

ORIGINAL ARTICLE

Life on the edge: Tadpoles of Cycloramphidae (Amphibia; Anura), anatomy, systematics, functional morphology, and comments on the evolution of semiterrestrial tadpoles

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Abstract

The evolutionary success of anurans can be partially explained by the occurrence of free-living larvae. Tadpoles occupy several distinct habitats, including the terrestrial environment. Semiterrestriality appears to have evolved seven times in anurans, and tadpoles of distantly related lineages have converged in a set of phenotypic characters, such as a depressed body, ventral mouth, massive, well-keratinized and laterally compressed jaw sheaths, low fins, and well-developed hind limbs. The semiterrestrial tadpoles of the South American family Cycloramphidae remain poorly studied. In this work, we perform a comparative analysis of the external and internal morphology of these larvae, we comment on the systematic and evolutionary implications for the family, and finally, we discuss the convergent evolution of semiterrestrial tadpoles in anurans. We studied the external, buccopharyngeal, and musculoskeletal morphology of semiterrestrial tadpoles of 14 species of Cycloramphidae. These tadpoles are highly modified and present several character-states associated with semiterrestrial life. Most of them are unique and restricted to the family, such as the novel configuration of the muscles subarcualis rectus I, rectus abdominis, and levator arcuum branchialium III. We propose 13 new synapomorphies for Cycloramphidae and one for *Thoropa*. The presence of similar, homoplastic, character-states in all semiterrestrial tadpoles of unrelated phylogenetic lineages seems to suggest that these character-states are adaptations for semiterrestriality.

KEYWORDS

buccopharyngeal cavity, chondrocranium, *Cycloramphus*, larval muscles, *Thoropa*

Resumo

O sucesso evolutivo dos anuros pode ser parcialmente explicado pela ocorrência de larvas de vida livre. Os girinos ocupam vários habitats distintos, incluindo o ambiente terrestre. A semiterrestrialidade parece ter evoluído sete vezes em anuros, e girinos de linhagens distantes relacionadas apresentam uma série de caracteres

fenotípicos convergentes, como corpo deprimido, boca ventral, lâminas mandibulares maciças, fortemente queratinizadas e comprimidas lateralmente, nadadeiras baixas e membros posteriores desenvolvidos. Entretanto, os girinos semiterrestres da família sul-americana Cycloramphidae permanecem pouco estudados. Neste estudo, fazemos uma análise comparativa da morfologia externa e interna dessas larvas, comentamos as implicações sistemáticas e evolutivas para a família e, por fim, discutimos a evolução convergente de girinos semiterrestres em anuros. Estudamos a morfologia externa, bucofaríngea e musculoesquelética de girinos semiterrestres de 14 espécies de Cycloramphidae. Esses girinos são altamente modificados e apresentam vários estados de caráter associados à vida semiterrestre. A maioria deles são estados únicos e restritos à família, como a nova configuração dos músculos subarcualis rectus I, rectus abdominis e levato arcuum branchialium III. Propomos 13 novas sinapomorfias para Cycloramphidae e uma para Thoropa. A presença de estados de caráter homoplásticos semelhantes em todos os girinos semiterrestres de linhagens filogenéticas não relacionadas parece sugerir que esses estados de caráter são adaptações para a semiterrestrialidade.

1 | INTRODUCTION

Anura comprises more than 7,000 species widely distributed on all continents except in Antarctica and several oceanic islands (Frost, 2020). The evolutionary success of anurans can be partially explained by the occurrence of free-living larvae, commonly known as tadpoles (Altig, 2006; Roelants et al., 2011), which allows frogs to exploit niches in both terrestrial and aquatic environments, reducing intraspecific competition. Tadpoles occupy habitats ranging from temporary ponds to phytotelmata in the canopy, dozens of meters above the ground, and in many cases, phenotypic characters can be associated with these habitats (Altig & Johnston, 1989; Altig & McDiarmid, 1999). The wide variety of forms and environments occupied can be explained by the hypothesis that morphological characters were selected independently in each developmental stage (Harris, 1999). As extreme examples, one can cite neustonic tadpoles with umbelliform oral discs that feed on the water surface (e.g., Dias et al., 2018, 2021; Grosjean et al., 2011), and fossorial tadpoles with reduced eyes, unpigmented skin, and vermiform bodies (e.g., Rada et al., 2019). Tadpoles can even occupy terrestrial environments (e.g., Menin & Rodrigues, 2013). Although some authors have reported that some suctorial tadpoles, such as *Ascaphus* Stejneger, 1899 (Noble, 1927), *Nasikabatrachus* Biju & Bossuyt, 2003 (Zachariah et al., 2012), and *Meristogenys* Yang, 1991 (Gan et al., 2015), can be found out of the water for short periods, very few species persist unsubmerged throughout their development.

Semiterrestrial tadpoles spend most of their life out (or partially out) of water, inhabiting wet rock faces and rivulets (Altig & Johnston, 1989). Semiterrestriality appears to have evolved seven times in anurans, occurring in the following taxa (a) *Cycloramphus* Tschudi, 1838 and *Thoropa* Cope, 1865 (Cycloramphidae, South

America; Bokermann, 1965; Caramaschi & Sazima, 1984; Cocroft & Heyer, 1988; Heyer, 1983a, 1983b; Heyer & Crombie, 1979; Lima et al., 2010; Moura et al., 2019; Nunes-de-Almeida et al., 2016; Silva & Oüvernay, 2012; Verdade et al., 2019), (b) *Arthroleptides* Nieden, 1911 and *Petropedetetes* Reichenow, 1874 (Petropedetidae, Africa; Barej et al., 2010; Channing et al., 2002, 2012; Drewes et al., 1989; Lawson, 1993), (c) *Nothophryne* Poynton, 1963 (Pyxicephalidae, Africa; Bitencourt-Silva et al., 2016; Conradie et al., 2018; Poynton & Broadley, 1985), (d) *Ptychadena broadleyi* Stevens, 1972 and *Ptychadena mutinondoensis* Channing & Willems, 2018 (Ptychadenidae, Africa; Channing & Willems, 2018; Stevens, 1972), (e) *Sclerophrys perreti* (Schizt, 1963) (Bufonidae, Africa; Channing et al., 2012; Onadeko et al., 2014; Schizt, 1963), (f) *Nannophrys ceylonensis* Günther, 1869 (Dicroglossidae, Asia; Kirstinghe, 1958), and (g) *Indirana* Laurent, 1986 and *Walkerana* Dahanukar et al., 2016 (Ranixalidae, Asia; Annandale, 1918; Gopalan et al., 2012; Modak et al., 2018; Padhye et al., 2014). The tadpoles of these distantly related lineages convergently evolved a set of phenotypic characters, such as a depressed body, ventral mouth, massive, well-keratinized and laterally compressed jaw sheaths, low fins, and strong, muscular, well-developed hind limbs (Altig & Johnston, 1989).

The semiterrestrial tadpoles of the family Cycloramphidae remain poorly studied. The family comprises the genera *Cycloramphus*, *Thoropa*, and *Zachaenus* Cope, 1866, with 36 recognized species endemic to eastern Brazil (Frost, 2020). Its monophyly is well supported (but see Grant et al., 2017), but its phylogenetic placement among other hyloid lineages is highly ambiguous (e.g., Frost et al., 2006; Grant et al., 2006; Jetz & Pyron, 2018; Pyron & Wiens, 2011). Among the species with known biology, two distinct reproductive modes have been reported: the two species of *Zachaenus* and the eight species of the *Cycloramphus bolitoglossus* and *Cycloramphus eleutherodactylus*

TABLE 1 Described tadpoles of Cycloramphidae

Species	External morphology	Buccopharyngeal morphology	Chondrocranium morphology	Muscles
<i>Cycloramphus bandeirensis</i>	Verdade et al. (2019)			
<i>Cycloramphus boraceiensis</i>	Heyer (1983a), this study	This study	This study	This study
<i>Cycloramphus brasiliensis</i>	Heyer (1983a), this study	This study	This study	This study
<i>Cycloramphus fuliginosus</i>	Heyer (1983a)	This study	This study	This study
<i>Cycloramphus izecksohni</i> (as <i>Cycloramphus duseni</i>)	Heyer (1983a)	Wassersug and Heyer (1983, 1988)	Wassersug and Heyer (1983, 1988)	
<i>Cycloramphus lithomimeticus</i>	Silva and Ouverney (2012), this study	This study	This study	This study
<i>Cycloramphus lutzorum</i>	Lima et al. (2010), this study	This study	This study	This study
<i>Cycloramphus rhyakonastes</i>	Nunes-de-Almeida et al. (2016)			
<i>Cycloramphus stejnegeri</i>	Heyer and Crombie (1979), Heyer (1983a)	Wassersug and Heyer (1983, 1988)	Lavilla (1991)	
<i>Cycloramphus valae</i>	Heyer (1983b)			
<i>Thoropa lutzi</i>	Bokermann (1965)	This study	This study	This study
<i>Thoropa megatympanum</i>	Caramaschi and Sazima (1984)	This study	This study	This study
<i>Thoropa miliaris</i>	This study	This study	This study	This study
<i>Thoropa petropolitana</i>	Bokermann (1965), this study	Wassersug and Heyer (1983, 1988)	This study	This study
<i>Thoropa saxatilis</i>	Cocroft and Heyer (1988), this study	This study	This study	This study
<i>Thoropa taophora</i>	Bokermann (1965), this study	This study	This study	This study
<i>Zachaeus carvalhoi</i>	Almeida-Silva et al. (2019)			
<i>Zachaeus parvulus</i>	Lutz (1944)			

groups breed independently from running water and develop endotrophic tadpoles (Heyer & Crombie, 1979; Lutz, 1944); the remaining *Cycloramphus* (*Cycloramphus fuliginosus*, *Cycloramphus granulosus*, and *Cycloramphus ohausi* groups, ca. 20 spp.) and all known *Thoropa* (6 spp.) are associated with saxicolous environments (Bokermann, 1965; Heyer, 1983a, 1983b; Lutz, 1944; Wassersug & Heyer, 1983).

External larval morphology has been described—although not always accurately or with properly defined characters—for approximately half of the species of Cycloramphidae, including both species of *Zachaeus* (Almeida-Silva et al., 2019; Lutz, 1944) and 10 of the 28 species of *Cycloramphus* (Heyer, 1983a, 1983b; Heyer & Crombie, 1979; Lima et al., 2010; Nunes-de-Almeida et al., 2016; Silva & Ouverney, 2012; Verdade et al., 2019). In *Thoropa*, assignation of tadpoles described is beyond doubt in four of the six species (Bokermann, 1965; Caramaschi & Sazima, 1984; Cocroft & Heyer, 1988; Moura et al., 2019). The description of *Thoropa miliaris* (Spix, 1824) tadpoles by Bokermann (1965) was based on 12 specimens of unspecified origin, except for the illustrated individual (WCAB 13307; Bokermann, 1965: 531) from Cubatão, São Paulo state. On the basis of morphometric and morphological analysis, Feio et al. (2006) revalidated *Thoropa taophora* for populations of *T. miliaris* from São Paulo state, which was corroborated by molecular evidence (Fitzpatrick et al., 2009; Sabbag et al., 2018). Consequently,

Bokermann's description corresponds to *T. taophora* (Miranda-Ribeiro, 1923) and the tadpole of *T. miliaris* is undescribed (but see Barth, 1956; Fatorelli et al., 2018; Lutz, 1954). A summary of published tadpole descriptions is shown in Table 1.

The buccopharyngeal cavity has been described for four cycloramphid species, including *T. miliaris* (partially; Barth, 1956), *Thoropa petropolitana* (Wandolleck, 1907), *T. taophora* (as *T. miliaris*; Wassersug & Heyer, 1983, 1988), and *Cycloramphus izecksohni* Heyer, 1983b (as *Cycloramphus duseni*; Wassersug & Heyer, 1983). The only chondrocranium known for the entire family is that of the endotrophic *Cycloramphus stejnegeri* (Noble, 1924) (Lavilla, 1991). Information on larval muscles is limited (Barth, 1956), and data on visceral elements are lacking for all species.

Given our limited knowledge, lack of accurate descriptions, poorly defined characters, and almost complete absence of information on internal morphology, a detailed review of Cycloramphidae larvae is most needed. In this study, we first describe the tadpole of *T. miliaris* from its type locality and then perform a comparative analysis of the external morphology, buccopharyngeal anatomy, and musculoskeletal morphology of cycloramphid larvae. Finally, we comment on the systematic and evolutionary implications for the family, consider the possible functional significance of apomorphic character-states, and assess the convergent evolution of semiterrestrial tadpoles in anurans.

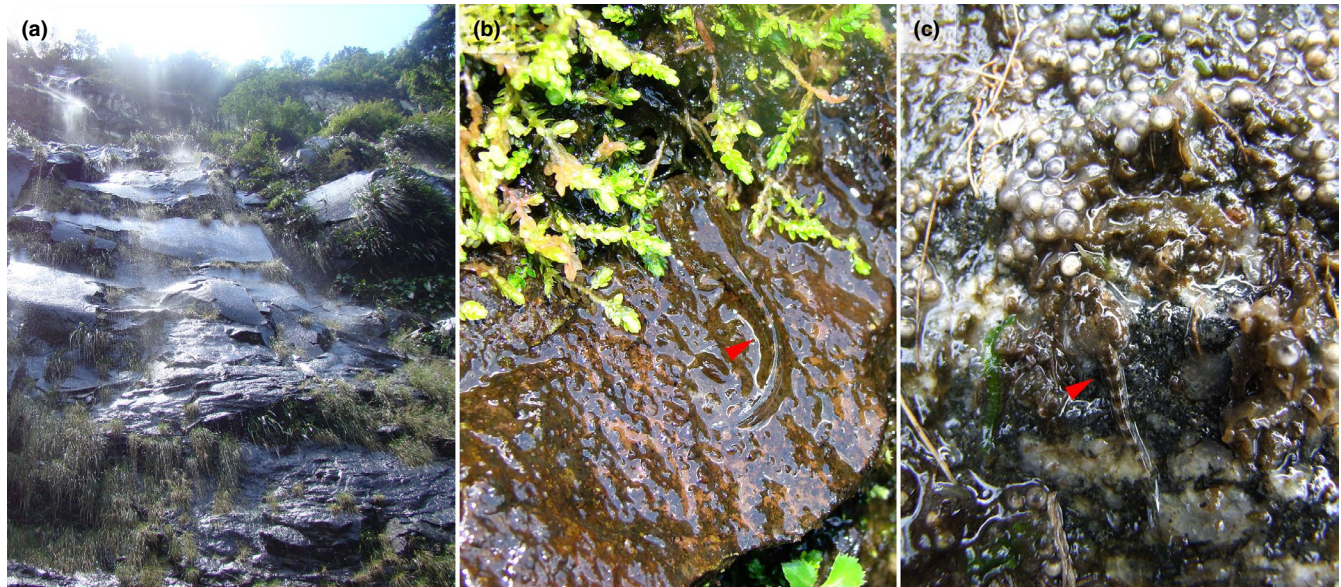


FIGURE 1 Tadpoles of *Thoropa* in their natural habitat. (a) Cachoeira das Pedras Brancas (Três Forquilhas, RS), habitat of *Thoropasaxatilis* (photograph T. Grant). (b) Tadpole of *T. saxatilis* (Três Forquilhas, RS; photograph T. Grant). (c) Tadpole of *Thoropataophora* in a highway rock outcrop (Bertioga, SP; photograph A. Fares Sabbag)

2 | MATERIAL AND METHODS

2.1 | Specimens

Examined tadpoles of *T. miliaris* were from the type locality, Praia Vermelha, Urca, Rio de Janeiro Municipality (22°57'14.4"S, 43°9'44.3"W). In addition to being the only species of *Thoropa* known at that locality, two individuals were raised to metamorphosis to confirm species identity. The description is based on 11 tadpoles in Gosner (1960) Stages 35–36. Tadpoles were measured to 0.1 mm precision with a digital caliper, following Altig and McDiarmid (1999) and Altig (2007): total length (TL), body length (BL), tail length (TAL), body width (BW), body height (BH), tail height (TH), nostril to snout distance (NSD), eye to snout distance (ESD), interorbital distance (IOD), eye to nostril distance (END), internarial distance (IND), oral disc width (ODW) and eye diameter (ED).

We also studied the external and internal larval morphology of other 13 cycloramphid species, namely, *Thoropa lutzi* Cochran, 1938, *T. megatympanum* Caramaschi & Sazima, 1984, *T. petropolitana*, *T. saxatilis* Cocrofr & Heyer, 1988, *T. taophora*, *Cycloramphus boraceiensis* Heyer, 1983a, *C. brasiliensis* (Steindachner, 1864), *C. fuliginosus* Tschudi, 1838, *C. izecksohni* Heyer, 1983b, *C. lithomimeticus* Silva & Oüvernay, 2012, *C. lutzorum* Heyer, 1983a, *C. stejnegeri*, and *C. valae* Heyer, 1983a. Figure 1 shows examples of common habitats of these tadpoles. Species assignment was based on comparison with the published tadpole descriptions and geographic distribution, given that species of Cycloramphidae are rarely syntopic (Frost, 2020; Sabbag et al., 2018). Additionally, we present behavioral observations on *T. saxatilis* based on fieldwork at Cachoeira das Pedras Brancas, Três Forquilhas, Rio Grande do Sul, Brazil (29°23.670'S, 50°02.551'W, 267 m).

To explore character evolution, we studied character-states in the closely related hyloid lineages Alsodidae, Batrachylidae, Ceratophryidae, Dendrobatoidea, Hyloidae, Rhinodermatidae, and Telmatobiidae, most of which (except Rhinodermatidae) possess aquatic tadpoles, in light of recent phylogenetic hypotheses (e.g., Grant et al., 2017; Jetz & Pyron, 2018); some data were taken from direct observation, but for most outgroup taxa character-states were obtained from the literature. For comparison, we also examined the semiterrestrial tadpoles of *Arthroleptides martiensseni* Nieden, 1911, *Petropedetes perreti* Amiet, 1973, and *Petropedetes vulpiae* Barej et al., 2010 (Petropedetidae) and *Indirana beddomi* (Günther, 1876) (Ranixalidae). The complete list of specimens examined is provided in Table 2; museum acronyms follow Sabaj (2016).

2.2 | Clearing and staining and dissection methods

After external morphology inspection, some specimens (see Table 2) were processed according to the clearing and double staining protocol of Dingerkus and Uhler (1977); the procedure was interrupted after the alcian blue step, and specimens were manually dissected for inspection of cranial muscles and the buccopharyngeal cavity (stained with methylene blue solution). After character description and illustration, the procedure was finished to study chondrocranial morphology.

2.3 | Micro-CT

One tadpole of *T. megatympanum* was treated with Lugol's (I/I2) solution for 48 h, following Metscher (2009), washed in distilled water,

TABLE 2 Examined material

Taxon	Collection	Locality	N	Stage	External morphology	Buccopharyngeal cavity	Muscles	Chondrocranium
Cycloramphidae								
<i>Cycloramphus bandeirensis</i>					Verdade et al. (2019)			
<i>Cycloramphus boraceiensis</i>	CFBH 36944; RU-GIR 69; USNM 217933	Angra dos Reis, RJ/XXX/ Salesópolis, SP	2, 8, 1	29–36, 34		DIS	DIS	C&S
<i>Cycloramphus brasiliensis</i>	RU-GIR 56	Nova Friburgo, RJ	5	30–32	✓	DIS	DIS	C&S
<i>Cycloramphus fuliginosus</i>	CFBH 37886	No information	2	28	✓	DIS	DIS	C&S
<i>Cycloramphus izecksohni</i>					Heyer (1983a)			
<i>Cycloramphus lithomimeticus</i>	RU-GIR 73	Itaguaí, RJ	12	30–37	✓	DIS	DIS	C&S
<i>Cycloramphus lutzorum</i>	LGE 10296	Guaratuba, PR	1					
<i>Cycloramphus stejnegeri</i>	USNM 209370,	Teresópolis, RJ	14	28–31	✓		DIS	Lavilla (1991)
<i>Thoropa lutzii</i>	MZUSP 79301	Sumaré, RJ	4	29	✓	DIS	DIS	C&S
<i>Thoropa megatympanum</i>	UFMG 158	Santana do Riacho, MG	8	34–37	✓	DIS; SEM	DIS; μ CT	C&S; μ CT
<i>Thoropa miliaris</i>	UNIRIO 4732	Praia Vermelha, Urca, Rio de Janeiro, RJ	20	34–37	✓	DIS; SEM	DIS	C&S
<i>Thoropa petropolitana</i>	MZUSP 80015	Petrópolis, RJ	4	28–30	✓	LIT	DIS	C&S
<i>Thoropa taophora</i>	CFBH 9016	Picinguaba, Ubatuba, SP	6	33–37	✓	DIS; LIT	DIS	C&S
<i>Thoropa saxatilis</i>	MZUSP 64785	Itambézinho, SC	4	28	✓	DIS	DIS	C&S
Other taxa								
<i>Alsodes neuquensis</i>	MACN 46544		2		✓	Barrasso et al. (2016)	Barrasso et al. (2016)	Barrasso et al. (2016)
<i>Arthroleptides martiensseni</i>	USNM 316556	Tanga, Tanzania	2	40	✓			
<i>Atelognathus patagonicus</i>						Wassersug and Heyer (1988)		
<i>Batrachyla taeniata</i>	KU 162051	Lago Chapo, Llaquihue, Chile	2	27–28	✓		DIS	
<i>Ceratophrys cranwelli</i>					✓	Vera Candiotti (2007)	Vera Candiotti (2007)	Vera Candiotti (2007)
<i>Crossodactylus gaudichaudii</i>	MNRJ 35073, 35087	Floresta da Tijuca, Rio de Janeiro, RJ	6	28–31	✓	DIS	DIS	C&S
<i>Eupsophus emiliopugini</i>					Vera Candiotti et al. (2011)	Vera Candiotti et al. (2011)	Vera Candiotti et al. (2011)	Vera Candiotti et al. (2011)
<i>Hylodes phyllodes</i>	MNRJ 35034	Angra dos Reis, RJ			✓	DIS; SEM	DIS	C&S

(Continues)

TABLE 2 (Continued)

Taxon	Collection	Locality	N	Stage	External morphology	Buccopharyngeal cavity	Muscles	Chondrocranium
<i>Hylorina sylvatica</i>					Cárdenas-Rojas et al. (2007)	Cárdenas-Rojas et al. (2007)	Cárdenas-Rojas et al. (2007)	Cárdenas-Rojas et al. (2007)
<i>Indirana beddomi</i>	USNM 232370	Kerala, India	3	28, 31, 40	✓			
<i>Insuetophrynus acarpicus</i>					Rabanal and Formas (2009)	Rabanal and Formas (2009)		Rabanal and Formas (2009)
<i>Limnomedusa macroglossa</i>	CFBH 40054		8	30–35	✓	DIS; SEM	DIS	C&S
<i>Megaelosia goeldi</i>	UNIRIO 2348	Parnaso, Tersópolis, RJ	2	25–26	✓	DIS	DIS	C&S
<i>Petropedetes perreti</i>	ZMB 73738	Mt. Manengouba, Cameroon	8	38	✓	DIS	DIS	C&S
<i>Petropedetes vulpiae</i>	ZMB 82846	Ebo Forest, Cameroon	2	37–38	✓			
<i>Rheobates palmatus</i>	ICN 9751, 55303, 55301	Guayabeta, Colombia/ San Vicente de Chucurí, Colombia	20	25–38	✓	DIS; SEM	DIS	C&S
<i>Rhinoderma darwini</i>					Lavilla (1987)	Wassersug and Heyer (1988)		Lavilla (1987)
<i>Telmatobius</i> spp						Vera Candiotti (2008)	Vera Candiotti (2008)	Vera Candiotti (2008)

Note: Acronyms are in accordance with Sabaj (2016).

Abbreviations: µCT, micro-computed tomography; C&S, clearing and staining; DIS, dissection; SEM, scanning electron microscopy.

and submitted to high-resolution micro-computed tomography (micro-CT) in 360° using a 40Kv X-ray beam in X-ray microscope Xradia 410 Versa by Carl Zeiss X-ray microscopy. Volumetric data were generated and explored in Amira 6.1 (Thermo Fischer Scientific).

2.4 | Scanning electron microscopy

Some individuals were manually dissected according to Wassersug (1976) to expose the buccopharyngeal cavity and, following inspection using a stereoscopic microscope, submitted to the protocol of Alcalde and Blotto (2006) for scanning electron microscopy (SEM). We also applied SEM methods to the tail fins of two tadpoles of *T. miliaris*.

2.5 | Histology

One whole tadpole of *T. miliaris* was decalcified (Dietrich & Fontaine, 1975), embedded in paraffin, and sectioned at 7–10 µm thickness. Serial slices were stained with toluidine blue and basic fuchsin and hematoxylin–eosin.

2.6 | Terminology and character optimization

External morphology and oral disc terminology follow Altig and McDiarmid (1999) and Altig (2007), and that of the lateral line system is in accordance with Schlosser (2002). Terminology for the musculoskeletal system follows Haas (2003). Buccopharyngeal cavity terminology follows Wassersug (1976).

Transformation series (Grant & Kluge, 2004; Hennig, 1966) were recorded (see Data S1) and the character matrix (Data S2) was constructed in Mesquite V. 3.51 (Maddison & Maddison, 2018). Variable phenotypic characters were optimized on the phylogenetic hypothesis of Jetz and Pyron (2018), which is currently the most comprehensive hypothesis of anuran relationships in terms of the number of analyzed taxa; we also optimized our characters onto Sabbag et al.'s (2018) more detailed hypothesis of cycloramphid relationships for comparison (Figure S1). Parsimonious (Fitch, 1971) optimization was performed in TNT software (Goloboff & Catalano, 2016).

3 | RESULTS

3.1 | External morphology

3.1.1 | The tadpole of *Thoropa miliaris* ($n = 11$; Gosner Stages 35–36; Figures 2 and 3)

Body depressed (BW/BH = 1.3–2.0), elliptical in dorsal view, snout rounded (Figure 2a). Eyes dorsal, large (ED/BL = 0.08–0.2), directed anterolaterad; meniscus on upper iris present, rounded, covering

part of the lens. Nares rounded, dorsal, directed anterolaterad; marginal rim present but fleshy projection absent. Nares closer to eyes than snout (NSD/END = 1.2–2.2). Internarial distance 50–75% of interorbital distance. Spiracle sinistral, tubular, lateral, ventral to midline of body, directed posterolaterad in dorsal view, dorsad at angle of 30–45° in lateral view; inner wall absent; opening round, equal to spiracle width, margin regular. Coiled gut with switchback point sinistral. Vent tube medial, short, conical, free of ventral fin, opening elliptical. Tail long (TAL/TL = 0.6–0.7); caudal muscles not reaching acute tail tip; dorsal fin reduced, very low, originating at midlength of tail; ventral fin forming a groove along the entire tail (Figure 3). Preorbital and dorsal lines of lateral line system visible in some specimens, remaining lines undetectable. Oral disc (Figure 2b) ventral, large (55%–80% of body width), not emarginated, bordered by single row of rounded, non-alternating marginal papillae; upper lip with large gap; submarginal papillae absent. Labial tooth row formula 2(2)/3(1); A1 and A2 lengths subequal; A2 interrupted with small gap; P1 and P2 lengths subequal, longer than P3. Jaw sheaths present, serrate, compressed laterally, entirely black; upper sheath U-shaped; lower sheath narrower, V-shaped.

Measurements, given in mm as mean $\pm$ standard deviation (range): TL 17.8 $\pm$ 0.5 (16.9–19.0); BL 5.6 $\pm$ 0.3 (5.1–6.3); BH 1.8 $\pm$ 0.1 (1.6–2.1); BW 3.0 $\pm$ 0.2 (2.5–3.4); TH 1.5 $\pm$ 0.2 (1.0–1.9); TAL 12.2 $\pm$ 0.3 (11.5–12.7); ESD 1.8 $\pm$ 0.2 (1.0–2.2); NSD 1.0 $\pm$ 0.2 (0.50–1.5); ED 0.7 $\pm$ 0.1 (0.5–1.1); IOD 0.9 $\pm$ 0.1 (0.6–1.2); END 0.6 $\pm$ 0.1 (0.4–1.0); IND 0.6 $\pm$ 0.1 (0.5–0.9); ODW 2.0 $\pm$ 0.1 (1.8–2.2).

3.1.2 | Comparison with other cycloramphid tadpoles (Figures 4–8)

Tadpoles of Cycloramphidae share several external morphological characteristics. The body is elliptical in dorsal view and distinctively depressed, with a long tail and very low fins (Figures 4 and 6). A meniscus is present in the upper iris of all tadpoles examined, with minor variations in shape and extent of lens covering. For instance, it is large, rounded, and covers a large portion of the lens in *C. boraceiensis* and *C. lithomimeticus*; small, rounded, and covers a small portion of the lens in *C. brasiliensis*, *C. fuliginosus*, and *T. lutzii*; and large, rounded, and covers a part of lens in *T. saxatilis* and *T. taophora*. Nares are dorsal, rounded, and marginally rimmed. The spiracle is sinistral, tubular, lateral, ventral to midline of body, and directed posterodorsad; its inner wall is absent. The coiled gut, usually visible through the abdominal skin, has a sinistral switchback point (Figure 5). The vent tube is medial, short, conical, and free of the ventral fin. The oral discs are similar among species, being wide, unemarginated, and surrounded by a single row of marginal papillae interrupted by a dorsal gap (Figure 8). Jaw sheaths are fully keratinized and laterally compressed, and the tooth row formula is 2(2)/3(1) in most species, 2(2)/3 in *Cycloramphus rhyakonastes* Heyer, 1983a; Nunes-de-Almeida et al., 2016). Submarginal papillae are absent. Endotrophic tadpoles show reduction in some larval characters, such as the absence of a spiracle in *Zachaenus* and a lower labial tooth row formula

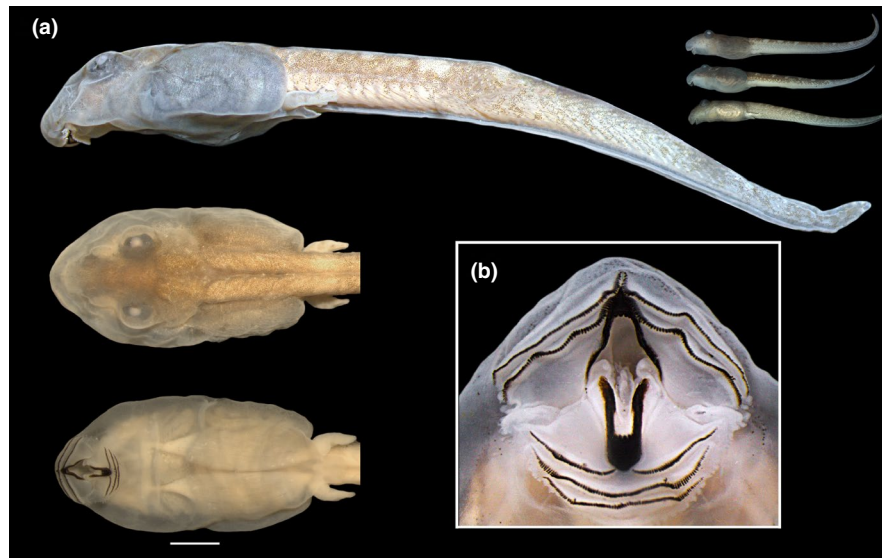


FIGURE 2 The tadpole of *Thoropa miliaris*. (a) Lateral, dorsal, and ventral views. (b) Detail of the oral disc. Three specimens from areas other than the type locality are shown at the upper right: Paraty, RJ (CFBH42222), Domingos Martins, ES (CFBH41089), Ibitirama, ES (ZUEC23660). Scale bar 1 mm. Note the typical streamlined body and the oral disc with highly compressed jaw sheaths

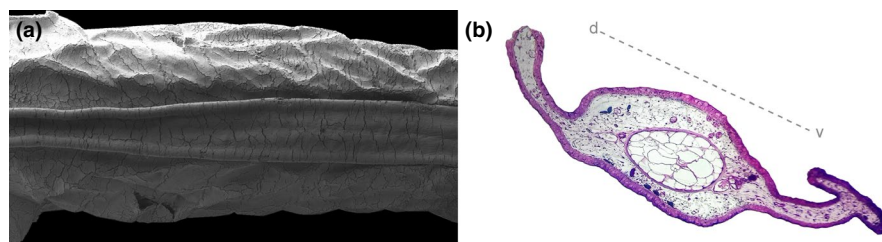


FIGURE 3 The tadpole of *Thoropa miliaris* showing details of tail morphology. (a) Scanning electron micrograph of the ventral aspect of the tail. (b) Cross section of the tail showing the arrangement of fins; the line indicates the dorso-ventral axis. Figures not to scale. Note the ventral fin distally expanded and modified into a groove

in *Zachaeus* and *C. stejnegeri*, 1(1)/2(1–2) and 2(1–2)/2(1–2) respectively (Almeida-Silva et al., 2019; Heyer & Crombie, 1979).

In contrast, some characters are highly variable both among and within genera. A well-developed, expanded abdominal flap is present in all *Cycloramphus*, *T. lutzi*, *T. petropolitana*, *T. saxatilis*, and *T. taophora*. In *T. megatympnum*, as in *T. miliaris*, it is poorly developed and almost unnoticeable (Figures 4–6); in *Zachaeus*, it is reduced, forming a small, rounded flap (Almeida-Silva et al., 2019). The posterior margin of the abdominal flap is deeply bilobate in *C. lithomimeticus*, *T. lutzi*, and *T. petropolitana* and unindented in *C. boraceiensis*, *C. brasiliensis*, and *C. fuliginosus*. In *T. miliaris*, *T. petropolitana*, *T. saxatilis*, and *T. taophora*, the spiracle opens above the midline of the posterolateral region of the flap; in *T. lutzi*, it opens below it and is directed posteriad; and in *C. lithomimeticus*, *C. boraceiensis*, *C. brasiliensis*, and *C. fuliginosus* it is aligned with the flap margin, directed posteriad. The ventral fin is low in all tadpoles of *Cycloramphus* but modified into a groove in all *Thoropa*. The length of the groove differs interspecifically, being differentiated along the anterior half of the tail in *T. lutzi* and *T. saxatilis*, only posteriorly in *T. petropolitana*, and along the entire fin in *T. megatympnum* and *T. taophora* (Figure 7). Unlike *T. miliaris*, in which the vent tube is free of the ventral fin, the

vent tube is attached to the ventral fin in *T. saxatilis* and *T. petropolitana* and to the fin and the abdominal flap in *T. lutzi* and *T. taophora*. Finally, angular and ventral lateral lines are visible in *C. brasiliensis* (not observed in *T. miliaris*).

3.2 | Internal morphology

We describe the main buccopharyngeal and musculoskeletal characteristics of larval *Thoropa* mainly on the basis of *T. miliaris*, highlighting differences between it and confamiliar tadpoles when pertinent.

3.2.1 | Buccopharyngeal cavity (Figures 9 and 10)

Buccal roof triangular, longer than wide (Figure 9a). Prenarial arena long, narrow, devoid of papillae, with arched, posteriorly oriented prominence or ridge. Internal nares elliptical, arranged obliquely; a flap-like papilla projecting mediad from wall lateral to each internal naris, partially occluding narial opening (see detail in *T. megatympnum*; Figure 10a); narial valve poorly developed or absent. Postnarial

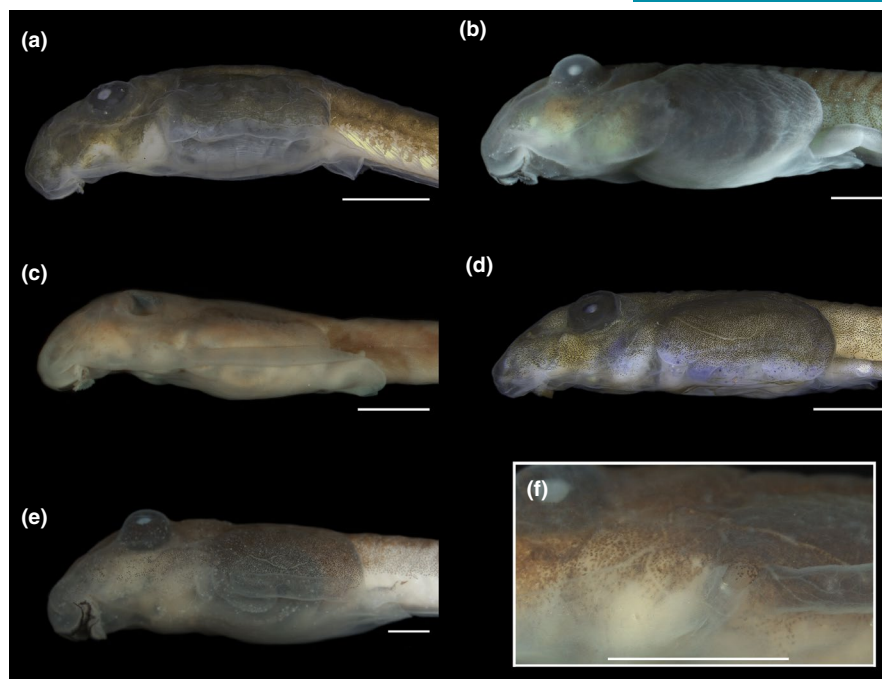


FIGURE 4 External morphology of tadpoles of *Thoropa*, lateral views. (a) *Thoropalutzi*. (b) *Thoropamegatympanum*. (c) *Thoropapetropolitana*. (d) *Thoropasaxatilis*. (e) *Thoropataophora*. (f) Detail of the spiracle of *T. saxatilis*. Scale bars 1 mm. Note the miniscule abdominal flap in *T. megatympanum*

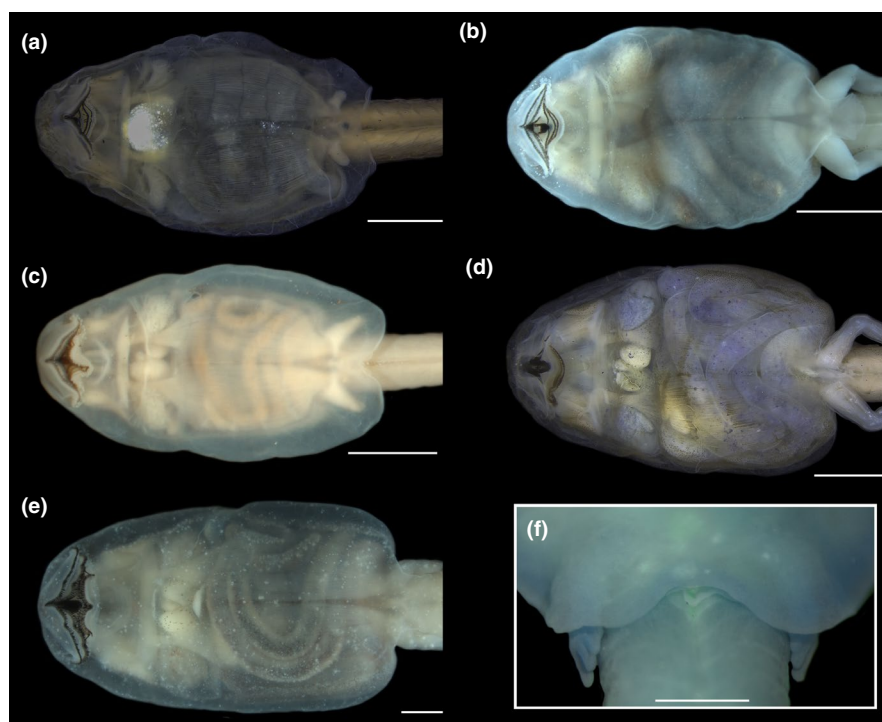


FIGURE 5 External morphology of tadpoles of *Thoropa* in ventral views. (a) *Thoropalutzi*. (b) *Thoropamegatympanum*. (c) *Thoropapetropolitana*. (d) *Thoropasaxatilis*. (e) *Thoropataophora*. (f) Detail of the vent tube opening in *T. petropolitana*. Scale bars 1 mm. Note the interspecifically variable shape of the posterior margin of the abdominal flap

arena triangular. Small papillae or ridges oriented obliquely, converging rostrally, weaker than in *Cycloramphus* tadpoles, forming large flaps almost reaching sagittal axis (Figure 10b). Median ridge trapezoid, low, with smooth or papillate margin in *Thoropa*; taller

and always papillate in *Cycloramphus*. Single pair of small lateral ridge papilla oriented transversely, bifurcated; larger and flap-like in *Cycloramphus*. Buccal roof arena rounded, delimited laterally by 5–6 (*Thoropa*) or 7–10 (*Cycloramphus*) pairs of conical papillae; pustulation

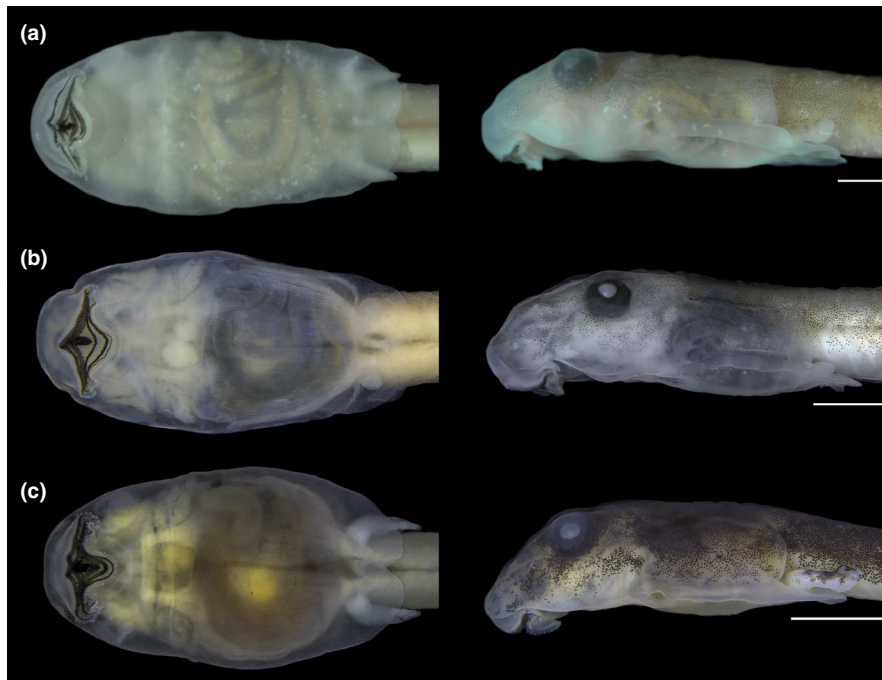


FIGURE 6 External morphology of tadpoles of *Cycloramphus* in ventral and lateral views. (a) *Cycloramphus boraceiensis*. (b) *Cycloramphus fuliginosus*. (c) *Cycloramphus lithomimeticus*. Scale bars 1 mm. Note the well-developed abdominal flaps in all species

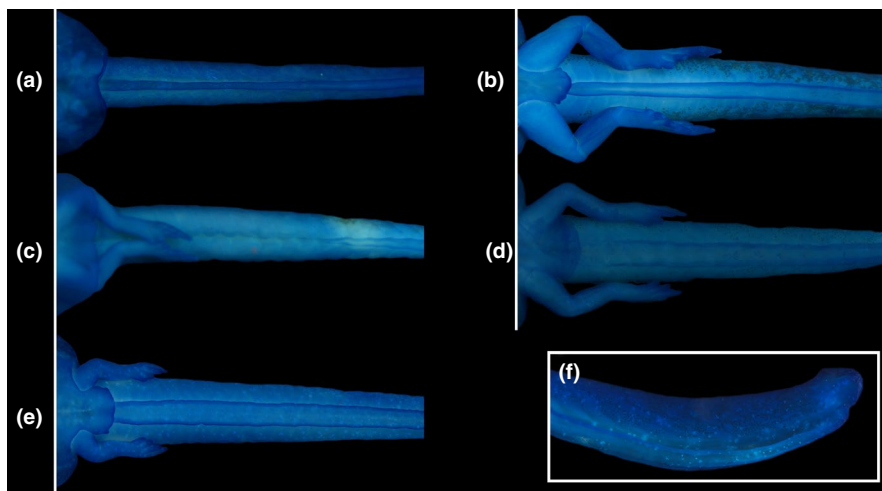


FIGURE 7 Comparative external morphology of tadpoles of *Thoropa*, details of the vent tubes and ventral fins. (a) *Thoropalutzi*. (b) *Thoropamegatympanum*. (c) *Thoropapetropolitana*. (d) *Thoropasaxatilis*. (e) *Thoropataophora*. (f) Detail of the distal portion of the tail of *T. taophora* showing the ventral fin modified to the tip. Methylene blue is used to contrast soft tissues. Figures not to scale. Note the variable arrangements of the ventral fin grooves

absent. Glandular zone not evident. Dorsal velum with smooth margin, interrupted medially, lacking papillae; some small papillae appear on the velum margin in *Cycloramphus*.

Buccal floor triangular (i.e., narrow anteriorly, wide posteriorly; Figure 9b). Two pairs of infralabial papillae: first pair large and globose (Figure 10c,d); second pair small and conical. Tongue anlage bell-shaped, bearing four conical lingual papillae in *Thoropa*, two or four in *Cycloramphus*. Buccal floor arena rectangular, bordered laterally by 10 (*Thoropa*) or 7–14 (*Cycloramphus*) pairs of long papillae, the anteriormost deeply bifurcated. Buccal pockets longer than wide, shallow,

oriented transversely. Margin of ventral velum with a few secretory pits, laterally smooth, medially undulate with wide median notch. Secretory ridges absent. Branchial basket triangular, shallow, bearing three filter cavities. Branchial plates bearing 6, 5, and 4 filter rows, respectively.

3.2.2 | Chondrocranium (Figures 11 and 12)

Chondrocranium longer than wide; greatest width at subocular bar (Figure 11a,b). Suprarostal cartilage tripartite; central corpora fused

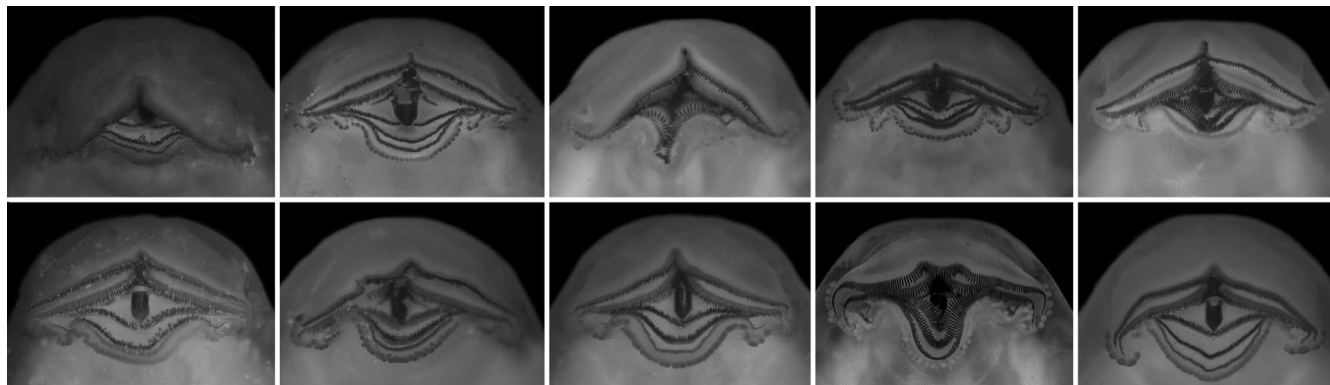


FIGURE 8 Oral morphology in cycloramphids. *Thoropa* (upper row, left to right): *Thoropalutzi*, *Thoropamegatympanum*, *Thoropapetropolitana*, *Thoropasaxatilis*, and *Thoropataophora*. *Cycloramphus* (lower row, left to right): *Cycloramphusbrasiliensis*, *Cycloramphusboraceiensis*, *Cycloramphusfuliginosus*, *Cycloramphuslithomimeticus*, and *Cycloramphuslutzorum*. Figures not to scale. Note the similar arrangements of marginal papillae, tooth rows, and jaw sheaths

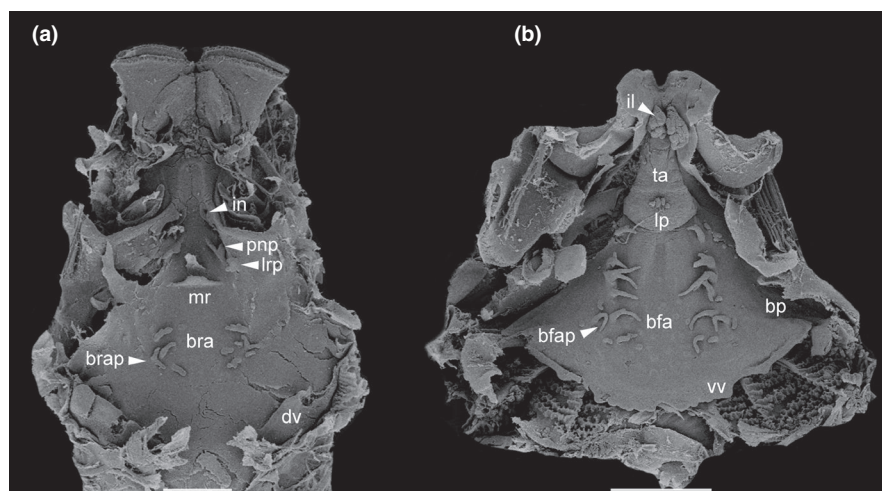


FIGURE 9 Buccal cavity of *Thoropa miliaris*. (a) Buccal roof. (b) Buccal floor. bfa, buccal floor arena; bfap, buccal floor arena papilla; bp, buccal pocket; bra, buccal roof arena; brap, buccal roof arena papilla; dv, dorsal velum; il, infralabial papilla; in, internal naris; lp, lingual papillae; lrp, lateral ridge papilla; mr, median ridge; pnp, postnarial papilla or ridge; ta, tongue anlage; vv, ventral velum. Scale bars 0.5 mm. Note the arched prenarial ridge and the distinctive arrangement of postnarial papillae converging rostrally

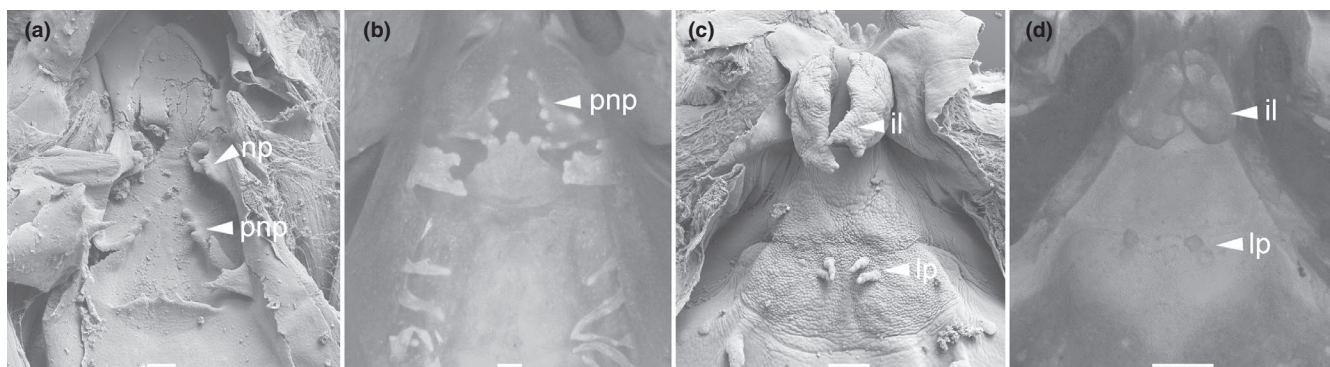


FIGURE 10 Comparative buccopharyngeal morphology in cycloramphids. Details of narial region of (a) *Thoropamegatympanum* and (b) *Cycloramphus brasiliensis*, and lingual regions of (c) *T. megatympanum* and (d) *Cycloramphusboraceiensis*. il, infralabial papilla; lp, lingual papillae; np, narial papillae; pnp, postnarial papilla. Scale bars 0.1 mm. Note the flap-like postnarial papillae in *Cycloramphus* and the similar globose infralabial papillae in all species

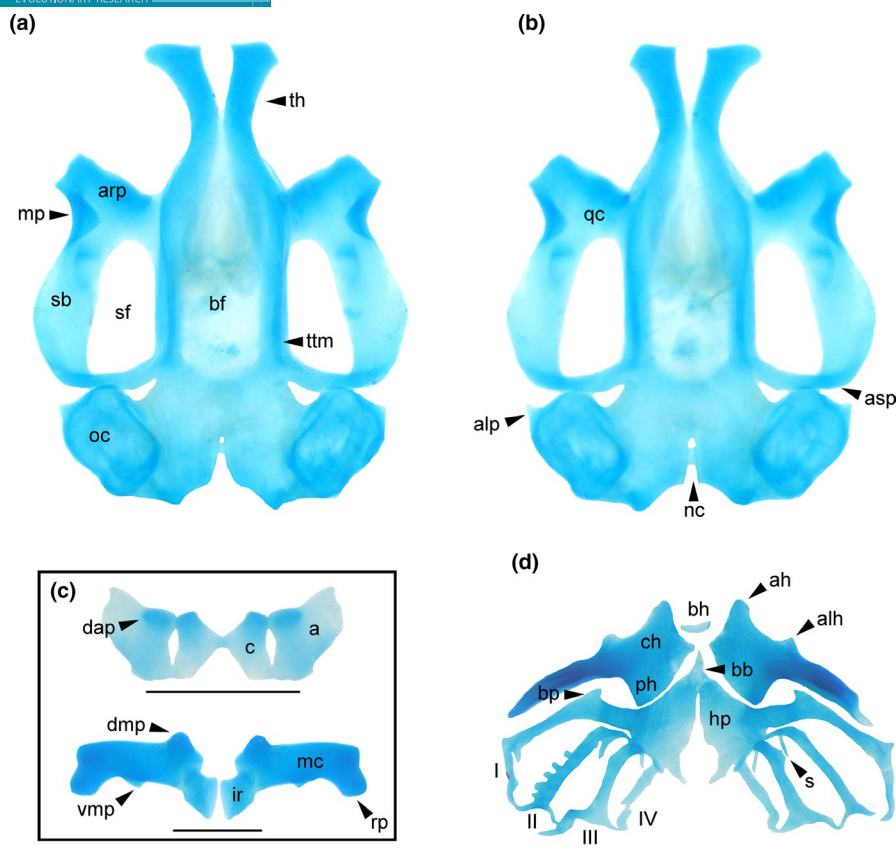


FIGURE 11 Chondrocranium of *Thoropa miliaris*. (a) Neurocranium in dorsal view. (b) Neurocranium in ventral view. (c) Detail of suprarostal and lower jaw cartilages in frontal views. (d) Hyobranchial skeleton in ventral view. a, ala; ah, anterior process of the ceratohyal; alh, anterolateral process of the ceratohyal; alp, anterolateral process of the otic capsule; arp, articular process; asp, ascending process; bb, basibranchial; bf, basicranial fenestra; bh, basihyal; bp, branchial process; c, corpus; ch, ceratohyal; dap, dorsal anterior process; dmp, dorsomedial process; hp, hypobranchial plate; ir, infrarostral; mc, Meckel's cartilage; nc, notochordal canal; mp, muscular process; oc, otic capsule; ph, posterior process of the ceratohyal; qc, quadratocranial commissure; rp, retroarticular process; s, spicule; sb, subocular bar; sf, subocular fenestra; th, trabecular horns; ttm, taenia tecti marginalis; vmp, ventromedial process; I–IV, ceratobranchials. Scale bars 0.5 mm. Note the low muscular processes and the distinctive shape of suprarostal cartilage

at midlength by cartilaginous bar; corpus and ala articulated along entire margins; suprarostal alae with well-developed dorsal anterior processes (Figure 11c). In *Cycloramphus*, the processes are more pronounced and laterally expanded. Ethmoid region very long, with trabecular horns diverging far distally; horns with free portion short, narrowly divergent to almost parallel in *Cycloramphus*, with expanded distal margin; lateral trabecular process absent. Intertrabecular plate poorly chondrified medially. Basicranial fenestra weakly chondrified, mostly occluded by a thin membrane; carotid and craniopalatine foramina barely visible. Orbital cartilages not contacting otic capsules; dorsal margin of prootic foramen open. Optic and oculomotor foramina present. Frontoparietal fontanelle large, almost rectangular, wider posteriorly; bordered laterally by taenia tecti marginales, anteriorly by planum ethmoidale, posteriorly by tectum synoticum. Otic capsules rhomboid with a thin crista parotica and pointed anterolateral process. Jugulare and inferior perilymphatic foramina visible in ventral view.

Palatoquadrate C-shaped; articular process very short, wide, with anterior margin slightly sinuous. Quadratocranial commissure thinner than articular process, lacking quadratoethmoid and

pseudopterygoid processes. Muscular process triangular, low, thin; hyoquadrate process evident ventrally. Antorbital process weakly differentiated. Ascending process rod-like, thin, slightly curved and arranged perpendicular to sagittal axis, attaching at level of oculomotor foramen (intermediate attachment). Lower jaw (Figure 11c) with L-shaped Meckel's cartilages, orientation deeply oblique relative to main axis of chondrocranium; dorsomedial, ventromedial, and retroarticular processes robust. Infrarostral cartilages rectangular, curved, connected medially by connective tissue.

In the hyobranchial skeleton (Figure 11d), ceratohyals long, flat, thin, subtriangular. Anterior margin bearing tall, rounded anterior process and low, wide anterolateral process. Articular condyle poorly developed. Posterior process triangular, tall, very wide. Pars reuniens poorly chondrified, not joining ceratohyals. Basihyal present, elliptical. Basibranchial weak, narrow, independent of ceratohyals; urobranchial process small. Hypobranchial plates long, triangular, leaving a wide, U-shaped notch between them. Branchial basket with four curved ceratobranchials with numerous lateral projections. Ceratobranchial I continuous with hypobranchial plate,

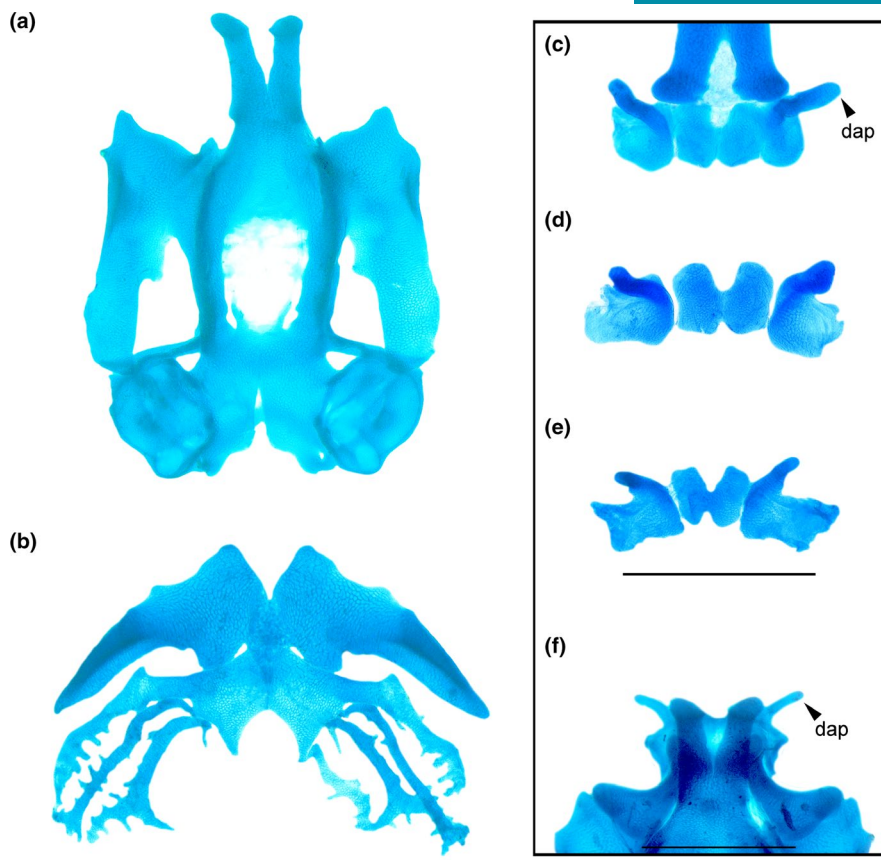


FIGURE 12 Skeletal morphology in cycloramphids. *Cycloramphus lithomimeticus* in (a) dorsal view of the neurocranium and (b) ventral view of the hyobranchial skeleton; right ceratobranchial IV was accidentally removed. (c) *Cycloramphus brasiliensis*, detail of the suprarostal cartilages articulated with trabecular horns in ventral view. Frontal views of suprarostal cartilages of (d) *C. brasiliensis* and (e) *C. lithomimeticus*. (f) *C. lithomimeticus*, detail of the rostral region showing the oblique arrangement of Meckel's cartilage. dap, dorsal anterior process. Scale bars 0.5 mm

bearing a tall, medially curved branchial process. Ceratobranchials II and IV fused to hypobranchial plate through a thin cartilaginous bridge; branchial process present at ceratobranchials II and III. Ceratobranchials joined distally by terminal commissures. Four long, curved spicules dorsally, the fourth one being wider and finger-like.

3.2.3 | Cranial muscles (Figures 13 and 14)

We identified 33 muscles in tadpoles of *Thoropa* and *Cycloramphus* (Table 3). Interhyoideus posterior present as a few loose fibers, continuous medially, originating near lateral edge of ceratohyal (Figures 13b,c and 14b,c). Diaphragmatopraecordalis continuous with interhyoideus posterior. Levator mandibulae externus with two slips (Figure 13a). Origins of levator mandibulae longus superficialis and profundus broadly overlapping. Levator mandibulae lateralis absent. Axial muscles covering dorsal area of otic capsule (Figure 14a).

We observed two remarkable conditions in tadpoles of *Thoropa* and *Cycloramphus*: (a) the subarcualis rectus I with two slips, one inserting on the dorsal ceratobranchial I and the other on an aponeurosis, in which fibers of the rectus abdominis anterior are also inserted (Figure 14d); and (b) the levator arcuum branchialium III with two

slips: one poorly developed and inserting on the distal ceratobranchial III and the second well developed, inserting on the peritoneum (Figure 14e,f). Additionally, the oblique musculature of the body wall is well developed in all species.

3.2.4 | Visceral components (Figure 15)

Gut long, coiled, concealing other organs, switchback point located laterally on the left side (Figure 15a,b). Lungs present, well developed, short, inflated in *C. boraceiensis*, *T. megatympnum*, and *T. miliaris* (Figure 15c), poorly developed, short, deflated in *T. petropolitana* and *T. taophora*.

4 | DISCUSSION

4.1 | Larval morphology and the systematics of Cycloramphidae

The phylogenetic hypotheses presented for Cycloramphidae differ substantially. For instance, Frost et al. (2006) recovered *Thoropa* as sister to dendrobatoids (i.e., Thoropidae + Dendrobatoidea)

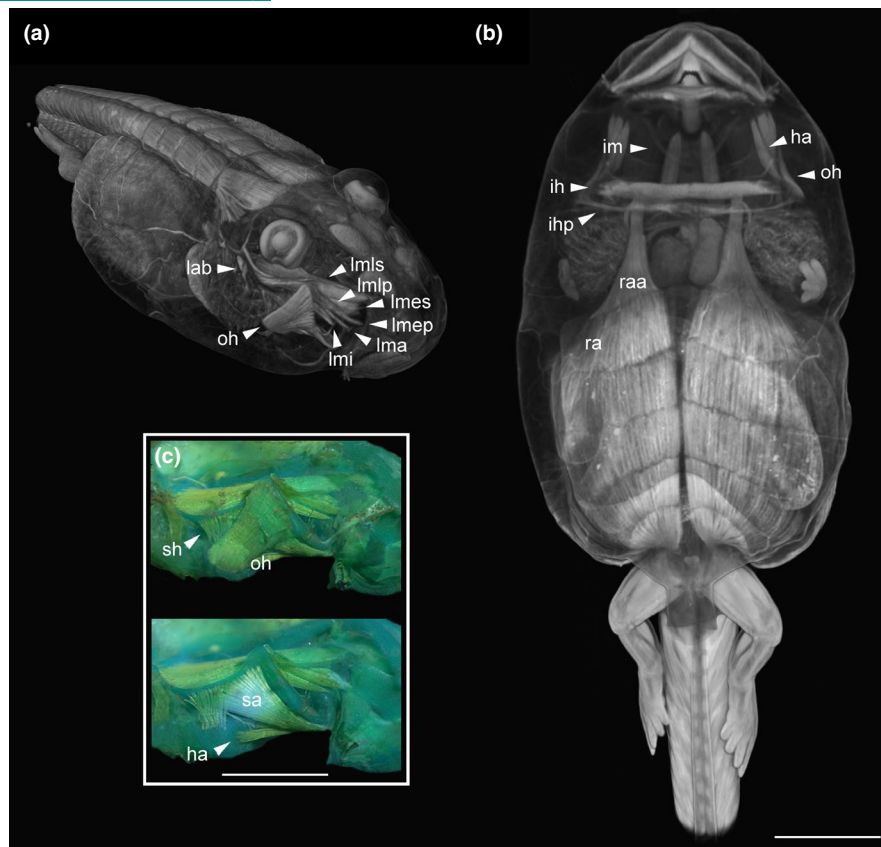


FIGURE 13 Cranial musculature of *Thoropa*. (a) Anterolateral view of the chondrocranium, showing levatores mandibulae muscles in *Thoropamegatympanum*. (b) Ventral view, showing superficial mandibular, hyoid and body muscles in *T. megatympanum*. (c) Detail of the hyoid and angular muscles in lateral view (for the sake of comparison, the original images have been reflected) in *Thoropamiliaris*. ha, hyoangularis; ih, interhyoideus; ihp, interhyoideus posterior; im, intermandibularis; lab, levator arcuum branchialium; lma, levator mandibulae articularis; lmp, levator mandibulae externus profundus; lmes, levator mandibulae externus superficialis; lmi, levator mandibulae internus; lmlp, levator mandibulae longus profundus; lms, levator mandibulae longus superficialis; oh, orbitohyoideus; ra, rectus abdominis; raa, rectus abdominis anterior; sa, suspensorioangularis; sh, suspensoriohyoideus. Scale bars 1 mm. Note the large size of the rectus abdominis

and *Cycloramphus* nested in a clade containing several lineages of Hyloides. Grant et al. (2006) did not recover *Thoropa* and *Cycloramphus* as sister taxa either; instead, *Thoropa* was recovered as sister to a large clade containing *Hylorina* Bell, 1843, *Eupsophus* Fitzinger, 1843, *Alsodes* Bell, 1843, *Limnomedusa* Fitzinger, 1843, *Proceratophrys* Miranda-Ribeiro, 1920, and *Odontophrynus* Reinhardt & Lütken, 1862, whereas *Cycloramphus* was the sister of *Rhinoderma darwinii* Duméril & Bibron, 1841. Later, Pyron and Wiens (2011) found *Thoropa* and *Cycloramphus* as sister taxa, and both sister to a clade containing Hyloidae + Alsodidae. Grant et al. (2017) found Cycloramphidae to be paraphyletic, with *Thoropa* as sister to Dendrobatoidea and *Cycloramphus* + *Zachaeus* as sister to Alsodidae + Hyloidae. Jetz and Pyron (2018) recovered *Thoropa* as sister to *Cycloramphus* + *Zachaeus* and this clade as sister to a clade containing Hyloidae, Batrachylidae, and Alsodidae. Sabbag et al. (2018) recovered Cycloramphidae as monophyletic—although *Zachaeus* was nested within *Cycloramphus* and *Thoropa* cf. *lutzi* was sister to *Cycloramphus* + *Zachaeus*—and sister to Alsodidae + Hyloidae. de Sá et al. (2019) recovered *Cycloramphus* and *Thoropa* as sister taxa with *Zachaeus* nested within *Cycloramphus*. Recently, Hime et al. (2020) found Cycloramphidae to be sister of a

clade composed by Hyloidae + (Alsodidae + Batrachylidae). Most of these studies employed only DNA evidence and treated insertions and deletions as nucleotides of unknown identity, with few exceptions (e.g., Grant et al., 2017), and all available hypotheses are based on poor taxonomic sampling that does not encompass the diversity of Cycloramphidae. Although a large-scale phylogenetic analysis is beyond the scope of this manuscript, we discuss the putative impact of larval morphology in the systematics of the family.

Our observations of tadpole morphology provide additional support for the monophyly of Cycloramphidae. Specifically, tadpoles of *Cycloramphus* and *Thoropa* share the following character-states that we propose as new synapomorphies for the family (Figure 16 and Figure S1): (a) jaw sheaths laterally compressed; (b) posterolateral portion of body integument expanded into an abdominal flap; (c) dorsal fin reduced; (d) ventral fin reduced; (e) dorsal fin originating on the tail; (f) eye meniscus present; (g) second slip of the levator arcuum branchialium III inserting on the peritoneum; (h) rectus abdominis anterior present, (i) inserting on a thin aponeurosis; (j) ventral slip of the subarcualis rectus I attached to a thin aponeurosis common with that of the rectus abdominis anterior (k) axial musculature reaching far anterior on the dorsal aspect of otic capsules; (l) suprarostal corpora fused

TABLE 3 Larval musculature in cycloramphids

Muscle	Insertions
Mandibular group, n. trigeminus (c.n. V)	
Levator mandibulae longus superficialis	External posterior margin of subocular bar and ascending process—dorsomedial surface of Meckel's cartilage. Via a long tendon
Levator mandibulae longus profundus	External margin of subocular bar and ventromedial area of ascending process—external margin of the suprarostal ala. Via a log tendon
Levator mandibulae externus superficialis	Inner, dorsal surface of muscular process—anterodorsal surface of Meckel's cartilage
Levator mandibulae externus profundus	Inner, middle surface of muscular process—suprarostal ala. It shares a tendon with levator mandibulae longus profundus
Levator mandibulae articularis	Inner, ventral surface of muscular process—dorsal surface of Meckel's cartilage
Levator mandibulae internus	Ascending process—lateral edge of Meckel's cartilage
Intermandibularis	Median aponeurosis—ventromedial surface of Meckel's cartilage
Mandibulolabialis	Lower lip—ventromedial surface of Meckel's cartilage
Hyoid group, n. facialis (c.n. VII)	
Hyoangularis	Anterodorsal, lateral edge of ceratohyal—retroarticular process of Meckel's cartilage
Quadratoangularis	Ventral area of palatoquadrate—retroarticular process of Meckel's cartilage
Suspensorioangularis	Posterior margin of muscular process—retroarticular process of Meckel's cartilage
Orbitohyoideus	Anterior and dorsal margins of muscular process—lateral edge of ceratohyal
Suspensoriohyoideus	Posterior margin of muscular process and subocular bar—lateral edge of ceratohyal. Fibers mostly parallel
Interhyoideus	Median aponeurosis—ventral surface of lateral edge of ceratohyal
Branchial group, n. glossopharyngeus (c.n. IX) and vagus (c.n. X)	
Levator arcuum branchialium I	Subocular bar—ceratobranchial I
Levator arcuum branchialium II	Subocular bar—ceratobranchial and terminal commissure II
Levator arcuum branchialium III	Lateral aspect of otic capsule—ceratobranchial III and peritoneum. Formed of two slips, the anterior with loose fibers, the posterior thick
Levator arcuum branchialium IV	Posterolateral aspect of otic capsule—ceratobranchial IV
Tympanopharyngeus	Posterolateral aspect of otic capsule—ceratobranchial IV and pericardium anterior to glottis
Dilatator laryngis	Posterior aspect of otic capsule—arytenoid cartilage
Constrictor branchialis II	Branchial process II—commissura terminalis I. It runs on the inner margin of ceratobranchial I
Constrictor branchialis III	Branchial process II—commissura terminalis II. It runs on inner margin of ceratobranchial II
Constrictor branchialis IV	Ceratobranchial III—commissura terminalis II. It runs on the inner margin of ceratobranchial III
Subarcualis rectus I	Base of posterior process of ceratohyal—ceratobranchial I and aponeurosis common with the rectus abdominis anterior. It includes two slips, the dorsal thin, and the ventral very thick and longer
Subarcualis rectus II-IV	Ceratobranchial IV—ceratobranchial I. It crosses the ceratobranchial III ventrally
Subarcualis obliquus II	Urobranchial process—branchial process II
Diaphragmatobranchialis	Peritoneum—distal point of ceratobranchial III
Spinal group, spinal nerve innervation	
Geniohyoideus	Hypobranchial plate and ceratobranchial III—infraorostal cartilage. It attaches at the level of ceratobranchial II and III, via tendon
Rectus abdominis	Peritoneum (diaphragm)—pelvic girdle. It is formed of six open myotomes of similar lengths
Rectus abdominis anterior	Peritoneum, aligned with m. rectus abdominis—aponeurosis shared with the m. subarcualis rectus I
Rectus cervicis	Peritoneum—ceratobranchial III. Some loose fibers appear to insert near ceratobranchial III
Interhyoideus posterior	Continuous fibers join ventrally the lateral edges of ceratohyals
Diaphragmatopraecordialis	Loose fibers surrounding the branchial chamber

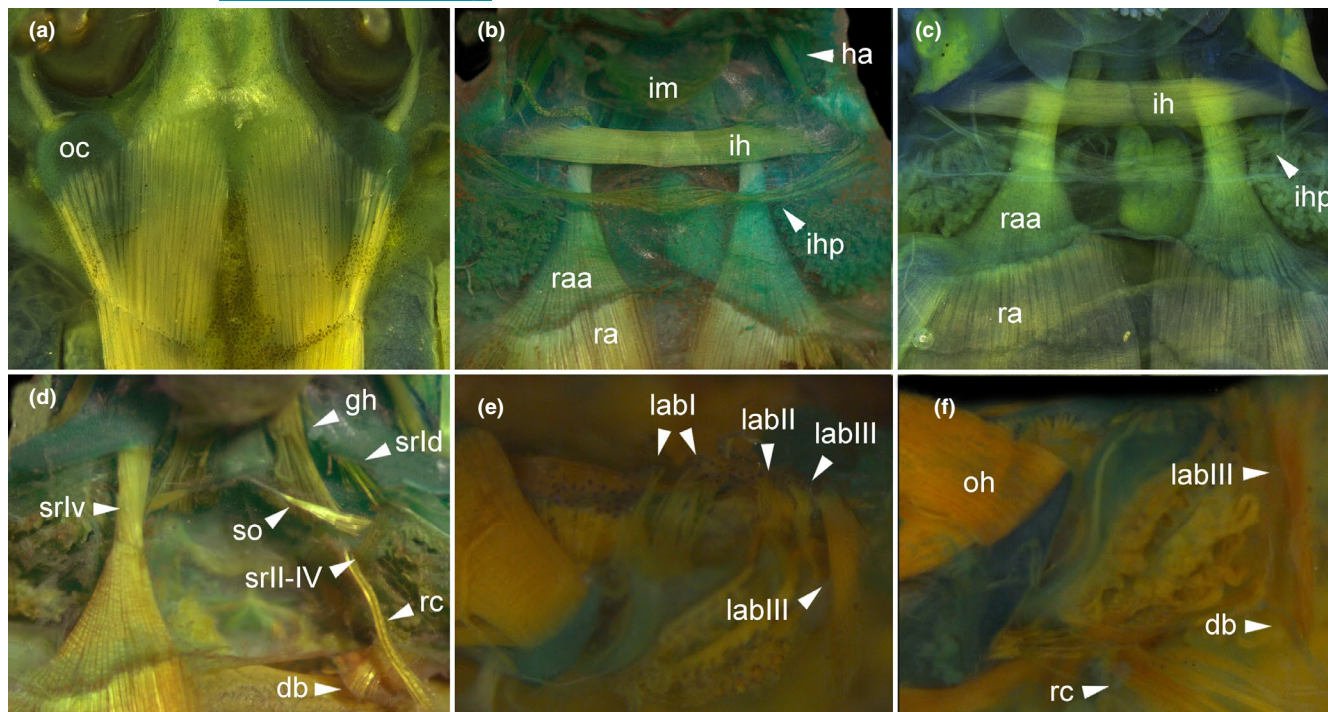


FIGURE 14 Details of muscles in *Thoropa* and *Cycloramphus*. (a) Dorsal tail musculature reaching the otic capsules in *Thoropasaxatilis*. (b, c) Ventral views showing the interhyoidei muscles in *Thoropamiliaris* and *Cycloramphuslithomimeticus*. (d) Ventral view showing subarcualis muscles in *T. miliaris*. (e, f) Lateral views showing levatores arcuum branchialium muscles in *T. miliaris* and *Cycloramphuslutzorum*. db, diaphragmatobranchialis; gh, geniohyoideus; ha, hyoangularis; ih, interhyoideus; ihp, interhyoideus posterior; im, intermandibularis; labI-III, levator arcuum branchialis I-III; oc, otic capsule; oh, orbitohyoideus; ra, rectus abdominis; raa, rectus abdominis anterior; rc, rectus cervicis; srlv, subarcualis rectus I ventral slip; srlI-IV, subarcualis rectus II-IV; so, subarcualis obliquus. Figures not to scale. Note the distinctive arrangement of the rectus abdominis anterior inserted on the ventral slip of subarcualis rectus I, and the two slips of the levator arcuum branchialium III

medially; and (m) secretory ridges of branchial food traps absent. Additionally, all tadpoles of *Thoropa* have a ventral fin modified into a groove, which we hypothesize to be a synapomorphy for the genus.

These characters are unique to Cycloramphidae among potential close relatives (some are convergently shared with other semiterrestrial tadpoles; see discussion below). Others are observed in distant related taxa. For instance, reduced tail fins have been reported in several species (e.g., *Gephyromantis sculpturatus* (Ahl, 1929), Mantellidae; Randrianiaina et al., 2011), and secretory ridges are absent in several macrophagous (e.g., *Dendropsophus decipiens* (Lutz, 1925), Hylidae; Dias et al., 2019), arboreal (e.g., *Tripurion spinosus* (Steindachner, 1864), Hylidae; Wassersug & Rosenberg, 1979), and endotrophic (e.g., *R. darwini*, Rhinodermatidae; Wassersug & Heyer, 1988) larvae. Some characters also deserve future investigation, such as the presence of the interhyoideus posterior; Haas (2003) hypothesized that its absence is synapomorphic for anurans, but he also reported its presence in several clades, (e.g., hylids, odontophrynids, some dendrobatids). We also observed the interhyoideus posterior in hylodids, but the lack of data for other taxa prevents us from further discussion.

Recently, several studies have demonstrated the disproportionate impact of phenotypic characters in phylogenetic analyses of predominantly molecular datasets, changing topologies and increasing or decreasing the relative branch support of multiple clades, (e.g., Cabra-García & Hormiga, 2020; de Sá et al., 2014; Sánchez-Pacheco

et al., 2018). We predict that the inclusion of phenotypic characters from larval morphology in a total evidence analysis of Cycloramphidae will impact the systematics of the group and support the monophyly of the family.

4.2 | Functional morphology of cycloramphid tadpoles

Thoropa and *Cycloramphus* larvae exhibit a number of apomorphic character-states that appear to be causally related to semiterrestriality. The modification of the posterolateral surface of the body to form a flattened integumentary expansion appears to play a role in adhering the body to the substrate. Wassersug and Heyer (1983) suggested that surface tension (capillarity) is key to enabling these tadpoles to adhere to rock surfaces. Surface tension increases with the greater area in contact with the rock surface provided by this abdominal flap. In *Thoropa*, surface tension is further increased by the modification of the ventral fin to form a groove that greatly increases the area of contact between the tadpole and the substrate (Movie S1). Lutz (1929) observed that *Cycloramphus* tadpoles, which lack this fin groove, adhere to vertical walls without using their tails, which are apparently only involved in propulsion (see also Verdade et al., 2019). Some authors (e.g., Barth, 1956; Bokermann, 1965) have suggested that the

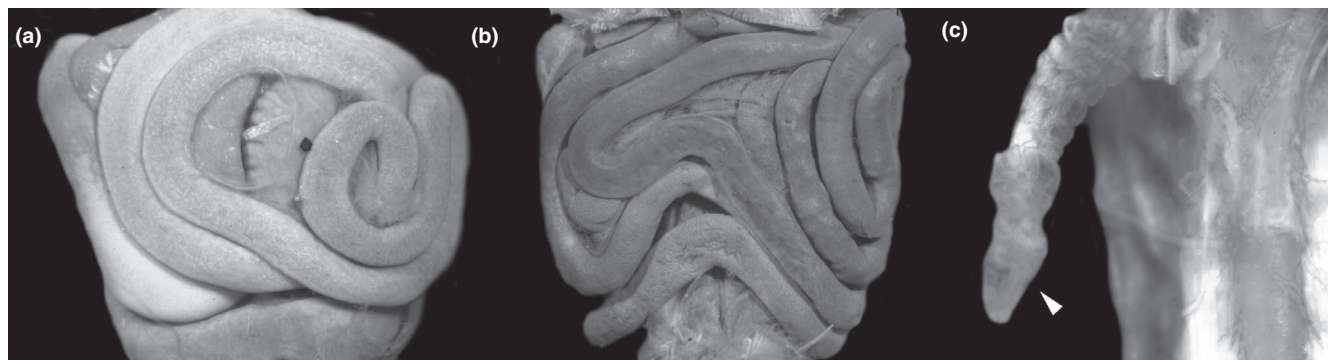


FIGURE 15 Soft anatomy of larval cycloramphids. Coiled guts of (a) *Cycloramphus boraceiensis* and (b) *Thoropa taophora*. (c) Right lung of *Thoropamiliaris*. Figures not to scale. Note the gut switchback point typically placed at the left of the abdominal cavity, and the inflated lung of *T. miliaris*

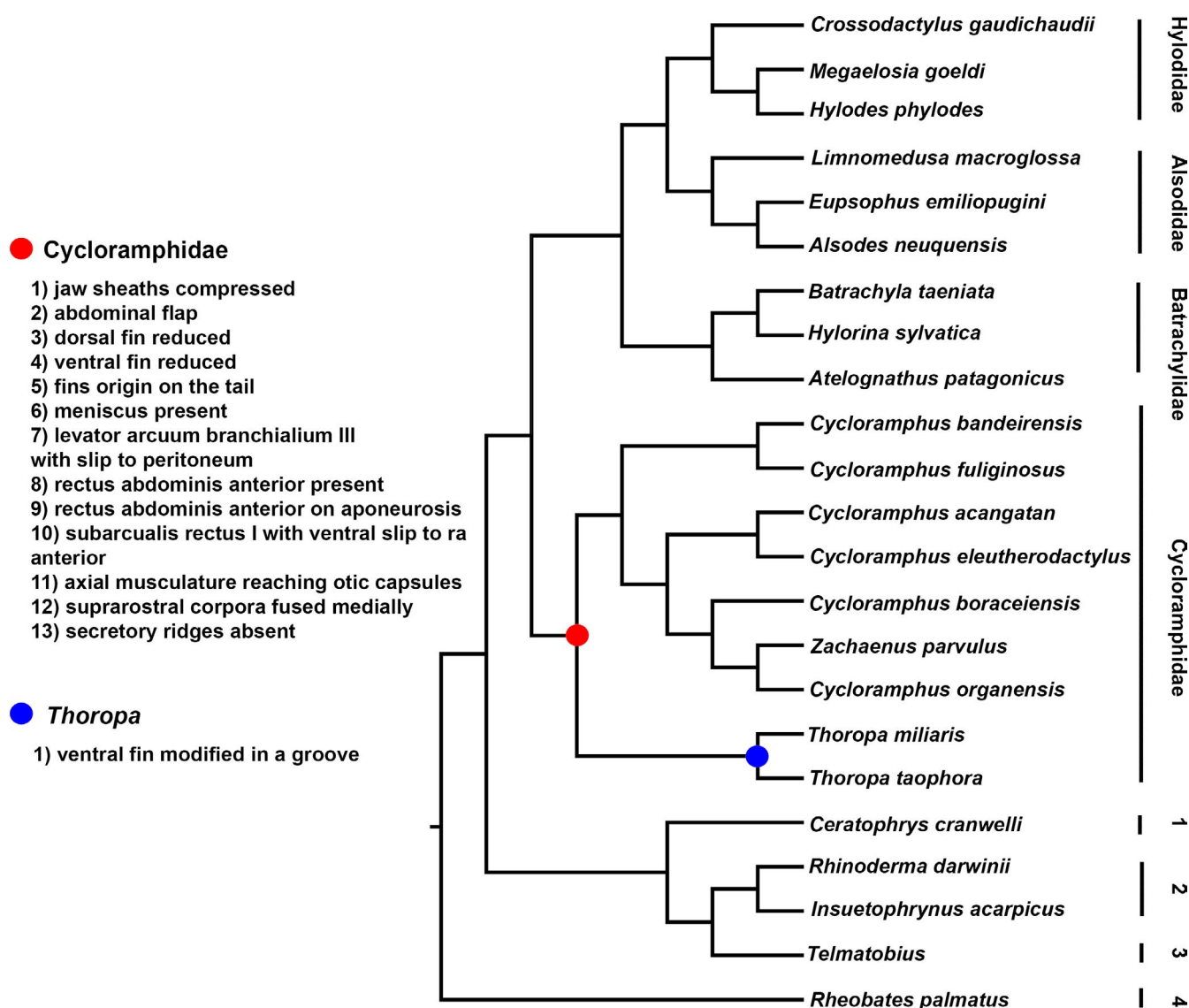


FIGURE 16 The phylogenetic hypothesis of Jetz and Pyron (2018) for Cycloramphidae showing newly proposed larval synapomorphies for the family. 1 = Ceratophryidae; 2 = Rhinodermatidae; 3 = Telmatobiidae; 4 = Aromobatidae



FIGURE 17 Live *Thoropa saxatilis* tadpole placed on a vertical glass surface in (a) lateral and (b–e) ventral views. Note the expansion of the abdominal flaps lateral to the white pigmentation in (b) and the usage of the mouth and legs for movement in (c, e)

oral disc and the well-developed jaw sheaths might be involved in hooking these tadpoles to the rocks. Recently, Verdade et al. (2019) reported that the larvae of *Cycloramphus bandeirensis* “moved across the wet surfaces of the rocks by affixing their mouth to the rock and then pulling the body forward by abdominal muscular contraction.” Similarly, field observations (G. Colaço, pers. comm.) indicate that the oral apparatus, tail, and abdominal flap, are involved in anchoring the tadpole of *T. miliaris* to the substrate. Tadpoles of *T. saxatilis* use their mouths to anchor their bodies and to aid in locomotion. Additionally, they employ alternating movements of the legs and abdominal muscular contraction (Figure 17; Movie S1).

In addition to external morphology, several internal anatomical features are likely related to life and locomotion in rocky environments. The rectus abdominis anterior is present in all cycloramphids examined. This muscle is rare among anuran larvae. Muscles with similar arrangements have been reported in some lineages, including *Ascaphus* (Gradwell, 1973), *Boophis* Tschudi, 1838, *Hyloscirtus* Peters, 1882, *Ranoidea* Tschudi, 1838 (Haas & Richards, 1998), *Leptobranchella* Smith, 1925 (Haas et al., 2006), *Occidozyga* Kuhl & Van Hasselt, 1822 (Haas et al., 2014), *Otophryne* Boulenger, 1900 (Wassersug & Pyburn, 1987), and *Telmatobius* Wiegmann, 1834 (Vera Candioti, 2008). We also confirm its presence in Hylodidae and some bufonids and mantellids (P.H.S. Dias, unpubl. data). In the aforementioned species, the muscle is a thin band of fibers that

originate near the medial fibers of the rectus abdominis and extends rostrad, usually to insert on the anteroventral palatoquadrate via a very long tendon. In contrast, in cycloramphids, this muscle is a discrete, thick slip of fibers that originate along the whole width of the rectus abdominis and converge to insert on the ventral slip of the subarcualis rectus I, in a condition that is unknown in any other anuran larvae. In tadpoles of *Ascaphus*, Gradwell (1973) suggested that the rectus abdominis anterior could pull the body toward the substrate after adhesion by the oral disc. It is likely that in cycloramphids the subarcualis rectus I assumes a comparable function by being the effective skeletal insertion of fibers of the rectus abdominis anterior.

The configuration of the levator arcuum branchialium III is another remarkable feature of cycloramphid tadpoles. The thick caudal slip is attached to the peritoneum, instead of the distal edge of ceratobranchials, as it is in most other described larvae. Further, the insertion is well ventral and slightly caudal to the level of the occipital region and close to the attachments of rectus cervicis, rectus abdominis, and diaphragmatobranchialis. A muscle with a comparable disposition was described by Haas et al. (2006) and Haas et al. (2014) in *Occidozyga* and *Leptobranchella* but interpreted as the diaphragmatobranchialis. Based on anatomical evidence and direct observations, Haas et al. (2006) showed that fossorial tadpoles of *Leptobranchella mjobergi* are capable of bending the body at a sagittal plane, and that bending can occur at the atlanto-occipital joint. The

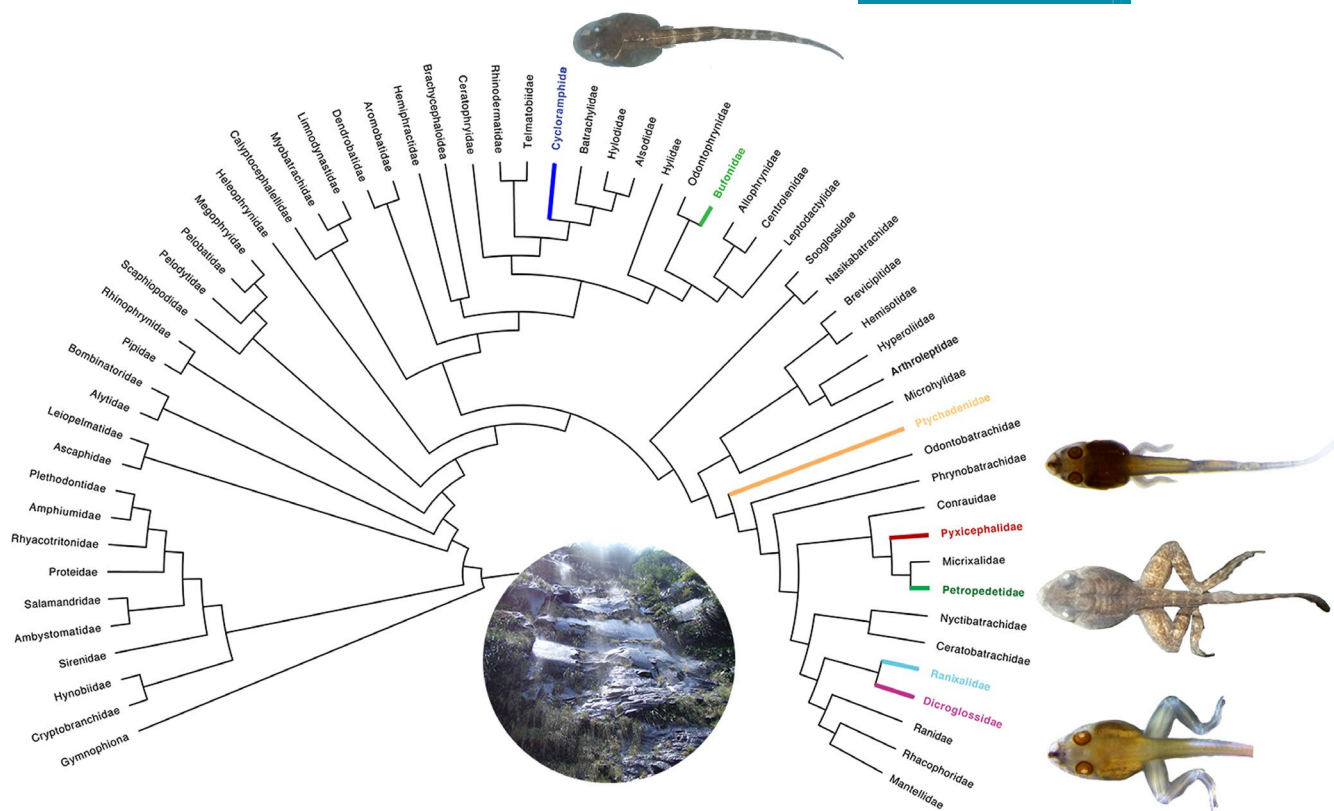


FIGURE 18 The phylogenetic hypothesis of Jetz and Pyron (2018) showing the families in which semiterrestrial tadpoles have evolved



FIGURE 19 Morphology of other semiterrestrial tadpoles. Dorsal views and details of the oral disc in two ranoid families. Petropedetidae: (a) *Petropedetes perreti*. (b) *Arthroleptides martiensseni*. Ranixalidae: (c) *Indirana beddomi*. Note the oral discs similar to those of cycloramphid tadpoles

resemblance of the arrangement of dorsal axial musculature, and of ventral recti abdominis and cervicis, and diaphragmatobranchialis/levator arcuum branchialium III in *Leptobranchella* and cycloramphids, leads us to suspect that dorsal extension and ventral flexion of the head are achieved similarly in both groups. Similar to the burrowing movements as in *Leptobranchella*, head maneuverability might be necessary to achieve the jumping and tail-flipping locomotion described for cycloramphid and other semiterrestrial larvae (Barej et al., 2010; Gopalan et al., 2012; Hoff et al., 1999; Veeranagoudar et al., 2009; G. Colaço, pers. comm.).

Wassersug and Heyer (1983) hypothesized that both *Cycloramphus* and *Thoropa* are obligate air breathers. Lutz (1929:20) asserted that *Cycloramphus* tadpoles “cannot stay in the water unless they emerge at least with the anterior part of their body,” and Bokermann (1965:527; free translation from the Portuguese) reported that *Thoropa* tadpoles “placed in water, they are clumsy and can only move around by clinging to some support point,” supporting the air-breathing hypothesis. We observed reduced and shrunken lungs in *T. megatympanum* and small and inflated lungs in *T. miliaris*, suggesting that lungs do not play an important role in gas exchange for either species. On the other hand, branchial filaments are present in the branchial baskets of cycloramphid tadpoles examined, but the greatly reduced spiracle suggests poor irrigation of gills within the branchial chamber—contra Barth (1956:490), who suggested that *Thoropa* tadpoles would breathe through strong branchial filaments. This morphology is compatible with ecological data showing that most cycloramphid larvae live in saxicolous environments with (sometimes very) limited water volume (e.g., Movie S1). According to Noble (1929), the long tail in tadpoles of *Cycloramphus* might perform an important role in respiration, and Verdade et al. (2019) suggested that the expanded abdominal flap might also play an important role in gas exchange. Thus, it is likely that most gas exchange in cycloramphid tadpoles occurs through the skin or through combined skin and lung respiration, with branchial respiration being negligible or absent.

Feeding habits of semiterrestrial tadpoles are as interesting as the adhesion mechanism and gas exchange, given that filter-feeding is unlikely in semiterrestrial environments. The semiterrestrial tadpoles of Cycloramphidae have well-developed, fully keratinized, compressed, massive jaw sheaths powered by robust jaw levator muscles, suggesting a role in macrophagous diets. Similarly, the buccopharyngeal cavity presents an overall reduction in papillae and secretory surfaces. Wassersug and Heyer (1983) reported mineral grains, algal filaments, and part of an arthropod exoskeleton in the guts of *T. petropolitana* and asserted that branchial food trap morphology seems to preclude planktonic suspension feeding. Barth (1956) reported diatoms, pteridophytes, spores, vegetal matter, and rests of small arthropods in the digestive tract of *T. miliaris*. Interestingly, similar feeding habits have been reported in other semiterrestrial tadpoles. Gut content of the tadpoles of *Indirana leithii* (Boulenger, 1888) presented filamentous algae and diatoms (Modak et al., 2018), and Wickramasinghe et al. (2007) found microflora, microfauna, detritus, and mineral particles in the tract of tadpoles of *N. ceylonensis*, as well as conspecific eggs and tadpoles.

4.3 | Adaptation for semiterrestrial life? Convergent evolution in semiterrestrial tadpoles

As noted above, semiterrestrial tadpoles are known in Bufonidae, Cycloramphidae, Dicroglossidae, Petropedetidae, Ranixalidae, Ptychadenidae, and Pyxicephalidae. In all seven lineages, they evolved from typical pond or stream dwellers ancestors (Figure 18), and, as early noted by Drewes et al. (1989), converged to very similar phenotypes (Figure 19). Among the material we examined, larvae of *A. martiensseni*, *I. beddomi*, *P. perreti*, and *P. vulpiae* have oval, elongated bodies; long tails with reduced tail fins; massive, fully keratinized, compressed jaw sheaths; poorly developed spiracle; large, dorsal eyes; long, coiled guts concealing other organs; and long, well-developed, muscular hind limbs. Most of these character-states (with exception of those from internal morphology ones, for which there is a dearth of information) have also been reported in the literature (e.g., Barej et al., 2010; Drewes et al., 1989; Gopalan et al., 2012). Moreover, the tadpoles of *P. perreti* also possess a short, poorly developed muscular process and strong, well-developed axial muscles covering the otic capsules dorsally; an additional slip of the levator arcuum branchialium III inserting on the peritoneum, and secretory ridges absent (P.H.S. Dias, unpubl. data).

The presence of homoplastic character-states in all semiterrestrial tadpoles of unrelated phylogenetic lineages seems to suggest that these character-states might be adaptations for semiterrestriality. Although adaptation can be difficult to test (Kluge, 2005), the correlation between transformation series ($A \rightarrow A'$) and transformation in the ecological aspects ($\alpha \rightarrow \alpha'$) provides a strong framework for more rigorous studies in the future (Losos, 2011).

5 | CONCLUSIONS

This study provides the hitherto most comprehensive account of semiterrestrial tadpole morphology. We described several new characters, proposed 13 new phenotypic synapomorphies for Cycloramphidae, and discussed the function and the evolution of these remarkable morphologies. Nevertheless, data are restricted to only part of Cycloramphidae, and species representing the *C. bolitoglossus* and *C. eleutherodactylus* groups and *Zachanenus*, which possess endotrophic, nidicolous tadpoles (Heyer, 1983a, 1983b; Heyer & Crombie, 1979), still need to be studied in detail. Additionally, data on the internal morphology of other semiterrestrial tadpoles are almost non-existent, and further research is necessary to understand the extent of the convergence among these lineages.

The importance of larval morphology to understand evolution and diversification of anurans has been recognized for a long time (e.g., Boulenger, 1892; Dias et al., 2013, 2021; Haas, 1995, 2003; Lataste, 1879; Noble, 1929; Orton, 1953), but we are far from fully understanding larval diversity. In the last 20 years, as more species were studied, several new, highly modified larval character-states have been described (e.g., Dias, 2020; Dias et al., 2019, 2021; Gan et al., 2015; Haas et al., 2006, 2014; Peixoto et al., 2003; Rada et al., 2019; Rowley et al., 2012; Vera Candioti et al., 2017; Zachariah et al., 2012). Our study provides

another example of how poorly studied groups can present novel and peculiar characters. The configuration in cycloramphid tadpoles of the muscles levator arcuum branchialium, subarcualis rectus I, and the morphology of the rectus abdominis anterior are unique among all anurans tadpoles. Larval morphology is an exciting field, and we predict that further research on poorly known groups will reveal novel phenotypes, synapomorphies, and complex evolutionary histories.

Note: Subsequent to the acceptance of our article, Dubois and colleagues (2021; Megataxa, 1, 1–738) transferred *Zachaeus* into the synonymy of *Cycloramphus*.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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

Data S1. Character definition and optimization.

Data S2. Character matrix in .tnt format.

Figure S1. Figure showing characters optimization onto Jetz and Pyron (2018) (A) and Sabbag et al. (2018) phylogenetic hypotheses, showing character-state transformations.

Movie S1. Movie of live *Thoropa saxatilis* tadpoles.

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