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**Evolution of Larval Characters in Dendrobatoidea Cope, 1865**  
**(Amphibia; Anura; Dendrobatidae and Aromobatidae)**

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## RESUMO

Girinos representam um elemento chave na história evolutiva e na diversificação dos anuros. Através de um ciclo de vida bifásico, os anuros conseguem aproveitar os recursos disponíveis tanto no ambiente terrestre como no aquático. Vários estudos demonstraram que a morfologia larvar pode representar uma importante fonte de evidências para estudos evolutivos. No entanto, girinos frequentemente são ignorados e pouco se sabe sobre sua anatomia e biologia. Um exemplo dessa problemática é a superfamília Dendrobatoidea, para a qual quase não há informações sobre seus girinos. O presente estudo visa contribuir para o preenchimento dessa lacuna. Eu realizei uma análise cladística da superfamília Dendrobatoidea, tendo como foco caracteres larvais. O dataset final também incluiu caracteres de adulto e sequências de DNA. A matriz final foi composta por 621 terminais e mais de 500 caracteres fenotípicos, dos quais 392 foram individualizados de sistemas larvais como condrocânio, musculatura craniana e cavidade buccopharíngeal. Em minha hipótese ótima, eu recuperei Dendrobatoidea bem como todas suas subfamílias e gêneros monofiléticos. Caracteres larvais otimizaram como sinapomorfias em diferentes níveis. Mediante a topologia e a distribuição dos caracteres, eu discuto a evolução de uma série de modos de vida e morfologias, como a oofagia, o endotrofismo e a carnivoría em Dendrobatoidea.

**Palavras-chave:** girinos; sistemática filogenética; fitotelmata; oofagia; endotrofia; morfologia.

## ABSTRACT

Tadpoles represent a key element in evolutionary history and the diversification of anurans. Through a two-phase life cycle, anurans can take advantage of the available resources in terrestrial and aquatic environments. Several studies have demonstrated that larval morphology may represent an important source of evidence for evolutionary studies. However, tadpoles are often ignored and little is known about their anatomy and biology. An example of this problem is the superfamily Dendrobatoidea, for which there is almost no information on tadpoles. This study aims to fill this gap. I performed a cladistic analysis of the superfamily Dendrobatoidae with emphasis on larval characters. The final dataset also included adult phenotypic characters and DNA sequences. The final matrix was composed of 621 terminals and more than 500 phenotypic characters of which 392 were individualized from larval systems, such as chondrocranium, cranial musculature and buccopharungeal anatomy. In my optimum hypothesis I recovered Dendrobatoidea as well as all its subfamilies and genera as monophyletic. Larval characters optimized as synapomorphies at different levels. Based on the topology and distribution of the characters, I discuss the evolution of several lifestyles and morphologies, such as oophagy, endotrophy, and carnivory in Dendrobatoidea.

**Keywords:** tadpoles; phylogenetic systematics; phytotelmata; oofagy; endotrophy; morphology.

## INTRODUCTION

One of the most remarkable characteristics in the evolution of anurans is the retention of a free-living swimming larva—commonly known as tadpole or polliwog—in about 80% of the known species (McDiarmid and Altig 1999; Roelants et al. 2011). The larva differs strikingly in morphology, ecology, physiology, and behavior from adult frogs (Noble 1929; Sokol 1981; Wassersug 1980; Altig and Johnston 1989; Haas 1995; Haas and Richards 1998; Handrigan and Wassersug 2007; Candiotti 2007); tadpoles have globular bodies and long flexible tails, whereas post-metamorphic frogs have stout bodies and lack a tail (Handrigan and Wassersug 2007). Moreover, tadpoles are usually aquatic suspension feeders, contrasting with terrestrial and strictly carnivorous adult frogs (Wassersug 1975; Altig et al. 2007).

This biphasic life cycle allows anurans to explore resources from both aquatic and terrestrial environments (Wassersug 1975; Downie et al. 2004; Wells 2007) and many studies indicate that evolutionary pressures can act decoupled in both adults and larvae (e.g., Sherratt et al. 2017; Valero et al. 2017), resulting in complex histories of character evolution. Such independent evolution and the large phenotypic variation among larvae have been pointed out as key elements in the evolution and diversification of anurans (Altig 2006a; Roelants et al. 2011).

Despite its poor preservation in fossil records, the evolutionary history of tadpoles can be tracked to the early Cretaceous; the oldest tadpole is almost as old as the oldest frog—*Prosalirus bitis*, from the early Jurassic—and they are both separated by approximately 45 million years (Shubin and Jenkins 1995; Gardner 2016). Regarding the extant anurans, phylogenetic interpretations of larval characters evolution (Haas 2003; Frost et al. 2006; Roelants et al. 2011) have shown a rapid diversification of tadpoles with different apomorphic characters evolving in several lineages.

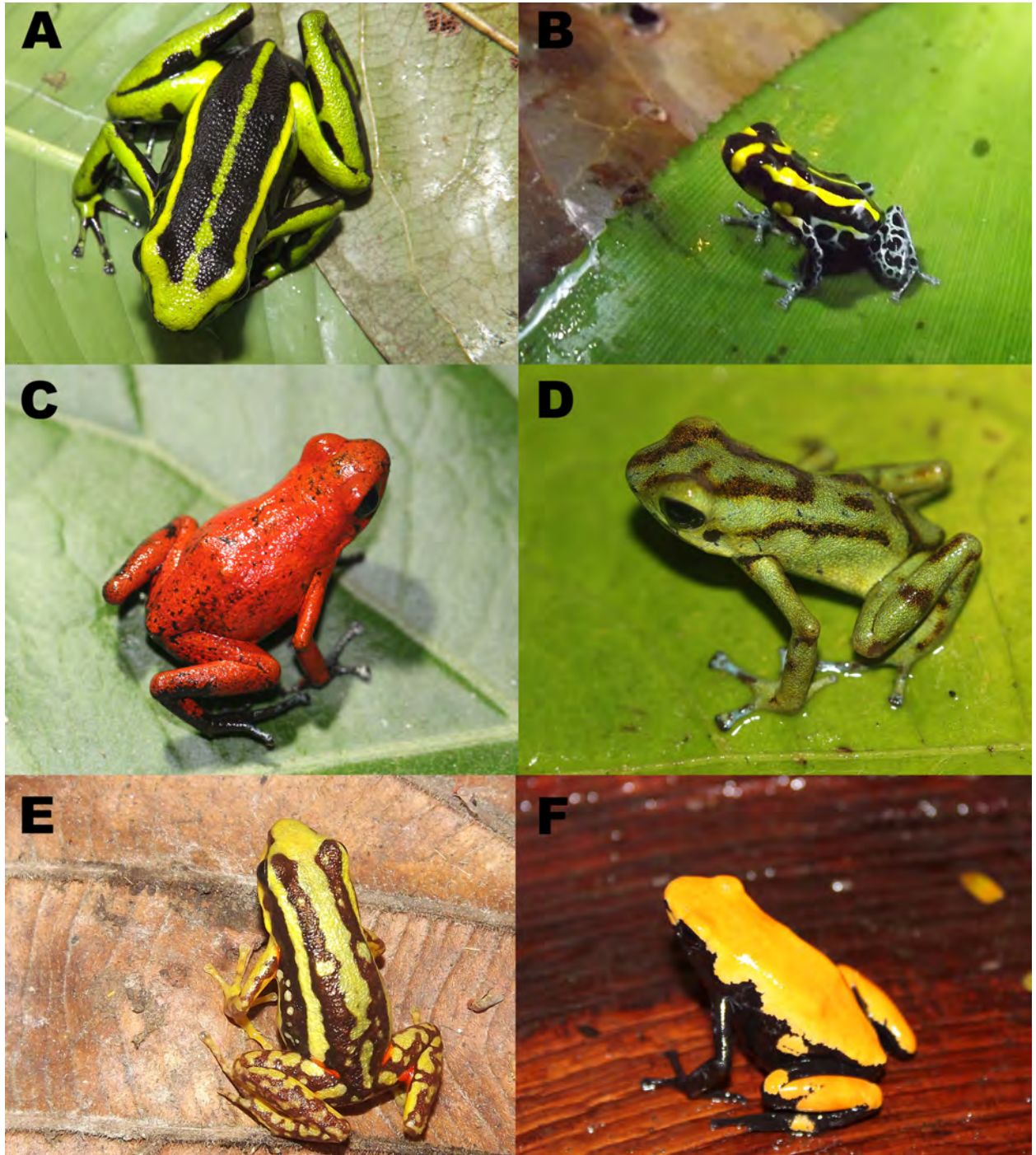
Ecologically, tadpoles are responsible for a high percentage of the total biomass in aquatic environments (Riis 1991) and they occupy a variety of niches (Altig and Johnston 1989). Tadpoles can be suspension feeders (e.g., Seale and Wassersug 1979), predators (e.g., Bowatte et al. 2013), filter feeders (e.g., Wassersug and Pyburn 1987) and can be found in streams (e.g., Downie et al. 2001), temporary or permanent ponds (e.g., Fabrezi 2011), phytotelmata (e.g., Lannoo et al. 1987; Lehtinen et al. 2004), and even outside of water in wet rocks (e.g., Bokermann 1965; Cocroft and Heyer 1988) or terrestrial nests (e.g., Caldwell and Lima 2003; Nuñez et al. 2012). They explore different layers of the water column, being found from benthic (e.g., Dias et al. 2014) to pelagic

zones (e.g., Savage 1968). Tadpoles are key elements in food webs, preying and being preyed on, playing different roles in the trophic chain (Werner and McPeck 1994; Schiesari et al. 2009; Caut et al. 2012).

Despite their importance in the evolution and diversification of Anura and the fact that they can figure in almost any field of evolutionary biology and ecology (e.g., phylogenetic systematics, evo-devo, population dynamic, evolutionary ecology, sociobiology, comparative morphology and physiology, adaptation studies), tadpoles have been highly neglected by herpetologists, and larval morphology is a largely unexplored field (McDiarmid and Altig 1999; Dias et al. 2013, 2014). Proof of that is the fact that we continue to be surprised by new remarkable tadpole phenotypes (e.g., Peixoto et al. 2003; Grosjean et al. 2004; Haas et al. 2006; 2014; Rowley et al. 2012; Zachariah et al. 2012; Gan et al. 2015; Candiotti et al. 2017). In 1999, for instance, McDiarmid and Altig estimated that only 2/3 of the known species had their tadpoles described. And, regarding internal morphology, the absence of data is more evident: Larson (2002) suggested that only 5% of the known tadpoles had their chondrocranium anatomy described.

A dramatic example of a poorly studied taxon regarding their tadpoles is the superfamily Dendrobatoidea (*sensu* Grant et al. 2006), which comprises two families—Aromobatidae and Dendrobatidae—of small tropical frogs commonly known as dart-poison frogs (Myers et al. 1978). Dart-poison frogs can be found in almost every ecosystem throughout Central and South America, occupying streams in dense forests, open fields, lowland rainforest, cloud forests and páramos in a wide range distribution, from Nicaragua to Bolivia and the Atlantic forest of Brazil and from the Pacific coast of South America to the French Antilles (Grant et al. 2006, 2017; Frost 2018).

There is a significant amount of knowledge on the biology of dart-poison frogs. All species but one have diurnal habits (Myers et al. 1991; Grant et al. 2006), many are characterized by bright colors (Fig.1), they lay their eggs on the ground or in phytotelma, and many species are characterized by complex breeding behaviors (Wells 1980; Poelman et al. 2013; Schulte and Lötters 2013) and parental care, which includes the transport of tadpoles on the dorsum of parent frogs (Noble 1927; Myers and Daly 1980; Weygoldt 1987; Grant 2004) and, in some cases, provisioning of nutritive oocytes for larval development (Weygoldt 1980; Caldwell and Oliveira 1999; Stynoski 2009). Also, about one third of the known species are able to sequester powerful toxins (such as lipophilic alkaloids; e.g., pumiliotoxins, histrionicotoxins, batrachotoxins, epibatidines) from their prey and use them as chemical defenses (Myers and Daly 1976; Myers et al. 1978; Daly et al. 1987, 2009; Saporito et al. 2004, 2012).



**Figure 1.** Some aposematic poison frogs: *Ameerega trivittata* (A), *Ranitomeya toraro* (B), *Oophaga pumilio* (C), *Oophaga vicentei* (D), *Epipedobates tricolor* (E), and *Adelphobates galactonotus* (F).

The phylogenetic relationships of Dendrobatoidea are also well understood. The monophyletic nature of Dendrobatoidea was originally proposed by Noble (1926) and consistently corroborated by subsequent works (e.g., Myers and Ford 1986; Ford and Cannatella 1993; Haas 2003; Vences et al. 2003). Phylogenetic knowledge on dart-poison frogs increased in the late 1990's and early 2000's (Summers et al. 1999; Santos et al. 2003; Graham et al. 2004; Darst et al. 2005), culminating with the seminal paper by Grant et al. (2006), who performed the severest test so far by performing a total evidence analysis—incorporating evidences for adult and



larval morphology, DNA sequences, behavior and karyological data. Recently, Grant et al. (2017) revisited the phylogenetic relationships of poison frogs and addressed several gaps in the sampling of phylogenetic diversity of the clade, resulting in a large, robust hypothesis and the proposition of new generic arrangements for these animals.

Contrasting with the scenario previously described, the understanding of larval morphology on Dendrobatoidea is a black hole. Tadpoles are frequently poorly described in only few lines of text; in many cases, the described specimens are not illustrated (e.g., *Paruwrobates erythromos*; Vigle and Miyata 1980) and taxonomic errors permeate the literature (e.g., Dunn 1924), with misleading comparisons and generalizations. Only 157 tadpoles have been described to date (e.g., Savage 1968; Silverstone 1975; Coloma 1995; Mijares-Urrutia and La Marca 1997; Páez-Vacas et al. 2010; Grant and Myers 2013; Dias et al. in press)—corresponding to less than 50% of the clade's diversity—and aspects of the internal morphology are known to c.a. 15 species (e.g., Wassersug 1980; Carr and Altig 1992; Haas 1995). Thus, an appraisal of larval morphology in Dendrobatoidea is most needed, so the evolution and diversification of tadpoles in that clade can be understood.

The present study aims to fill this gap by approaching the evolution of larval morphology in dart-poison frogs. Characters were individualized from several larval phenotypic systems such as external morphology, chondrocranium, buccopharyngeal cavity, cranial muscles, nervous system, and visceral components for as many dendrobatoids as possible, covering the phylogenetical and ecological diversity of the clade. Larval evidence was added to all previous evidence available from adult morphology and DNA sequences in order to provide the severest test to our hypothesis of larval evolution. Therefore, the goals of this work are: 1) to test the phylogenetic relationships of dart-poison frogs and their relatives; 2) to understand the evolution of larval characters; 3) to provide an ideographic explanation for larval characters distribution. I propose a new phylogenetic hypothesis, provide several new larval synapomorphies for poison frogs and their relatives at different levels of inclusion, and discuss the evolution of larval characters systems in a phylogenetic framework.

### **Tadpoles and the Systematics of Dendrobatoidea—an overview**

Scientific knowledge on Dendrobatoidea tadpoles is very scarce and the numbers cloak the reality; about half of the known species of Dendrobatoidea have their tadpoles described (Appendix 1). However, the descriptions are poorly detailed and frequently limited to a single paragraph or few lines in the accounts of new species; papers dealing only with tadpole descriptions are wondrously rare. Notwithstanding, there are many interesting studies in the

literature. The present review does not intent to cover every tadpole description, but it aims to provide a broad view on the relevance of larval morphology to the systematics of Dendrobatoidea.

The history of the dart-poison frog larvae can be tracked down to the XIX century, when Wyman (1859) first described the tadpole of *Ameerega trivittata*—originally assigned by him to *Hylodes lineatus* (= *Lithodytes lineatus*) and posteriorly identified as *Phyllobates trivittatus* by Dunn (1941), who examined the specimens deposited at the Museum of Comparative Zoology, Harvard University (MCZ 10164 and 11030). Rather than describe the tadpole, Wyman was more interested in describing some reproductive particularities of vertebrates, or as he attested (p.5) the "unusual modes of gestation" observed. Wyman's description was based on 12–20 tadpoles obtained from the dorsum of an adult frog collected at the Rio Suriname. He dissected some specimens hoping to find some feature responsible for the adherence of the tadpoles to the parent's dorsum. Thereby, he described some aspects of internal anatomy, such as the presence of internal gills disposed in "three hyoid arches" and not fully developed lungs.

Wyman failed to find any structure out of the common morphology of known larvae, which led to his hypothesis that the tadpole's mouth should play some suctional role in the back-riding individuals. He also speculated about egg deposition and the feeding habits of the tadpoles:

*"I was not able to ascertain whether the eggs were primarily deposited in the water or not, but it is well known to some of the colonists that after the larvae have reached a certain degree of development they are carried about in the manner just described and they do not known (sic) them under any other circumstances. The existence of yolk cells in the intestine, shows that for a period at least they may have from these a supply of nutriment. But after this is exhausted, and it appeared to be nearly so in those which I have dissected, how do they obtain their food? In the absence of limbs adapted to terrestrial locomotion can they leave the body of the parent? and if they cannot, do they, as in the case of Pipa and probably in Notodelphys, depend upon a secretion from her?"*  
(p.7)

Still in the XIX century, Boulenger (1895) described the tadpole of *Mannophryne trinitatis* (as *Phyllobates trinitatis*). Boulenger emphasized that "the "tadpoles are perfectly normal, of the Ranoid type" (p.210). However, the characteristics mentioned by Boulenger—viz., LTRF 2/3, marginal papillae with dorsal diastema, sinistral spiracle, dextral vent tube, and the tail twice as long as the body—are those of any generalized pond tadpole (Altig and McDiarmid 1999) and did not support his assertion of the Ranoid type.

In the early XX century Dunn was the first to employ larval characters in the taxonomy of poison-frogs. In a paper on some Panamanian frogs, Dunn (1924) described the tadpoles of



*Colostethus latinasus*, *Allobates talamancae* and *Silverstoneia nubicola* (all as *Phyllobates*). According to his descriptions the tadpoles of *C. latinasus* possess the "normal tadpole of the genus, with labial teeth 2/3" and that of *A. talamancae* "has no labial teeth, but a highly developed labial disc like that of *Microhyla achatina* and *Megophrys montana* and entirely different from anything hitherto described from America " (p.7). In the same paper he described a new species—*Silverstoneia nubicola* (as *Phyllobates nubicola*)—that had an adult frog so similar to those of *C. latinasus* and *A. talamancae* that they could be considered conspecific (p.12). The tadpole of that species, however, presented a well-developed oral disc that would ally it to *A. talamancae* (p.7). Nevertheless, the tadpoles of *nubicola* and *talamancae* possessed "some obvious differences" (p.12), aiding Dunn to describe *Silverstoneia nubicola* as a different species. Currently, it is clear that Dunn (1924) did not describe the tadpoles of *A. talamancae* but those of a *Silverstoneia*, that, given the presence of labial teeth and dorsal and ventral emargination of the oral disc, is herein considered to be *Silverstoneia flotator*—contra Savage (1968: 755), who considered it as *Silverstoneia nubicola*—(see also Grant and Myers 2013).

In 1946, Breder described and illustrated the tadpole of *Allobates talamancae* from Panama and it was clearly different from the described by Dunn (1924), which in fact was the tadpole of *Silverstoneia flotator* (see above). Breder (1946) also clarified that the tadpole described by Dunn (1924) as *Colostethus latinasus* was indeed *Colostethus pratti* and that this name also should be applied to *Hyloxalus panamensis* (= *Colostethus panamensis*), whose behavior of carrying tadpoles on the dorsum was described by Dunn (1944).

Stebins and Hendrickson (1959) described the tadpoles of *Hyloxalus subpunctatus* (as *Phyllobates subpunctatus*) from Colombia; they also reported the parental care of a male with his clutch and the behavior of carrying tadpoles. Their field observations were used to refute the hypothesis that the oral discs possess some suckorial function to keep the tadpole adhered to parents' dorsum as suggested by Wyman (1859). To Stebins and Hendrickson (1959), mucous secretions play the fundamental role in the maintenance of tadpoles in the back of adults, and movements of the body and tail muscles were important for the tadpoles to release themselves from the parent frog.

Savage (1968) revised the Central America species of dendrobatoids and also provided some comments on South American taxa. Based on larval characters he suggested (p.748) four groups could be recognized:

**Group A:** lateral emargination, dextral vent tube, single row of marginal papillae, LTRF 2(2)/3(1), oral disc not umbelliform—contained *Colostethus inguinalis*, *Colostethus latinasus*, *Colostethus pratti*, *Allobates talamancae*, and *Phyllobates lugubris*.

**Group B:** oral disc not emarginated—*Dendrobates auratus*.

**Group C:** oral disc not emarginated, medial vent tube, enormous beak, large papillae (except anteriorly), LTRF 1/1—*Oophaga pumilio*.

**Group D:** oral disc not emarginated, oral disc umbelliform, dextral vent tube, labial teeth absent, numerous flattened submarginal papillae anterior and posterior to mouth, absence of marginal papillae—*Silverstoneia nubicola*.

Savage's (1968) four groups are quite consistent with the current taxonomy of poison frogs, with exception of his group A that would represent a polyphyletic assemblage supported by plesiomorphic characters. Unfortunately, Savage did not investigate South American tadpoles, and besides that, he also based his taxonomic arrangements on adult characters. Thus, he recognized three groups for dendrobatids, for which some larval characters were considered diagnostic:

**Group I:** composed by *inguinalis*, *latinasus*, *nubicola*, *pratti*, and *talamancae* and "also most species called *Phyllobates* in South America". Larval character supporting this group were: lateral emargination of oral disc or umbelliform oral disc and dextral vent tube.

**Group II:** composed by *lugubris* (also *bicolor* and *auroteania* in South America). Larval traits evoked to diagnose this group were: lateral emargination on oral disc and dextral vent tube.

**Group III:** comprised *auratus*, *granuliferus*, *minutus*, *pumilio*, and *speciosus* (also *tinctorius*, *histrionicus*, and *trivittatus* among approximately 15 South American forms); larvae of this group were defined as sharing oral disc not emarginated and a median vent tube.

Savage (1968) resurrected *Colostethus* for his group I, defined the group II as *Phyllobates* and the group III as *Dendrobates*. The larval characters were included in an artificial identification key. He considered larval morphology particularly important to define *nubicola* (item 8b; p.768) and gave special attention to this species, describing aspects of the oral disc and its peculiarities:

"The mouth parts of the larvae of *C. nubicola* are specially modified for feeding near the surface of the water. The oral disc is expanded, lacks denticles, and is usually directed dorsally. The papillae over the surface of the disc apparently aid in sorting particles out of the water as it flows toward the mouth. The tadpole can orient the umbrella-like oral disc ventrally to attach to rocks or other substrate features when resting." (p.757)

Silverstone (1975, 1976) took the analysis of larval morphology more deeply into the systematics of dart-poison frogs. His descriptions are more complete than most of the previous works, several of his species groups were characterized by some larval trait, and some relationships were hypothesized by overall tadpole similarities.

Silverstone (1975) defined the *histrionicus* group for *histrionicus* and *leucomelas*. Larval characters used to diagnose this group were the reduced number of teeth rows, the oral disc not emarginated laterally, and the medial position of the vent tube. The tadpoles of *leucomelas* were not known, and Silverstone united those species in the *histrionicus* group because they were the only dendrobatid species lacking the omosternum. However, he noticed the morphological similarities between the tadpoles of *histrionicus* and *pumilio*, and suggested that those two groups could be related:

*"The tadpole of D. histrionucus resembles that of D. pumilio in its reduced number of denticles and papillae. This suggests that histrionicus group is more closely related to the pumilio group than to the other two groups of Dendrobates."* (p.23)

Silverstone was right, and today, *histrionicus* and *pumilio* are members of the genus *Oophaga*. In his definition of the *minutus* group he emphasized the fact that the tadpoles of *minutus* and *opisthomelas* were unique among dendrobatids in sharing an emarginated oral disc, labial teeth not reduced in number, and a dextral vent tube:

*"Tadpoles of D. minutus and D. opisthomelas are the only ones in the genus known to have indented lips and a dextral anus; this and their small size suggest that they belong in the same species group."* (p.31)

Silverstone (1975) also commented about tadpoles collected and tentatively assigned *altobueyensis* and *fulguritus* that also shared the *minutus*-like morphology, but he could not precisely identify them. Once again, accretions made by Silverstone (1975) based on larval morphology were corrected; all of those *minutus*-like species currently form a well-supported clade, the genus *Andinobates* (Brown et al. 2011).

In his revision of the genus *Phyllobates*, Silverstone (1976) also employed larval characters in his analysis. However, he found less variation than in *Dendrobates* and larval morphology played a discreet role in his taxonomic revision. He listed a set of characteristics common to all known tadpoles of the so called *Phyllobates*, such as the emargination of the oral

disc, jaw sheets inconspicuous and thin, larval tooth row formula 2(2)/3, dextral vent tube, among others.

Myers and Daly (1980) described *Andinobates bombetes* (as *Dendrobates*) and suggested that *abditus*, *bombetes*, and *opisthomelas* formed a monophyletic group supported by the presence of a gap in the papillation of the lower lips in the tadpoles of those species:

*"Based on a larval synapomorphy, we suggest that at least D. abditus, D. bombetes, and D. opisthomelas form a monophyletic subgroup. The character state is the median gap that interrupts the papillate fringe on the posterior (lower) edge of the oral disc."* (p.20)

Wassersug (1980) described the buccopharyngeal anatomy for several anuran taxa, including *Hyloxalus subpunctatus* and *Silverstoneia nubicola*—both referred to as *Colostethus*. He stated that there is no anatomical element that could distinguish dendrobatid frogs from all other anuran larvae. However, he pointed out that the differences observed between the two analyzed dendrobatid species are striking and suggest that both could be considered as part of separate genera:

*"Of the two families remaining, there are no internal oral features that readily distinguish the dendrobatid larvae from other advanced families. The differences between Colostethus subpunctatus and Colostethus nubicola are massive and, again, if internal oral features of the larvae are taken into consideration, the funnel-mouthed form could justifiably be separated into a different genus."* (p.121)

La Marca (1994) revised the taxonomy of the collared frogs of genus *Mannophryne*. He provided data on the larval morphology for *M. cordilleriana*, *M. herminae*, *M. neblinae*, *M. olmonae*, and *M. riveroi*, and for many of those, La Marca (1994) described that the “internarial distance was wider than the interorbital distance”. He proposed that some character could be useful to diagnostic the species, but there was no larval character in his artificial key. He stated (p.62) that “*neblinae* is unique in having larvae with large labial papillae, a condition not seen in other *Mannophryne* tadpoles”, but did not discussed further this character.

Coloma (1995) incorporated tadpole external morphology in his revision of the Ecuadorian species of *Colostethus*. He proposed a general morphology based on comparisons only among back-riding tadpoles. Nevertheless, he did not include any larval trait in his artificial key.

La Marca (1995) hypothesized an evolutionary scenario in which the transformation of small labial papillae to large papillae would be a diagnostic character of *Mannophryne neblinae*:

*"Small papillae are widespread among the Dendrobatidae. The large papillae of Mannophryne neblinae is a unique condition among collared frogs, although they are present in some Dendrobates. Polarity of character state is uncertain. It is hypothesized that large papillae is the derived condition."* (p.53)

Haas (1995) described the chondrocranium morphology for seven species of Dendrobatoidea—*Epipedobates anthoni*, *Epipedobates boulengeri*, *Epipedobates tricolor*, *Dendrobates tinctorius*, *Hyloxalus subpunctatus*, *Phyllobates bicolor*, and *Silverstoneia nubicola*—and compared them with all known chondrocranium by that time. He strongly rejected a possible evolutionary relationship with ranoid frogs. Instead, he pointed that several characteristics such as the lack of the larval processus oticus, the presence of three foramina Acustica and the lack of a foramen perilymphaticum accessorius were shared with bufonoid larvae. He listed 26 chondrocranial characters for dendrobatids, but given the absence of a robust outgroup hypothesis, he stressed that the polarity of several characters could not be established. Notwithstanding, Haas (1995) concluded that the free proximal end of the ceratobranchials II and III (commissura proximalis II–III) is an unambiguous synapomorphy for Dendrobatoidea (as Dendrobatidae), supporting its monophyly.

Haas (1997) employed for the very first time characters derived from larval morphology of a dart-poison frog in a formal cladistic analysis. He described the hyobranchial apparatus for several frogs of different families and performed a parsimony analysis of 31 characters. *Phyllobates bicolor* (the only dendrobatid species included) was recovered as sister to *Odontophrynus achalensis* (Odontophrynidae). Such relationship was supported by the origin of the musculus subarcualis rectus II (character 28.1) and by the change in the configuration of insertion point of the m. rectus cervicis (on the processus branchialis II and/or III to both proximal ceratobranchialia III and IV; character 29.2). Once more, Haas (1997) rejected the ranoid hypothesis dendrobatid relationships. The sister relationship of *Phyllobates bicolor* with *Odontophrynus achalensis* was congruent with the assertion that Dendrobatidae belongs to Bufonoidea (Lynch 1971; Haas 1995; Hay et al. 1995).

Mijares-Urrutia and La Marca (1997) performed the only comprehensive study with the tadpoles of the genus *Aromobates* (as *Nephelobates*). They described the tadpoles of *A. alboguttatus*, *A. duranti*, *A. haydeae*, *A. meridensis*, *A. orostoma*, and *A. serranus* and concluded that the larvae of *Aromobates* shared the overall phenotypic pattern of the so-called *Colostethus*

larvae, which was the typical pond type 4 of Orton (1953). However, they listed some characters that allowed the comparisons between groups (p.141). They hypothesized that *A. mayorgay* (data from La Marca and Mijares-Urrutia 1988), *A. meridensis*, and *A. molinari* (data from La Marca 1985) could be grouped by the coloration of body-edges, the oval body shape, the spiracular opening located at mid-body, and the posterolateral orientation of spiracle. They also concluded the *A. alboguttatus*, *A. haydeae*, *A. orostoma* share a set of larval characters, although they did not list them. They also compared the tadpoles of *Nepheleobates* with other Venezuelan dendrobatids, differencing them from *Aromobates nocturnus* (Myers et al. 1991) by organization of marginal papillae, from *A. leopardalis* (as *Colostethus*; Mijares-Urrutia 1991) by the structure of jaw sheaths, and from *Mannophryne* by the internarial/interorbital distance relation (La Marca 1994).

In 1998, de Sá and Hill described the chondrocranium morphology of *Dendrobates auratus*. They found that this species shared most of the characters with other dendrobatids described by Haas (1995). Particularly, they drew attention to the fusion between the orbital cartilage and the otic capsule and to the absence of processus anterolateralis hyalis of the ceratohyal in *Dendrobates auratus* and *Dendrobates tinctorius*, which they suggested to be derived within the family, but craving as a putative synapomorphy for *Dendrobates*. It is important to note that de Sá and Hill (1998) wrongly interpreted the results of Haas (1995) and concluded that *Dendrobates auratus* would differ from *Dendrobates tinctorius* by the absence of commissura proximalis II–III, which in fact is also missing in the later (Haas 1995: 253, Fig.7b).

Another finding of de Sá and Hill (1998) concerns the plate-like cartilage on the terminal processus posterior hyalis in *Dendrobates auratus*. Haas (1995) observed the same character in *Dendrobates tinctorius* and suggested that it could be the fourth spicule. However, de Sá and Hill (1998) noted a small curving process in the ceratobranchial IV, which they interpreted as the fourth spicule, leaving the plate-like cartilage as a feature of undetermined homology that is shared by both *Dendrobates* species.

Haas (2001) performed one of the most comprehensive studies on anuran mandibular arch musculature. The only dendrobatid species included was *Phyllobates bicolor*, which was reported to possess a functional, differentiated musculus levator mandibulae lateralis and the ramus mandibularis ( $V_3$ ) running dorsally to the musculus levator mandibulae externus. Haas (2001) interpreted his results in a topology that reflected the hypothesis of Ford and Cannatella (1993) and Haas (1997). *Phyllobates bicolor* was placed in a large polytomy that included several neobatrachians plus Ranoidea.

Haas (2003) expanded significantly his studies on larval morphology. He performed a broad phylogenetic analysis of anuran larvae, including 81 species of several families and 156

characters, primarily derived from chondrocranium and cranial muscles. He included four dendrobatid terminals: *Dendrobates tinctorius*, *Epipedobates tricolor*, *Mannophryne herminae*, and *Phyllobates bicolor*. He provided new insights into larval evolution and proposed synapomorphies at different taxonomic levels; regarding dart-poison frogs, his topology recovered Dendrobatoidea (as Dendrobatidae) monophyletic and sister to Hylodidnae (=Hylodidae).

Synapomorphies of Dendrobatoidea were 1) insertion of the *m. rectus cervicis* on the processus branchialis II and/or III to both proximal ceratobranchialia III and IV (39.2); 2) the presence of the taenia tecti medialis only on the roof of the cavum cranii (96.1); 3) the transport of larva on the dorsum by parental frog (137.1); and 4) pseudofirmisternal shoulder girdle (144.1). Additionally, *Dendrobates tinctorius* + *Phyllobates bicolor* was supported by the absence of amplexus. There was no resolution within *Epipedobates*, *Mannophryne* nor in the clade composed by *Phyllobates* and *Dendrobates*. Dendrobatoidea + Hylodidae were supported by: 1) occurrence of a guiding behavior (142.1), where male leads female from the calling site to oviposition site and 2) T-shaped terminal phalanges (156.2).

Frost et al. (2006) in their seminal paper included the dataset of Haas (2003) together with DNA sequences. As a result, they recovered Dendrobatidae as monophyletic and, besides the reported synapomorphic traits described by Haas (2003), the presence of a small adrostral cartilage (90.1) and cephalic amplexus (139.2) optimized as unambiguous synapomorphies for that clade.

Grant et al. (2006) opted for not including the dataset of Haas (2003) in their analysis due to the very small sample size (p.51). Nevertheless, they employed twelve larval characters (characters 87–98). The genus *Silverstoneia* was supported by three unambiguous synapomorphies: 1) loss of emargination of the oral disc (89.0); 2) origin of submarginal larvae papillae (91.1); and 3) loss of posterior keratodont rows in larvae (94.3). Several other larval traits were listed as complementary characteristics for many taxa.

Páez-Vacas et al. (2010) performed a systematic revision of the *Hyloxalus bocagei* complex based on phylogenetic analysis of DNA sequences, external morphology and morphometric data from adults and tadpoles, parameters of advertisement call. They described the tadpoles of *H. bocagei*, *H. italoii*, *H. maculosus*, and *H. yasuni*, from which they took several diagnostic characters, specially some related with color patterns (p.67; Table 17). They also suggested (p.68) that color pattern characters should be included in future studies with *Hyloxalus* larvae.

Brown et al. (2011) revised the genus *Ranitomeya* and described the genus *Andinobates*. Besides DNA sequences, they analyzed several morphological characters from adults and tadpoles and advertisement calls (not included in the phylogenetic hypothesis). They redefine the



genus *Ranitomeya* and species groups within both *Ranitomeya* and *Andinobates*, suggesting putative synapomorphies for some clades. Larval characters, as expected, provided insights into their taxonomy; for instance, the *Andinobates bombetes* group can be diagnosed from the *fulguritus* + *minutus* groups on the basis of a wide medial gap in the papillae on the posterior lip (see also Myers and Daly 1980). Brown et al. (2011) also succinctly described several tadpoles; however, they did not provide illustrations for most of them nor collection numbers.

Grant and Myers (2013) reviewed the genus *Silverstoneia*. They described five new species, including the one mentioned by Grant et al. (2006:168). They also provided descriptions and illustrations of the tadpoles of *Silverstoneia dalyi* and *Silverstoneia minima*, plus illustrations and character discussions for *Silverstoneia flotator* and *Silverstoneia nubicola*. Larval characters such as the presence of keratodonts and oral disc emargination were employed in the diagnosis of the species.

Sánchez (2013) analyzed several museum specimens as well as the available literature of dendrobatoids. He focused his discussion on three characters: 1) jaw sheets, that could be U-shaped, massive and well-developed as in most Dendrobatinae or presenting a medial notch that he called W-shaped, which was the plesiomorphic condition for several taxa; 2) fleshy projection on nostril marginal rim, absent in most Dendrobatinae; and 3) intestine configurations, for which Sánchez recognized two conditions: a long, well-developed intestine that covers other visceral components in ventral view (S condition) or a short intestine, that leaves the visceral organs exposed in ventral view (D condition).

Sánchez (2013) drew a tree topology based on the hypothesis of Grant et al. (2006) and Brown et al. (2011) and interpreted the evolution of his larval characters within that tree. He found that the U-shaped jaw sheets, nostril without fleshy projections, and short gut (D condition) are restricted to Dendrobatidae minus *Phyllobates*, whereas the other conditions were shared by Colostethinae, Hyloxalinae and to all genera of Aromobatidae. Sánchez (2013) himself admitted that his interpretation lacked the cladistic rigor, however, his work provided some insights in the evolution of some characters in poison-frogs.

Recently, Grant et al. (2017) revisited the phylogenetic relationships of Dendrobatoidea. They employed a total evidence analysis of the available DNA sequences, plus several new data from many taxa never included in any previous hypothesis (e.g., *Hyloxalus picachos*, *Silverstoneia erasmios*). Additionally, they included a phenotypic dataset, which was the same used by Grant et al. (2006), but with new characters and modification of others that were coded for more terminal taxa.

Regarding larval morphology, Grant et al. (2017) included most of the characters proposed by Grant et al. (2006) plus the three characters of Sánchez (2013). They divided the character

larval oral disc (character 88) of Grant et al. (2006) in two: larval disc occurrence (character 94: absent; present) and larval disc morphology (character 95: normal; umbelliform; suctorial). They also divided the character larval diet (character 112) of Grant et al. (2006) into larval trophic guild (character 125: exotrophic; endotrophic) and exotrophic larval diet (character 126: detritivorous; predaceous; oophagous).

Grant et al. (2017) found larval characters as unambiguous synapomorphies at different levels. For instance, the U-shaped jaw sheaths and the absence of projection on marginal rim represented synapomorphies for Dendrobatini (new tribe), in accordance with Sánchez (2013). Additionally, several larval features supported the genus *Silverstoneia*, in accordance with Grant et al. (2006). Interestingly, the larval character long gut covering other viscera provided the first phenotypic synapomorphy for the genus *Adelphobates*, which was previously supported only by DNA characters (see Grant et al. 2006: 172).

Dias et al. (in press) described the tadpole of *Epipedobates darwinwallacei* and revised some larval characters in the genus. They suggested as putative synapomorphies for the genus *Epipedobates* the following larval character-states: 1) shelf on the upper jaw sheath, and 2) subcutaneous melanophores distributed in two transverse bands in the peribranchial area. Additionally, they stressed that the presence of white spots on the anterolateral and ventrolateral surfaces of the body could be another synapomorphic character, but it would require further studies on the genus' morphology, distribution and nature.

## CONCLUSIONS

- ✓ Knowledge on the larvae of the superfamily Dendrobatoidea is scarce.
- ✓ Several transformation series can be individualized from larval morphology.
- ✓ The concept of semaphoronts should be treated as character-specific.
- ✓ The sister group of Dendrobatoidea is a clade composed by the families Alsodidae, Cycloramphidae, and Hylodidae.
- ✓ Dendrobatoidea, Dendrobatidae, Aromobatidae and all subfamilies and genera were recovered monophyletic.
- ✓ Evidence suggest that the generic diversity of the families Aromobaidae and Dendrobatidae will increase.
- ✓ The inclusion of phenotypic larval characters had a profound impact on the relationships of poison frogs and their relatives.
- ✓ Larval characters allowed taxonomic positioning of several taxa, as *Aromobates mandelorum* com.nov. and the recognition of new species, as *Allobates aff. talamancae*.
- ✓ Larval characters optimized as unambiguous synapomorphies at different levels across the tree.
- ✓ Tadpoles of dart-poison frogs are highly diverse and present different lifestyles.
- ✓ Predaceous and endotrophic larvae evolved independently several times and possess several specialized characters.

- ✓ Obligatory oophagy in *Oophaga* can be studied in larval characters that include the development of a larval stomach.
  
- ✓ Larval morphology will contribute to further studies on systematics, ecology and evolution of anurans.

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