the terminology of the larval cranium and muscles with English names, when available. For this procedure we took photographs with a Leica M205A stereomicroscope.

2.3 | Feeding Behavior and Oral Disc Movement

At the laboratory, about 2 h after collection, we placed the tadpoles and the emergent vegetation in the same aquarium with clean water, and filmed with a Canon D60 camera, at a rate of 60 frames (each 0.016 s) per second for an hour and a half. We conducted observations in which oligochaetes, obtained in the same location as the tadpoles, were continuously offered. We based the description of the feeding behavior and oral disc mechanics on the single suction event recorded at 00:30 am (Supporting Information, Video S1). After recording, we euthanized the tadpoles as described in the sampling section.

3 | Results

3.1 | Tadpole Identification

The sequences of tadpoles and adults show no nucleotide differences, confirming their semaphorontic association. Our sequences exhibit 99.7% identity with reference sequences of *Dendropsophus cerradensis* (*sensu* Nakamura et al. 2025) available in Genbank (accession numbers: MT503752–53) (details in Supporting Information and Table S2).

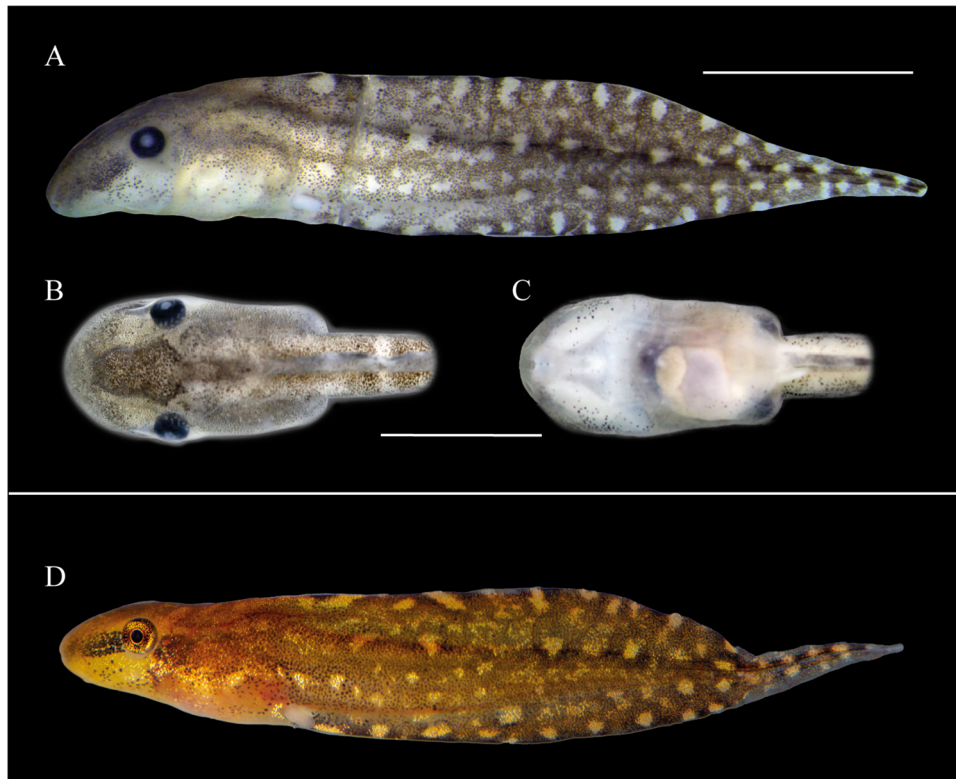


FIGURE 2 | Tadpole of *Dendropsophus cerradensis* (UFMG-GIR 2581) at stage 32: (A) lateral, (B) dorsal, and (C) ventral views. A specimen photographed in life (D) at stage 34 (UFMG-GIR 784). Scale bars (A) = 5 mm, (B, C) = 2 mm.

3.2 | External Morphology

Body depressed (Figure 2) (BH/BW 0.76–0.88), elongate elliptical with a medial constriction in dorsal view, triangular depressed in lateral view; body height about 50% of body length (BH/BL 0.43–0.50). Snout rounded in dorsal (BWN/BWE 0.33–0.39) and lateral views. Eyes laterally positioned (IOD/BWE 0.85–0.88) dorsolaterally directed, approximately 25% of the body width (ED/BWE 0.22–0.26). Nostrils elliptical, positioned and directed anteriorly, represent about 5% body length (ND/BL 0.04), laterally and ventrally visible, located approximately the oral disc, corresponding about 70% of oral disc width (ND/ODW 0.50–0.80). Ciliated cells around nostrils, concentrated in external margin (Figure 3). Spiracle sinistral, visible in lateral view (SDV/BH 0.37–0.64), small-sized (SL/BL 0.09–0.13), directed posteriorly; inner wall attached to the body and slightly longer than its external wall; opening located at the second third of the body length. Intestinal tube circularly coiled, switchback point dislocated from the center of abdominal region. Vent tube dextral, directed posteriorly, short, attached and positioned above ventral fin margin; ventral wall longer than dorsal. Oral disc modified into an oral tube (Figure 4), anteroventral (ODP 36°), about 11% of body width (ODW/BW 0.07–0.14), marginal and submarginal papillae absent; LTRF 0/0; jaw sheaths wide, finely serrated; upper jaw sheath arc shaped, lower jaw sheath U-shaped; sheaths not apparent when oral disc is retracted. The oral orifice is small, covered by well-developed upper and lower external folds, which are the continuation of the rostral and gular skin (Figures 3a,b and 5). Lower external fold with ciliated cells (Figure 3). The external folds are composed of smooth, loose connective tissue. Upper and lower labia are present. The upper labium is short and

thin, whereas the lower is supported by connective tissue being longer and thicker. An upper ridge lies between the upper labium and the upper jaw sheath. The distal surface of the lower labium is concave and upper labium convex. Tail low (MTH/TAL 0.25–0.30), higher than body (MTH/BH 1.32–1.57), tail musculature height about 30% of body height (TMH/BH 0.30–0.34), reaching tail tip; tail tip in a distinct flagellum. Dorsal and ventral fins of intermediate height (DFH/TAL 0.09–0.16 0.12 ± 0.02 , VFH/TAL 0.06–0.11 0.08 ± 0.01). Dorsal fin higher than ventral fin (DFH/VFH 1.30–1.73), originating at the posterior third of the body. Ventral fin less arched than dorsal fin, originating at level of vent tube. Lateral line system distinct just in the supraorbital line, starting posteromedially to the eyes and converging dorsally towards the snout, with a concentration of five rows of approximately 26 stitches on top of the oral disc and between the nostrils.

3.3 | Measurements

Table 1.

3.4 | Color

In life, body marbled with golden and white spots. In dorsal view, a medial brown spot at the level of the brain. Laterally, a brown longitudinal stripe extends from the eye to the snout, faded anteriorly; iris with an orange-brown longitudinal stripe with superior and inferior golden blotches; ventral surface, below eye line to the belly, cream color with golden dots at the branchial basket area; belly silver. Tail, including muscle and fins, homogeneously

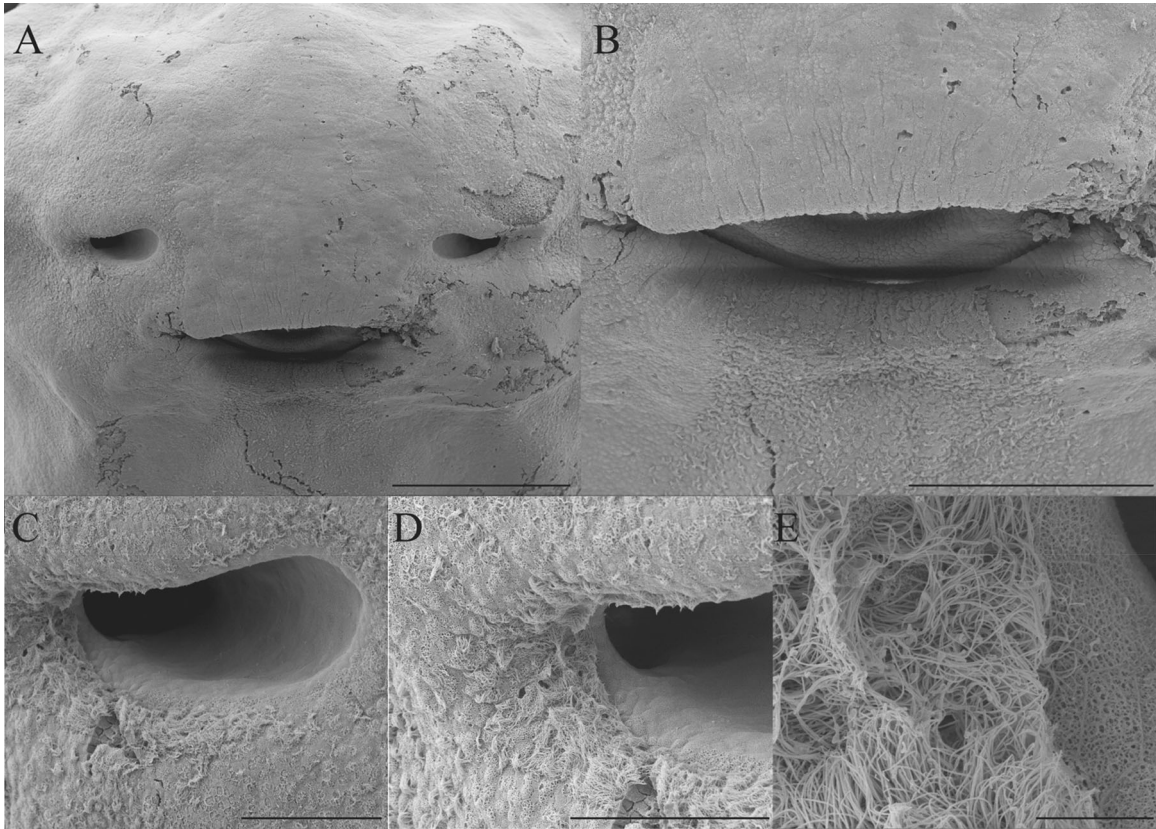


FIGURE 3 | Anterior view of *Dendropsophus cerradensis* tadpole at stage 37 (UFMG-GIR 2581). (A, B) Oral orifice and the internalized oral tube. Note that the anterior fold (an extension of the rostral epithelium) covers the upper lip; the lower lip is partially covered by the posterior fold, (C) right nostril, (D, E) with details of the ciliated cells. Scale bars (A) 500.0 μm , (B) 300.0 μm , (C, D) = 100.0 μm , (E) = 10.0 μm .

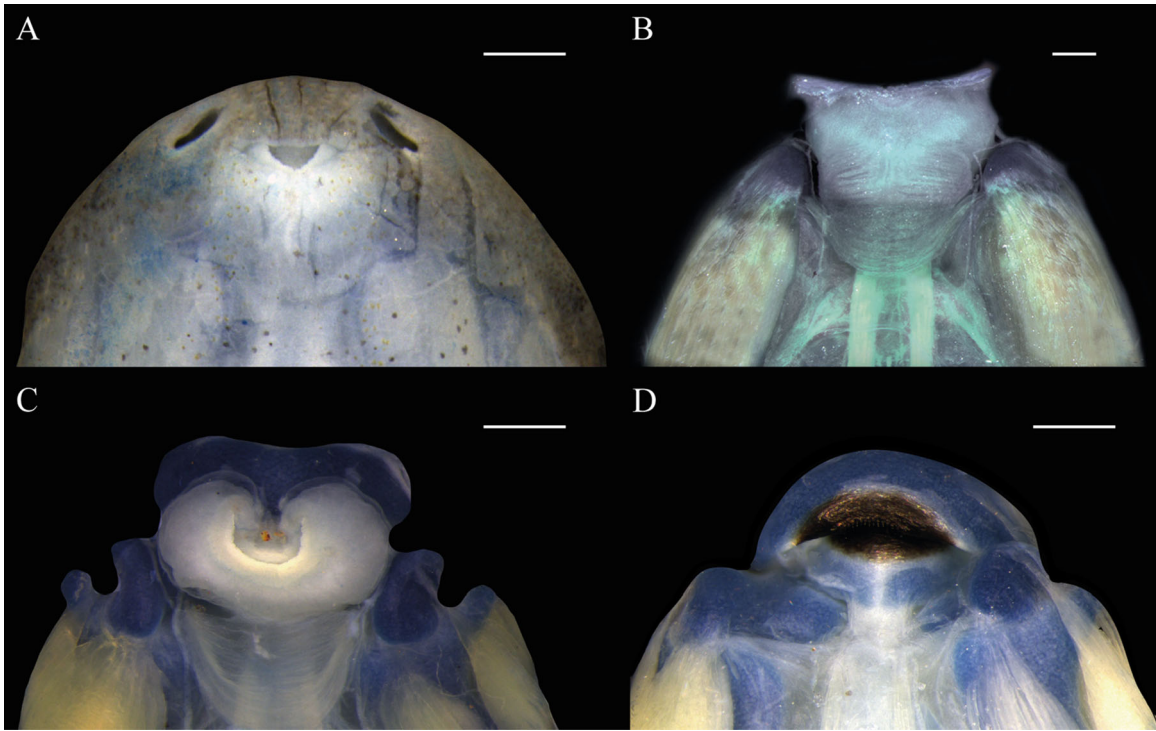


FIGURE 4 | The oral disc of *Dendropsophus cerradensis* (UFMG-GIR 2581) in a stained specimen at stage 32, observed in a sequential dissection. (A) ventral view showing the small oral orifice (B) with the external fold pulled forward, (C) without external fold showing the oral tube, and (D) without the oral tube showing jaw sheaths. Scale bars = 0.2 mm.

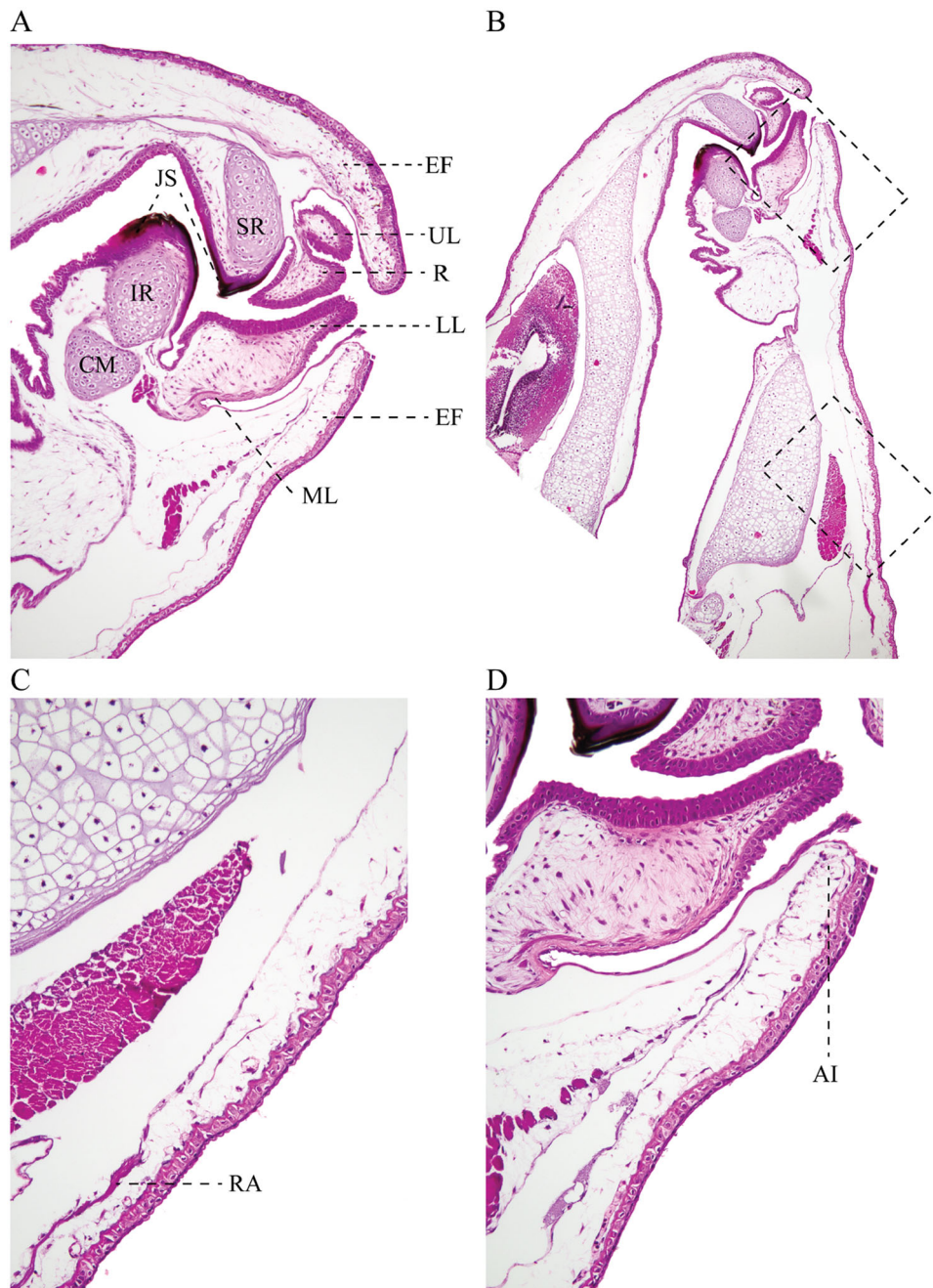


FIGURE 5 | Histological sagittal sections of the body of *Dendropsophus cerradensis* at stage 35, (UFMG-GIR 2581). (A) An almost medial section of the snout showing the oral tube region: EF = external fold, UP = upper labium, R = upper ridge, LL = lower labium, ML = m. mandibulolabialis, JS = jaw sheaths, SR = suprarostrol, IF = infrarostrol, CM = Meckel's cartilage. (B) A more lateral section of the body. Squares in the bottom and top are shown in details respectively in (C) and (D) to highlight the RA = m. rectus abdominis and the AI = anterior insertion of m. rectus abdominis.

marbled with rounded dark-brown and golden spots. Fins translucent in the tail tip. In preservative, the coloration fades, but the melanophore spots remain the same.

3.5 | Buccopharyngeal Cavity

Buccal floor triangular with a central pair of well-developed, globose, infralabial papillae of uneven margins (Figure 6). Tongue anlage well-developed. Lingual papillae absent. Buccal floor arena not defined, with some pustulations near the lateral portion of the buccal floor. Buccal pocket not discernible.

Glandular zone absent. Ventral velum smooth, without secretory pits and not supported by spicules.

Buccal roof triangular. Internal nares positioned 34° degrees in relation to the longitudinal axis, partially covered with a pre-narial papillae (Figure 6). No other structure present.

3.6 | Muscles

Thirty-one cranial muscles were identified in the tadpoles of *D. cerradensis* (Figure 7; Table 2). Most muscles followed the

TABLE 1 | Measurements (in mm) of tadpoles of *Dendropsophus cerradensis*.

Measurement	Stage				Mean	SD	Min	Max
	28 (n = 1)	30 (n = 3)	31 (n = 3)	32 (n = 2)				
TL	16.5	20.8 ± 1.0	19.1 ± 1.4	22.3 ± 2.0	19.7	2.5	16.5	22.3
BL	4.8	6.1 ± 0.7	5.9 ± 0.4	6.8 ± 0.3	5.9	0.8	4.8	6.8
TAL	11.6	14.7 ± 0.3	13.2 ± 1.1	15.5 ± 1.7	13.8	1.7	11.6	15.5
MTH	3.1	4 ± 0.3	3.7 ± 0.2	4.3 ± 0.0	3.8	0.5	3.1	4.3
DFH	1.2	1.6 ± 0.2	1.4 ± 0.2	1.8 ± 0.0	1.5	0.2	1.2	1.8
VFH	0.8	1.2 ± 0.2	0.9 ± 0.2	1.3 ± 0.0	1.0	0.2	0.8	1.3
TMH	1.6	2 ± 0.1	1.9 ± 0.2	2.1 ± 0.1	1.9	0.2	1.6	2.1
BH	2.2	2.7 ± 0.3	2.7 ± 0.0	3.1 ± 0.2	2.7	0.3	2.2	3.1
SL	0.5	0.7 ± 0.1	0.7 ± 0.1	0.7 ± 0.0	0.6	0.1	0.5	0.7
SVD	1.4	1.5 ± 0.4	1.5 ± 0.1	1.5 ± 0.4	1.5	0.1	1.4	1.5
SED	3.6	4.5 ± 0.5	4.6 ± 0.2	4.6 ± 0.2	4.3	0.5	3.6	4.6
ED	0.7	0.8 ± 0.1	0.8 ± 0.0	1 ± 0.1	0.8	0.1	0.7	1.0
BW	2.9	3.4 ± 0.3	3.2 ± 0.0	3.7 ± 0.5	3.3	0.3	2.9	3.7
BWN	1.1	1.2 ± 0.0	1.2 ± 0.1	1.4 ± 0.0	1.2	0.1	1.1	1.4
BWE	2.9	3.5 ± 0.2	3.4 ± 0.2	3.9 ± 0.2	3.4	0.4	2.9	3.9
TMW	1.1	1.5 ± 0.1	1.4 ± 0.1	1.7 ± 0.2	1.4	0.2	1.1	1.7
ESD	2.4	3.1 ± 0.3	3 ± 0.1	3.1 ± 0.1	2.9	0.3	2.4	3.1
NSD	0.5	0.6 ± 0.0	0.6 ± 0.0	0.6 ± 0.1	0.6	0.0	0.5	0.6
ND	0.3	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3	0.0	0.3	0.3
IND	0.9	1 ± 0.1	1 ± 0.1	1.1 ± 0.0	1.0	0.1	0.9	1.1
IOD	2.5	3.1 ± 0.1	3 ± 0.2	3.4 ± 0.2	3.0	0.4	2.5	3.4
ODW	0.4	0.4 ± 0.0	0.4 ± 0.1	0.4 ± 0.0	0.4	0.0	0.4	0.4
DFiA	175.1°	171° ± 7.7°	167.2° ± 6.0°	161.3° ± 7.5°	168.7°	5.9°	161.3°	175.1°
ODP	40.1°	40.5° ± 6.3°	28.5° ± 3.2°	38.3° ± 0.9°	36.8°	5.7°	28.5°	40.5°

Note: Total length (TL), body length (BL), tail length (TAL), maximum tail height (MTH), dorsal fin height (DFH), ventral fin height (VFH), body height (BH), spiracle length (SL), spiracular-venter distance (SVD), snout-spiracle distance (SED), eye diameter (ED), body width (BW), body width at level of nostrils (BWN), body width at eyes level (BWE), tail muscle width (TMW), eye-snout distance (ESD), nostril-snout distance (NSD), narial diameter (ND), internarial distance (IND), interorbital distance (IOD), oral disc width (ODW), dorsal fin insertion angle (DFiA), oral disc position (ODP). All measures in millimeters (mm) except for DFiA and ODP which are in degrees, values expressed as mean ± standard deviation (SD) (range) for each stage and for the measurement.

generalized insertion patterns (Vera-Candioti 2007; Dias et al. 2019; Dias et al. 2023), with a few exceptions already described for other related species (i.e., levator mandibulae lateralis insert on nasal sac; mandibular and hyoid groups are robust, especially the m. levator mandibulae longus superficialis and profundus, m. l. m. internus, m. orbitohyoideus, and m. hyoangularis; m. subarcualis rectus II–IV is interrupted with two slips, from ceratobranchial I to branchial process III and from branchial process III to ceratobranchial IV). The configuration of m. levator mandibulae longus profundus inserting on Meckel's cartilage is described for the first time in the tribe.

Table 2.

3.7 | Larval Cranium

No cranial ossification at the examined stages (Figure 8). Larval cranium longer than wide. Suprarostrals as a single piece of cartilage, almost straight; the proximal border decreases towards the midline. The highest part at the level of the posterior process. Suprarostrals

cartilage articulates syndesmotically with the trabecular horns. Trabecular horns short, acuminate, curved downwards anteriorly. In dorsal view, both horns almost parallel. Medial margin directed inwards. Quadratoethmoid ligament connects the processus lateralis trabeculae and the process quadrato ethmoidal. Cranial floor lightly chondrified anteriorly. Fenestra basicranial not occluded; planum intertrabecular not developed in medial region; cranial floor pierced by the carotid foramen. Craniopalatine foramen not visible. Orbital cartilage tall, with two indentations, assuming a W-shaped border. Prootic foramen visible. Larval cranium opens dorsally; frontoparietal fenestra bordered by the taeniae tecti marginal and posteriorly by the tectum synoticum. Otic capsules quadrangular and robust; the two capsules are bridged by the tectum synoticum.

Palatoquadrate long and robust. Articular process robust with the anterior outer margin projecting upward. Processes pseudopterygoideus absent. Muscular process wide, quadrangular with anterior triangular process at anterior margin. Palatoquadrate attaches to the braincase by quadratocranial commissure, ascending process, and larval otic process. Quadratocranial commissure wide. Subocular bar thin and curved. Ascending process attached to cranial

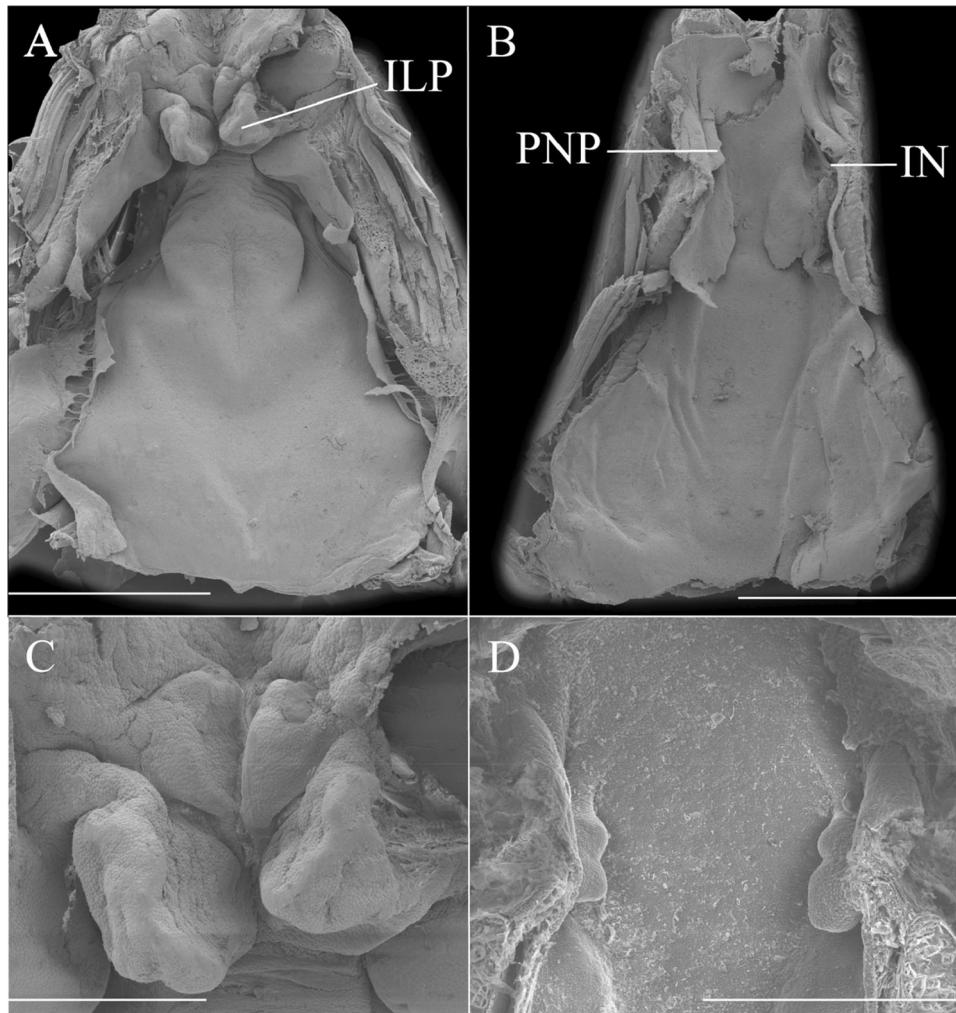


FIGURE 6 | Buccopharyngeal cavity of a tadpole of *Dendropsophus cerradensis* (UFMG-GIR 2581) at stages 32 (A–C) and 37 (D). (A) Buccal floor, (B) buccal roof, (C) detail of infralabial papillae, and (D) detail of prenarial papillae above internal nares. ILP = infralabial papillae, PNP = prenarial papillae, IN = internal nares. Scale bars (A) = 0.5 mm, (B) = 2.0 mm, (C) = 300.0 μ m, (D) = 500.0 μ m.

floor. Meckel's cartilage wide, sigmoid-shaped, transversely oriented. Infrarostral cartilages short, independent, medially joined syndesmotically.

Ceratohyals triangular, curved relative to the sagittal axis and robust; anterior process, lateral process, articular condyle rounded and robust, and small and barely visible anterolateral process. Medial ceratohyal margins parallel. Basihyal absent. Basibranchial long and devoid of urobranchial process. Pars reuniens poorly chondrified. Branchial basket reduced, poorly chondrified (difficult to visualize in the prepared specimen) with four ceratobranchials. Hyobranchial plates well-developed, quadrangular, articulated with a medial gap. Ceratobranchials lack projections and spicules. Ceratobranchials connected by terminal commissures.

3.8 | Feeding Behavior and Oral Disc Movement

The tadpoles remained most of the time quiet at the bottom of the aquarium. They did not actively chase the worms in the water column, and for a few moments, they bent the body downwards in the direction of the prey. Tadpoles moved along the bottom of the aquarium by bending the body, without moving the tail. The

predation event captured in frontal view regards a tadpole at stage 36 preying on a worm that moved in front of its snout (Video in Supporting Information, Figure 9). Initially, a body depression movement was observed along the longitudinal snout stripe. Then, the snout began to depress. Finally, the oral tube was fully protruded, and the worm had already been sucked in. These three initial movements occurred within 0.048 s, lasting 0.016 s each. In the subsequent frames, the tadpole moved forward and then sucked in the worm through a series of coordinated movements involving the oral tube and lower jaw. After 0.13 s, the final movement was a complete suction action using the oral tube. Once the labia were fully retracted, the lower jaw continued to move. The entire predation event, from the first movement to the end, lasted 2.56 s. As the camera recorded at 60 frames per second, each frame lasting 0.016 s, the actual movements may have occurred even faster than observed.

4 | Discussion

Larval morphology appears to be conserved within the *Dendropsophus microcephalus* group. For instance, all characterized tadpoles i.e. *D. bipunctatus*, *D. branneri*, *D. leali*, *D. mathiassoni*,

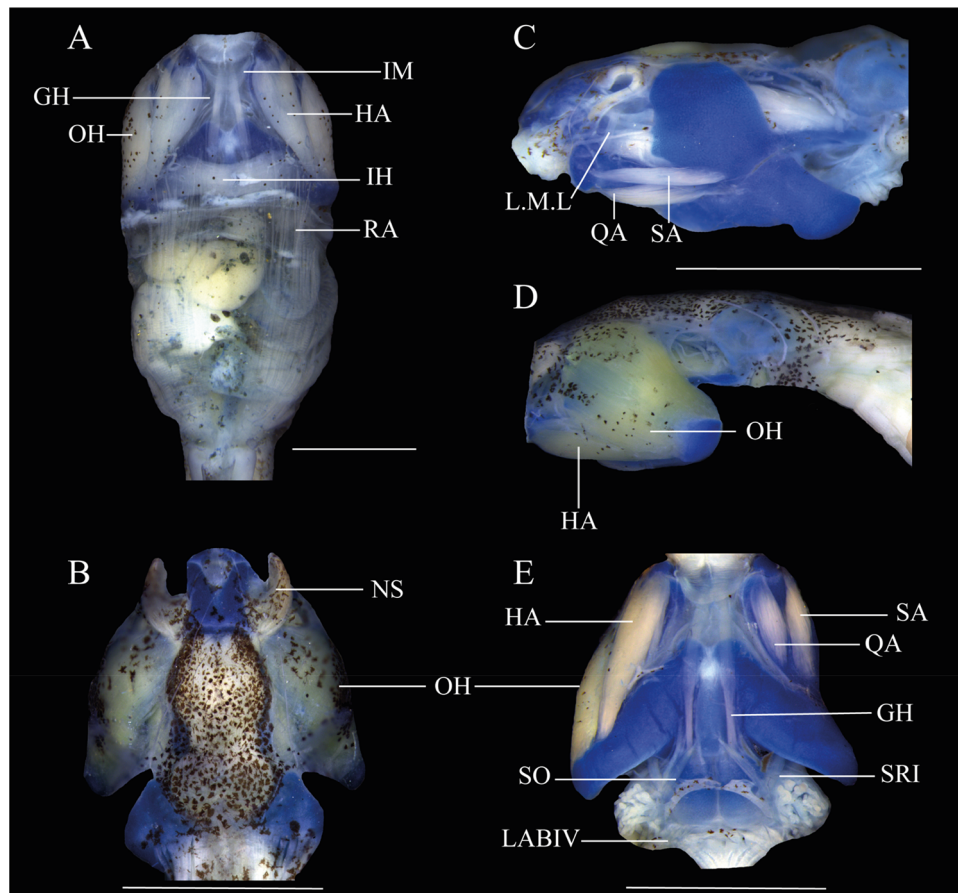


FIGURE 7 | Larval cranial musculature of *Dendropsophus cerradensis* at stage 32 (UFMG-GIR 2581). (A) Ventral view, showing levatores mandibulae muscles. (B) Dorsal view, showing nasal sac. (C–D) Lateral view, showing mandibular and hyoid muscles. (E) Ventral view showing hyoangularis muscle at right and without HA at left and details of hyobranchial muscles. GH geniohyoideus, HA hyoangularis, IH interhyoideus, IM intermandibularis, LABIV levator arcuum branchialium IV, LML levator mandibulae lateralis, ML mandibulolabialis, NS nasal sac, OH orbito-hyoideus, QA quadratoangularis, RA rectus abdominis, SA suspensorioangularis, SRI subarcualis rectus I, SO subarcualis obliquus. Scale bars = 1 mm.

D. meridianus, *D. microcephalus*, *D. nanus*, *D. phlebodes*, *D. rhodopeplus*, *D. robertmertensi*, *D. rubicundulus*, *D. sanborni*, *D. sartori*, and *D. studerae* have an elongated and depressed body, lateral eyes, oral disc without papillae and labial tooth rows modified in an oral tube, nostrils located at the tip of the snout near the oral disc, low tail and fins, distinct flagellum tip, and anteroventral brown stripe ranging from the nostril to the end of the body (Duellman and Fouquette 1968; Duellman 1972; Bokermann 1963; Altig 1987; Hero 1990; Cruz and Dias 1990; Pugliese et al. 2001; Carvalho-e-Silva et al. 2003; Lynch 2006; Lynch and Suárez-Mayorga 2011; Schulze et al. 2015; De Abreu et al. 2015).

The oral disc modified into an oral tube has been recovered as a synapomorphy of the group (Faivovich et al. 2005; Orrico et al. 2021). Besides the similarity discussed in the literature, there are some differences in the oral tube configuration among some species. While in most species the lower labium is folded into a U-shape (e.g., *D. nanus*, *D. branneri*, *D. leali*; see Figure 9, p. 218, Vera-Candioti et al. 2004; Schulze et al. 2015; De Abreu et al. 2015), in *D. cerradensis* and *D. mathiassoni* the external fold covers almost the entire labia (Kaplan 2017; this study). In *D. microcephalus* and *D. rhodopeplus* the external fold that covers the upper labium is short and wrinkled, with the upper labium and upper ridge visible,

while in *D. cerradensis* and *D. mathiassoni* it is long and smooth, covering the upper labium and almost total of lower labium. Because of this condition, the oral orifice may be more ventrally positioned in both species, and only a margin of lower labium and the upper ridge are visible.

The *Dendropsophus microcephalus* group (i.e., *D. microcephalus*, *D. nanus*, *D. phlebodes*; Wassersug 1980; Vera-Candioti 2007) presents a reduction of buccopharyngeal elements, a condition related to macrophagy. In contrast, *Dendropsophus decipiens*, *D. parviceps*, *D. marmoratus*, *D. minutus*, and *D. leucophyllatus* species groups have more elements in buccal floor and roof (e.g., papillae, medial ridge, lateral ridge papillae; Echeverría 1997; Kaplan and Ruiz 1997; Wassersug 1980; Vera-Candioti 2007; Dias et al. 2019; Costa et al. 2024). These groups (except *D. leucophyllatus* group), as well as *Xenohyla truncata* (Dias et al. 2023), share fan-like papillae delimiting the buccal floor (Wassersug 1980; Dias et al. 2019). Considering the phylogenetic relationships of Dendropsophini (Orrico et al. 2021; Whitcher et al. 2025), it is possible that the loss of these papillae has evolved in the common ancestor of *D. leucophyllatus* + *D. microcephalus* groups.

The presence of prenasal papillae covering the internal nares in *D. cerradensis* is reported for the first time in the tribe

TABLE 2 | Patterns of origin and insertion of *Dendropsophus cerradensis* muscles at stages 28 and 31.

Muscle	Origin	Insertion	Comments
<i>Mandibular group, n. trigeminus (c.n. V) innervated</i>			
Levator mandibulae longus superficialis	External and posterior margin of the subocular bar and part of the ascending	Dorsomedial region of Meckel's cartilage	Insertion via long tendon
Levator mandibulae longus profundus	Medial margin of the subocular bar	Internal medial margin of the Meckel's cartilage	Insertion via fiber weft
Levator mandibulae externus superficialis	Medial, inferior surface of the muscular process	Medioventral surface of suprarrostral	
Levator mandibulae externus profundus	Medial, inferior surface of the muscular process	Ventral margin of the edge of the suprarrostral	
Levator mandibulae articularis	Inferior part of the medial surface of the muscular process	Dorsal surface of the lateral edge of Meckel's cartilage	
Levator mandibulae lateralis	Articular process of the palatoquadrate	Nasal sac	
Intermandibularis	Medial region of Meckel's cartilage	Median aponeurosis	
Mandibulolabialis	Ventromedial region of Meckel's cartilage	Lower, medial and lateral surface of the oral tube	
Levator mandibulae internus	Ventral surface of the ascending process	Internal edge of Meckel's cartilage	Insertion via a long, very thin tendon
<i>Hyoid group, n. facialis (c.n. VII)</i>			
Hyoangularis	Anterior surface of the edge of the ceratohyal	Retroarticular process of Meckel's cartilage	
Quadratoangularis	Ventral surface of the palatoquadrate		
Suspensorioangularis	Ventral margin of the muscular process	Retroarticular process of Meckel's cartilagem	
Orbitohyoideus	Anterior and dorsal margins of the muscular process	Lateral edge of the ceratohyal	
Suspensoriohyoideus	Posterior descending margin of the muscular process	Posterior surface of the lateral process of the ceratohyal	
Interhyoideus	Ventral surface of the ceratohyal, near the lateral edge	Median aponeurosis	
<i>Branchial group, n. glossopharyngeus (c.n. IX) and vagus (c.n. X)</i>			
Levator arcuum branchialium I	Lateral margin of the subocular bar	Ceratobranchial I	
Levator arcuum branchialium II	Larval otic process	Ceratobranchial I and ceratobranchial II	
Levator arcuum branchialium III	Lateral part of the otic capsule	Ceratobranchial III	
Levator arcuum branchialium IV	Posterolateral part of the otic capsule	Ceratobranchial IV and hypobranchial plate	
Tympanopharyngeus	Lateral part of the otic capsule	Connective tissue anterior to the glottis	
Dilator laryngis	Posterolateral surface of the otic capsule	Arytenoid cartilage	
Constrictor branchialis II	Branchial process II	Terminal commissure I	
Constrictor branchialis III	Branchial process II	Terminal commissure II	

(Continues)

TABLE 2 | (Continued)

Muscle	Origin	Insertion	Comments
Mandibular group, n. trigeminus (c.n. V) innervated			
Constrictor branchialis IV	Terminal commissure II and the distal part of the ceratobranchial III		Fibers are continuous with those of the anterior part of the m. subarcualis rectus II–IV
Subarcualis rectus I	Two slips: lateral part of the posterior process of the ceratohyal – proximal, lateral part of the ceratobranchial I (dorsal slip) and branchial process III (ventral slip)		
Subarcualis rectus II–IV	Two slips: anterolateral part of the ceratobranchial I – branchial process III (anterior slip) and branchial process III – ventromedial part of the ceratobranchial IV (posterior slip)		
Subarcualis obliquus II	Posterior edge of the basibranchial	Branchial process II and III	
Diaphragmatobranchialis	Peritoneum	Distal edge of the ceratobranchial III	
Spinal group, spinal nerve innervation			
Geniohyoideus	Posterior, ventral surface of the infrarostral	Hypobranchial plates, near the anterior edge	
Rectus abdominis	Pelvic girdle	Anterior insertion at anterior end of the external fold	
Rectus cervicis	Peritoneum	Branchial process III	

Dendropsophini. Like *D. cerradensis*, *D. microcephalus* and *D. nanus* also have internal nares positioned at an acute angle relative to the longitudinal axis, although prenarial papillae have not been described for these species (Vera-Candioti 2007). However, projections were figured in the internal nares of *D. nanus* (see fig. 29, in Vera-Candioti 2007: 59), and this feature could represent a derived character in the group. Since the papillae cover the internal nares, they may have a mechanical protective function when food is engulfed by suction (see a similar hypothesis in Wassersug 1980: 113).

Dendropsophus cerradensis and other species of the *D. microcephalus* group have globose infralabial papillae (Wassersug 1980; Vera-Candioti 2007). It has been suggested that tadpoles use their infralabial papillae to detect the position of vegetal food items (Wassersug 1980). In this regard, it is possible that the *D. microcephalus* group use their jaw sheaths to bite or hold food items, as observed in *D. cerradensis*, in contrast with other anurans, that use their jaws mainly to scrape food particles from the substrate.

The suprarostral as a single element is a putative synapomorphy of Dendropsophini (except in *D. ebraccatus*; Haas 2003; Dias et al. 2023). Otherwise, the absence of anteroposterior process in the suprarostral may be a synapomorphy of the *D. microcephalus* group (i.e., anteroposterior process is present in *D. decipiens*, *D. molitor*, and *D. soaresi*, with the latter exhibiting a small medial V-shaped notch). Other features may also be exclusive to the *D. microcephalus* group, such as the muscular process, which is quadrangular in this group, but triangular in *D. decipiens*, *D.*

molitor, and *D. soaresi* (Dias et al. 2019; Arenas-Rodríguez et al. 2018; Costa et al. 2024). The m. subarcualis rectus II–IV is interrupted in *D. cerradensis*, *D. microcephalus*, and *D. nanus* (Vera-Candioti 2007), while it is a continuous slip in another Dendropsophini tadpoles, such as *Xenohyla truncata*, *D. decipiens*, and *D. ebraccatus* (Haas 2003; Dias et al. 2019, 2023).

The insertion of the m. levator mandibulae longus profundus in Meckel's cartilage, as observed in *D. cerradensis*, represents a rare occurrence in Neobatrachia, since this configuration has only been described for *Rhacophorus vampyrus* (Vera-Candioti et al. 2021). In species with a single slip of m. l. m. longus, such as *Ascaphus truei* (Ascaphidae), *Rhinophrynus dorsalis* (Rhinophrynidae), *Pipa carvalhoi* (Pipidae), the insertion occurs on the lower jaw (Haas 2003). In contrast, in species with the m. l. m. longus in two portions (i.e., superficialis and profundus), the m. levator mandibulae longus profundus portion inserts in the suprarostral cartilage, which is a common condition in Anura (e.g., Haas 2003; Vera-Candioti 2007).

Although the feeding behavior of this group has been discussed in the literature (i.e., Lavilla 1990; Vera-Candioti et al. 2004; Vera-Candioti 2007; Kaplan 2017), no video records existed until our study. The video showed a complete and fast protrusion of the oral tube, demonstrating an efficient suction feeding mechanism. This behavior may also occur in other species of *D. microcephalus* group, but behavioral and/or mechanical differences could occur due to differences in the degree of oral tube internalization (see above). Our data corroborates that the m. r. ab. anterior is inserted in the most anterior end of the external

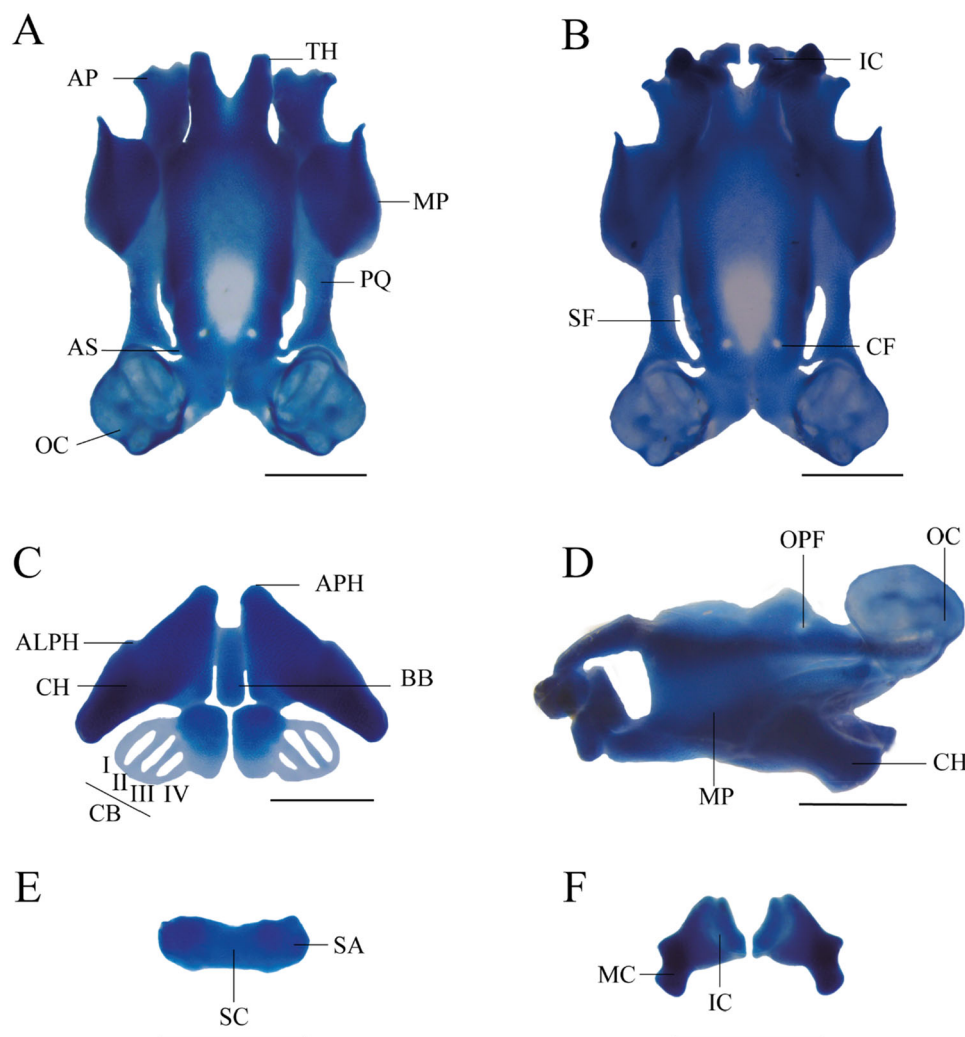


FIGURE 8 | Larval cranial skeleton of *Dendropsophus cerradensis* at stage 32 (UFMG-GIR 2581). (A, B) Neurocranium, dorsal and ventral views. (C) Hyobranchial skeleton. (D) Neurocranium in lateral view. (E) Suprarostrale cartilage, frontal view. (F) Lower jaw, frontal view. APH anterior branchial process, ALPH anterolateral process, AP articular process, APH anterior process, AS ascending process, BB basibranchial, BF basicranial fenestra, BH basihyal, CB ceratobranchial, CH ceratohyal, HP hypobranchial plate, IC infrarostral, MC Meckel's cartilage, MP muscular process, OC otic capsule, ORC orbital cartilage, PQ palatoquadrate, QC anterior quadratoarticular commissure, RAP retroarticular process, SA suprarostrale ala, SC suprarostrale corpus, SF subocular fenestra, TH trabecular horn. Scale bars = 5 mm.

fold (Kaplan 2017), a unique condition in Anura. Anterior insertion of the m. r. ab. has been reported in suctorial and rheophilous tadpoles (e.g., Noble and Pope 1929; Haas and Richards 1998; Dias et al. 2024), but never inserting on soft tissue.

Despite we are still unable to fully resolve the mechanism of oral tube protrusion, our observations support the oral tube protrusion hypothesis (Lavilla 1990; Vera-Candioti et al. 2004; Vera-Candioti 2007). However, it is also possible that the external fold is retracted by the contraction of the m. rectus abdominis anterior, contributing to the exposure of the oral tube, as suggested by Kaplan (2017). Thus, the suction feeding behavior of *D. microcephalus* group may result from a dual mechanism involving the retraction of the external fold and the simultaneous or subsequent protrusion of the oral tube itself. Also, the m. mandibulolabialis may play a role in the fine motor control of the oral tube, since it might be involved, at least in the retraction of the tube (see Vera-Candioti et al. 2004). In

species with tooth rows, the m. mandibulolabialis usually inserts at ridges and probably functions to distort them distally (Carr and Altig 1991; but see Dias 2020). Further investigation of these muscles, using an electromyographic approach for instance, could elucidate their function.

Suction feeding is a strategy found in many vertebrate groups (e.g., Deban and Olson 2002; Kleinteich et al. 2014; Bellwood et al. 2015). Among several strategies and adaptations associated with this feeding mode, jaw protrusion is one of the most important innovations in vertebrate feeding (Wainwright et al. 2015). Within amphibians, suction feeding is utilized by aquatic salamanders (both adults and larvae), caecilian larvae, and some anurans (e.g., O'Reilly 2000; Deban 2003; Carreño and Nishikawa 2010; Barrionuevo 2016; Duport-Bru and Abdala 2024).

Regarding anurans, suction feeding is observed in aquatic species, such as those of Pipidae (Duellman and Trueb 1994), but most tadpoles predominantly feed by scraping and/or filtering.

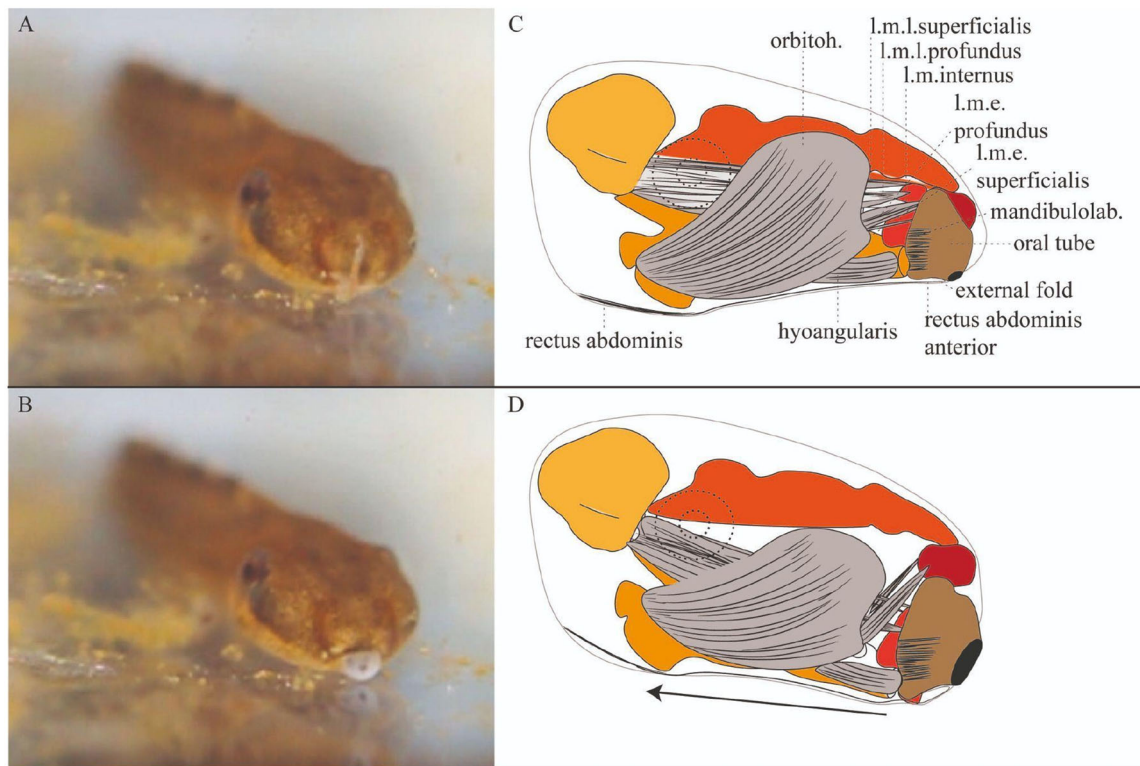


FIGURE 9 | Feeding behavior and a hypothesis of oral tube movement of *Dendropsophus cerradensis*. Two sequential frames depicting (A) the moment before the suction act—note the presence of the Oligochaete in front of the tadpole—and (B) the moment after the suction, with the oral tube fully protruded. (C) In the first moment, when the oral tube is retracted, the m. mandibulolabialis may be contracted. (D) Possibly, the contraction of the m. rectus abdominis (indicated by the black arrow) pushes back the external fold, resulting in the protrusion of the oral tube.

Although suction is an ancestral feeding behavior of vertebrates, including tadpoles, *D. cerradensis* and possibly other species of the *D. microcephalus* group exhibit an innovation: an oral tube that remains retracted and is only protruded at the moment of suction. *Occidozyga baluensis* (Dicroglossidae) is the only species with a similar oral tube, sharing other features, such as robust jaw sheath and ceratohyals, and reduced branchial baskets (Haas et al. 2014; Vassilieva et al. 2025). However, in *O. baluensis*, the m. rectus abdominis anterior inserts from diaphragm to ventral skin. The presence of whole worms or worm-like insects in its gut contents provides evidence of suction feeding, though protrusion of the oral tube has not yet been documented in this species (Haas et al. 2014; Vassilieva et al. 2025).

Hymenochirus boettgeri (Pipidae) is another macrophagous tadpole that utilizes suction feeding. The oral disc of *H. boettgeri* is an external tube that is folded anterodorsally in a resting position and is “stretched” during feeding behavior (see Figure 2, p. 275, Sokol 1962). Although the duration of the suction event in *D. cerradensis* was not precisely calculated, it is equal or less than 0.016 s, similar to that reported for *H. boettgeri* (0.04–0.012 s), which is faster than larval teleosts (Deban and Olson 2002). Given that the size of the oral orifice is inverse to the pressure generated (Wassersug and Hoff 1979), the suction imprinted by a small oral tube and the robustness of the hyoid muscles in *D. cerradensis*, possibly results in a great suction power, enabling the predation of entire oligochaetes hidden in the plant roots or in the substrate. Whether there is dietary flexibility in the tadpoles of this group, consuming both worms and plant material, or whether plants are a

secondary component ingested, remains unknown and requires further investigation (Wassersug and Rosenberg 1979; Vera-Candioti et al. 2004; Vera-Candioti 2007).

Another difference between these three unrelated lineages regards the mechanism of prey localization. Both *H. boettgeri* and *O. baluensis* have anterior eyes with stereoscopic vision (Deban and Olson 2002; Haas et al. 2014), which probably plays a role in detecting food items, while *D. cerradensis* has dorso-lateral eyes and possibly relies on other senses for “hunting”. *Dendropsophus cerradensis* has a well-developed nasal sac that serves as an attachment point to the l. m. lateralis. As suggested by Haas (2003), the contraction of this muscle could dilate the nasal sac, potentially enhancing its olfactory function.

5 | Conclusions

The suction behavior reported here for tadpoles of *D. cerradensis* demonstrates a unique feeding mode in Anura, characterized by the full protrusion of the oral tube exclusively during feeding. *Dendropsophus cerradensis* has a fully internalized oral tube, while its remaining external and internal morphology is similar to the other known species of *D. microcephalus* group, indicating an adaptation to macrophagy. Key features of this adaptation include: (1) oral disc modified in oral tube, (2) oral tube anteroventrally positioned, (3) body elongated and depressed, (4) position of the nostrils at the tip of the snout, (5) development of nasal capsules, (6) reduced elements in bucco-pharyngeal cavity, (7) orbitohyoideus as the main robust

muscle, (8) insertion of m. rectus abdominis superficialis in external fold, (9) robust and curved ceratohyal, (10) reduced branchial baskets. Although some behavioral aspects were observed, such as body bending to forage for food in the substrate, it is difficult to draw conclusions about other predatory behaviors of *D. cerradensis*. It remains unknown whether this tadpole is an active predator or relies on a sit-and-wait strategy. Despite the convergence observed in the buccopharyngeal cavity and musculoskeletal system with other anuran families, the internalized oral tube remains a unique feature of the *D. microcephalus* group. Further research is essential to address if this specialization could represent an evolutionary novelty that facilitated the occupation of new adaptive zones and the exploitation of novel resources.

Author Contributions

Barbara Caroline Marcondes: conceptualization, formal analysis, investigation, methodology, writing – original draft, writing – review and editing. **Pedro Henrique dos Santos Dias:** writing – original draft, writing – review and editing, supervision. **Raíla Brena Araújo:** methodology, writing – review and editing. **Guilherme Castro Franco Lima:** investigation, writing – review and editing. **Caroline Cuervo-Santos:** investigation, writing – review and editing. **Caroline Batistim Oswald:** methodology, writing – review and editing. **Rafael Felix Magalhães:** investigation, writing – review and editing, methodology. **Sebastião Roberto Taboga:** writing – review and editing, methodology. **Tiago Leite Pezzuti:** conceptualization, investigation, supervision, writing – original draft, writing – review and editing.

Acknowledgements

We are grateful to F.V. Candiotti and the anonymous reviewers for critically reviewing the manuscript. B.C.M. thanks FAPEMIG (13580) and CAPES (88887.892985/2023-00). T.L.P. acknowledges CAPES for the PNPd fellowship (8887.468027/2019-00). PHD thanks the Marie Skłodowska-Curie Actions (MSCA-IF-2020, MEGAN; 101030742).

Data Availability Statement

The data that support the findings of this study are available from the corresponding authors upon request. Gene sequences used in the present study will be deposited and available at GenBank upon manuscript acceptance.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.