RESEARCH ARTICLE

Larval anatomy of *Dendropsophus decipiens* (A. Lutz 1925) (Anura: Hylidae: Dendropsophini) with considerations to larvae of this genus

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Abstract

The *Dendropsophus decipiens* clade comprises four species: *D. berthalutzae*, *D. decipiens*, *D. haddadi*, and *D. oliveirai*. Tadpoles of these species were described, but data on their internal morphology are lacking. We provide the first description of the buccopharyngeal anatomy, chondrocranial morphology, and cranial, hyoid and hyobranchial musculature of the tadpole of *D. decipiens*. Larvae of *D. decipiens* are characterized by the absence of lingual papillae, presence of fan-like papilla on the buccal floor, presence of a single-element suprarostral cartilage, presence of a small triangular process at the basis of the processus muscularis, m. levator mandibulae lateralis inserted on the nasal sac, and m. subarcualis rectus II-IV with a single, continuous slip. Tadpoles are likely macrophagous, although not as specialized as those of other species of the genus, suggesting some degree of diversification on the feeding habits within *Dendropsophus*.

Introduction

Dendropsophini is a well-supported tribe of hylid treefrogs composed of the genera *Dendropsophus* and *Xenohyla* [1,2]. The relationships of Dendropsophini with other hylid tribes remain uncertain; it is poorly supported as sister taxon of Sphaenorhynchini [3] or as sister taxon of Pseudini [1,4–8]. *Dendropsophus* is a speciose clade of Neotropical treefrogs comprising 105 species distributed from Southern Mexico to Central-eastern Argentina [9], and the relationships between its species remain poorly known [1,3–8]. Three putative synapomorphies were suggested for the genus: diploid chromosome number of 30, the extreme reduction of quadratojugal, and labial tooth row formula 1/2 in tadpoles [3,10]. 105 species groups are recognized in *Dendropsophus*: the *D. columbianus*, *D. garagoensis*, *D. labialis*, *D. leucophyllatus*, *D. marmoratus*, *D. microcephalus*, *D. minimus*, *D. minutus*, and *D. parviceps* groups [3], whose composition have been slightly modified in the last few years (e.g. [11–13]).
The *Dendropsophus microcephalus* species group comprises more than 30 species, of which 13 are included in the two tentatively recognized clades: the *D. decipiens* and *D. rubicundulus* clades [3,11,13]. Two known morphological synapomorphies for this group are the absence of labial tooth rows and marginal papillae on the oral disc of larvae (with a reversal in the *D. decipiens* clade; [3,14]). The *D. microcephalus* group is the latest diverging taxon of *Dendropsophus*, and the relationship with other groups, as well as between its species remains controversial (e.g. [1,3,8]). The *D. decipiens* clade comprises four species: *D. berthaltuzae, D. decipiens, D. haddadi*, and *D. oliveirai*. *Dendropsophus berthaltuzae* is the only species of this clade included in molecular phylogenetic analyses (e.g. [1,3,15]), and therefore, the monophyly of the *D. decipiens* clade lacks a rigorous test. Putative synapomorphies for this clade are the presence of a posterior row of marginal papillae on the oral disc and oviposition on leaves overhanging water [3,16,17].

The external larval morphology in the *Dendropsophus decipiens* clade has been described for *D. berthaltuzae* [18], *D. decipiens* [16], *D. haddadi* [19,20], and *D. oliveirai* [16], but no aspect of their internal anatomy has been analyzed so far. We describe the buccopharyngeal anatomy, chondrocranial morphology, and cranial, hyoid and hyobranchial musculature of the tadpole of *D. decipiens*. We also provide comments on the larval internal morphology of *Dendropsophus* based on our observations complemented with data from the literature.

**Materials and methods**

Tadpoles were collected (ICMBio/RAN permit # 13256–1) in a dam of Rio Borboleta (22°59′19″S, 44°06′13″W) at Reserva Rio das Pedras, Mangaratiba, Rio de Janeiro, Brazil. Specimens were euthanized by topical application of 20% benzocaine anesthetic mixed with water, preserved in 5% formaldehyde and deposited in the Coleção de Anfíbios do Laboratório de Biossistemática de Anfíbios da Universidade Federal do Estado do Rio de Janeiro (Lot UNIRIO 3635). Some tadpoles were raised in the laboratory to corroborate species identification. Developmental stages were determined according to Gosner [21].

Two individuals (stages 34 and 35) were dissected according to Wassersug [22] to expose the buccopharyngeal cavity. One individual (stage 34) was submitted to the protocol of Alcalde and Blotto [23] for scanning electron microscopy (SEM). Descriptive terminology follows Wassersug [22,24]. For observations of the chondrocranium and cranial muscles, six individuals (stages 30–36) were treated following the protocol of Dingerkus and Uhler [25] for clearing and staining; we interrupted the procedure just after the staining with alcian blue for two individuals (stage 36) which were then dissected manually for the study of larval muscles. After observations and illustrations, we finished the clearing protocol. Terminology for the chondrocranium and muscles follows Haas [26–28]. The character-states discussed through the text were optimized on the phylogenetic hypothesis proposed by Duellman et al. [1] with the software TNT v1.5 [29].

**Results**

**External morphology**

The tadpole of *Dendropsophus decipiens* (stage 37) was described by Pugliese et al. [16]. It is characterized by having a triangular body, high tail fins with brown stripes, and a reduced oral disc with blunt marginal papillae and absence of labial teeth.
Buccopharyngeal anatomy

Buccal floor triangular with two pairs of infralabial papillae; medial pair conical; lateral pair flap-like (Fig 1A). Lingual bud elliptical, lacking lingual papillae. Buccal floor arena U-shaped, laterally delimited by single fan-shaped papilla, with few pustulations. Prepocked pustulations present. Buccal pocket deep, oriented transversely. Glandular zone well-developed, with evident secretory pits, and well-marked spicular support. Ventral velum arch-shaped, lacking marginal projections; medial notch discreet. Branchial basket triangular, with three well-developed filter cavities. Filter plates unconnected, bearing many filter rows. Glottis exposed.

Buccal roof triangular (Fig 1B). Prenarial arena half-circle shaped, with few pustulations. Internal nares elliptical, oriented transversely; anterior border with four to five conical pustulations; posterior margin lacking valve. Postnarial papillae absent. Median ridge triangular, low. Lateral ridge papillae conical. Buccal roof arena poorly defined, delimited posterolaterally by two conical papillae. Glandular zone undistinguished. Dorsal velum arch-shaped, smooth, medially interrupted.

Chondrocranium morphology

Suprarostral cartilage single (Fig 2D); suprarostral alae and suprarostral corpus completely fused. Suprarostral alae triangular, bearing two processes: processus posterior dorsalis and anterior dorsalis. Cornu trabeculæ short, thin, uniform along their extension, and parallel to each other; articulates with suprarostral (Fig 2A and 2B). Planum ethmoidale developed and distinct. Foramen nasalis present, elliptical. Fenestra basicranialis not occluded; planum intertrabeculare not formed in medial region; pierced by the foramen caroticum primarium.

Fig 1. Buccopharyngeal anatomy of Dendropsophus decipiens (stage 34). (A) Buccal floor and (B) buccal roof. Abbreviations: BFA, buccal floor arena; BFAP, buccal floor arena papillae; BP, buccal pocket; BRA, buccal roof arena; DV, dorsal velum; G, glottis; GZ, glandular zone; IL, infralabial papillae; IN, internal nares; LB, lingual bud; LRP, lateral ridge papillae; MR, median ridge; VV, ventral velum. Scale bars = 400 μm.

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Cartilago orbitalis tall, reaching the capsula auditivae posteriorly, forming the dorsal margin of the foramen prooticum; foramina oculomotorium, opticum, and prooticum pierce the cartilago orbitalis. Frontoparietal fontanelle large, rectangular and open (Fig 2A and 2B); laterally bordered by taenia tecti marginales, anteriorly by the planum ethmoidale, and posteriorly by the tectum synoticum. Capsula auditivae robust, rhomboid-shaped, representing c.a. 28% of chondrocranium length. Anterolateral process of crista parotica absent. Jugulare and inferior perilymphaticum foramina present, visible in ventral view.

Palatoquadrate thin, long, slightly curved (Fig 2A and 2B); articular process articulate with cartilago Meckeli. Processes quadrateethmoidalis and pseudopterygoideus absent. Processus muscularis triangular, lower than cartilago orbitalis; triangular process present at the anterior...
margin of the process muscularis, triangular, anteriorly directed. Commissura quadrato-orbita-
lis absent. Processus antorbitalis reduced. Subocular bar with small, triangular, lateral expan-
sions. Processus ascendens attached to cranial floor with an angle of approximately 90°.
Hyoid过程 evident on ventral surface of processus muscularis. Cartilago Meckeli
sigmoid-shaped, orientated almost perpendicular to chondrocranium axis (Fig 2E). Infracra-
tral cartilages rectangular, curved, joined medially by connective tissue.

Ceratohyals long, flat, and subtriangular (Fig 2C); their anterior margin bearing two trian-
gular, well-developed processes: processus anterior hyalis and processus anterolateralis hyalis.
Posterior processes triangular, tall. Ceratohyals are joined by a pars reuniens, which is chon-
drified. Basibranchial rectangular, bearing a rounded processus urobranchialis. Basihyal pres-
ent, slim, cylindrical. Planum hypobranchiale long, triangular, contacting each other along
their anterior half. Branchial basket has four curved ceratobranchials with numerous lateral
projections. Ceratobranchial I continuous with the planum hypobranchiale; dorsally, it bears a
triangular processus anterior branchialis. Ceratobranchials II and III also fuse to the planum
hypobranchiale plate and bear round branchial processes. Ceratobranchial IV is shorter,
wider, and fused to the planum hypobranchiale. Four long, curved spicules develop dorsally;
the third and fourth spicules are connected to the planum hypobranchiale by a thin cartilagi-
nous bridge. Ceratobranchials are distally joined by terminal commissures.

Cranial, hyoid and hyobranchial musculature
We found a total of 31 muscles in larvae of Dendropsophus decipiens (origins and insertions in
Table 1; Figs 3 and 4). Interhyoideus posterior and diaphragmatopraecordialis absent. Subar-
cualis obliquus present in two slips, inserting on the processus branchialis II and III. Subarcu-
alis rectus II-IV continuous, inserting on the ceratobranchial I. Mandibulolabialis with single
slip, corresponding to mandibulolabialis inferior. Intermandibularis arch-shaped. Larval leva-
tor mandibulae externus with two slips, superficialis and profundus. Levator mandibulae later-
alis inserting in the nasal sac. Ramus mandibularis (cranial nerve V₃) runs dorsally to longus
and externus groups.

Discussion
Larval internal morphology
Dendropsophus has been repeatedly found as sister taxon of Xenohyla (always well supported)
in molecular phylogenetic analyses for Hylidae (e.g. [1,3,6,8]). However, the phylogenetic rela-
tionships of the tribe Dendropsophini (Dendropsophus + Xenohyla; sensu [2]) within Hylidae
remain controversial. It is recovered as sister taxon of Sphaenorhynchini, closely related to Pse-
udini and Scinaxini [3] or alternatively, as sister taxon of Pseudini, distantly related to Sci-
navinini and Sphaenorhynchini (e.g. [1,8]).

Descriptions of the internal larval anatomy are scarce for Dendropsophus. The buccophar-
yngeal anatomy is known for D. ebraccatus, D. garagoensis, D. minutus, D. microcephalus, D.
nanus, D. padreluna, D. phlebodes, D. sarayacuensis, D. stingi, and D. virolinensis [24,30–32].
Similarly, descriptions of cranial muscles and the chondrocranium morphology are only avail-
able for D. ebraccatus, D. microcephalus, and D. nanus [28,32–34]. Dendropsophus ebraccatus
was included in the phylogenetic analyses of Haas [28]. Aside from those studies, there is some
scattered information available as the relative size of the buccal depressors muscles of D. micro-
cephalus and D. phlebodes [35], buccal pumping anatomy and secretory ridges of D. microce-
phalus [36,37], hyobranchial morphology of D. nanus [38], and some character-states of chondrocranium for D. microcephalus [39].
Table 1. Cranial, hyoid and hyobranchial musculature of the tadpole of *Dendropsophus decipiens* (stage 36). Abbreviations: CB I, II, and III = Ceratobranchial I, II, and III. c.n. = cranial nerve. LMLP = m. levator mandibulae longus profundus. n. = nerve.

| Muscle | Origin | Insertion | Comments |
|--------|--------|-----------|----------|
| Levator mandibulae longus superficialis | External posterior margin arcus subocularis and processus ascendens | Dorsomedial cartilago Meckeli | Via long tendon |
| Levator mandibulae longus profundus | External margin (curvature) arcus subocularis | External margin of the suprarostral ala | Via a long tendon; tissue mass near the upper lip |
| Levator mandibulae externus superficialis | Inner processus muscularis (superior) | Processus posterior dorsalis of suprarostral ala | |
| Levator mandibulae externus profundus | Inner processus muscularis (medial) | External, anteroven tral margin of suprarostral ala | Share a tendon with LMLP |
| Levator mandibulae articularis | Inner processus muscularis (inferior) | Dorsal cartilago Meckeli | |
| Levator mandibulae lateralis | Processus articularis quadrati | Nasal sac | |
| Submentalis (intermandibularis anterior) | - | - | |
| Intermandibularis | Median aponeurosis | Ventromedial cartilago Meckeli | |
| Mandibulolabialis | Ventromedial cartilago Meckeli | Lower lip | Single slip (inferior) |
| Levator mandibulae internus | Ventr al processus ascendens and few fibers on the lateral curvature | Distal cartilago Meckeli | |

**Hyoid group, n. facialis (c.n. VII)**

| Muscle | Origin | Insertion | Comments |
|--------|--------|-----------|----------|
| Hyoangularis | Dorsal ceratohyal | Retroarticular process of cartilago Meckeli | |
| Quadratoangularis | Ventral palatoquadrate | Retroarticular process of cartilago Meckeli | |
| Suspensorioangularis | Descendent posterior margin of the processus muscularis | Retroarticular process of cartilago Meckeli | |
| Orbitohyoideus | Processus muscularis | Lateral edge of ceratohyal | |
| Suspensoriohyoideus | Posterior descending margin of processus muscularis | Lateral process of ceratohyal | |
| Interhyoideus | Median aponeurosis | Ventral ceratohyal | |

**Branchial group, n. glossopharyngeus (c.n. IX) and vagus (c.n. X)**

| Muscle | Origin | Insertion | Comments |
|--------|--------|-----------|----------|
| Levator arcus branchialium I | Arcus subocularis | Ceratobranchial I | |
| Levator arcus branchialium II | Lateral otic capsule | Ceratobranchial II | |
| Levator arcus branchialium III | Lateral otic capsule | Ceratobranchial III | |
| Levator arcus branchialium IV | Otic capsule | Ceratobranchial IV | |
| Tympanopharyngeus | Otic capsule | Ceratobranchial IV and pericardium | |
| Dilator laryngis | Otic capsule | Arytenoid cartilage | |
| Constrictor branchialis I | - | - | |
| Constrictor branchialis II | Processus branchialis II | Commissura terminalis I by the inner margin of CB I | |
| Constrictor branchialis III | Processus branchialis II | Commissura terminalis II by the inner margin of CB II | |
| Constrictor branchialis IV | Processus branchialis II | Commissura terminalis II | Along the CB III |
| Subarcualis rectus I | Posterior lateral base of ceratohyal | Processus branchialis III, dorsal CB II and CB I | |
| Subarcualis rectus II-IV | Ceratobranchial IV | Ceratobranchial I | Crossing the CB III |
| Subarcualis obliquus II | Processus urobranchialis | Processus branchialis II and III | Two slips |
| Diaphragmatobranchialis | Peritoneum (diaphragm) | Distal Ceratobranchial III | |

**Spinal group, spinal nerve innervation**

| Muscle | Origin | Insertion | Comments |
|--------|--------|-----------|----------|
| Genyoohoideus | Planum hypobranchiale | Infrarostral cartilage | Originating between CB II and III |
| Rectus abdominis | Peritoneum (diaphragm) | Abdominal wall | Five open myotomes |
| Rectus cervices | Peritoneum (diaphragm) | Processus branchialis III | Single slip |

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The controversial phylogenetic position of the tribe Dendropsophini (e.g. [1,3]) within Hylidae, added to the poor knowledge about on internal larval anatomy in *Dendropsophus* prevents us to assess the polarity of most character-states and, therefore, to enhance broad discussions about larval character evolution in *Dendropsophus*; however, there are some interesting exceptions that deserve comments.

Several species of *Dendropsophus* have a reduced number of elements in the buccopharyngeal cavity [24,30–32]. For example, the median ridge is missing in *D. ebraccatus* and *D. nanus* [24,32], and a lower number of papillae in both buccal floor and roof and the absence of lingual papillae were also reported for larvae of *Dendropsophus* (e.g. [31,32]). Faivovich et al. [3] suggested the absence of lingual papillae as a putative synapomorphy for the clade composed of *Dendropsophus*, *Lysapsus*, *Pseudis*, *Scarthyla*, *Scinax*, and *Sphaenorhynchus* (the former Dendropsophini tribe sensu [3]), with reversion in *Lysapsus* and *Pseudis*. Our observations showed that lingual papillae are also present at least in some species of *Sphaenorhynchus* (*S. dorisae*, *S. lacteus*, *S. prasinus*; P.H.S. Dias and K. Araujo-Vieira personal observations). This character-state is unknown for *Xenohyla*. The absence of lingual papillae optimizes ambiguously in the phylogenetic hypothesis of Duellman et al. [1] due to the unknown character-state of *Xenohyla*. The absence of lingual papillae optimizes ambiguously in the phylogenetic hypothesis of *Xenohyla*; it is a synapomorphy of *Dendropsophus* or of a more inclusive clade, the tribe Dendropsophini (*Dendropsophus + Xenohyla* sensu [2]).

*Dendropsophus decipiens* (*D. microcephalus* group) has a fan-like papilla on the buccal floor, adjacent to the buccal pockets. This character was first described by Kaplan and Ruiz-Carranza [31] for *D. garagoensis*, *D. padreluna*, *D. virolinensis* (*D. garagoensis* group), and *D. stingi*.

![Cranial, hyoid and hyobranchial muscles of Dendropsophus decipiens (stage 36).](https://doi.org/10.1371/journal.pone.0219716.g003)

(A) Ventral and (B) dorsal views. Abbreviations: CB (II-IV), constrictor branchialis; GH, genyohyoideus; HA, hyoangularis; IH, interhyoideus; IM, intermandibularis; LBI, levator arcuum branchialium I; LBIV-TP, levator arcuum branchialium IV + tympanohyoides; LMA, levator mandibulae articularis; LMEP, levator mandibulae externus profundus; LMES, levator mandibulae externus superficialis; LMI, levator mandibulae internus; LMLS, levator mandibulae longus superficialis; ML, mandibulolabialis; OH, orbitohyoideus; RC, rectus cervicis; SO, subarcualis obliquus; SRI, subarcualis rectus I; SRII-IV, subarcualis II-IV. Scale bars = 0.5 mm.
(D. parviceps group) and illustrated for D. minutus (D. minutus group; [30]). Fan-like papillae are absent in larvae of D. ebraccatus, D. microcephalus, D. nanus, D. phlebodes, and D. sarayacuensis [24,28,32]. The presence of a fan-like papilla on the buccal floor in members of the D. garagoensis, D. microcephalus, D. minutus, and D. parviceps groups suggest that it could be a
putative synapomorphy of the genus *Dendropsophus*; however, the taxonomic distribution of this character-state within *Dendropsophus* remains poorly known.

A putative synapomorphy of the *Dendropsophus garagoensis* group is the presence of two pairs of infralabial papillae, which were reported for *D. garagoensis* and *D. padreluna* [31]—with independent evolution in *D. decipiens* [this work]. Other species of *Dendropsophus* that have been studied present a single pair of infralabial papillae (e.g. *D. minutus*, *D. nanus*, *D. phlebodes*; [24,30,32]).

Larvae of *Dendropsophus decipiens* differ from those of its related species *D. microcephalus* and *D. nanus* (characters in parenthesis) in having generalized processus muscularis (broad processus muscularis), marginal projections on arcus subocularis of palatoquadrate (smooth margin), thin ceratohyals (stout and thick ceratohyals), regular branchial basket (reduced branchial basked), and presence of spicules on the ceratobranchialia (absence of spicules) [32–34]. However, *D. decipiens* share with those species short and narrow cornu trabeculae, the presence of a small triangular process at the basis of the processus muscularis, and a single-element suprarostral cartilage. The latter could be a synapomorphy of *Dendropsophus* (with one reversion to a separated element suprarostral cartilage in *D. ebraccatus* within the *D. leucophyllatus* group; [28]) or of the *D. microcephalus* group. In larvae of *Lysapsus*, *Pseudis*, and some *Scinax*, the suprarostral corpora are fused distally, but with a medial indentation that allow the identification of both elements; several other hylids have completely separated suprarostral cartilage (e.g. [32,33,40–43]). This character-state is still unknown for *Scarthyla*, *Sphaenorhynchus*, and *Xenohyla*.

It is worth to note that a single-element suprarostral cartilage is not very common in anuran larvae. Besides some *Dendropsophus*, such morphological condition have been reported in some microhylids [32], *Occidozyga baluensis* (Dicroglossidae) [44], and *Ceratophrys* and *Lepidobatrachus* (Ceratophryidae) [32,45–47]. It is interesting to point that, regarding Ceratophryidae, *Chacophrys pierotti* possesses the suprarostral alae and corpora completely fused (with a small fenestra), but both corpora have a medial indentation [48]. Lavilla and Fabrezi [49] suggested that the complete fused suprarostral could be a synapomorphy of *Ceratophrys + Lepidobatrachus*. Given the phylogenetic relationships within Ceratophryidae [50]—*Chacophrys* and *Lepidobatrachus* are sister taxa, and both sister to *Ceratophrys*—this is not possible. However, the complete fusion between the alae and corpora could be a synapomorphy for the family. While microhylids are filter-feeders, *Ceratophrys*, *Lepidobatrachus*, and *Occidozyga* are macrophagous larvae. Further information are still needed to understand the relationship between macrophyg and the fusion of the elements of the suprarostral cartilage.

*Dendropsophus decipiens* shares with *D. ebraccatus* the m. subarcualis rectus II-IV with a single, continuous slip; whereas *D. microcephalus* and *D. nanus* have this muscle discontinued at the processus branchialis II [28,32,41]. Larvae of *Scinax* and distantly related hylids (e.g. *Agalychnis, Boana, Osteocephalus, Trachycephalus*; [28,32,42]) have a single subarcualis rectus II-IV, while larvae of *Lysapsus* and *Pseudis* have a discontinued subarcualis rectus II-IV [28,32,34]. The taxonomic distribution of these character-states on the phylogenetic hypothesis of Duellman et al. [1] suggests that *D. decipiens* and *D. ebraccatus* have the plesiomorphic condition (single subarcualis rectus II-IV), being the m. subarcualis rectus II-IV discontinued at the processus branchialis II a putative synapomorphy of *Lysapsus + Pseudis*, with instances of homoplasy in *D. microcephalus* and *D. nanus*.

Larvae of *Dendropsophus*, *Lysapsus*, and *Pseudis* that have been studied share the m. levator mandibulae lateralis inserted on the nasal sac [32,41] [this work]—although Haas [28] mentioned that it inserted on the processus posterior dorsalis of the suprarostral or in the rostral tissue in *D. ebraccatus* [28: ch. 57.0]. In larvae of *Scinax*, the m. levator mandibulae lateralis inserts on the pars alaris of the suprarostral cartilage [32,34,42]. The taxonomic distribution of
these character-states on the phylogenetic hypothesis of Duellman et al. [1] suggests that the m. levator mandibulae lateralis inserted on the nasal sac could be a synapomorphy of the Dendropsophini + Pseudini clade (sensu [2]) or arose twice independently in Dendropsophus and the Lysapsus + Pseudis clade. Other character-state, the absence of the superior slip of the m. mandibulolabialis also optimize ambiguously as a synapomorphy of the Dendropsophini + Pseudini clade or of Dendropsophus and the Lysapsus + Pseudis clade (with some instances of reversion within Pseudis; [28,41]). Larvae of Scinax have the superior slip of the m. mandibulolabialis [42]. The optimizations of both character-states mentioned above are dependent on the conditions, still unknown, present in larvae of Scarthyla, Sphaenorhynchus, and Xenohyla.

Feeding habits

Tadpoles can be distinguished regarding their feeding habits accordingly with the size of their prey (macrophagous or microphagous) and the nature of the feeding items (herbivore, carnivore, or omnivore). Larvae of Dendropsophus have been described as macrophagous feeders (e.g. [51]), or macrophagous herbivores according to Wassersug [24]. However, other reports suggest that tadpoles of Dendropsophus could be omnivorous. For example, Vera Candioti [32] described the presence of entire oligochaetes in the digestive system of D. nanus. Ruas et al. [52] observed tadpoles of D. novaisi chasing and preying on tadpoles of Rhinella crucifer. Also, larvae of D. minutus were observed attacking and preying on living tadpoles of Physalaemus sp.—although it was considered a facultative behavior, given that D. minutus feeds commercial fish food and plant residues in captivity [53].

Most of the macrophagous tadpoles (both herbivorous or carnivores) have terminal mouth, reduced branchial basket, well-developed orbitohyoideus, reduced labial tooth rows, reduced or lost elements of the buccopharynx, massive jaw sheaths, fused elements of suprarostral cartilages, and short intestines [32,35–36,44–47,54] [P.H.S. Dias personal observation]. Almost all these character-states are present, with different combinations, in larvae of Dendropsophus. Wassersug [24] pointed out several buccopharyngeal characters associated with macrophagy in larvae of Dendropsophus, and also reported that D. phlebodes “presented the most extreme reduction in structures associated with fine suspended matters”.

We observed that larvae of Dendropsophus decipiens have some character associated with a macrophagy as a terminal mouth lacking labial teeth, reduction in the elements of the buccopharyngeal cavity, such as papillation and secretory tissue, and single-element suprarostral cartilage. Nevertheless, tadpoles of D. decipiens differ from those of D. microcephalus and D. nanus, which have marked reduction of branchial baskets (well-formed and bearing spicules in D. decipiens) and massive orbitohyoideus [32] that is correlated with powerful suction capacity [35]. This combination of characters suggests that larvae of D. decipiens feed on large elements and have reduced filter capacity, although they are not as specialized for predation (carnivory/omnivory) as the tadpoles of D. microcephalus and D. nanus. Morphological and behavioral observations for more species, as well as the usage of techniques such as stable isotope (see [55]) are necessary for a fully appreciation of the evolution of feeding habits in Dendropsophus.

Our results suggest that larval internal morphology could provide interesting insights into the evolution and diversification of Dendropsophus. However, additional studies on other species of Dendropsophus and its related taxa (e.g. Scarthyla, Sphaenorhynchus, and Xenohyla) are required to corroborate the different putative synapomorphies mentioned in this work. Furthermore, the feeding habits of tadpoles of the genus are, putatively, more diverse than previously observed, with variable degrees of specialization for a macrophagous diet.
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