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Larval morphology of *Discoglossus scovazzi* (Amphibia: Anura: Alytidae) and its phylogenetic implications

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Abstract. *Discoglossus scovazzi*, an endemic North African species within Alytidae, has long been understudied in terms of its larval morphology. This work presents a comprehensive description of its tadpole (Gosner stages 20–28), based on 52 specimens reared under controlled laboratory conditions. We document the external morphology, coloration, and cranial and hyobranchial musculature using high-resolution imaging and histological data. The tadpole exhibits an elliptical body shape, an anteroventrally directed oral disc with a labial tooth row formula of 2/3(1), and distinct pigmentation patterns. Muscle reconstructions revealed 34 cranial and branchial muscles, including the presence of the m. tympanopharyngeus, a newly reported autapomorphy. Through phylogenetic optimization, we identify five synapomorphies supporting the Costata clade, and three autapomorphies unique to *D. scovazzi*. These findings not only refine the morphological diagnosis of *D. scovazzi* but also enhance our understanding of character evolution within basal anurans. The inclusion of this species broadens the morphological dataset for Alytidae and underlines the importance of larval characters in phylogenetic inference. Our results underscore the need for further research on larval morphology across understudied taxa to illuminate early anuran diversification.

Key words. Morphology, musculature, development, phylogeny, synapomorphy, tadpole.

Introduction

Alytidae Fitzinger, 1843 is the sister taxon to Bombinatoridae Gray, 1829, and both form a clade called Costata (suborder), whose members are thought to retain plesiomorphic traits within anurans. Alytidae comprises 12 species (Frost 2024) belonging to two distinct monotypic subfamilies: the Alytinae and the Discoglossinae (Blackburn & Wake 2011, Zhang et al. 2013). The genus *Discoglossus* Otth, 1837 comprises five species, which are all primarily distributed across the eastern Mediterranean region (Garcia-Paris & Jockusch 1999, Frost 2024).

The phylogeny and distribution of the genus *Discoglossus* have been the subject of extensive investigation and revision over the past decades (see, for example, Lanza et al. 1984, 1986, Martínez-Solano 2004, Real et al. 2005, Pabijan et al. 2012, Vences et al. 2014). The molecular data indicate that *D. montalentii* Lanza, Nascetti, Capula & Bullini, 1984 is the most basal taxon, while *D. sardus* Tschudi, 1837 and *D. pictus* Otth, 1837 and in addition, *D. scovazzi* Camerano, 1878 and *D. galganoi* Capula, Nascetti, Lanza, Bullini & Crespo, 1985 are identified as the respective sister taxa (Pabijan et al. 2012). The Moroccan painted frog, *D. scovazzi*, is distributed in north Africa, specifically to the west of the Moulouya River, which acts as a significant geographical barrier, dividing the west and east Maghreb region (Velo-Antón et al. 2008). The misinterpretation of *D. scovazzi* as a subspecies of *D. pictus* has resulted in a lack of precision and completeness in the available information regarding the exact habitat and distribution of *D. scovazzi*. It is therefore necessary to undertake a critical revision in order to separate the information on both species, which were summarized under the name *D. pictus*, and to assign them to the respective species (Vences et al. 2014).

This study seeks to contribute to the existing knowledge about the larval morphology of *D. scovazzi*, which is, to date, poorly unknown. This tadpole was previously illustrated by Beukema et al. (2013) and briefly described by Escoriza & Ben Hassine (2019). Herein, we describe important aspects of the external morphology, provide new data on the musculature, and presents potential synapomorphies at different levels within Costata, which contribute to a more detailed understanding of this fascinating species.

Material and methods

Husbandry and staging

Fertilized eggs of *Discoglossus scovazzi* were obtained from a private breeder. Approximately 20 eggs per petri dish were cultured in 0.1x modified Barth's salt solution and maintained at temperatures between 18 and 25 °C. Specific stages were collected every two hours. Anesthesia was administered using 1% tricaine methanesulfonate (MS-222) in accordance with the animal welfare protocols of the Friedrich Schiller University of Jena. The specimens were then fixed in 4% phosphate-buffered formalin (PFA). All specimens were staged according to the simplified staging table introduced by Gosner (1960), and these stages were labelled as 'Go stages'. A developmental series between Go 20 and Go 28 with a total of 52 specimens was used as baseline for the morphological description in this study. Fixed larvae were preserved in 70% ethanol and stored at the Institute of Zoology and Evolutionary Research, Friedrich Schiller University, Jena, Germany. Histological data from a previous study (Lukas & Ziermann 2022) was used for the description of the musculature.

Image acquisition and procession

Photographs of the whole tadpoles were developed in Adobe Lightroom classic (version 11.5) (Adobe, San Jose, USA), single images denoised (option: standard) with Topaz DeNoize AI (Topaz Labs, Dallas, USA) and merged with Zerene Stacker 1.04 (Zerene System LLC, Richland, USA). Photographs of whole tadpoles were taken with a Canon EOS R5 (Canon, Krefeld, Germany) equipped with a Canon MP-E 65 mm f/2.8 1–5× Macro Photo Objective. (Canon, Krefeld, Germany). Stack shots were realized with a StackShot macrorail (Cognisys, Traverse City, MI, USA) and Zerene Stacker (Zerene Systems LLC, Richland, WA, USA). For stable positioning the different stages of tadpoles were placed in Balea Hygiene Handgel (Dalli GmbH & Co. KG, Stolberg [Rhld.], Nordrhein-Westfalen) (septigel) within a petri dish (Weingardt et al. 2023), and a cover slip on top. Even illumination was achieved by covering the whole petri dish with a plastic dome (Rayher, Laupheim, Germany), which was ground with abrasive paper (Starcke, Melle, Germany) and colored with white (RAL 9010) spray paint (Maston, Veikkola, Finland). Specimens were illuminated with two flashlights (Phottix Juno Li60 Flash, New York, USA) controlled with two Yongnuo RF603C II wireless triggers (Yongnou, Shenzen, China). All samples photographed were placed on a glass plate that was staged on four snap lid jars with silicone and gray paper underneath to get an evenly blurred gray background. All images were edited (cropping, white balance, sharpening filter) and arranged using Adobe Photoshop 2024 and Adobe Illustrator 2024 (Adobe Inc.)

Character evolution

We used the character matrix of Haas (2003) and scored characters of the external morphology (this study), and musculoskeletal system (this study; Lukas & Ziemann 2022). The matrix was edited in Mesquite V. 3.51 (Maddison & Maddison 2018) and optimized under parsimony (Fitch 1971) into the phylogenetic hypothesis of Portik et al. (2023), pruned to represent the relationships of Costata,

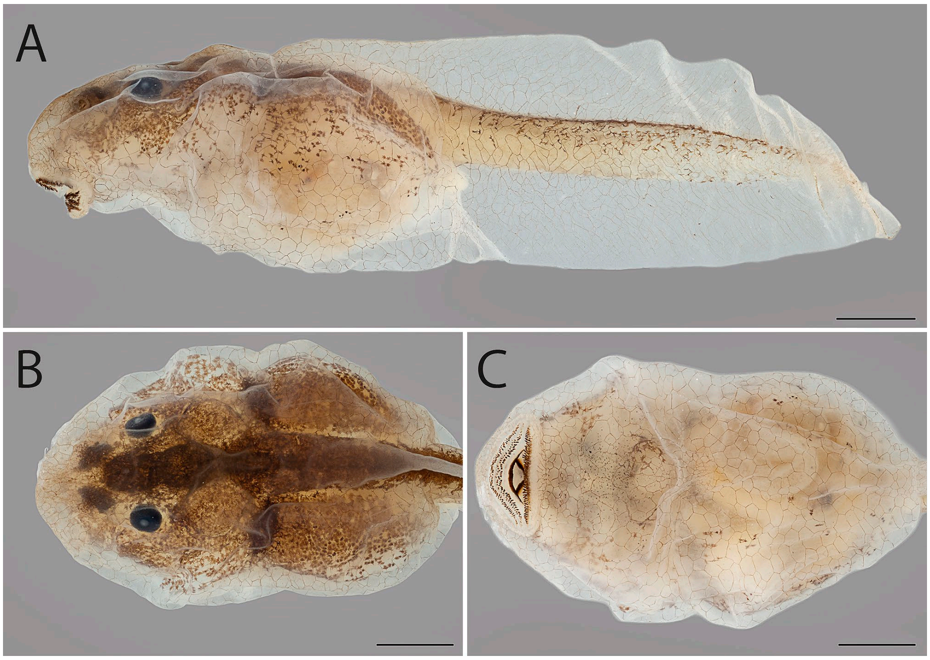

Figure 1. Tadpole of *Discoglossus scovazzi*, stage 28 Go, in (A) lateral, (B) dorsal and (C) ventral view. Scale bar is 1 mm.

using T.N.T. 1.6 (Goloboff & Morales 2023). Additionally, we kept the representatives of Anomocoela (Scaphiopodidae Pelodytidae Pelobatidae Megophryidae) and Xonoanura (Pipidae and Rhinophrynidae), immediately less inclusive clades to Costata, as well as *Ascaphus truei* (Ascaphidae) and the salamander *Ambystoma mexicanum*, to optimize the characters. We treated non-ambiguous optimized characters as putative synapomorphies. To depict the optimizations, we used the script 'wincladtree', as described by Goloboff (2024). The character list, character matrix, and complete list of synapomorphies are listed in Supplementary document S1.

Results

Tadpole description

Body elliptical in dorsal and lateral views (Fig. 1). Snout rounded in dorsal view, sloped in lateral view. Nostrils positioned dorsolaterally, elliptical, with a marginal rim (Fig. 2C). Eyes dorsolateral. Spiracle single, medial, ventral, short (Fig. 2B). Digestive tract coiled; switchback point ventrally located. Vent tube dextral, tubular, short, fully attached to the ventral fin (Fig. 2D). Tail fins slightly higher than body; tail muscle almost reaching tail tip; tail tip acute. Dorsal and ventral fins arch-shaped, about the same height, higher portions between the middle and posterior thirds of the tail. Dorsal fin originating on the posterior third of the body. Oral disc positioned and directed anteroventrally, laterally emarginate; a single row of conical, marginal papillae; small diastema present in the upper lip; submarginal papillae absent (Fig. 2A). Labial tooth row formula (LTRF) 2/3(1); double lines of teeth per row; A1 and A2 length subequal; P2 and P3 length subequal, slightly longer than P1. Jaw sheaths present, serrate, keratinized; upper jaw sheath arch-shaped; lower jaw sheath V-shaped.

Color of the tadpole in preservative: Skin translucent. Dorsolateral body parts light brown, medially above the brain and the tail dark brown, dark brown spots around the nostrils and behind the otic capsules, snout fawnish. From dorsal to ventral a gradually fading from light brown to light fawn. Single spots of dark melanophores ventrally. Tail fins translucent, with light brown line forming a reticulated pattern.

Musculature: The skeletal morphology of this tadpole has been described by Lukas & Ziermann (2022). The patterns of muscles origin and insertions are based on the cranium and hyobranchial apparatus described by those authors. We observed 34 muscles in the larvae of *Discoglossus scovazzi* (Table 1).

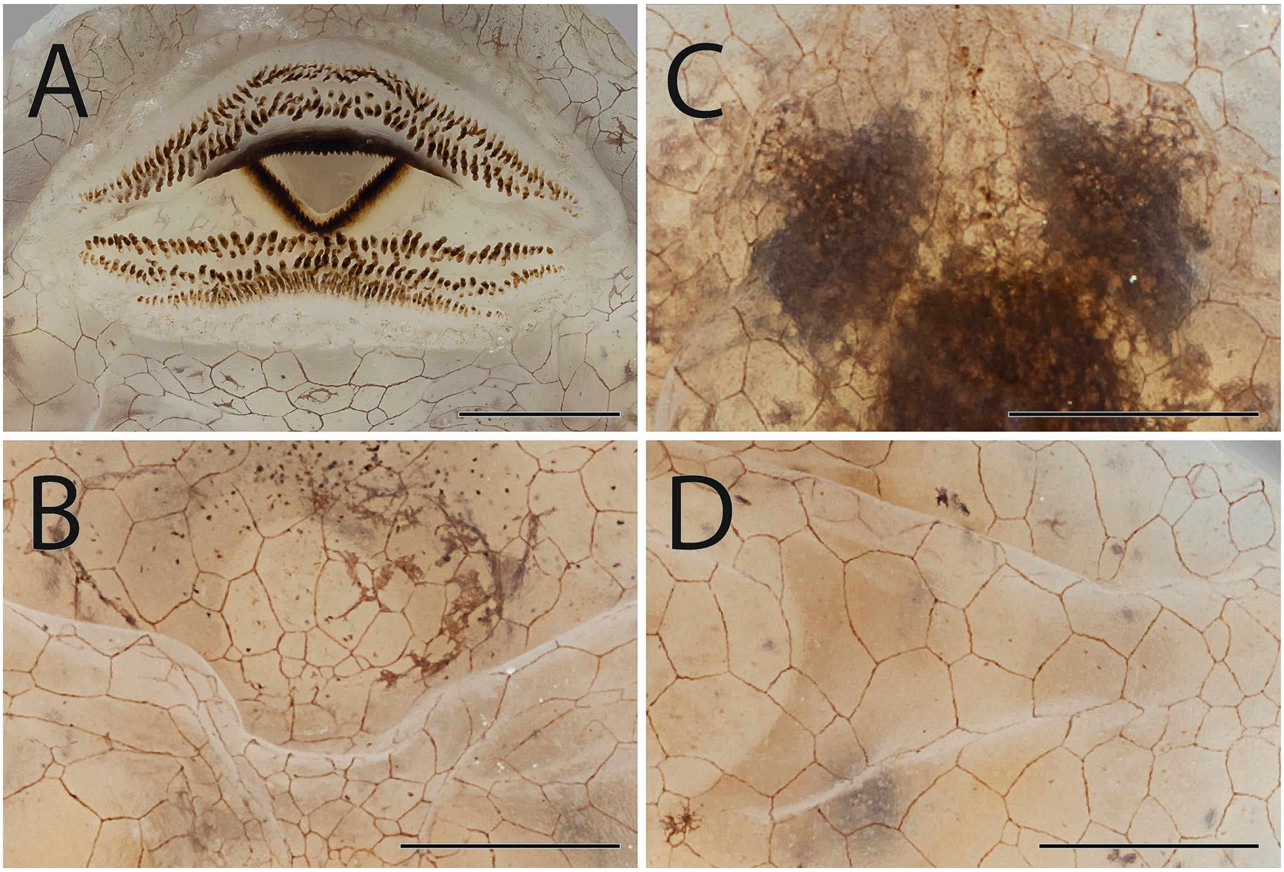

Figure 2. Details of the external morphology of *Discoglossus scovazzi*, stage Go. 28. (A) oral disc in ventral view; (B) external nares in dorsal view; spiracle in ventral view; (D) vent tube in ventral view. Scale bar is 500 µm.

Table 1. Patterns of origin and insertions of cranial and hyobranchial muscles of *Discoglossus scovazzi*.

Muscle	Origin	Insertion	Comments
Eye			
Obliquus inferior	ventral margin of oculomotor foramen	anteroventral bulbus oculi	
Obliquus superior	dorsal margin of oculomotor foramen	anterodorsal bulbus oculi	
Rectus anterior	posterior to optic foramen	anteromedial bulbus oculi	
Rectus posterior	posterior to oculomotor foramen	posteromedial bulbus oculi	
Rectus inferior	mediolateral margin of orbital cartilage	caudoventral bulbus oculi	shared origin with rectus superior
Rectus superior	mediolateral margin of orbital cartilage	caudodorsal bulbus oculi	shared origin with rectus inferior
Mandibular			
Jaw levators			
Lev. mand. longus superficialis	caudolateral surface of subocular bar	dorsomedial surface of Meckel´s cartilage	
Lev. mand. longus profundus	caudolateral surface of subocular bar	lateral surface of suprarostral ala	shared origin with M. lev. mand.
Lev. mand. internus	ventral surface of ascending process, inferior surface of subocular bar	dorsolateral surface of Meckel´s cartilage	insertion is via long tendon
Lev. mand. externus superficialis	medial, inferior surface of muscular process	ventroletral surface of Meckel´s cartilage	only a few fibers
Lev. mand. externus profundus	medial, inferior surface of muscular process	ventrolateral surface of suprarostral ala	
Lev. mand. articularis	ventromedial, inferior surface of muscular process	dorsamedial surface of retroarticular process	
Ventral muscles			
Mandibulolabialis inferior	dorsolateral surface of Meckel´s cartilage	lower lip	frayed
Intermandibularis	dorsolateral surface of Meckel´s cartilage	median aponeurosis	
Hyoid			
Interhyoideus anterior	ventrolateral surface of ceratohyal	median raphe	
Jaw depressors			
Orbitohyoideus	anterior and dorsal surface of muscular process	lateral surface of lateral process of ceratohyal	
Suspensoriohyoideus	posterodorsal surface of the descending margin of muscular process	caudodorsal surface of lateral process of ceratohyal	
Quadratoangularis	ventral surface of muscular process	dorsolateral tip of Meckel´s cartilage	
Suspensorioangularis	caudoventral margin of the subocular bar	lateral tip of Meckel´s cartilage	insertion via short tendon
Branchial			
Subarcualis rectus I	one head, proximal surface of ceratobranchial I	caudodorsal surface of ceratohyal	
Subarcualis rectus II-IV	ventral, proximal surface of ceratobranchial IV	proximalsurface of ceratobranchial I	
Subarcualis obliquus	proximal, lateral surface of ceratobranchial II	urobranchial process of basibranchial	
Constr. branchialis II	anteroventral surface of ceratobranchial I	terminal commissure I	
Constr. branchialis III	anteroventral surface of ceratobranchial III	terminal commissure II	
Constr. branchialis IV	anteroventral surface of ceratobranchial IV	terminal commissure II	
L. arc. branchialium I	caudolateral surface of subocular cartilage	lateral surface of ceratobranchial I	
L. arc. branchialium II	caudal surface of subocular cartilage	caudolateral surface of ceratobranchial I	
L. arc. branchialium III	lateral surface of otic capsule	terminal commissure I	
L. arc. branchialium IV	caudolateral surface of otic capsule	terminal commissure II and III	
Tympanopharyngeus	caudolateral surface of otic capsule	dorsal margin of ceratobranchial IV, connective tissue anterior to the glottis	
Dilatator laryngis	ventrolateral surface of otic capsule	arytenoid cartilage	
Constrictor laryngis	around glottis		
Hypobranchial			
Geniohyoideus	medial surface of proximal commissure II	lateral margin of infrarostral cartilage	
Rectus cervicis	peritoneum	medial surface of proximal commissure II	

Character evolution

In our optimizations, we identified 16 putative syapomorphies for Costata and for its genera, as well as 3 autapomorphies for *Discoglossus scovazzi* (Fig. 3).

Costata is supported by 5 synapomorphies: (i) M. geniohyoideus inserting on ceratobranchial III; (ii) M. intermandibularis restricted to the medial face of Meckel`s cartilage; (iii) M. levator mandibulae in two portions; (iv) double posterior process of pars alaris; and (v) cartilaginous roofing of the cavum cranii, formed only by the taenia transversalis.

Bombinatoridae is supported by a single synapomorphy: the presence of the mandibulolabialis superior. Alytidae has two synapomorphies: (i) presence of admandibular cartilage; and (ii) presence of the processus postcondylaris of the ceratohyal.

The genus *Alytes* has five synapomorphies: (i) M. subarcualis rectus with two slips; (ii) presence of the larval crista parotica; (iii) presence of long spiculae; (iv) anterior processus ascendens intracranial endolymphatic system present; and (v) presence of secretory ridges. *Discoglossus* has a single synapomorphy, the absence of the m. hyoangularis.

Finally, *Discoglossus scovazzi* is characterized by three autapomorphic transformations: (i) presence of the m. tympanopharyngeus; (ii) cornu trabeculae articulating with the suprarostral cartilage by the pars alaris; and (iii) absence of the cartilaginous roofing of the cavum crani.

Discussion

The history of larval morphology of *Discoglossus* species is quite old and began with Dúgés (1834), and ever since, many descriptions, reports, or illustrations of tadpoles from the five species of the genus have been scattered throughout the literature (e.g., Salvidio et al. 1988, Kwet

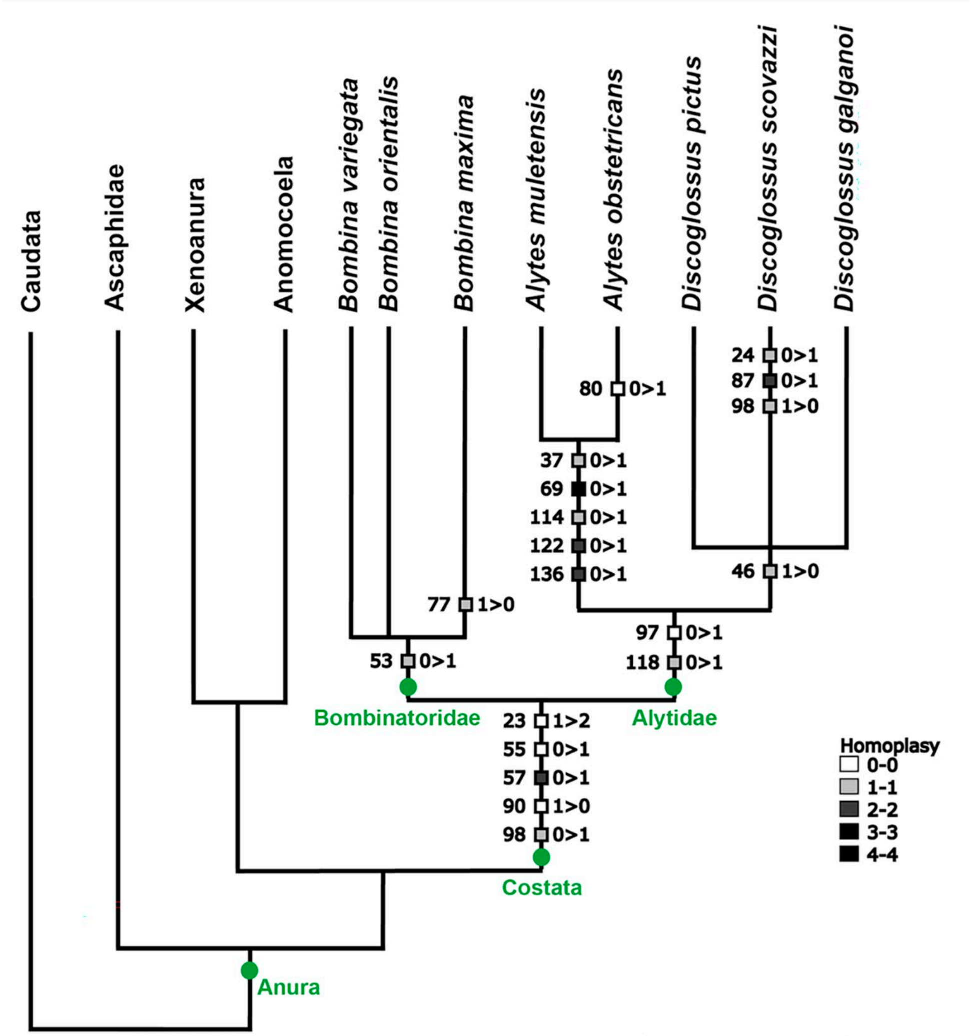

Figure 3. Optimization of phenotypic characters into the topology of Portik et al. (2023) pruned to represent the relationships of the sampled taxa. Boxes at the branches shows the synapomorphies recovered, the transformation between states, and the homoplasy of characters as described by Goloboff (2024).

2009, Ambrogio & Mezzadri 2014). Moreover, internal larval morphology has been investigated in a few species (e.g., Wassersug 1980, Viertel 1982, Lukas & Ziermann 2022).

Recently, Vera Candioti et al. (2024) reviewed the musculoskeletal system in anuran larvae, reporting on definition, variation, homology propositions, and character evolution. They optimized data from Haas (2003) into the phylogenetic hypothesis of Jetz and Pyron (2018). Our optimizations are quite similar to theirs, as we retrieved the same larval synapomorphies for Costata as did Vera Candioti et al. (2024), although we possess a larger taxon sampling, including *Alytes muletensis* and *D. scovazzi* in our dataset. Despite the fact that the inclusion of these two taxa did not affect optimizations for neither Costata, nor Alytidae, they revealed novel phenotypic variation within the family. For instance, *A. muletensis* do not share the presence of a pseudopterygoideus process with *A. obstetricans* – a unique autapomorphy for that species. As for *D. scovazzi*, we recovered three autapomorphies for that species (see results).

Our results highlighted that we are far from understanding the real phenotypic diversity and the phylogenetic history of larval morphology within early diversified lineages of anurans, such as Costata. Many gaps in our knowledge still need to be addressed. For example, the larvae of *Latonia nigriventer* are poorly known (Perl et al. 2017), with no information about its internal morphology available (Dias et al. 2024a, Vera Candioti et al. 2024). Also, elements of the buccopharyngeal system have never been explored within a phylogenetic context, despite some characters seeming to have phylogenetic variation (Wassersug 1980). The recent discovery of the bizarre, endotrophic tadpoles of *Barbourula busuangensis* by Miñaro et al. (2024) reinforce that idea.

Larval morphology is a box of surprises; the two last decades have been marked by the descriptions of novel and unique tadpoles and their exquisite traits (e.g., Grosjean et al. 2011, Randrianiania et al. 2011, Rowley et al. 2012, Haas et al. 2014, Dias et al. 2024a, b, Vera Candioti et al. 2021, Marcondes et al. 2025). Many new and exciting discoveries are, however, still waiting to be unveiled.

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Supplementary data

The following data are available online:

Supplementary document S1. Character matrix and complete optimization.