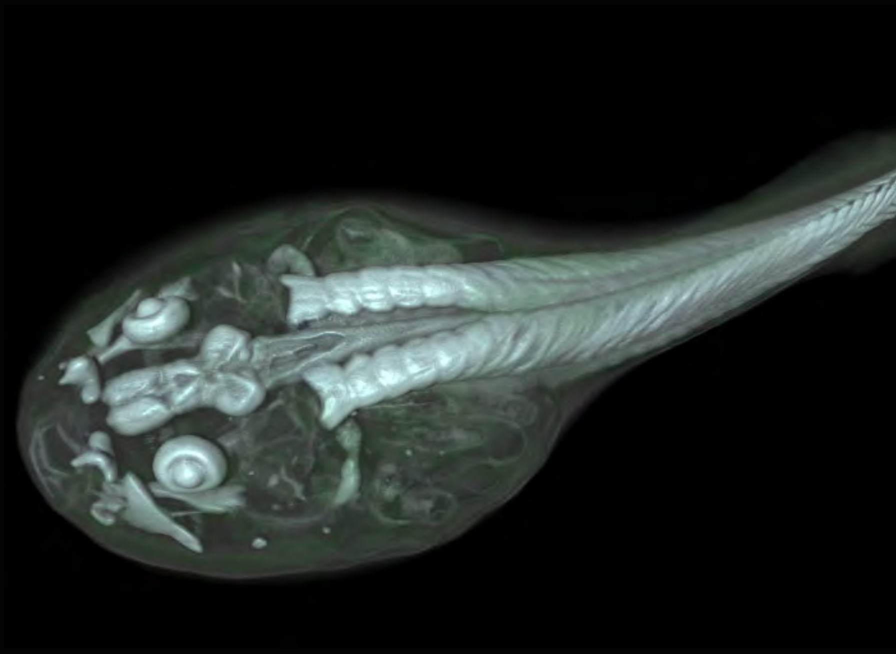
Universidade de São Paulo
Programa de Pós-Graduação em Zoologia

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

Pedro Henrique dos Santos Dias



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Tese apresentada ao Programa de Pós-Graduação em Zoologia do Instituto de Biociências da Universidade de São Paulo como parte dos requisitos necessários à obtenção do Título de Doutor em Ciências Biológicas, na área Zoologia

Orientador: Dr. Taran Grant

São Paulo
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Frontispiece. Adulto de *Oophaga pumilio* em Isla Solarte, Bocas del Toro, Panamá.

Nomenclatural Disclaimer

The taxonomic changes presented herein, including new taxa, combinations, and synonymy, are disclaimed as nomenclatural acts and are not available, in accordance with Article 8.3 of the International Code of Zoological Nomenclature.

São Paulo
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Orientador

São Paulo
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Aos meus pais, Rosangela e Luiz Henrique.

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“True ignorance is not the absence of knowledge, but the refusal to acquire it.”

Karl Popper

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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 Dendrobatoidae, 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 condrocrânio, musculatura craniana e cavidade buccopharingeal. 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 carnivoria 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; Candioti 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 McPeek 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; Candioti 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 know 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 (Meyers 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 and 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 suctorial 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 trininitatis*). 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 described 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 pratii* 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 suctorial 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 ceratobracnhials II and III (commissura proximalis II–III) is an unambiguous synapmorphy 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. haydeeae*, *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. haydeeae*, *A. orostoma* share a set of larval characters, although they did not list them. They also compared the tadpoles of *Nephelobates* 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 internatial/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 *Dendroabates 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 adrostal 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. italoi*, *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 de *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 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 museums 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) intestines 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*, *Silvertoneia 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 sheets 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.

MATERIALS AND METHODS

Conventions and Abbreviations

To carry out the present study, I examined several tadpoles from 46 different scientific collections and field series from eleven countries, as listed below.

Acronyms: American Museum of Natural History (**AMNH**); Amphibian Collection Célio Fernandes Baptista Haddad, at the Universidade Estadual Paulista, Rio Claro (**CFBH**); Amphibian Collection, Universidade Federal do Estado do Rio de Janeiro **(UNIRIO)**; Carnegie Museum, Departament of Herpetology **(CM)**; Centro Jambatu de Investigación y Conservación de Anfíbios **(CJ)**; Coleção Herpetológica da Universidade Federal do Mato Grosso **(UFMT)**; Coleção Zoológica Paulo Bührhneim, Universidade Federal do Amazonas **(CZPB-UFAM)**; Colección de Herpetología, Escuela de Biología, Universidad de Costa Rica **(UCR)**; Colección Herpetológica de la Universidad de Santa Marta **(SM)**; Departamento de Zoologia, São José do Rio Preto, Universidade Estadual Paulista **(DZSJRP)**; Escuela Politecnica Nacional, Ecuador **(EPN)**; Herpetological Collection, Universidade Federal de Minas Gerais **(UFMG)**; Institut Royal des Sciences Naturelles de Belgique **(IRSNB)**; Instituto de Ciencias Naturales, Universidad Nacional de Colombia **(ICN)**; Instituto Nacional de Pesquisa da Amazônia **(INPA)**; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" **(MACN)**; Museo de Historia Natural de San Marcos, Universidad Nacional Mayor de San Marcos, Lima, Peru **(MUSM)**; Museo de Historia Natural La Salle **(MHNLS)**; Museo de Zoología da Pontificia Universidad Católica del Ecuador **(QCAZ)**; Museo de Zoología de la Universidad Tecnologica Indoamerica **(MZUTI)**; Museu de Ciências e Tecnologia da PUC-RS **(MCT)**; Museu de História Natural Capão do Imbuia **(MHNCI)**; Museu de História Natural da Universidade Federal de Alagoas **(MUFAL)**; Museu de História Natural, Universidade Estadual de Campinas **(ZUEC)**; Museu de Zoologia da Universidade de São Paulo **(MZUSP)**; Museu de Zoologia da Universidade Estadual de Feira de Santana **(MZUEFS)**; Museu de Zoologia, Universidade Federal da Bahia **(UFBA)**; Museu Nacional, Rio de Janeiro **(MNRJ)**; Museu Paraense Emilio Goeldi **(MPEG)**; Muséum National d'Histoire Naturelle **(MNHN)**; Museum of Comparative Zoology **(MCZ)**; Natural History Museum of Los Angeles County **(LACM)**; Royal Ontario Museum **(ROM)**; The Museum, Michigan State University **(UMMZ)**; The Sam Noble Oklahoma State Museum of Natural

History **(OMNH)**; Universidade Federal de Uberlândia **(UFU)**; University of Kansas, Museum of Natural History **(KU)**; University of the West Indians, Zoological Museum **(UWIZM)**; Zoologische Staatssammlung, Munchen, Germany **(ZSM)**.
Field series: Albertina P. Lima **(APL)**; Antoine Fouquet **(AF)**; Gustavo González Duran **(GGD)**; John Douglas Lynch **(JDL)**; Marco A. Rada **(MAR)**; Pedro Henrique Dias **(PD)**; Philippe Kok **(PK)**.

Additional specimens were obtained through fieldwork. Two expeditions were conducted: the first one in March 2015 along the Içá River, Brazilian Amazon, and the other in July 2017 in several localities in Panamá, from the Pacific to the Atlantic coast. All species authorships are listed in the Appendix 2. The list of examined material and voucher numbers are provided in the Appendix 3

Species assignment

The studied tadpoles were assigned to a species based on one or several of the following criteria: 1) the material was used for the original tadpole description; 2) specimens were from the type locality or immediate vicinities; 3) specimens were from localities where a single dendrobatoid species was recorded; 4) tadpoles were reared from egg clutches; 5) tadpoles were collected from the back of an adult specimen; 6) DNA analysis of tissues collected from the specimens; 7) tadpoles from lots in which one or several specimens in different developmental stages, preferably with froglets; 8) tadpoles in late developmental stages in which adult characters were present; 9) comparison with the original descriptions. Specimens that could not be assigned to a species or with a dubious identification were excluded from this study.

General Methods and Terminology

Specimens were examined under stereoscopic microscope; in many cases, I used methylene blue or crystal violet (Ronald Altig, pers. com) to aid character identification. External morphology and oral disc characters follow the anatomical terms proposed by McDiarmid and Altig (1999) and Altig (2007); for the lateral line system I followed Schlosser (2002a,b) terminology based on the development of the lateral line placodes.

For the study of the buccopharyngeal cavity, individuals were manually dissected according to Wassersug (1976a). After exposition, features were preliminary analyzed with the aid of methylene blue and some individuals were selected for further detailed inspection under

Scanning Electron Microscopy (SEM); these individuals were washed in tap water and then submitted to gradual alcoholic dehydration: 1) two hours in 25% ethanol; 2) 24 hours in 70% ethanol; 3) three baths of 15 min in 100% ethanol, 20 minutes prior to the critical point dryer. Dehydrated samples were submitted to the critical point dryer in carbon dioxide and then mounted in double-face carbon tape on stubs, which were covered with a thin layer of gold. Images were generated in a Zeiss SIGMA Microscope; magnification, work distance, and accelerating voltage (EHT; kVs) were adjusted according to each sample. Terminology for buccopharyngeal anatomy follows Wassersug (1976a, 1980).

Cranial muscles and cartilages were accessed by manual dissection or microCT scanning. For manual dissection, individuals were stained with alcian blue for 24 hours and had their skin removed to expose the muscles. Lugol solution (aqueous solution of I_2 at 1% and KI at 2%) was employed to increase contrast between the muscle fibers and cartilages. After muscle inspection and visceral components inspection, standard protocols of clearing and staining (e.g., Dingerkus and Uhler 1977; Wassersug 1976b; Taylor and Van Dyke 1985; Dias et al. 2013) were carried out for chondrocranium study. For some rare species for which only one specimen was available for dissection, before the clear and staining procedures, the hyobranchial apparatus was disarticulated to expose the buccopharyngeal cavity for character coding.

For microCT analysis, tadpoles were washed in tap water and stained with lugol, phosphotungstic acid ($H_3PW_{12}O_{40}$), or a combination of both to increase the density of soft tissues (see Metcher 2009). Cranial muscles terminology is that of Haas (1997, 2001) with some additions of Carr and Altig (1991, 1992) for the mandibulolabialis and rectus abdominis muscles. Chondrocranium and hyobranchyal apparatus terminology follows Haas (1995). Visceral components terms are in accordance with Griffiths (1961), Viertel and Richter (1999), Sánchez (2013) and Haas et al. (2014). Cranial nerves were studied during manual dissection or through specific preparations following the protocols of Nishikawa (1987) and Song and Parenti (1999) that employ Sudan Black B. Terminology follows Lannoo (1999), Haas (2001, 2003) and Quinzio and Fabrezi (2014).

For histological preparations I dehydrated samples and embedded them in Leica historesin solution. Blocks were serial cut at 10µm in a semi-automatic microtrome and samples stained with general protocols with hematoxylin and eosin or fucsin and toluidine blue (Mulish and Welsch 2010).

Laboratory Protocols

Total Genomic DNA was extracted from ethanol-preserved tissues samples using the Quiagen DNeasy (Quiagen, Valencia, CA, USA) extraction kit following the manufacture's guidelines. PCR amplification was carried out in 25µl reaction. The standard PCR program consists of initial denaturing step of 3 min at 95–96°C followed by 35–38 cycles of 30s at 96°C, 30s at 45–48°C and 1 min at 72°C; the process is ended with a final extension of 72°C for 3 min—variations related to specific genes regions (Table 1). The amplified product of the PCR was purified with Agencourt AMpure XP DNA Purification and Cleanup Kit (Beckman Coulter Genomics, Brea, CA, USA). Sequencing reactions were performed using fluorescent-dye labeled terminators (ABI Prism Big Dye Terminators v. 1.1; Applied Biosystem, Foster City, CA, USA), with an ABI 3730XL (Applied Biosystem, Foster City, CA, USA). We sequenced all in both directions (i.e., 3'→5' and 5'→3') in order to double check for errors during the sequencing and/or editing process. Chromatograms were read and contigs generated using Geneious v.6.1.6 (Kearse et al. 2012). Sequences were formatted according to Grant et al. (2006). The primers employed are listed in Table 2.

Table 1. PCR cycles condition per gene region.

Pair of Primers	Initial Denature	Denature	Annealing	Extension	Final Extension	Storage
AR/BR	96°C/3'	96°C/60"	48°C/60"	72°C/60"	72°C/3'	4°C/∞
L2a/H10	96°C/3'	96°C/60"	48°C/60"	72°C/60"	72°C/3'	4°C/∞
L2a/Titus 1	96°C/3'	96°C/60"	48°C/60"	72°C/60"	72°C/3'	4°C/∞
MVZ59/MVZ50	96°C/3'	96°C/60"	45°C/60"	72°C/60"	72°C/3'	4°C/∞
12A-L/tVAL-H	96°C/3'	96°C/60"	45°C/60"	72°C/60"	72°C/3'	4°C/∞
LCO1490/HCO2198	96°C/3'	96°C/60"	48°C/60"	72°C/60"	72°C/3'	4°C/∞
ANF1/ANR1	96°C/3'	96°C/60"	48°C/60"	72°C/60"	72°C/3'	4°C/∞
MVZ15/cytB2	96°C/3'	96°C/60"	45°C/60"	72°C/60"	72°C/3'	4°C/∞
Rhod1a/Rhod1C	96°C/3'	96°C/60"	58°C/60"	72°C/60"	72°C/3'	4°C/∞
TyrC/TyrG	96°C/3'	96°C/60"	58°C/60"	72°C/60"	72°C/3'	4°C/∞
H3F/H3R	96°C/3'	96°C/60"	48°C/60"	72°C/60"	72°C/3'	4°C/∞
28sV/28sJJ	96°C/3'	96°C/60"	50°C/60"	72°C/60"	72°C/3'	4°C/∞
RAG1 TG1F/RAG1 TG1R	96°C/3'	96°C/60"	52°C/60"	72°C/60"	72°C/3'	4°C/∞
SIA1/SIA2	96°C/3'	96°C/60"	55°C/60"	72°C/60"	72°C/3'	4°C/∞

Table 2. Primers employed in this study.

Gene region	Primer name	Direction	Primer sequence (5` to 3`)	Reference
16S rDNA	AR	Forward	CGCCTGTTTATCAAAAACAT	Palumbi et al. 1991
	BR	Reverse	CCGGTCTGAACTCAGATCACGT	Palumbi et al. 1991
	L2A	Forward	CCAAACGAGCCTAGTGATAGCTGGTT	Hedges 1994
	H10	Reverse	TGATTACGCTACCTTTGCACGGT	Hedges 1994
	L13	Forward	TTAGAAGAGGCAAGTCGTAACATGGTA	Feller and Hedges 1998
	TITUS 1	Reverse	GGTGGCTGCTTTTAGGCC	Feller and Hedges 1998
12S rDNA	MVZ59	Forward	ATAGCACTGAAAAYGCTDAGATG	Graybeal 1997
	MVZ50	Reverse	TYTCGGTGTAAGYGARAKGCTT	Graybeal 1997
	12S A-L	Forward	AAACTGGGATTAGATACCCCACTAT	Goebel et al. 1999
	tRNAval-H	Reverse	GGTGTAAGCGARAGGCTTTKGTTAAG	Goebel et al. 1999
Cytochrome oxidase subunit 1	LCO1490	Forward	GGTCAACAAATCATAAAGATATTGG	Folmer et al. 1994
	HCO2198	Reverse	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. 1994
	ANF1	Forward	ACHAAYCAYAAAGAYATYGG	Lyra et al. 2017
	ANR1	Reverse	CCRAARAATCARAADARRTGTTG	Lyra et al. 2017
Cytochrome b	MVZ15	Forward	GAACTAATGGCCCACACWWTACGNAA	Moritz et al. 1992
	CytB2	Reverse	AAACTGCAGCCCCTCAGAAATGATATTTGTCCTCA	
Rhodopsin exon 1	Rhod1A	Forward	ACCATGAACGGAACAGAAGGYCC	Bossuyt and Milinkovitch, 2000
	Rhod1C	Reverse	CCAAGGGTAGCGAAGAARCCTTC	Bossuyt and Milinkovitch, 2000
Tyrosinase exon 1	TyrC	Forward	GGCAGAGGAWCRTGCCAAGATGT	Bossuyt and Milinkovitch, 2000
	TyrG	Reverse	TGCTGGCRTCTCTCCARTCCCA	Bossuyt and Milinkovitch, 2000
Histone H3	H3F	Forward	ATGGCTCGTACCAAGCAGACVGC	Colgan et al. 1999
	H3R	Reverse	ATATCCTTRGGCATRATRGTGAC	Colgan et al. 1999
28S rDNA	28sV	Forward	AAGGTAGCCAAATGCCTCATC	Hillis and Dixon 1991
	28sJJ	Reverse	AGTAGGGTAAAACTAACCT	Hillis and Dixon 1991
Recombination activing gene 1	RAG1 TG1F	Forward	CCAGCTGGAAATAGGAGAAGTCTA	Grant et al. 2006
	RAG1 TG1R	Reverse	CTGAACAGTTTATTACCGGACTCG	Grant et al. 2006
Seven in absentia	SIA1	Forward	TCGAGTGCCCCGTGTGYTTYGAYTA	Bonacum et al. 2001
	SIA2	Reverse	GAAGTGGAAGCCGAAGCAGSWYTGCATCAT	Bonacum et al. 2001

General Analytical Approach: Theoretical considerations

Choice of optimality criteria

The choice of the analytical method employed in any scientific inference is arguably one of the most important steps in discovery operations (Grant 2002). Many researchers, however, do not give the necessary attention to this important step. Contrary to the scientific method, subjective values are often evoked to justify the analytical choices; general acceptance or the usage of the most recent and advanced methods are frequently the justification of many colleagues to employ method A instead of B. Moreover, many scientists opt for "not taking sides" and employ different, incomparable methods in order to avoid taking a philosophical position. Such naïve approach ignores the fact that "not taking sides" is *per se* a philosophical stand.

Science should be objective and the scientist should be able to base his choices on philosophical, empirical and/or theoretical grounds. Any method can be evaluated regarding its ability to increase knowledge, and that should guide scientific inference. Methods in phylogenetic systematics use transformations from one character state into another as evidence of historical relationships. As I will argue, parsimony has strong philosophical, theoretical and even operational bases, which makes it a more robust criterion for phylogenetic inference.

Parsimony is a non-parametrical, non-statistical criterion that maximizes hypothesis explanatory power by minimizing the number of causal explanations required for the hypothesis to explain the data (Kluge and Grant 2006); this is known as the principle of anti-superfluity (Barnes 2000; Baker 2003). In phylogenetic systematics, parsimony minimizes the number of evolutionary events required to explain character variation (Grant and Kluge 2009).

By minimizing the required number of events, parsimony increases the explanatory power of a hypothesis. The explanatory power can be defined as the ability of a hypothesis to explain the evidences given the background knowledge. Parsimony assumes only descent with modification (Kluge 2007), and a phylogenetic hypothesis chosen under parsimony optimality will provide the best explanation for character distribution with the minimal background required.

Parsimony relies on popperian refutationism (Kluge 2009) and is coherent with the historical nature of phylogenetic systematics. Phylogenetic systematics, differently from nomothetic sciences such as physics, is an ideographic science, i.e., it deals with singular historical events that have happened in the past. Historical events are singular and not subjected to the laws of statistical frequencies. Each character transformation along the history of a lineage is unique. By treating all characters as individuals (Grant and Kluge 2004), parsimony avoids mistreating unique events as units of a class of events.

Probabilistic model-based approaches such as likelihood, in contrast, are statistical, parametric methods that seek to maximize accuracy by incorporating the most realistic model of evolution. Defenders of likelihood (and similar criteria) mistreat the concepts of historical identity. Likelihood treats individual historical transformations as evidence for classe membership when they try to create distributions for independent, unrelated events. For example, the fact the nucleotide G (guanine) changed to T (thymine) independently in two or three organisms does not provide evidence for the creation of a distribution of probabilities of “Gs turns into Cs” in the future. Even if that transformation occurred in hundreds of individuals, they would still represent individual transformations.

Besides the theoretical inconsistency, likelihood has less explanatory power when compared to parsimony by logic. Maximum likelihood hypotheses necessarily incorporate models of evolution; in other words, they incorporate more elements to the background knowledge, and this will decrease the explanatory power of a given hypothesis.

Many researchers however will ignore the philosophical and theoretical justifications of parsimony and will use operationalists arguments. Since Felsenstein (1978), the default argument has been that parsimony lacks statistical consistency. Several studies have demonstrated that likelihood is inconsistent as well (e.g., Siddal 2001), also suffers from long branch attraction and will perform badly many times.

Additionally, if parsimony is inconsistent whereas probabilistic methods are consistent, one may expect to find great divergence in phylogenetic analysis based on parsimony vs probabilistic methods. Empirical evidence supports the opposite. Rindall and Brower (2011) evaluated 1,000 studies employing both parsimony and probabilistic methods and found that in only three cases the authors complained about topological differences. Goloboff et al. (2017) demonstrated that parsimony outperforms probabilistic methods with phenotypic datasets.

Parsimony is defensible in theoretic, philosophical, empirical and operational grounds, unlike likelihood and other probabilistic approaches. Therefore, I choose parsimony as the optimality criteria for the present study.

Nucleotide homology

As important as the choice of optimality criteria is the alignment method. Slowinski (1998) demonstrated that the number of possible alignments increases exponentially. For example, for a dataset of five taxa and 10 nucleotides, the number of possible alignments is 1.35 X 10^{38}—comparatively, the Milky Way has approximately $2{,}510^{10}$ stars.

Alignment softwares often provide a single alignment without a justification of that choice. This is due to the absence of an objective criteria for choosing among the alignments. Sokal (1965) proposed that tree search and alignment search should be performed simultaneously. Wheeler (1996) provided a computational implementation for this matter—an approach known as direct optimization. According to this procedure, tree search and the hypothetization of optimal homology relationships between nucleotides are performed together. As a consequence, the optimality criteria used for selecting the best hypothesis is the same as used to select the best alignment. I performed a total evidence parsimony analysis and used dynamic homology as implemented in POY for my analysis.

Semaphoront

Hennig (1966: 6) defined the semaphoront as the "organism or the individual at a particular point of time, or even better, during a certain, theoretically infinitely small, period of its life". The concept of semaphoront was central to Hennig theory; semaphoronts are the individuals in which character states are expressed, or in Hennig's words the "character bearer". Thus, the recognition of proper semaphoronts is pivotal for phylogenetic systematics, in which the historical transformation of one character state into another provides the evidence for choosing among the competing hypothesis (Farris 1967; Kluge and Grant 2006).

One difficulty faced is that the delimitation of semaphoronts is not that simple in organisms with complex life cycles such as anurans. Hennig (1966) was aware of this problem and stated that nothing can be said about "how long a semaphoront exists as constant systematically useful entity. It depends on the rate at which its **characters (sic) changes**" (p.6; my bold). Hennig`s definition of a comparable semaphoront was clearly based the expressions of character states.

He went further on this argumentation: "We will call those peculiarities that distinguish a semaphoront (or a group of semaphoronts) from other semaphoront "characters" (p.7). Note that Hennig`s usage of the term character is equivalent to our usage of character-state (see Grant and Kluge 2004: 23). This way, any empirical delimitation of a comparable semaphoront is related to the characters evaluated and on the expression of its states along organism development (Dias and Grant, manuscript in preparation).

Empirical definition – To empirically determine an equivalency of semaphoronts, large ontogenetic series of the most abundant species sampled across the phylogeny of Dendrobatoidea (viz *Rheobates palmatus*, *Dendrobates truncatus*, *Andinobates virolinensis*, *Colostethus* *fraterdanieli*, and *Hyloxalus subpunctatus*) were examined and all the transformational series (including internal morphology) evaluated, to identify developmental stages in which a character state could not be scored due to ontogenetic transformation.

Regarding external morphology and buccopharyngeal cavity, from the time the parent frog deposits the larva in the water until the pre-metamorphosis (around Gosner stage 41), there was no variation in the character state observed, and all species shared the same overall pattern. In the pre-metamorphosis phases, the forelimbs emerge through the spiracle, the mouthparts degenerate and the vent tube retracts; also there are changes in the overall shape of the body and snout, and the tail and tail fins are absorbed; therefore, the characters states associated with the aforementioned structures cannot be scored properly. In other words, there is a developmental transformation in the characters and their states. At this phase, new transformation series could be identified, as well as their own semaphoront; however, this was beyond the scope of this study for several reasons, including: 1) the aim of this study is to address morphological variation in larval morphology, and those pre-metamorphic individuals represent a distinct moment of the anuran`s life-cycle; 2) regarding tadpole biology and population dynamics, few individuals reach this moment, due to predation, completion, etc.. Moreover, the development of frogs from the appearance of the forelimbs to the complete metamorphosis is really fast, as tadpoles suffer more with predation at this stage and as the strong selective pressure accelerates development. Thus, very few individuals are available in collections to identify semaphoronts and transformation series at this phase. Thus, based on my detailed study of these species, free-swimming tadpoles in Gosner stages 25–41 comprise a single, equivalent semaphoront for most of the transformation series I studied.

General Analytical Approach: Implementation

Taxon Sampling

Ingroup selection was driven to cover the largest diversity of poison frogs as possible. Sampling limitation was due to the availability of tadpoles in scientific collections and/or collected in the field. Nevertheless, I was able to include species of all nominal genera of Dendrobatoidea with the exception of *Ectopoglossus* and *Leucostethus.*

In order to have the most complete dataset possible, I mostly included morphological data for species with available DNA sequences or tissues preserved in ethanol, for which molecular sequences could be obtained. Nevertheless, several species with no molecular data were coded with the intention of clarifying their placement and the evolution of characters (e.g., *Andinobates viridis*, *Hyloxalus edwardsi*, *Hyloxalus pinguis*, '*Prostherapis*' *dunni*).

Several dendrobatoid species are well known for having taxonomic issues that include paraphyly, cryptic diversity, synonyms, etc. (see Grant et al. 2017 for further comments). Thus, I tried to shed light in some of these problems by performing the best taxon sampling as possible. For taxa with systematic problems, I directed sampling to cover: 1) as much populations as possible; 2) lineages currently under synonym; 3) representatives of clades recovered in previous (e.g., Grant et al. 2006, 2017; Santos et al. 2009; Pyron and Wiens 2011) phylogenetic analysis.

Whenever as possible, I coded each population individually, or at least representatives of each lineages separately. Unfortunately, however, in some cases I was not able to match several populations to the available DNA evidence; in these situations, the taxonomic and evolutionary boundaries within these species were blurred, and it proved very complicated to associate some of the examined to specific lineages that were hypothesized based on genotypic evidence. In those situations, I opted to code morphological variation as polymorphisms and to duplicate phenotypic entrances for every molecular terminal. Grant et al. (2006: 56) discussed three possible methods to include phenotypic data for specimens coded separately for genotypic data, i.e., in cases in which the individual coded for phenotypic characters is not the same individual that was sequenced:

1) Phenotypic characters coded for each individual separately;
2) Phenotypic data coded for the species as a whole and duplicated for each molecular terminal;
3) Phenotypic data coded for the species as whole, and entered for a single terminal, leaving the other conspecific terminals with molecular data but with missing morphological data.

I agree with Grant et al. (2006) in rejecting the first approach because it may lead to incoherent results due to comparisons among incomparable semaphoronts and to the exclusion of previous evidence (obtained from other individuals not sequenced), which may represent significant part of a matrix. The third approach would lead to a large number of missing entrances that certainly would interfere in character optimization (ambiguous optimizations). Therefore, I opt for the second method, as it maximizes the severity of the test. Below, I specify in which cases more than one lineage was sampled.

The brilliant-tight poison frog, *Allobates femoralis*, is a well distributed species throughout the amazon drainage, from Peru to French Guiana and east Brazilian Amazonia (Frost

2018). Many studies (e.g., Grant et al. 2006, 2017; Simões et al. 2010) pointed to the existence of several lineages under the name *Allobates femoralis*. I examined tadpoles from Loreto, Peru (near the type locality), Brazil, Ecuador and French Guiana. These tadpoles were morphologically very similar and, given that I could not properly assign the coded individuals to particular lineages, I coded the variable characters as polymorphisms for these frogs.

Ameerega trivittata is another phylogenetically diverse group with a wide range distribution (Grant et al. 2006; Frost 2018). Silverstone (1976) reported a large color pattern variation. Grant et al. (2006) sampled 13 populations that covered approximately all the geographic distribution of the species but found low genetic variation within the species—pairwise distances for cytochrome b varied from 0.5% to 3.4%. This led Grant et al. (2017) to include less terminals of *Ameerega trivittata* in their study; they included one individual from Brazil, Acre (Ameerega_trivittata_MPEG12504) and one from Colombia, Letícia (Ameerega_trivittata_TNHCFS9966). I had access to several populations of *Ameerega trivittata* tadpoles: some from Brazilian Amazonian sites, from Letícia, Colombia and from San Martín, Peru. As I found some variation in character-states among these populations, I opted to include another terminal from Grant et al. (2006), (Ameerega_trivittata_MJH7483) from San Martín, Peru (see appendix 4 for GenBank numbers).

As *Allobates femoralis* and *Ameerega trivittata*, *Ameerega hahneli* is also well distributed species. It occurs throughout the Amazonian lowlands, from Peru to French Guiana (Frost 2018), and currently comprises several different lineages (Twomey and Brown 2008). I examined tadpoles from Letícia, Colombia, Puerto Inca, Peru, and Mitaraka, French Guiana. Grant et al. (2006: 136) suggested that the population from Letícia were not conspecific with the remaining sampled specimens, but they were unclear to determine which of these terminals were conspecific with *hahneli sensu stricto*. I included the Peruvian and Colombian populations in the analysis, and data from French Guiana tadpoles were scored for comparisons.

Muñoz-Ortiz et al. (2015) studied the relationships among different populations of *Rheobates palmatus* and *Rheobates pseudopalmatus* in Colombia. They found that many populations grouped as specific clades, a result confirmed by Grant et al. (2017). Given the complex taxonomy for both nominal species and the large phylogenetic diversity, I tried to sample individuals from different clades; I examined individuals from the Central Cordillera, referred to as *Rheobates pseudopalmatus*, and from different populations of the Eastern Cordillera (viz Albán and Tibacuy, Cundinamarca; Restrepo, Meta; Charalalá and San Vicente de Chucurri, Santander).

Tarvin et al. (2017) studied the evolution of aposematism in the genus *Epipedobates*. They provided a phylogenetic tree for the genus and suggested that *Epipedobates boulengeri* represents a polyphyletic assemblage, with one clade as sister to the remaining species and other as sister to

Epipedobates tricolor. However, Tarvin et al. (2017) did not include all available sequences for *Epipedobates* and all sequences of *Epipedobates boulengeri* used in their study are from Bilsa, Ecuador. Grant et al. (2017) found a paraphyletic *Epipedobates boulengeri*, with individuals from the type locality of Gorgona Island, in the Pacific coast of Cauca department, Colombia, as sister to all other *Epipedobates*, and a second less inclusive clade including individuals from Esmeraldas, Ecuador. I examined tadpoles from three different populations of *E. boulengeri* from Gorgona Island, continental populations of Nariño department, also in Colombia, and a third population from Alto Tombo, Esmeraldas, Ecuador. However, no DNA sequences of specimens from Nariño were avaiblable, so data on tadpoles from this locality were not included in the final matrix.

Oophaga pumilio is widely distributed in lowland forests of Caribbean drainage of Central America, from eastern Nicaragua to western Panama (Frost 2018). Many studies, however, have demonstrated that there is a hidden diversity within *Oophaga pumilio*. Haegman and Pröhl (2007) performed an analysis including DNA sequences of three mitochondrial markers for several populations and found two well supported clades (with three genetic lineages), but paraphyletic regarding *Oophaga arborea* and *Oophaga speciosa*. Hauswaldt et al. (2011), while analyzing mitochondrial and nuclear genes plus microsatellites, found similar results: a northern lineage, including Costa Rican individuals, and a southern one, including Costa Rican and Panamanian individuals. Similar results were also found by Galindo-Uribe et al. (2014). I examined different populations of *Oophaga pumilio*—insular individuals from Isla Solarte, Bocas del Toro, Panama, continental Panamanian populations from the national park La Amistad, Changuinola, and Costa Rican populations from Zona Protectora La Selva.

Allobates talamancae is a species distributed from Nicaragua to Colombia. Previous studies (e.g., Grant et al. 2017) found that Central America and South American populations of *Allobates talamancae* formed independent clades. Grant et al. (2017) reported that a specimen from Ecuador differ from individuals of Nicaragua by 9.6% and from Panama by 8.2%. I sampled tadpoles from Panama and from the Colombian Chocó—I also added new DNA sequences from Colombian population, from Quibdo, Cochó—Allobates_talamancae_MCP1306. In the results of Grant et al. (2007), Panamanian and Costa Rican populations formed a supported clade; therefore, I assumed them to be conspecific and code phenotypic evidence from Panamanian tadpoles for both terminals. On the other hand, I had no evidences that Colombian and Ecuadorian terminals would be conspecific, so I coded the phenotypic, larval characters observed in tadpoles of Quibdo, Colombia to a terminal sequenced from the same region.

Lutz (1925) described *Allobates olfersiodes* from Angra dos Reis, Rio de Janeiro, Brazil. Later, Bokermann (1967) described three new *Allobates* associated to *Allobates olfersiodes*—

Allobates alagoanus, *Allobates capixaba*, and *Allobates carioca*. Verdade and Rodriguez (2007) revisited the taxonomic status of the four species and could not find any phenotypic differences among them, concluding that they should be synonymized under *Allobates olfersiodes*. Until very recently, the hypothesis of Verdade and Rodrigues (2007) could not be tested, but Grant et al. (2017) included DNA sequences from two different populations: one from Alagoas state (from the type locality of nominal *Allobates alagoanus*) and another two from Rio de Janeiro state (from a site near the type locality of nominal *Allobates carioca*). They found 15.3% of differences in the pairwise distances of the cyt b, as well as large branch lengths, suggesting that both populations were not conspecifics. Forti et al. (2017) described and compared the acoustic repertory of different populations, including representative samples from a wide range of distribution of *Allobates olfersiodes* and concluded that, in agreement with Bokermann (1967), acoustic parameters support the existence of many taxa under *Allobates olfersiodes*. In the present study, I included samples from different localities; I examined tadpoles from Tijuca, Rio de Janeiro (*Allobates carioca*), Espírito Santo (*Alloabtes capixaba*), Maceió, Alagoas (*Allobates alagoanus*), and from Igrapiúna, Bahia (that may be representative of *Allobates capixaba* or may represent an undescribed species; see discussion on Forti et al. 2017: 148). Unfortunately, I could not find any tadpoles of nominal *Allobates olfersiodes*.

Recently, Grant et al. (2017) revisited the phylogenetics of poison frogs and partially addressed the complex taxonomic problem of the Colombian species complex of *Colostethus fraterdanieli* (see also Grant et al. 2006). They sampled specimens from most of the *Colostethus fraterdanieli* distribution, and found four monophyletic clades, for most of which there were available names. They restricted the first clade that contained individuals from Urrao, Antioquia in the northern Cordillera Occidental, to *Colostethus ramirezi*. A second clade that contained individuals distributed along the Valle del Cauca was recognized as being *Colostethus brachihistriatus*. Finally, they hypothesized *Colostethus fraterdanieli* to be restricted to the third clade that contained individuals from the Cordillera Central. The fourth clade, from Cordillera Occidental, remains a complex taxonomic problem. I examined representatives of all clades found by Grant et al. (2017)—I included *Colostethus ramirezi* from the Parque Natural Las Orquídeas, Urrao (MAR 2781), *Colostethus brachihistriatus* from Pereira, Risaralda (GGD 1084), *Colostethus fraterdanieli* from La Unión (ICN 45928) and Amalfi (MHUA 084), Antioquia. I sample tadpoles from Betania, in the Cordillera Occidental to represent the fourth clade.

Hyloxalus elachyhistus is a widespread Andean species (Frost 2018). Grant et al. (2006: 139) demonstrated that more than one species was conflated within the *elachyhistus* epithet. The optimal hypothesis of Grant et al. (2017) showed that the elachyhistus from Cajamarca, Peru were sister to *Hyloxalus idiomelus*, whereas the population of Piura, also in Peru, was sister to the

Ecuadorian population from Torata-Balsas, El Oro. I examined tadpoles from Ayabaca, Peru and La Mercedez, Ecuador. I associated the tadpoles from La Mercedez to the population of El Oro, separated by approximately 220 Km. Tadpoles from Ayabaca were associated to the terminals of Piura, distant c.a 180 Km, in contrast with Cajamarca, distant c.a 640 Km. Moreover, given the topologies of Grant et al. (2006, 2017) individuals of Cajamarca are not part of the same lineage as Piura + El Oro.

Non-examined material and literature data

Some tadpoles described in the literature could not be personally examined for this study, but I coded part of the characters from the published descriptions and illustrations. Tadpoles of *Allobates chalcopis* and *Allobates mcdiarmid* were respectively described by Kaiser and Altig (1994) and Reynolds and Foster (1992) and were deposited in the scientific collection of the Smithsonian Institution (NMNH). Unfortunately, some of them were damaged or bleached (Kenneth A. Tighe pers.com) and could not be examined. External morphology characters were coded from the original descriptions.

The Venezuelan political instability made it impossible to visit scientific collections in that country, and given their politics of not sending material through postal service, the following Venezuelan taxa were not examined: *Allobates pittieri*, *Anomaloglossus whotuja*, *Aromobates alboguttatus*, *Aromobates duranti*, *Aromobades haydeae*, *Aromobates leopardalis*, *Aromobates mayorgai*, *Aromobates orostoma*, *Aromobates serranus*, and *Mannophryne yustizi*; these species were coded exclusively from literature (La Marca 1985; Mijares-Urrutia 1991; La Marca and Mijares-Urrutia 1997; Mijares-Urrutia and La Marca 1997; Barrio-Amóros and Rivas 2004).

Brown et al. (2008) reviewed the *Ranitomeya fantastica* species complex, described two new species (*Ranitomeya benedicta* and *Ranitomeya summersi*) and provided some data on tadpole morphology for the three species of the group. Unfortunately, they did not provide any voucher numbers for the examined material. According to them, one tadpole of *Ranitomeya benedicta* was destroyed (p.8). They mentioned that all type material was housed at MUSM; during visitation of the collection, no tadpole of any one of three species was found, nor within the tissues collections (Alfredo Guzman, pers.com). Thus, I incorporated only the data provided by Brown et al. (2008).

Twomey and Brown (2008) described briefly the tadpoles of *Ameerega altamazonica*. They referred the material to the East Carolina University field collection (ECU-F; numbers 102–104), but I had no access to that collection; therefore, I only code the few characters possible from their description and illustration.

Brown et al. (2011) described the tadpoles of *Ranitomeya amazonica*, *Ranitomeya flavovitata*, *Ranitomeya imitator*, *Ranitomeya toraro*, *Ranitomeya uakarii* and *Ranitomeya variabilis*, but they did not provide museum voucher numbers for most of the specimens—the exceptions are those of *Ranitomeya vanzolinii* (OMNH 36057) and *Ranitomeya toraro*, for which they said that tadpoles were removed from the back of adult frogs (OMNH 3667 and MPEG 12037). I examined tadpoles from *Ranitomeya amazonica*, *Ranitomeya imitator*, *Ranitomeya toraro* and *Ranitomeya variabilis* from other collections, but I could not examine those used by Brown et al. (2011).

Two species of *Excidobates* were coded from the literature: *Excidobates captivus* (Twomey and Brwon 2008) and *Excidobates mysteriosus* (Schulte 1990). Reiner Schulte (pers.com) informed that the specimens (CRS 13–15) were lost. Twomey and Brown (2008) did not provide any information on voucher numbers for their examined tadpoles. I searched for these tadpoles at MUSM, but with no success.

Hyloxalus azureiventris (Lotters et al. 2000) were coded from the literature as well as from photos kindly provided by Dr. Alexander Kupfer from the Staten Museum of Natural History, Stuttgart. *Ameerega rubriventris* (Lotters et al. 1997) was also coded from the literature and from photos, gently provided by Dr. Flecks Morris and Miss Ursula Bott, from the Zoologisches Forschungsmuseum Alexander Koenig, Bonn. Grant et al. (1997) and Grant and Castro (1998) described tadpoles of *Allobates niputidea* and *Hyloxalus fascianigrus* respectively; I did not have access to those larvae (housed at the Universidad Javieriana [MUJ 3534], Bogota and Universidad del Valle [UVC 11784], Cali, both in Colombia) and the only characters we could code were those provided in the descriptions.

During my visitation to the herpetological collection of INPA, I was not able to find tadpoles of *Allobates hodli, Allobates magnussoni, Allobates tapajos* and *Anomaloglossus stepheni* housed at that collection. I was informed (Ariane Silva, pers.com) that at least part of this material was with Dr. Albertina Lima, who was working in the description of a *Allobates* species. Tadpoles of *Ameerega braccata* described by Haddad and Martins were not located at the ZUEC, CFBH or MZUSP—Haddad and Martins (1994: 295) did not specify which voucher numbers correspond to each individual, adult or tadpole. The tadpoles of *Oophaga granulifera* housed at UCR (10710) were also damaged and dry, as informed me Gerardo Chavez (pers.com). Tadpoles of *Anomaloglossus degranvillei* (Lescure 1984) were not found either. Thus, all the aforementioned specimens were coded from the literature: Lescure (1984); Hersek et al. (1992), Van Wijngaarden and Bolaños (1992), Haddad and Martins (1994), Juncá et al. (1994), Savage (2002), Simões et al. (2010), Lima et al. (2014, 2015).

Some outgroup species were also not observed, and characters were scored from the literature, such as *Alsodes vanzolinii* (Formas and Brieva 2004), *Eupsophus emiliopuginii* (Candioti et al. 2011), *Hylorina sylvatica* (Cárdenas-Rojas et al. 2007a), *Insuetophrynus acarpicus* (Formas et al. 1980; Rabanal and Formas 2009) and *Rhinoderma darwinii* (Lavilla 1987).

Outgroup sampling

Outgroup rationale

Generally, phylogenetic hypotheses are designed to test the relationships within a particular group of interest: the ingroup. However, in order to properly test such relationships, it is necessary to include taxa that are not part of the ingroup: the outgroup. The outgroup selection is essential for a robust phylogenetic hypothesis (Nixon and Carpenter 1993), given that the outgroup taxa and their characters states help to provide biological meaning to cladograms by establishing the polarization of character transformation (Farris 1982). Moreover, outgroups may increase the explanatory power of a phylogenetic hypothesis by providing a severe test to both tree topology and character optimizations. As Farris (1967) made clear (see also Kluge and Grant 2006), phylogenetic hypotheses are composed by two components: a cladistics element, which is related to the tree topology and to the vector relationships between nodes and leaves, and a patristic element, which concerns characters transformations, i.e., homologies and synapomorphies. The selected outgroup taxa may provide a test for both components.

The most obvious way in which an outgroup can refute the cladistic relationships is by being placed as part of the ingroup, refuting its monophyly (Farris 1982). The outgroup may also change the global optimization and the optimal arrangements within the ingroup taxa, resulting in different tree topologies.

Regarding the patristic component, outgroups may interfere in the distribution of character states` optimization within the ingroup (Donoghue and Cantino 1984). The inclusion of new outgroup taxa can also refute transformation series hypothesis by presenting a different state (new or combined/different conditions) and can also refute the hypothesized direction of transformation (0 → 1 into 1 → 0).

Theoretically, outgroup comparison (and rooting) can be done based on a single taxon; the outgroup does not need to form a clade, nor does it need to be the sister taxa of the interest group (Nixon and Carpenter 1993). However, the more outgroup taxa are added, the more severe is the test of homology and relationships. Moreover, sampling the sister taxa increases the probability of refuting cladistic hypotheses (both of its components), because less evidence would have to be refuted (T. Grant unpublished data). Thus, ideally, the best hypothesis would include as much outgroups taxa as possible, with denser sampling among the more closely related taxa.

Outgroup selection

The monophyly of Dendrobatoidea is strongly supported by both phenotypic and genotypic characters (e.g., Noble 1926, Myers et al. 1991; Grant et al. 2006, 2017), and will hardly be put to test. However, the internal relationships, the patristic components as well as the sister taxa relationships can be severely challenged by a broad outgroup selection. Given the above, I tried to target the largest number of outgroups possible. The choice of outgroup taxa was driven by previous knowledge on the relationships of dart-poison frogs. However, note that the incorporation of previous knowledge does not follow a Bayesian approach (see Grant et al. 2006: 39); in Bayesian inference, the prior knowledge (priors) is used in order to constrain hypothesis selections in function of the that knowledge, whereas in the context of outgroup selection I used previous knowledge to maximize the probability of refuting the cladistic and patristic components of the phylogenetic hypotheses, thus, increasing the severity of test (Popper 1959; Kluge 1997, 2009).

Noble (1926) was the first to propose the monophyly of Dendrobatoidea and suggested a close relationship with Hylodidae frogs, a position adopted by other scientists subsequently (e.g., Lynch 1971). Haas (2003), with a dataset composed primarily by larval morphology, found Hylodidae to be the sister group to Dendrobatoidea—although that relationship was supported by two adult characters, viz., the male guiding behavior (character 142) and the T-shaped phalange (character 156). Subsequently, Frost et al. (2006), using a large molecular dataset plus Haas (2003) characters, found *Thoropa miliaris* as sister of Dendrobatoidea, and both as sister to Bufonidae.

In a broad study on poison frogs, Grant et al. (2006) recovered Hylodidae as the sister taxon of poison frogs, and both as sister to Bufonidae. Pyron and Wiens (2011) and Pyron (2014), in studies based on DNA sequences, found Bufonidae to be the sister of all Dendrobatoidea, whereas Hylodidae was distant related.

Zangh et al. (2013) explored the phylogenetic implications of the mitochondrial genome in anurans. They found *Mannophryne trinitatis* and *Dendrobates auratus* as sister to several lineages of Hyloides[*], a very different position when compared to previous studies (e.g., Frost et al. 2006; Grant et al. 2006; Pyron and Wiens 2011; Pyron 2014). Vacher and colleagues (2016) published the complete mitochondrial genome of *Anomaloglossus baeobatrachus* and provided a phylogenomic hypothesis including all available genomes by then. They recovered the four dendrobatoids (*Anomaloglossus baeobatrachus*, *Dendrobates auratus*, *Hyloxalus yasuni*, and *Mannophyne trinitatis*) at the base of Hyloides, as sister to the remaining lineages (including 13 different families).

Recently, Feng et al. (2017) presented a phylogenetic hypothesis of anuran relationships based on genomic data including approximately 88,000 bp from 95 nuclear protein-coding genes. Their results suggested Dendrobatoidea as sister to a large clade containing Brachycephaloidea (*sensu* Padial et al. 2014), Odontophrynidae, Leptodactylidae and Bufonidae—a result incongruent with that obtained previously with their analysis of mitogenomes (Zhang et al. 2013).

In the same year, Grant et al. (2017) revisited the phylogenetic relationships of Dendrobatoidea and, despite not incorporating as many genes as Feng et al. (2017), gathered a large matrix of phenotypic characters and the largest sampling of dendrobatoids so far. Their results suggested that *Thoropa* is the sister group of Dendrobatoidea, as did Frost et al. (2006).

Given the above, it is clear that there is no consensus regarding the sister group of dart-poison frogs. Nevertheless, several independent studies employing different sources of evidence and taxa sampling suggested that Hylodidae, Bufonidae and Cycloramphidae (particularly *Thoropa*) are closely related to Dendrobatoidea. Therefore, I focused the outgroup sampling in those groups—see comments on outgroup above.

Regarding tadpole morphology, I included representatives of all nominal genera of Hylodidae—*Crossodactylus* (7/14), *Hylodes* (16/26) and *Megaelosia* (2/7), covering all the phylogenetic diversity of Hylodidae (Montesinos et al. in prep.). Regarding Cycloramphidae, I included nominal taxa from *Thoropa* (4/6) and *Cycloramphus* (2/28). I did not have access to any nidicolous tadpoles of *Zachaenus*, for which only DNA data was sampled.

Bufonidae is a large cosmopolitan family of toads (Frost 2018). In this study, I focused on the New World lineages that are basal among bufonids (Frost et al. 2006; Pramuk et al. 2008; Pyron and Wiens 2011; Pyron 2014) and more likely to refute cladistic hypothesis regarding poison frogs. I included larval morphology evidence for representatives of most clades of South, Central, and North American bufonids: *Amazophrynella* (2/7), *Anaxyrus* (1/23), *Atelopus* (1/96),

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[*] Hylodes was proposed by Frost et al. (2006) to include all Hyloidea of the traditional usage, excluding Heleophrynidae. They opt for that name to avoid family-group regulation (p.191), so other superfamylies could be recognized. I use this name in that sense.

Frostius (1/2), *Dendrophryniscus* (2/10), *Incilius* (4/39), *Melanophryniscus* (1/29), *Nannophryne* (1/4), *Peltophryne* (1/12), *Rhaebo* (1/13), and *Rhinella* (1/93).

Finally, I also included representative taxa from different clades of Leptodactyliformes (*sensu* Frost et al. 2006). Although Grant et al. (2017) stated that Dendrobatoidea is always recovered within Chthonobatrachia, however subsequent analyses to that of Frost et al. (2006) recovered several lineages of Diphybatrachia nested with Chthonobatrachia. Thus, the most conservative sampling should include taxa from Leptodactyliformes. Given the above, I included species of Alsodidae, Batrachylidae, Centrolenidae, Leptodactylidae and Odontophrynidae in my analysis. Rhinodermatidae taxa were coded only from the literature and for Ceratophryidae I included only DNA sequences. See Appendix 3 for complete list of examined taxa.

Genotypic characters sampling

Given the wide variation in the diversities levels included in this study, I follow Grant et al.`s (2006) reasoning by sampling genes with different degrees of variability. I target the mitochondrial H-strand transcription 1 (H1), which includes 12S ribosomal, tRNA^{val}, and 16S ribosomal sequence (2,400 bp, generated in 5–7 fragments), fragments of the cytochrome oxidase c subunit I (COI; 658 bp), cytochrome b (CytB; 385 bp). Additionally to the fast evolving mitochondrial genes, I target the nuclear protein coding genes histone H3 (328 bp), rhodopsin (316 bp), tyrosinase (532 bp), recombination activating gene 1 (RAG-1; 435 bp), seven in absentia (SIA; 397 bp), and the 28S ribosomal gene (ca. 700 bp)—part of generated sequences were already incorporated in the analysis of Grant et al. (2017).

Additionally, I complemented the dataset by incorporating previously analyzed sequences available at GenBank (NCBI, The National Center for Biotechnology Information); incorporated sequences were generated by: La Marca (2002), Santos et al. (2003, 2009, 2014), Vences et al. (2003), Pauly et al. (2004), Faivovich et al. (2005, 2012, 2014), Wiens et al. (2005), Frost et al. (2006), Grant et al. (2006, 2017), Pramuk (2006), Roberts et al. (2006), Twomey and Brown (2008a,b, 2009), Amaro et al. (2009), Fitzpatrick et al. (2009), Heinicke et al. (2009), Manzanilla-Puppo et al. (2009), Páez-Vacas et al. (2010), Van Bocxlaer et al. (2010), Simões et al. (2010, 2013b), Barrio-Amorós et al. (2011), Brown et al. (2011), Medelson III et al. (2011), Alonso et al. (2012), Amendáriz et al. (2012), Barrio-Amóros and Santos (2012), Fouquet et al. (2012, 2013a,b), Irisarri et al. (2012), Kok et al. (2012, 2018), Peloso et al. (2012), Amézquita et al. (2013), Blotto et al. (2013), Dias et al. (2013), Kiefer et al. (2013), Brandvain et al. (2014), Lima et al. (2014), Rojas et al. (2014); Muñoz-Ortiz et al. (2015), Sá et al. (2015), Machado et al. (2016), Ibáñez et al. (2017), Lyra et al. (2017), Montesinos et al. (in prep).

The complete genomic data included 15 loci (Table 4). The extensive amount of missing data for some terminals does not represent an analytical issue for parsimony (see Choice of Phylogenetic Method section) in opposition to model-based methods (see Goloboff and Pol 2005; Simmons and Goloboff 2013; Padial et al. 2014). Updates in previously published sequences follow Grant et al. (2017). Also, I removed part of the H1 sequence for the terminal "C_fraterdanieli_CZPUV4186" (GenBank accession number MF624209), due to contamination by DNA sequences of a species of *Andinobates*; I included only the last 1664 bp, that in fact correspond to *Colostethus fraterdanieli*. GenBank accession numbers for all sequences employed in this study are listed in Appendix 4.

Phenotypic characters sampling

Character Matrix

The final matrix of larval characters contained 426 terminals of 238 species, including 161 dendrobatoids and 77 outgroup taxa. I included tadpoles of all nominal genera of Dendrobatoidea, with the exception of *Ectopoglossus* and *Leucostethus*, for which there is no available material—tadpoles of species of these genera are not known. Some genera were well sampled, and I included all nominal species (e.g., *Phyllobates*), whereas for others, a single representative was sampled; for the complete list of examined material, see Appendix 3.

Table 3. Gene regions and number of sample terminals.

Gene Region	Number of Terminals
H-strand transcription unit 1 (H1)	621
mitochondrially encoded cytochrome b (cyt b)	357
mitochondrially encoded cytochrome c oxidase I (CO1)	236
rhodopsin exon 1 (RHO)	208
H3 histone family member 3C (H3)	203
recombination activating 1 (RAG1)	182
28S ribosomal RNA (28S)	172
seven in absentia (SIA)	160
tyrosinase exon 1 (TYR)	148
proopiomelanocortin (POMC)	77
solute carrier family 8 member A1 (SLC8A1)	59
brain derived neurotrophic factor (BDNF)	55
bone morphogenetic protein 2 (BMP2)	54
3'-nucleotidase (NT3)	54
zinc Finger E-box binding homeobox 2 (ZEB2)	54

Phenotypic Characters

Character 0 to 169 are related to adult morphology and have been discussed elsewhere (Grant et al. 2006, 2017) and are listed in the Appendix 5. Herein, I comment only the larval phenotypic characters. I separated them by phenotypic systems in order to make the reading easier.

External morphology characters

ORAL DISC

The typical tadpole oral disc is composed by an upper labium with two tooth rows and free edges, a lower labium, usually larger than the upper labium, free on its edges, and bearing three tooth rows, jaw sheaths, marginal papillae surrounding the both labium but with a dorsal gap, and submarginal papillae laterally and lateroventrally (Altig 2006, 2007). Ontogenetically, the oral disc develops surrounding the stomodeum (Thibadeau and Altig 1989), and the presence of ciliated cells characteristic of larval epidermis on the disc face suggests that it is homologous with the general surface surrounding the mouth in other anurans and vertebrates (Altig 2006). This transient feature is usually well formed in hatched tadpoles and atrophy in the pre-metamorphic stages (Gosner 1960 stages 41+). Several transformation series can be observed in the oral disc and its features (Fig. 2).

170. ORAL DISC ORIENTATION: VENTRAL, 0° ANGLE (0); ANTEROVENTRAL OR SUBTERMINAL, 45° ANGLE (1); ANTERIOR OR TERMINAL, 90° (2); UPTURNED, MORE THAN 90° (3). ORDERED. ADDITIVE.

The orientation of the oral disc regarding tadpoles` longitudinal axis (i.e., longitudinal) usually reflects variation of the feeding habits and habitat selection (Altig and McDiarmid 1999). For example, terminal mouths have been suggested to be correlated with macrophagous/carnivorous diets (Altig and Johnston 1989) and have been described in several taxa, as *Ceratophrys* (e.g., Candioti 2005), *Dendropsophus* (e.g., Lavilla 1990) *Leptobatrachus* (Ruibal and Thomas 1988), and *Occidozyga* (e.g., Haas et al. 2014). We follow Altig and Johnston (1989: 83) in considering the main axis as the line connecting the tip of the tail and the point where the myotomes contact the body, and the plane of the oral disc as the line connecting the base of the lower lip with the body. With this in account, we recognized four states: ventral, if the plane of the oral disc is parallel to the body`s longitudinal axis (state 0); anteroventral or subterminal, if the plane forms a 45° angles (state 1); terminal or anterior, when the oral disc plane is perpendicular to the body`s axis (state 2); and upturned, when the mouth is oriented upwards, forming an angle superior to 90° (state 3).

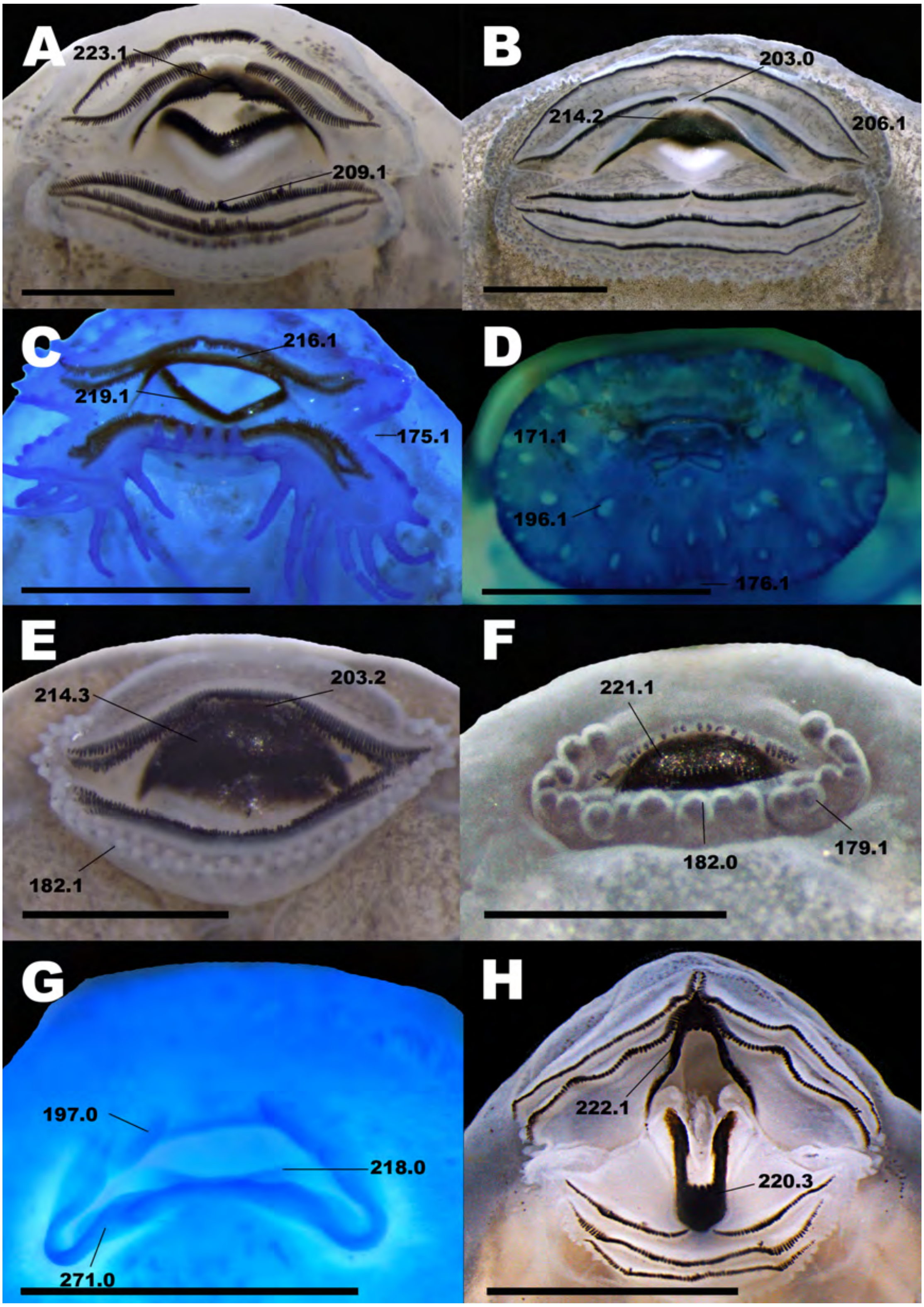

Figure 2. Variation in the oral disc characters within Dendrobatoidea and their relatives. *Colostethus fraterdalieli* (A), *Rheobates palmatus* (B), *Allobates grillisimilis* (C), *Silverstoneia flotator* (D), *Dendrobates truncatus* (E), *Oophaga vicentei* (F), *Anomaloglossus apiau* (G), and *Thoropa miliaris* (H); character and their states pointed. Scale bar = 10 mm.

LARVAL LABIA

There are some evidences that upper and lower labium are independently subject to variation. Altig (2006b: 102) exemplifies it as follows: he evoked the results of Haertel and Storm (1970) on the hybrids of two species of *Rana* that possess different tadpoles with different tooth row formulas—*Rana cascadae* has LTRF 3(2-3/4), *Rana pretiosa* has LTRF 2(2)/3(1) and their hybrid presents LTRF 2(2)/4(1), the upper formula of *pretiosa* and the lower of *cascadae*. According to Altig (2006), this could suggest independent genetic control of teeth rows formation on each labium. Moreover, there several funnel-mouthed tadpoles, as those of the genus *Mantidactylus* that evolved from a regular mouth ancestor but have a modified lower labium (Grosjean et al. 2011); similar condition can be observed in *Megophrys* larvae (e.g., Li et al. 2011), in which the upper lip is more developed than the lower. Given the above, I considered the upper and the lower labia as independently evolving individuals.

171. LOWER LABIUM OCCURRENCE: ABSENT (0); PRESENT (1).

Grant et al. (2006: character 88) used this character in an amalgam with the morphological condition of the labia in a single transformation series, a position changed by Grant et al. (2017: characters 94 and 85) that divided it in two independent characters. Nevertheless, in both works, they treat the oral disc as a single element. Haas (2003: character 7: 54) used this character but, as in Grant et al. (2006), he considered both lips as a single evolutionary individual. The absence of one of the labia in tadpoles in very rare. Nevertheless, some endotrophic nidiculous larvae may present one or both labia absent, as in the Madagascan *Gephyromantis granulatus* (Randrianiania et al. 2011). Within dendrobatoids, the labia are absent, for example, in the larvae of *Anomaloglossus apiau* and *Anomaloglossus stepheni*.

172. UPPER LABIUM OCCURRENCE: ABSENT (0); PRESENT (1).

See comments on character 1.

173. LARVAL LOWER LABIUM MORPHOLOGY: "NORMAL" (0); UMBELLIFORM (1); SUCTORIAL (2); FLAP (4).

Grant et al. (2006: character 88: 95; see also Grant et al. 2017) used this character in his phylogenetic analysis of dart-poison frogs and their relatives, although he did not make a distinction between both labia. As discussed above, each labium can evolve independently, so I divided the Grant et al. (2006; 2017) character in two: one regarding the upper labium and the other regarding the lower labium. When the labia are present, they may present different conformations. Typically, the upper labium is attached to the snout and lack marginal papillae on its medial portion (Altig 2006, 2007), which I refer to as "normal" labium (state 0; Grant et al. 2006, 2017). In the umbelliform, or upturned condition (state 1) the labia are enlarged, and the upper lip is usually free from the snout, has a semi-circular shape and lacks marginal papillae (Grant and Myers 2013). The oral disc of some sectorial tadpoles (state 2) is also enlarged and usually does not fold shut, even in preserved specimens (e.g., *Ascaphus truei*), although this is not a rule. Many species present lateral pleats, which probably seals the mouth (Altig and McDiarmid 1999). Endotrophic tadpoles tend to have a reduction of mouthparts and associated features (e.g., Randrianiania et al. 2011); it happens the same with the labia, that when present, are drastically reduced, forming only a pair of flaps surrounding the mouth`s opening, lacking papillae and every other mouthpart. Most dendrobatoids examined present a regular labial morphology (state 0), but all examined larvae of *Silverstoneia* have umbelliform oral disc (state 1) and several endotrophic tadpoles have reduced labia, giving rise to dermal flaps (state 2), which in some cases, was completely absent (see character 1).

174. LARVAL UPPER LABIUM MORPHOLOGY: "NORMAL" (0); UMBELLIFORM (1); SUCTORIAL (2); FLAP (4).

See comments on character 3.

175. LATERAL EMARGINATION ON THE ORAL DISC: ABSENT (0); PRESENT (1).

Emarginations are indentations on the oral disc (Altig and McDiarmid 1999); in fact, in the literature they have been termed indentation as well (e.g., Silverstone 1975). Emarginations are formed prior to hatching by the extension of a shallow groove that divides the labia superior and inferior (Thibaudeau and Altig 1988); this process is not well known, but apoptosis seems to be a plausible mechanism. Emarginations may occur in different points of the oral disc (see characters 6, 7 and 8). Most dendrobatoids tadpoles possess a lateral emargination on their oral disc, with few exceptions, as *Silverstoneia flotator*. Grant and Myers (2013) suggested that the emargination observed anterolaterally in the oral disc of *Silverstoneia minima* and *Silverstoneia nubicola* should be termed "anterolateral" (p.47). I agree with Grant and Meyers regarding the overall position of the emargination, however, not with the term. Herein, I call it lateral emargination. By inspecting the oral disc of several individuals of different *Silverstoneia* species, I found that the line of the anterolateral emargination can be tracked to the lateral corner of the mouth`s opening, at the point of articulation of upper and lower jaw sheaths, the same as de regular, lateral emargination of other poison frogs. The umbelliform oral disc is formed by the enlargement of the upper and lower lips, however, one lip may develop more than the other, giving rise to such asymmetry;in some taxa, as *Megophrys*, the lips are enlarged only laterally, giving rise to a triangular shape (Leong and Chou 1985; Stuart et al. 2006; Oberhummer et al. 2014; pers. observation), and in some *Mantydactilus* and *Leptodactylodon*, the lower lip is well-developed whereas the upper lip is reduced (Grosjean et al. 2011; Mapoyat et al. 2014). So, I hypothesize that the dislocate lateral emargination of some *Silverstoneia* larvae is the product of unbalanced growth between lips.

176: CENTRAL EMARGINATION ON THE LOWER LIP: ABSENT (0); PRESENT (1).

As discussed above, emarginations may occur at different points of the oral disc. In the *Silverstoneia* larvae, there is a central emargination on the lower lip (Dunn 1924; Ibáñez and Smith 1995; Savage 2002; Grant and Myers 2013). Besides finding this emargination present in all *Silverstoneia*, I also observed this state (state 1) in all *Crossodactylus* tadpoles.

177. VENTROLATERAL, PAIRED EMARGINATION ON THE LOWER LIP: ABSENT (0); PRESENT (1).

Contrasting with the central emargination (see character 6), in some taxa there is a pair of emarginations on the lower lip; they are located laterally, following, approximately, the lines of the lower jaw. The presence of these paired emarginations (state 1) was observed in outgroup taxa, as *Proceratophrys appendiculata* and *Thoropa* species, for instance. This character was described by de Sá and Langone (2002), that described the larva of *Proceratophrys avelinoi*; the authors mentioned that the "two folds of the posterior labium" (p.493) could be considered a diagnostic character for the genus *Proceratophrys*. The usage of the term folds is becoming common in the literature regarding the larvae of that genus (e.g., Nascimento et al. 2010; Dias et al. 2014); however, herein I follow Altig and McDiarmid (1999: 37) in distinguishing folds from emarginations with a careful inspection of the oral disc aperture. Thus, I suggest the usage of emargination instead of folds for this character state.

178. CENTRAL EMARGINATION ON THE UPPER LIP: ABSENT (0); PRESENT (1).

This character reflects the exact same condition as character 6, but for the upper lip. The presence of such emargination was restricted to *Silvertoneia erasmios* and *Silverstoneia nubicola*.

MARGINAL PAPILLA

The oral discs are very often bordered with marginal papillae that may vary in density, size, length, shape, orientation, and pigmentation (Altig and Johnston 1986; Altig 2007). Altig and McDiarmid (1999: 37) recognized four different possible arrangements for marginal papillae: 1) completely distributed around the oral disc, with no gap, which is a rare condition, present specially in suctorial forms (e.g., *Colomascirtus lindae*; Duellmand and Altig 1978); 2) presenting a dorsal gap (or diastema), which is the most taxonomically and ecologically common (e.g., *Proceratophrys bigibbosa*; Dias 2018); 3) ventral gap only, which is very uncommon; and 4) dorsal and ventral gaps, typical of bufonids, but also occurring in other families (e.g., *Rhaebo hematiticus*; McDiarmid and Altig 1990). Altig and Johsnton (1989) recognized a fifth condition, the total absence of papillae (p.83), which is very often the condition presented by endotrophic tadpoles (e.g., *Frostius pernambucensis*; Cruz and Peixoto 1982). Embriologically, the marginal papillae are formed after the formation of jaw sheaths. The ventrolateral margin of the oral disc is the first to differentiate from the surrounding area and marginal papillae appear first in that area than in any other portion of the oral disc (Thibaudeau and Altig 1988; Altig 2006b). Given the difference in time formation plus the fact that gaps on different portions of the oral disc can vary in every different combination, I hypothesize that different regions of the oral disc can suffer different pressures and evolve independently from each other. Thus, I divided the oral disc into four regions: 1) medial region of the lower lip; 2) medial region of the upper lip; 3) ventrolateral region, lower lip; and 4) dorsolateral region, upper lip. I used the mouth`s corner as a landmark to define the ventrolateral and the dorsolateral regions, i.e., tracing a straight line on the mouth`s corner, I considered ventrolateral the region from that line until the division (emargination) between the lower and upper lip; the same for the dorsolateral in the upper lip.

179. SHAPE OF MARGINAL PAPILLAE, MEDIAL REGION, LOWER LIP: CONICAL (0); ROUNDED (1).
I recognized two shapes for the marginal papillae in dart-poison frogs and their relatives: conical (state 0) and rounded (state 1). These states have been described in the literature of poison frogs, although with different terminologies. For instance, Simões and Lima (2012:86) stated that the tadpoles of *Allobates sumtuosus* have "pyramidal" (what I am calling conical) papillae on the upper lip and rounded in the lower lip; Haddad and Martins (1994) call the conical papillae "pointed". Given the tridimensional shape of the marginal papillae, I found conical a more accurate term. Within dart-poison frogs, the conical papillae are the most common, and few taxa, as *Oophaga*, present the rounded condition.

180. SHAPE OF MARGINAL PAPILLAE, VENTROLATERAL REGION, LOWER LIP: CONICAL (0); ROUNDED (1).
See character 12.

181. SHAPE OF MARGINAL PAPILLAE, DORSOLATERAL REGION, UPPER LIP: CONICAL (0); ROUNDED (1).
See character 12.

182. ORGANIZATION OF MARGINAL PAPILLAE, MEDIAL REGION, LOWER LIP: STRAIGHT (0); ALTERNATED (1).

Marginal papillae usually occur in a single row (uniserial), although in several taxa it may be biserial or even multiserial (e.g., Sánchez 2010). In some taxa the marginal papillae may be organized alternately, emulating the biserial condition (Altig and McDiarmid 1999) as is in most dendrobatoids (state 1). Nevertheless, the straight, uniserial condition is also observed in several taxa, as *Anomaloglossus baeobatrachus*.

183. ORGANIZATION OF MARGINAL PAPILLAE, VENTROLATERAL REGION, LOWER LIP: STRAIGHT (0); ALTERNATED (1).

See character 15.

184. ORGANIZATION OF MARGINAL PAPILLAE, DORSOLATERAL REGION, UPPER LIP: STRAIGHT (0); ALTERNATED (1).

See character 15.

185. SUBMARGINAL PAPILLAE, MEDIAL REGION, LOWER LIP: ABSENT (0); PRESENT (1).

In some tadpoles, several papillae may occur on the face of the oral disc, usually in packs, parallel to the line of marginal papillae (Altig and McDiarmid 1999); generally, they are located close to the lateral end of tooth rows, but, in some cases, they can be ventral to the lower teeth row. In some particular cases, the submarginal papillae may be scattered on the face of the oral disc and present a round, elongated form. Developmentally, they are derived from the same totipotent tissue surrounding the stomodeum (Thibaudeau and Altig 1988; Altig 2006). Most poison frogs lack submarginal papillae (Grant et al. 2006), but several outgroup taxa presented it. As I did for marginal papillae, I also recognized that submarginal papillae may occur independently in different regions of the oral disc.

186. SUBMARGINAL PAPILLAE, VENTROLATERAL REGION, LOWER LIP: ABSENT (0); PRESENT (1).

See character 18.

187. SUBMARGINAL PAPILLAE, VENTROLATERAL REGION, LOWER LIP: ABSENT (0); PRESENT (1).

See character 18.

188. SUBMARGINAL PAPILLAE, DORSOLATERAL REGION, UPPER LIP: ABSENT (0); PRESENT (1).
See character 18.

189. SUBMARGINAL PAPILLAE, MEDIAL REGION, LOWER LIP, SHAPE: CONICAL (0); PRESENT (1).
When present, submarginal papillae, as well as marginal ones, may vary regarding their shape. I also recognized two states for this character (see character 12).

190. SUBMARGINAL PAPILLAE, VENTROLATERAL REGION, LOWER LIP, SHAPE: CONICAL (0); PRESENT (1).
See character 21.

191. SUBMARGINAL PAPILLAE, DORSOLATERAL REGION, UPPER LIP, SHAPE: CONICAL (0); PRESENT (1).
See character 21.

192. SUBMARGINAL PAPILLAE, MEDIAL REGION, LOWER LIP, SIZE: SMALL, WIDER THAN LONGER (0); MEDIAL, APPROXIMATELY AS LONG AS WIDE (1); LARGE, LONGER THAN WIDER.
Submarginal papillae may vary regarding their size. Differently from the approach used in the marginal papillae, in which there is a significant amount of variation, I evaluated the size of submarginal papillae by taking into account its length and width. I opt for this approach given that I did not observed any relation between density and size; there were always few (two or three) submarginal papillae.

193. SUBMARGINAL PAPILLAE, VENTROLATERAL REGION, LOWER LIP, SIZE: SMALL, WIDER THAN LONGER (0); MEDIAL, ABOUT AS LONG AS WIDE (1); LARGE, LONGER THAN WIDER.
See character 24.

194. SUBMARGINAL PAPILLAE, DORSOLATERAL REGION, UPPER LIP, SIZE: SMALL, WIDER THAN LONGER (0); MEDIAL, ABOUT AS LONG AS WIDE (1); LARGE, LONGER THAN WIDER.
See character 24.

195. SUBMARGINAL PAPILLAE, SCATTERED ON THE FACE OF LOWER LIP: ABSENT (0); PRESENT (1).
In some tadpoles, the submarginal papillae, instead of following the line of marginal papillae, are scattered along the face of the oral disc (Altig and McDiarmid 1999). This condition is generally

present in the upturned, umbelliform larvae. The presence of this submarginal papillae (state 1) is characteristic of *Silverstoneia* larvae (Dunn 1924; Savage 1968; 2002; Ibáñez and Smith 1995; Grant and Myers 2013). It is interesting to note that several other umbelliform tadpoles of different families present the same kind of submarginal papillae—*Leptodactylodon* (e.g., Cruz et al. 2012; Mapoyat et al. 2014); *Mantidactylus* (e.g., Grosjean et al. 2011); *Megophrys* (e.g., Leong and Chou 1985; Stuart et al. 2006; Oberhummer et al. 2014) *Phasmahyla* (e.g., Cruz 1980, 1982; Carvalho-e-Silva et al. 2009).

196. SUBMARGINAL PAPILLAE, SCATTERED ON THE FACE OF UPPER LIP: ABSENT (0); PRESENT (1).

See character 195.

LABIAL TOOTH RIDGES AND TOOTH ROWS

Tooth ridges are transverse features on the face of the oral disc that vary interspecifically in number, length, position and shape (Altig and McDiarmid 1999). On these ridges there are mitotic sites arranged linearly, from which labial teeth develop (Altig 2006), although the entire surface of the oral disc seems to be potent for teeth formation (Thibaudeau and Altig 1988). Tooth ridges are high and flexible structures, that may contribute to a plasticity in the position of the labial teeth during feeding (Altig 2006). Such variation in the tooth ridges may be useful for tadpoles to grasp on to substrates, or it may contribute to fixation in torrent, suctorial forms. Altig (2006: 99) suggested that the flexible ridges contribute to the motion of fluid particles during feeding. Altig (1970; see also Altig and McDiarmid 1999; Altig 2007) proposed a notation system to designate the tooth rows, that can also be applied to tooth ridges; according to that system, the most distal row of the upper lip will be A-1, and the subsequent rows would A-2, A-3…A-N, where "N" is the total number of rows in the upper lip. On the lower lip, the most proximal row, i.e., the closest to the mouth, would be noted as P-1, and the subsequent rows P-2, P-3…P-N. If one wants to refer to the labial tooth ridges instead of tooth rows, he should add an "R"; in this case the first tooth ridge is AR-1, and so forth. Ontogenetically, dermal ridges appear in a specific order: AR-1 + PR-1 AR-1 + PR-2, PR-1, AR-2, PR-3 (but see Candioti et al. 2011 for variation from this general pattern). In many taxa, the tooth ridges are medially interrupted, creating gaps, which are formed due to incomplete development of the ridges (Thibaudeau and Altig 1988). Both tooth ridges and rows can be expressed as a formula in short notation (Altig 1970) by giving the number of rows on the upper and in the lower lips separated by an "/", with the interrupted (if present) rows expressed in parenthesis. For instance, a tadpole with two superior and three inferior rows, in which the second superior and the first posterior rows are interrupted, presents the labial tooth row formula (LTRF) of 2(2)/3(1). Tooth ridges and labial teeth develop in different moments and independently (Thibaudeau and Altig 1988). Moreover, it is not uncommon to observe species in which the tooth ridges are completely formed, but lack labial teeth, as occurs in some *Silverstoneia* tadpoles. These facts suggest that labial teeth and tooth ridges evolve independently and, therefore, should be treated as different individuals during character conceptualization, as emphasized by Altig (2006: 102). He attested that "the formation of tooth ridges is independent then of and occurs ontogenetically prior to the presence of mitotic beds for tooth formation in the ridges". Thus, I considered tooth ridges and tooth row as different historical individuals and coded different characters for each of them. Regarding the tooth ridges, I coded each row independently as absent/present, the presence of gaps and, in some cases, the extension of the gaps.

197. LABIAL DERMAL RIDGE, AR-1: ABSENT (0); PRESENT (1).

198. LABIAL DERMAL RIDGE, AR-2: ABSENT (0); PRESENT (1).

199. LABIAL DERMAL RIDGE, PR-1: ABSENT (0); PRESENT (1).

200. LABIAL DERMAL RIDGE, PR-2: ABSENT (0); PRESENT (1).

201. LABIAL DERMAL RIDGE, PR-3: ABSENT (0); PRESENT (1).

202. AR-1, GAP: ABSENT (0); PRESENT (1).

203. AR-2, GAP: ABSENT (0); PRESENT, SHORT (1); PRESENT, LARGE (2). ADDITIVE.
The second anterior tooth row is very often the most variable among tadpoles. The presence of a gap or not has been used in several studies as an important taxonomic character. For instance, Dias et al. (2014: 191) discussed the possible loss of the gap in AR-2 in the genus *Proceratophrys*, suggesting it as a putative synapomorphy for the *Proceratophrys appendiculata* clade. Nevertheless, few authors discussed the extension of such gap; Dias (2018), for example, noted that in the species of the *Proceratophrys bigibbosa* group the gap on AR-2 was larger than in other species of *Proceratophrys*, when present; in *Proceratophrys bigiboosa*, *Proceratophrys avelinoi*, and *Proceratophrys palustris* the AR-2 gap is very wide and the upper jaw sheath occupies its medial portion, in contrast with other species, in which the gap is restricted to a small area above the apex of the upper jaw sheath. He suggested this condition as a putative synapomorphy for the *Proceratophrys bigibbosa* group. I observed this large gap (state 2) in all

Dendrobatini minus the Central American *Phyllobates* (*lugubris* and *vittatus*) and "*Colostethus*" *ruthveni*. I also found this character state present in several *Allobates* tadpoles.

204. PR-1, GAP: ABSENT (0); PRESENT (1).

205. PR-2, GAP: ABSENT (0); PRESENT (1).

LABIAL TOOTH ROW AND KERATODONTS

Usually, the tooth ridge present keratodonts or labial teeth on is borders (Altig and McDiarmid 1999). The may provide stabilization during feeding (Wassersug and Yamashita 2002; Altig 2006) and may vary in size, shape and. The tooth row formula (LTRF) is species specific (Altig and McDiarmid 1999: 41) and is very often used in taxonomic and evolutionary studies (e.g., Haas 2003; Grant et al. 2006; Dias et al. 2014). As occur in tooth ridges, teeth formation follows a general order: A1 + P2, P1, A2, P3 (Thibaudeau and Altig 1988), however, some deviation exists (e.g., Candioti et al. 2011), including in dart-poison frogs (e.g., Anganoy-Criollo 2013). Altig and Johnston (1989: 89) proposed a system in which the number of tooth rows of both upper and lower lips are used to calculate a balance value; they recognized three conditions: 1) balanced, if the number of tooth rows in upper and lower lips are equal (e.g., LTRF 3/3 > 0, balanced; 2) positively imbalanced, in which the number of upper lip are superior to those of the lower lip (e.g., LTRF 4/3 > +1; 3) negatively imbalanced, in which there are more rows on the lower lip than on the upper lip (e.g., LTRF 2/3 > -1)—the most common condition. In some taxa (e.g., ascaphids, discoglossids), the tooth rows may be organized in a biserial way, possibly as a compensation for the total number of rows (Altig and Johnston 1989). I coded the presence/absence of teeth in each tooth ridge. Given that all specimens examined in the present study, including outgroup taxa, present at most two superior and three inferior rows, I limited the number of characters to reflect that range of variation. However, I stress that in other taxa, as in many hylids and ranids, there are up to 17 superior and 21 inferior tooth rows (Altig and Johnston 1989).

206. A-1, LABIAL TEETH: ABSENT (0); PRESENT (1).

207. A-2, LABIAL TEETH: ABSENT (0); PRESENT (1).

208. P-1, LABIAL TEETH: ABSENT (0); PRESENT (1).

209. CONTINUITY OF LABIAL TEETH ON P-1: CONTINUOUS (0); DISCONTINUOUS (1).

As discussed above (see comments on tooth ridges), gaps may be present in the dermal ridge structure. Nevertheless, in some particular cases, as pointed by Altig (2007b: 2 malformations), the tooth row gap may be present due to the absence of teeth in part of the ridge (state 1), even when the tooth ridge is intact and complete, creating a discontinuity in the labial teeth row. Such a condition has been reported in the literature as a true gap on the tooth row—for example, La Marca (194) described the tadpole of *Mannophryne riveroi* as having the LTRF 2(2)/3(1); personal examination of tadpoles of that species showed that the P-1 gap is in fact an interruption of the labial teeth, and the tooth ridge is complete. I considered it a false gap, that may have evolved to compensate the absence of gap on the ridge, although it is only a hypothesis. This false gap was observed in taxa of different lineages (e.g., *Colostethus brachyhistriatus*, *Aromobates saltuensis*). If the species presents a true gap on PR-1, this character becomes inapplicable.

210. P-2, LABIAL TEETH: ABSENT (0); PRESENT (1).

211. P-3, LABIAL TEETH: ABSENT (0); PRESENT (1).

212. P-3, RELATIVE SIZE REGARDING P-2: SHORTER THAN P-2 (0); EQUAL TO P-2 (1).

Among dart-poison frogs the P-3 row is the most variable regarding its length. In some taxa it may be shorter than the P-2 (state 0), as in several *Ameerega*, whereas in others it is about the same size (state 1), as in most *Colostethus*. In all examined specimens, it was never longer than P-2.

JAW SHEATHS

The jaw sheaths are keratinized structures present in the oral disc of anuran larvae, also known as "beaks"; they are well-developed in most anurans, with the exception of pipoids and microhylids (Orton 1953; Starrett 1973; Haas 2003). The column cells that form the units of the jaw sheaths appear by Gosner (1960) stage 23 (Thibaudeau and Altig 1988) and the keratinization process begins first on the upper jaw and then on the posterior jaw sheath; in the same stage the traditional serrations begin to form. The jaw sheaths function as the primary food removal feature in tadpoles (Altig 2006) and may present different conditions, although difficult to describe their morphologies (Altig and McDiarmid 1999). Usually, the upper jaw sheath is an arch-shaped structure with a pair or lateral processes, with serrated borders and well-keratinized, whereas the lower jaw sheath is a v-shaped structure, also with serrated border (Altig 1970; Altig and McDiarmid 1999). Several deviations from this pattern have been reported in the literature; for instance, some *Ansonia* tadpoles have the upper jaw medially interrupted (e.g., Inger 1985; 1992; Haas and Das 2008) and in *Meristogenys*, both jaws are divided (e.g., Matsui et al. 2010). Projections like fangs, as in *Leptodactylodon* (e.g., Mapoyat et al. 2014), or notches, as in many poison frogs (e.g., Sánchez 2013), are also common. Within dart-poison frogs I found variation in the occurrence, development, keratinization, shape and structure of the jaw sheaths.

213. UPPER JAW SHEATH: ABSENT (0); PRESENT (1).

The upper jaw sheath was present in almost all individuals examined. Exceptions were the endotrophic tadpoles of *Allobates nidicola*, *Allobates masniger*, and *Anomaloglossus apiau*. I also coded absent for the tadpoles of *Anomaloglossus stepheni* and *Anomaloglossus degranvillei*, based on the literature (Lescure 1984; Juncá et al. 1994).

214. UPPER JAW SHEATH, KERATINIZATION: ABSENT (0); PRESENT, ONLY IN THE EXTERNAL BORDER (1); PRESENT IN APPROXIMATELY 50% OF THE JAW AREA (2); FULLY KERATINIZED (3). ADDITIVE.

There is some controversy regarding whether the jaw sheaths and the larval teeth are or not pigmented. Despite the available evidences that jaw sheaths present some granules of pigment (e.g., Fellers et al. 2001), it is more likely that the dark color present in the jaw sheaths is due to the keratinization process. Altig (2007b: 2) provided several arguments against the pigmentation view; a strong argument provided is the fact that many albino tadpoles presented dark-colored jaw sheaths and labial teeth (see also Luna et al. 2012). In dart-poison frogs I found variation in the degree of keratinization of jaw sheaths. In some tadpoles, the dark-colored area is restricted to the border of the jaw sheaths (state 0); this is the condition of most *Allobates* tadpoles—also of several bufonids. Most of the taxa, instead, present a large proportion, c.a. 50%, of the jaw sheath area keratinized (state 1). In Dendrobatini, I observed a third condition in which the entire jaw sheath was keratinized (state 2).

215. STRUCTURE OF THE MARGIN OF UPPER JAW SHEATH: SMOOTH (0); WITH A MEDIAL PROJECTION (1); WITH A MEDIAL NOTCH (2).

Sánchez (2013) discussed the significance of the medial notch on the upper jaw sheaths of dart-poison frogs. According to Sánchez (2013), most dendrobatoids present a medial notch (his W condition), whereas the smoot margin (his U condition) would be restricted to Dendrobatinae minus *Phyllobates* and some other few species (e.g., *Hyloxalus sylvaticus*). I found the same overall pattern as Sánchez, with some differences in some taxa (e.g., *Hyloxalus sylvaticus*, contra Duellman and Wild 1993; *Colostethus panamansis*, contra Sánchez 2013). I also observed some outgroup taxa with this medial notch (e.g., *Limnomedusa macroglossa*). Also, in the outgroup taxa I found a third condition (state 1), in which the medial region of the upper jaw sheath is projected ventrally; this condition was particular common in Hylodidae larvae.

216. UPPER JAW SHEATH, SHAPE: ARCH (0); TRAPEZOID (1); INVERTED V (2); LATERALLY COMPRESSED, CYLINDRICAL (3).

Altig and McDiamird (1999: 44) commented on the difficulty of recognizing the overall shape of the jaw sheaths. Nevertheless, it is possible to recognize some patterns. I found that in most poison frogs, the upper jaw sheath presents an arch form, with a constant curvature from one lateral process to another (state 0). In several *Allobates*, however, the transition from the lateral process to the main body of the jaw sheath is angular, conferring a trapezoid shape to the upper jaw sheath (state 1); this is also the shape observed in several bufonids. Hylodids, in general, present a massive upper jaw sheath that extends dorsally, conferring an inverted "V" morphology (state 2). In Cycloramphidae larvae, both upper and lower jaws are laterally compressed (Bokermann 1965; Heyer 1983; Cocroft and Heyer 1988); in those species, the jaw sheaths assume a more cylindrical shape (state 3).

217. UPPER JAW SHEATH, LATERAL PROCESS: ABSENT (0); PRESENT (1).

In most anuran larvae, the lateral margin of the upper jaw sheath is expanded laterally, forming a lateral process. I could not detect the lateral process in some tadpoles (e.g., some *Dendrobates*).

218. LOWER JAW SHEATH: ABSENT (0); PRESENT (1).

Lower jaw sheaths were present in all examined tadpoles, including those in which the upper jaw was lacking (see character 45); however, in those taxa they were completely lacking keratinization, although it was still possible to identify the V-shaped jaw basis (see Altig 2007b 4). Nevertheless, Juncá et al. (1994) and Lescure (1984) stated that the lower jaw was absent in *Anomaloglossus stepheni* and *Anomaloglossus degranvillei*. As I did not examine those specimens personally, I followed the authors in their statements.

219. LOWER JAW SHEATH, KERATINIZATION ABSENT (0); PRESENT, ONLY IN THE EXTERNAL BORDER (1); PRESENT IN APPROXIMATELY 50% OF THE JAW AREA (2); FULLY KERATINIZED (3). ADDITIVE.

220. LOWER JAW SHEATH, SHAPE: ARCH (0); V-SHAPED (1); LATERALLY COMPRESSED, CYLINDRICAL (3).

See character 47.

221. ROBUSTNESS OF JAW SHEATHS: SIMPLE, CORRESPONDING TO LESS THAN 50% OF ORAL DISC HEIGHT (0); MASSIVE, CORRESPONDING TO MORE THAN 50% OF ORAL DISC HEIGHT (1).

In many dendrobatoids, particularly in Dendrobatini, the jaw sheaths are well-developed. Silverstone (1975) noticed this and call this condition “massive”, although he did not provide a way to measure it. I propose that if the height of both jaw sheaths corresponds to more than 50% of the oral disc, they should be treated as massive jaw sheaths (state 1).

222. AXIS OF MAJOR DEVELOPMENT OF THE JAW SHEATHS: HORIZONTAL (0); VERTICAL (1).

Usually, the jaw sheaths are laterally wide and with variable height. In other cases, however, the jaw sheaths are higher than wider. In this character I use the length and the width of the jaw sheaths to determine those axis.

223. SHELF: ABSENT (0); PRESENT (1).

In some taxa there is a scouring surface on the upper jaw sheath, the shelf (Fig. 3), which is more common in hylids. This character was first described by Cadle and Altig (1991) in tadpoles of *Colomascirtus armatus*. Duellman et al. (1997) revised the systematics of the Andean *Colomascirtus armatus* and *Boana pulchella* species groups; they defined the shelf as “a broad plate below the serrations on the upper jaw sheath” (p. 13) and used its presence as a diagnostic character. Sánchez (2010) also employed the presence of the shelf in his diagnosis of the tadpoles of the then *Hyloscirtus* larvae. This character has been poorly studied, and it was not described in many occasions, even when present; for instance, in figure 6B of Haas et al. (2012), there is a similar feature in the upper jaw of *Rhacophorus penamorum*, although the authors did not mention it. Anganoy-Criollo and Cepeda-Quilindo (2017) and Dias et al. (2018) almost simultaneously* reported the presence of the shelf in several tadpoles of unrelated dendrobatoids, but both studies suggested the presence of that feature as a putative synapomorphy for the genus *Epipedobates*—Anganoy-Criollo and Cepeda-Quilindo (2017) confirmed it in *Epipedobates anthonyi*, *Epipedobates boulengeri*, *Epipedobates narinensis*, and *Epipedobates tricolor,* and Dias et al. (2018) confirmed it in *Epipedobates darwinwallacei* and *Epipedobates espinosai*, besides the aforementioned species. Herein, I confirm the findings of both studies and expanded the codification of the character for all examined tadpoles.

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*When Anganoy-Criollo and Cepeda Quilindo`s (2017) paper came out, the manuscript by Dias et al. was already accepted for publication in South American Journal of Herpetology.

224. STRUCTURE OF DORSAL MARGIN OF UPPER LIP: SMOOTH (0); CRENELLATED (1).

When not bordered by marginal papillae, the margin of the oral disc may present an irregular surface with small indentations that provide a faired aspect. The presence of a crenellated margin (state 1), is particularly common in *Silverstoneia* larvae.

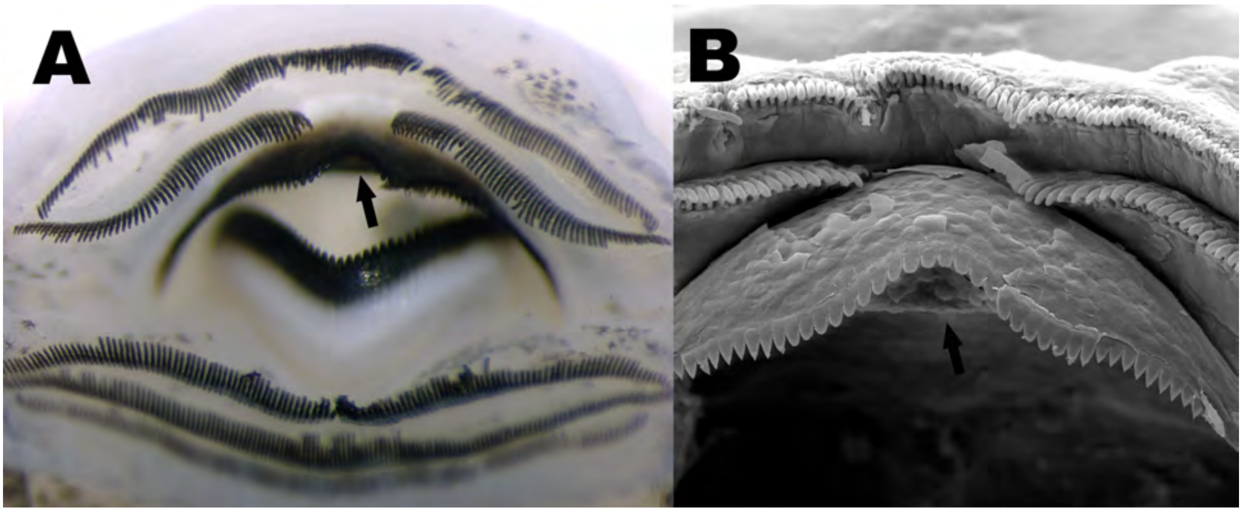

Figure 3. Details of the upper jaw sheath of *Colostethus fraterdanieli* (A) and SEM images of the upper jaw of *Colostethus ramirezi* (B) showing the shelf behind the medial notch.

225. STRUCTURE OF VENTRAL MARGIN OF LOWER LIP: SMOOTH (0); CRENELLATED (1).

See character 56.

226. BODY SHAPE, DORSAL VIEW: ELLIPTICAL (0); CYLINDRICAL (1); GLOBULAR, PLUMP (2).

Tadpoles bodies can vary drastically in their shape (Altig and McDiarmid 1999). In dorsal view, I recognized three different morphologies: in the first (state 0), the body is wider medially to posteriorly, and is very similar to an ellipse or oval-shape; this is the most common shape presented by dart-poison frog larvae. In the second condition (state 1), the body presents a constant, regular width, with a slight curvature, resulting in the appearance of a cylinder; this state was observed in some taxa, as *Ameerega hahneli*. The third state (state 1) was observed mainly in Dendrobatini; in this condition, the body is almost uniform in width, slightly larger at the level of the eyes (rather than posteriorly), with rounded body edges.

227. SNOUT SHAPE, DORSAL VIEW: OVAL, SLIGHTLY ROUNDED (0); RHOMBOID (1).

Rhomboid snout was observed in most Dendrobatini larvae.

228. BODY SHAPE, LATERAL VIEW: OVAL (0); DEPRESSED (1).

In lateral view, I recognized two different conditions. In state 0, the body is oval, very often shorter at the gular/branchial region and taller at the intestines area. In state 1, the body is short, and uniform in height, from the vent to the snout; this condition is common in Dendrobatini tadpoles.

229. SNOUT SHAPE, LATERAL VIEW: ROUNDED (0); TRUNCATED (1).

In lateral view, the snout may be rounded, with smooth curves (state 0), or it may present a more gradual sloping, and turns more abruptly downward near the oral disc, resulting in a truncated shape (state 1).

230. BUMPS, ANTERIOR VENTRAL SURFACE OF THE BODY: ABSENT (0); PRESENT (1).

In ventral view, some tadpoles, particularly the predaceous Dendrobatini tadpoles, present a pair of protuberances in the anteroventral surface, near the oral disc corner; these bumps are the external evidence of a well-developed hyoangularis muscle and robust Meckel`s cartilage.

231. BUMPS, LATEROVENTRAL SURFACE OF THE BODY: ABSENT (0); PRESENT (1).

In lateral view, the well-developed orbitohyoideus forms a bump slightly anterior to the eyes (state 1). This condition was common in Dendrobatini tadpoles.

232. ANTERIOR, MEDIAL, BODY DEPRESSION: ABSENT (0); PRESENT (1).

Haddad and Pombal (1995) were the first to describe this "ventral depression anterior to the region of the coiled intestine" (p.284) and Pombal et al. (2003) suggested it as a synapomorphy for the genus *Hylodes*. I found this character state present in several hylodids, as well as in some poison frogs.

233. DARK THROAT COLLAR, WITH WHITE BANDS: ABSENT (0); PRESENT (1).

Silverstone (1976: 7) was the first to describe this character as a "dark brown transverse band on the posterior portion of the throat" in species of his *femoralis* group. That character-state consists of subcutaneous melanophores distributed in two (well-marked or not) transverse bands in the peribranchial area. Although some other dendrobatoid species present dark coloration on the anterior ventral surface (e.g., *Allobates femoralis*), the presence of these two bands is exclusive to *Epipedobates*.

SPIRACLE

The spiracle is the opening through which the water exits the buccopharynx (Altig 2007). Developmentally, it is formed by interactions between the opercular fold and the body wall, which may create variation in the position, aperture, degree of attachment, and orientation of the spiracle in free living tadpoles (Altig and McDiarmid 1999). Historically, the spiracle has been used in the systematics of anurans. Orton (1953) proposes groups of frogs based on mouthparts, and number and position of spiracle. Her system, as updated by Starrett (1973) comprises four groups:

Type 1 or Xenoanura: including Pipidae and Rhinophrynidae—paired ventral spiracle; mouthparts lacking.
Type 2 or Scoptanura: including Microhylidae—single medial spiracle; mouthparts lacking.
Type 3 or Lemanura: including Ascaphidae and Discoglossidae—single ventromedial spiracle; mouthparts present.
Type 4 or Acosmanura: including the remaining (then) frogs—single lateral spiracle; mouthparts present.

Several other authors used and discussed different conditions of the spiracle. For example, Kluge and Farris (1969) started the era of quantitative phylogenetics and the spiracle was present among their characters. I found several individual transformation series regarding the spiracle morphology within poison frogs (Fig. 4).

234. SPIRACLE: ABSENT (0); PRESENT (1).

The spiracle was present in most examined species, including back-riders tadpoles of *Silverstoneia* (*contra* Grant and Myers 2013). The only tadpoles lacking spiracle were the endotrophic larvae of *Allobates* and *Anomaloglossus*.

235. SPIRACLE, SHAPE: TUBULAR (0); CONICAL (1).

I considered the spiracle tubular if its width was constant from the basis to the aperture.

236. INNER WALL OF THE SPIRACLE: ABSENT (0); PRESENT (1).

In some taxa, the opercular fold is poorly developed and the inner wall of the spiracle is absent in free living larvae. This may generate two conditions: a) the spiracle is a simple hole in the abdominal wall, as in *Thoropa miliaris*; b) the inner wall of the spiracle is formed only by the body wall, as in *Phyllobates terribilis*.

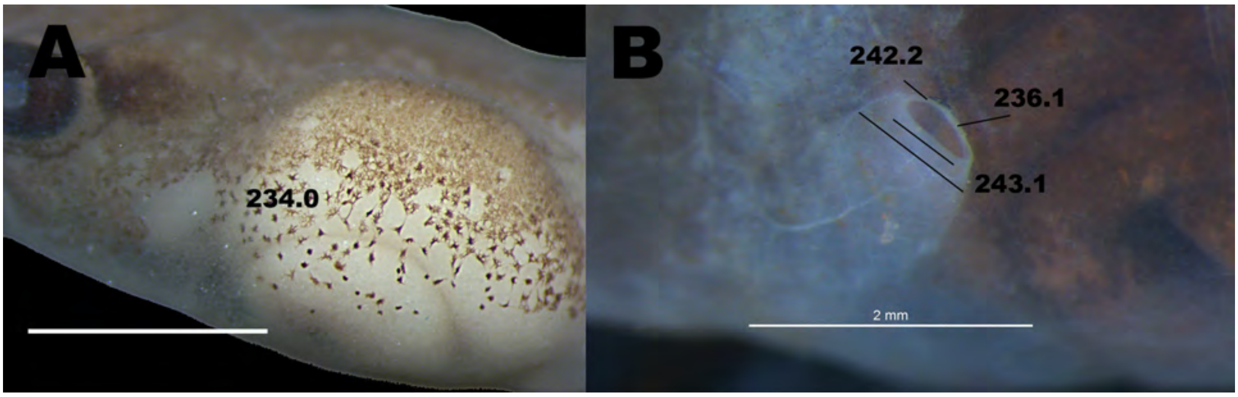

Figure 4. Absence of the spiracle in *Allobates masniger* (A), and character variation in the spiracle of *Ameerega flavopicta* (B). Scale bar = 2 mm.

237. INNER WALL OF THE SPIRACLE, DEGREE OF FUSION: COMPLETELY FUSED (0); FREE MEDIALLY AND DISTALLY (1); FREE DISTALLY (2); ONLY THE BORDER FREE (3).

When present, the inner wall is the point of attachment of the spiracle to the body. In most dendrobatoids, the two initial thirds of the spiracle are attached to the body and only its terminal portion is free (state 2). In some taxa (e.g., *Epipedobates anthonyi*) this free portion is smaller, and only the terminal borders are free, as simple projections of the tube (state 3).

238. SPIRACLE, MARGIN STRUCTURE: SMOOTH (0); IRREGULAR (1).

239. SPIRACLE, OPENING SHAPE: ROUNDED (0); ELLIPTICAL (1).

240. SPIRACLE, POSITION REGARDING THE MEDIAL, LONGITUDINAL AXIS OF THE BODY: AT THE SAME LINE (0); BELOW (1); VERY LOW, DISLODGED TO NEAR THE VENTRAL SURFACE OF THE BODY (2).

Tracing a longitudinal line from snout to tail tip, the spiracle of most dendrobatoids is located below that line (state 1). In Dendrobatini tadpoles, the spiracle is lower than that, and is located on the edge of the lateral/ventral surfaces of the body (state 2). In some rare cases, as in *Allobates kingsburyi*, I found the spiracle positioned at the level of the longitudinal line (state 0).

241. SPIRACLE, ANGULATION REGARDING THE LONGITUDINAL AXIS: PARALLEL TO THE LONGITUDINAL AXIS (0); DORSAL (1).

Considering the same longitudinal line of character 240 and considering the spiracle axis as a straight line from its basis to its aperture, the spiracle of most dendrobatoids and their relatives forms an angle of 30–45° with the longitudinal axis. The effect is that in poison frogs, the spiracle is dorsal. In few taxa, as *Silverstoneia erasmios*, the spiracle axis is approximately parallel to the longitudinal axis (state 0).

242. INNER WALL OF SPIRACLE, RELATIVE SIZE: EQUAL TO EXTERNAL WALL (0); SMALLER THAN EXTERNAL WALL (1); LARGER THAN EXTERNAL WALL (2).

Usually, the inner wall of the spiracle is more developed than the external wall; i.e., the length of the free edge of the inner wall is larger than that of the external wall; thus, when observed in lateral view, the inner wall of the spiracle is always visible (state 2). In few tadpoles, the external wall of the spiracle growth larger than the inner wall, and, in lateral view, it obstructs the inner wall (state 1), as in some populations of *Ameerega hahneli*.

243. SPIRACLE, RELATIVE SIZE OF ITS OPENING: EQUAL TO SPIRACLE WIDTH (0); SMALLER THAN SPIRACLE WIDTH (1).

I scored the state 0 whenever the spiracle opening diameter was approximately equal to the spiracle diameter immediately before the opening. In several tadpoles, however, the diameter of the aperture was smaller than diameter of the spiracle tube (state 1).

244. SPIRACLE, PIGMENTATION: FREE OF PIGMENTS (0); WITH SCATTERED MELANOCYTES AND WHITE BORDER (1); ONLY SCATTERED MELANOCYTES (2).

The spiracle may vary significantly from the body color; it may lack pigments (state 0) or present a clear white stripe on the border (state 1).

245. EYES POSITION: DORSAL (0); LATERAL (1).

According to Altig and McDiarmid (1999), lateral eyes are typically larger than dorsal yes, and it is possible to see them from the ventral view (state 1); in dart poison frogs, lateral eyes were very rare, occurring in few taxa, as in the nidicolous tadpole of *Anomaloglossus apiau*. I followed this definition, and I also recognized that position and orientation of eyes should be treated as different characters.

246. EYES ORIENTATION: LATERAL (0); ANTEROLATERAL (1).

I recognized that the orientation of the eyes varies independently from its position. I recognized two conditions for eye orientation. In state 0, the axis running through the center of pupil forms a straight line with the longitudinal axis of the tadpole. In the anterolateral eyes, the intersection between both axis forms an angle of 30–45°.

247. IRIS ORNAMENTATION: ABSENT (0); WITH A RING (1).

In several tadpoles, both alive and preserved, it was possible to identify a white circle in the iris, around the pupil (state 1). This circle was present in several taxa, as *Anomaloglossus tamacuarensis*, *Hyloxalus elachyhistus*, among others.

248. EYE SIZE: REGULAR (0); REDUCED (1); LARGE (2).

249. EXTERNAL NARES: ABSENT (0); PRESENT (1).

The external nares were present in all dendrobatoids, but they were very reduced in some endotrophic tadpoles. In one particular case, I could not find the external nares in *Allobates nidicola*; the nares were simple concavities in the snout. Although it may be an error, I coded the polymorphism for the species.

250. EXTERNAL NARES, POSITION: DORSAL (0); LATERAL (1).

I followed the same criteria used to delimit eye position. See character 245.

251. EXTERNAL NARES, ORIENTATION: LATERAL (0); ANTEROLATERAL (1); FORWARD (2).

I followed the same criteria used to delimit eye orientation. See comments on character 246.

252. EXTERNAL NARES, OPENING SHAPE: ELLIPTICAL (0); ROUNDED (1); RENIFORM (2).

The shape of external nares opening varies considerably within dendrobatoids (Fig. 5). In state 2, reniform, I considered only the narial shape *per se*, excluding the marginal rim.

253. PLANE OF NARIAL OPENING: AT THE LEVEL OF SURROUNDING SURFACE (0); BELOW SURROUNDING SURFACE (1); PROMINENT, ABOVE SURROUNDING SURFACE (2).

Considering the plane surrounding the narial opening, it is possible to see that the narial aperture may be located slightly below (state 0) or even above the surrounding surface (state 2), although in the most common condition it is located at the same level (state 1).

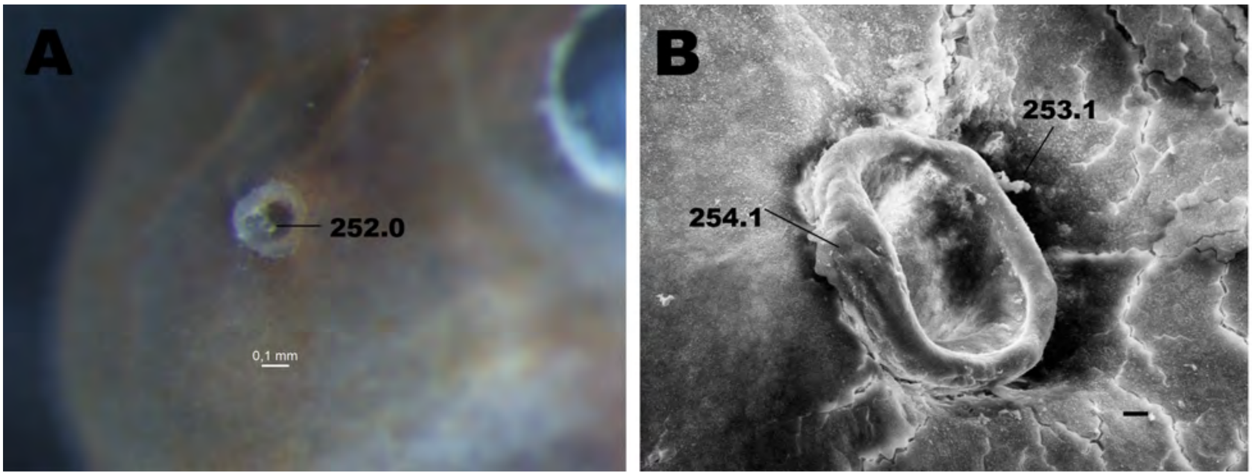

Figure 5. External nares of the tadpole of *Ameerega flavopicta* (A). SEM detail showing the marginal rim (B). Characters and their states are indicated.

254. Fleshy rim: absent (0); present in all narial opening (1).

In most anurans, the border of the external nares is surrounded by a marginal rim. This rim is present in most species, but I found some tadpoles lacking it (state 0), as some *Thoropa*. Altig and McDiarmid (1999) stressed that this rim may vary in development and structure, which I found to vary independently and are treated as other characters.

255. Structure of the marginal rim: flat (0); prominent upward (1).

In some species, the marginal rim is low, flattened, and restricted to the border of the narial opening (state 9). In other cases, it is robust, well-developed, and prominent. When observed in a sagittal plane, the prominent marginal rim (state 1) is clearly distinguished from the surrounding surface.

256. Structure of the marginal rim: smooth (0); irregular (1).

Several hylodids present the marginal rim irregular, crenulated (state 1). State 1 was present in few dendrobatoid, as *Hyloxalus maculosus* and *Hyloxalus chrocraspedus*.

257. Lateral projection on the inner margin of the nares: absent (0); present (1).

Sánchez (2013) described the variation of this character in Dendrobatoidea. I found that most species present the lateral projection of the marginal rim.

258. Structure of the ventral wall the body: smooth (0); modified into a belly sucker [gastromizophorous] (1).

Altig and Johnston (1989) proposed the ecomorphological guild of gastromizophorous tadpoles to contemplate tadpoles with a belly sucker, which they hypothesized as being a specialization for living in fast-flowing waters. Gan et al. (2015: 55) followed the same thought and considered gastromyzophorous tadpoles a subclass of suctorial tadpoles. Gastromyzophorous tadpoles evolved independently several times in three different families: Bufonidae, Hylidae, and Ranidae (Candioti et al. 2017a). In the present study, I included gastromyzophorous tadpoles of the bufonid genus *Atelopus* (Fig. 6), and character state 1 was restricted to them.

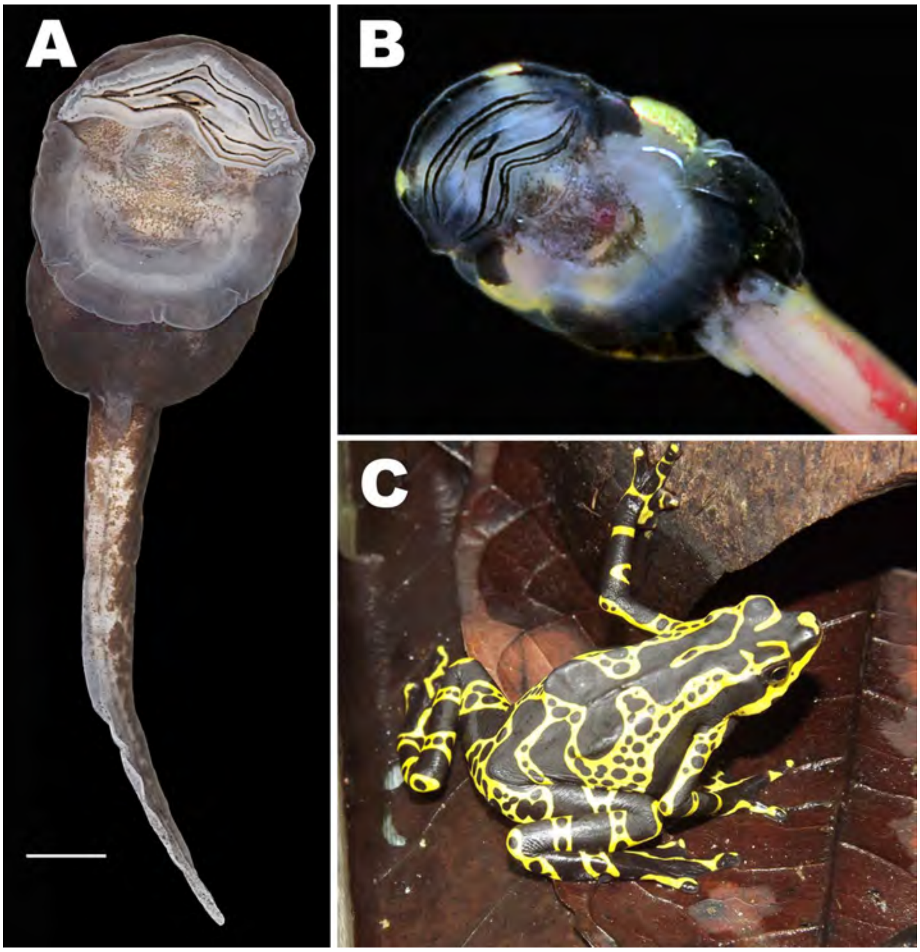

Figure 6. Ventral view of the tadpole of *Atelopus carrikeri* (A) and living specimens of *Atelopus subornatus* (B) and *Atelopus* sp. Note the presence of the belly sucker. Scale bar = 10 mm. *Atelopus subornatus*, photo by Marvin. Anaganoy.

259. STRUCTURE OF THE VENTRAL, POSTEROLATERAL BODY: SMOOTH (0); FORMING A DERMAL EXPANSION POSTEROLATERALLY (1).

In most of cycloramphid larvae, the posterolateral portion of the body presents a dermal expansion (state 1; Fig. 7). This character was first described by Bokermann (1965) and possibly represents a specialization for semi-terrestrial life style (Dias et al. in prep.).

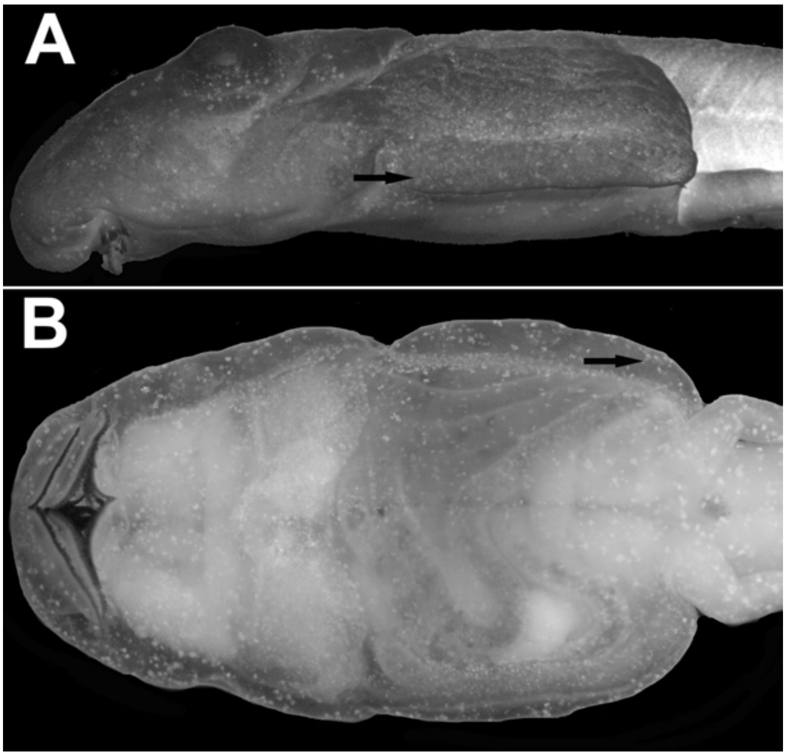

Figure 7. Lateral (A) and ventral (B) views of the tadpole of *Cycloramphus braceiensis*, showing (arrows) the posterolateral dermal expansion.

VENT TUBE

Altig and McDiarmid (1999: 33) discuss the usage of vent tube, anus, and cloaca. The digestive tract of tadpoles ends in an external tube. Such vent tube is often associated with the ventral fins, and may vary regarding size, shape, orientation, and degree of attachment to ventral fin. The vent tube as a character(s) has been used in the systematics of frog for more than 200 years, since Camerano (1890). Even nowadays, it plays an important role in our understanding of frog relationships; for example, this year Dias (2018) proposed that the conical vent tube would represent an unambiguous synapomorphy for the poorly known *Proceratophrys bigibbosa* species group. Below I address all variation observed in poison frogs.

260: VENT TUBE, OPENING: OPEN (0); CLOSED (1).

Most frogs present an open vent tube; however, non-feeding tadpoles sometimes present a closed vent tube, which makes senses given they clearly don`t need to eliminate feces. I found this condition in some endotrophic tadpoles, as *Frostius*.

261. VENT TUBE, POSITION: MEDIAL, AT THE SAME PLANE AS VENTRAL FIN (0); RIGHT, LATERAL TO VENTRAL FIN (1).

This character has been used in Dendrobatoidea systematics for many years. Silverstone (1975) defined species groups based on several characters, including the position of the vent tube. In the most common condition, the vent tube is located at the right side of the ventral fin (state 1), but in many dendrobatini it may be positioned at the same plane as the ventral fin in a medial condition (state 0).

262. VENT TUBE, OPENING DIRECTION: MEDIAL (0); RIGHT (1).

I recognized that the position of the vent tube regarding the ventral fin and the direction of its aperture represent different transformation series. In other words, even in the medial vent tube, for example, its aperture may be direct towards the right (state 1).

263. VENT TUBE, SHAPE: CONICAL (0); TUBULAR (1); ENLARGED DISTALLY (2).

I considered the vent tube tubular (state 1) if the diameter of the tube was constant from the origin of the vent tube until its aperture. If the diameter of the base was larger than that of the extremity, I considered it conical (state 0). In some rare cases, as in *Atelopus*, the greatest diameter is on the aperture level (state 2).

264. VENT TUBE, LEFT WALL ATTACHMENT: ATTACHED TO THE LATERAL MARGIN OF VENTRAL FIN (0); FREE FROM VENTRAL FIN (1).

If the spiracle is dextral, then it attaches (or not) to the ventral fin`s left wall.

265. VENT TUBE, DORSAL WALL ATTACHMENT: ATTACHED TO THE LATERAL MARGIN OF VENTRAL FIN (0); FREE FROM VENTRAL FIN (1).

This character is applied only for medial vent tubes.

266. VENT TUBE, LEFT WALL, EXTENSION OF ATTACHMENT: FULLY ATTACHED (0); MEDIALLY ATTACHED (1); ATTACHED AT THE BASIS (2).

For comments on how I evaluated the degree of fusion of the vent tube, see comments on the spiracle attachment, character 237.

267. VENT TUBE, DORSAL WALL, EXTENSION OF ATTACHMENT: FULLY ATTACHED (0); MEDIALLY ATTACHED (1); ATTACHED AT THE BASIS (2).

Same as character 266.

268. VENT TUBE, POSITION REGARDING THE VENTRAL FIN IN LATERAL VIEW: POSITIONED ABOVE THE LINE OF THE VENTRAL FIN (0); POSITIONED AT THE SAME LINE AS THE DISTAL MARGIN OF THE VENTRAL FIN (1).

Faivovich (2002) was the first to employ this character in a cladistic analysis. Echevería (2004) studied the vent tube in several anurans. She recognized the terms "external tube" for the vent tube that followed the margin of the ventral fin (state 1), and "non-marginal external tube" when the vent tube was located above the line of the ventral fin (state 1). In dart poison frogs both conditions were observed, although the character state 1 was more common.

269. VENT TUBE, ORIENTATION REGARDING BODY`S LONGITUDINAL AXIS IN LATERAL VIEW: PARALLEL TO LONGITUDINAL AXIS (0); VENTRALLY DIRECTED, FORMING A 30–45° ANGLE WITH THE LONGITUDINAL AXIS (1).

Considering the longitudinal axis, the line connecting the tail tip and the snout of the larvae, and the vent tube axis the line traced from its basis to its aperture, in lateral view both lines may be parallel (state 0), or the vent tube may be ventrally directed, and both lines will form an angle of 30–45°.

270. VENT TUBE, ORIENTATION REGARDING BODY`S LONGITUDINAL AXIS IN VENTRAL VIEW: PARALLEL TO LONGITUDINAL AXIS (0); LATERALLY DIRECTED, FORMING A 30–45° ANGLE WITH THE LONGITUDINAL AXIS (1).

In ventral view, the axis of the vent tube may be parallel to the tadpole`s longitudinal axis or pointing to the right; see character 269.

271. VENT TUBE, LENGTH: SHORT, NEAR THE BODY WALL (0); LONG, FORMING A LARGE TUBE (1); SHORT, ALMOST FUSED AT THE BODY WALL (2).

In some taxa, particularly in outgroup species, the vent tube is almost absent, and the exit of the digestive tract is through a small aperture in body`s wall (state 2). In other cases, it may be short, if its length is about the same size as its diameter (state 0) or long, if its longer than the diameter (state 1).

272. VENT TUBE, OPENING SHAPE: ELLIPTICAL (0); ROUNDED (1).

273. VENT TUBE, MARGIN TEXTURE: SMOTH (0); IRREGULAR (1).

274. DORSAL FIN, ORIGIN: AT THE BODY/TAIL JUNCTION (0); AT THE POSTERIOR THIRD OF THE BODY (1); POSTERIOR TO BODY/TAIL JUNCTION, ON THE TAIL (2).

The anuran dorsal fin usually originates near the body tail junction. I follow Altig and Mcdiarmid (1999) and Altig (2007) in delimiting body and tail. Under their concept, three states can be recognized for the origin of dorsal fin: at the body/tail junction (state 0), at the posterior third of the body (state1), or even on the tail (state 2).

275. TAIL TIP, SHAPE: ROUNDED (0); ACUTE (1).

The tip of the tail is formed by the junction of the dorsal and ventral fin posteriorly. In some species such junction is abrupt, and the tail tip is acute. In other species, as in most dendrobatini, the tail tip is rounded.

276. CAUDAL MUSCLES, EXTENSION: NOT REACHING THE TAIL TIP (0); REACHING THE TAIL TIP (1).

In most poison frogs, the myotomes of the tail do not extend until the tip of the tail, and the terminal portion of the tail is composed only by the dorsal and ventral fins. In some taxa, however, the myotomes reach the tail tip, and no or very few fins can be observed (state 1).

277. DORSAL FIN, RELATIVE HEIGHT REGARDING BODY`S HEIGHT: REGULAR, ABOUT THE SAME HEIGHT OR HIGHER THAN THE BODY (0); LOW, LOWER THAN BODY`S HEIGHT, BORDERING CAUDAL MUSCLES.

In cycloramphid larvae, both dorsal and ventral fins are poorly developed and in lateral view they are at approximately the same height as the tadpole`s body (state 1); this state was not observed out of Cycloramphidae).

278. VENTRAL FIN, RELATIVE HEIGHT REGARDING BODY`S HEIGHT: REGULAR, ABOUT THE SAME HEIGHT OR HIGHER THAN THE BODY (0); LOW, LOWER THAN BODY`S HEIGHT, BORDERING CAUDAL MUSCLES.

See character 277.

279. DORSAL FIN, SHAPE: ARCH-SHAPED, BOTH EXTREMITIES WITH THE SAME SLOPE (0); STRAIGHT LINE, SAME ANGULATION ALONG ITS EXTENSION (1); SIGMOID, PROXIMALLY LOW, GRADUALLY INCREASING ITS HEIGHT (2).

280. VENTRAL FIN, SHAPE: ARCH-SHAPED, BOTH EXTREMITIES WITH THE SAME SLOPE (0); STRAIGHT LINE, SAME ANGULATION ALONG ITS EXTENSION (1); SIGMOID, PROXIMALLY LOW, GRADUALLY INCREASING ITS HEIGHT (2).

281. VENTRAL FIN, MARGIN STRUCTURE: SIMPLE (0); WITH A MEDIAL GROOVE (1).

Barth (1956: 490) noticed the presence of a "projection edge" of the tail of the tadpole of *Thoropa miliaris*, however, he mentioned the absence of tail fins for that species. The first to formally describe this character state were Cocroft and Heyer (1983). They recognized that *Thoropa saxatilis* had a groove on the ventral portion of the tail. Histological cross sections and SEM images of the tail of *Thoropa miliaris* showed that this groove is formed by the ventral fin (Fig. 8). This character state was restricted to species of *Thoropa*.

LATERAL LINE SYSTEM

The lateral line system (Fig. 9) is a mechanoreceptive and electroreceptive system that evolved in amniotic vertebrates (Lannoo 1987; Quinzio et al. 2014). Schlosser (2002a,b) revised the lateral line system in anurans. He used the lateral line placodes to establish hypothesis of homology between each individual line. Most anurans present the stitches of the lateral line well-developed and easy to identify under stereoscopic. In other cases, these stitches are not observable. I considered each lateral line to be a historical individual and, for each of them, I code the presence or absence of its stitches. Grant et al. (2006) used this character in his phylogenetic analysis, however, he treated the lateral line system as a single character. Following Grant et al. (2006: 96) I also highlight the need for caution in interpreting "absence", as it may only be an inability to detect the stitches.

282. STITCHES OF THE SUPRAORBITAL LATERAL LINE: ABSENT (0); PRESENT (1).

283. STITCHES OF THE ANTERIOR PIT LATERAL LINE: ABSENT (0); PRESENT (1).

284. STITCHES OF THE INFRAORBITAL LATERAL LINE: ABSENT (0); PRESENT (1).

285. STITCHES OF THE MIDDLE PIT LATERAL LINE: ABSENT (0); PRESENT (1).

286. STITCHES OF THE PREOPERCULAR LATERAL LINE: ABSENT (0); PRESENT (1).

287. STITCHES OF THE GULAR LATERAL LINE: ABSENT (0); PRESENT (1).

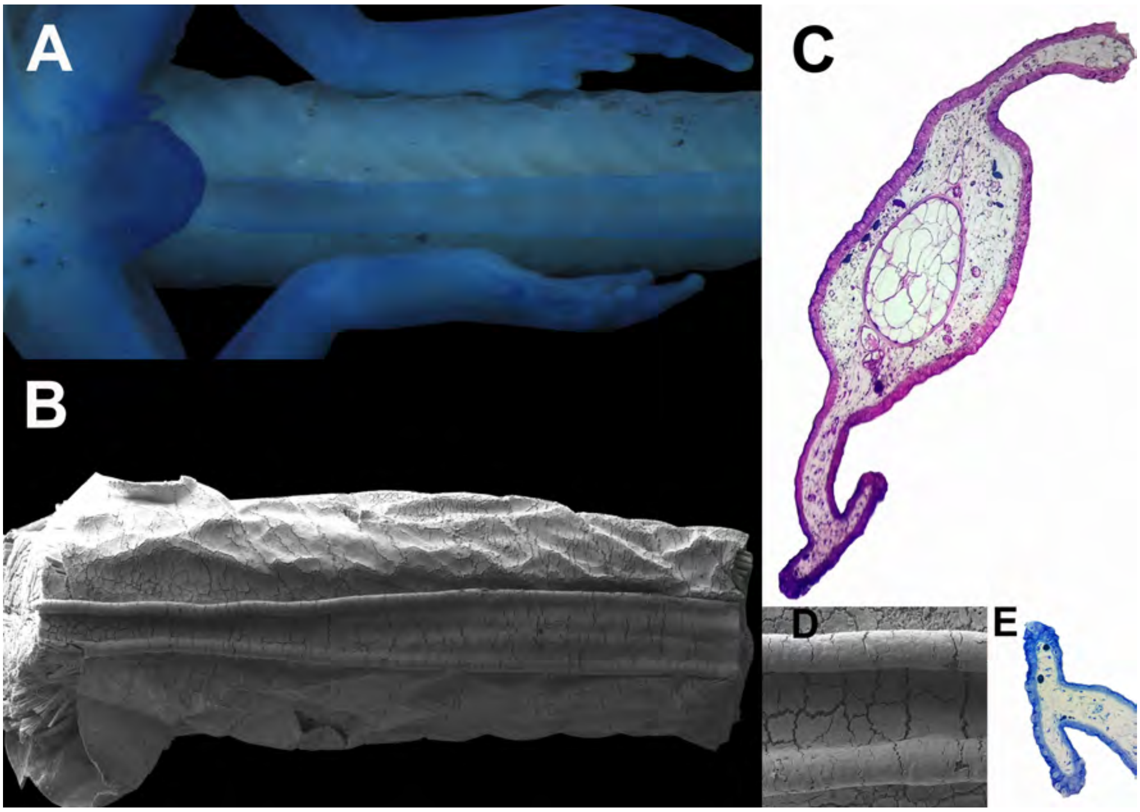

Figure 8. Ventral fin of tadpoles of *Thoropa miliaris* (A) forming a medial groove. SEM images (B) and cross section (C) of that structure. SEM (D) and histological (E) details of the ventral fin tip, showing no differentiated tissue.

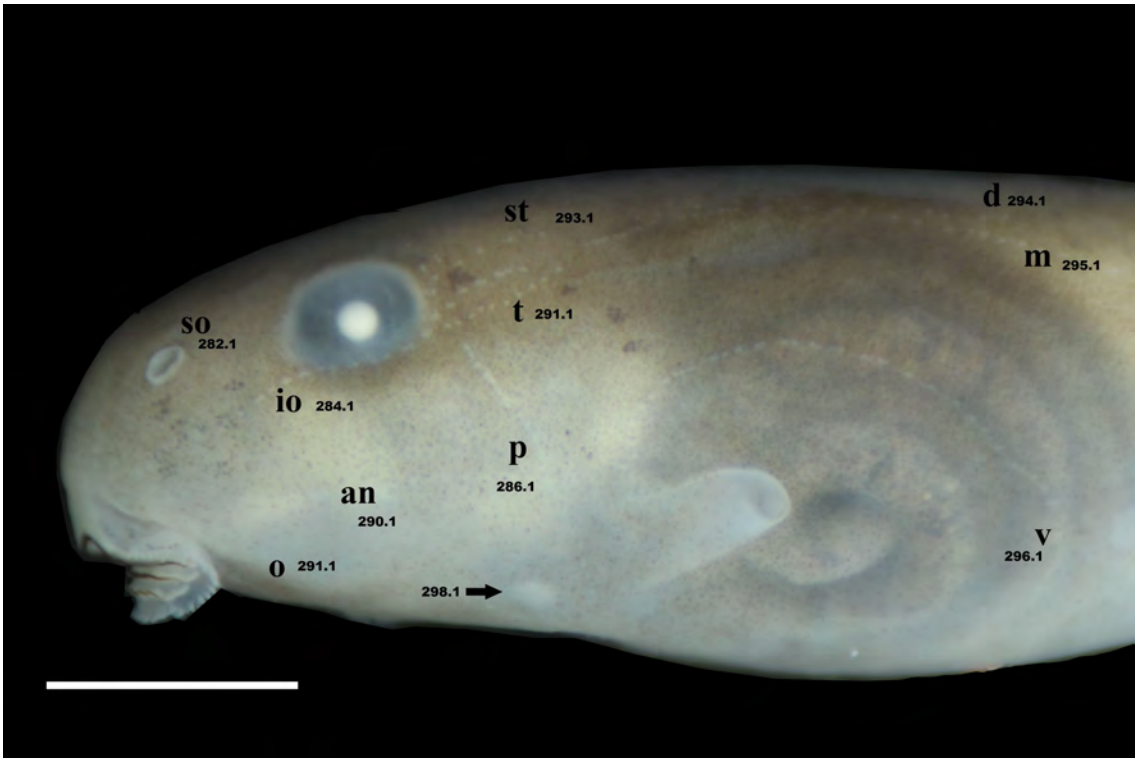

Figure 9. Lateral line system in the tadpole of *Epipedobates darwinwallacei*. AN, angular; D, dorsal trunk; IO, infraorbital; M, middle trunk; O, oral; P, preopercular; SO, supraorbital; ST, supratemporal; T, temporal; V, ventral. Detail of the anterolateral white spots. Scale bar = 10 mm.

288. STITCHES OF THE JUGAL LATERAL LINE: ABSENT (0); PRESENT (1).

289. STITCHES OF THE MANDIBULAR LATERAL LINE: ABSENT (0); PRESENT (1).

290. STITCHES OF THE ANGULAR LATERAL LINE: ABSENT (0); PRESENT (1).

291. STITCHES OF THE ORAL LATERAL LINE: ABSENT (0); PRESENT (1).

292. STITCHES OF THE TEMPORAL LATERAL LINE: ABSENT (0); PRESENT (1).

293. STITCHES OF THE SUPRATEMPORAL LATERAL LINE: ABSENT (0); PRESENT (1).

294. STITCHES OF THE DORSAL TRUNK LATERAL LINE: ABSENT (0); PRESENT (1).

295. STITCHES OF THE MIDDLE TRUNK LATERAL LINE: ABSENT (0); PRESENT (1).

296. STITCHES OF THE VENTRAL TRUNK LATERAL LINE: ABSENT (0); PRESENT (1).

WHITE SPOTS ON THE VENTRAL AREA

The white spots on the body were first mentioned by Altig and McDiarmid (1999: 29) who suggested that it “appears glandular, but it may be associated with the lateral line system”. Kolenc et al. (2008) reported it for several species of *Hypsiboas* (see also Sánchez 2010; Pezzuti et al. 2010; Pirani et al. 2011; Merces et al. 2015; Pinheiro et al. 2016) and provided SEM images suggesting that they are accumulation of neuromasts. More recently, they were observed in *Alsodes neuquensis* larva by Barrasso et al. (2016), who suggested a glandular structure by the analysis of SEM images. In dendrobatoid tadpoles they were first reported for *Hyloxalus subpunctatus* by Anganoy-Criollo (2013). Dias et al. (in press) report them in *Epipedobates* and suggest that they could represent a synapomorphy for that genus. I observed these white spots in several taxa. After SEM and histological techniques (Fig. 10), I reject the neuromast hypothesis. No cilia or similar structure was observed. I found a regular epithelium with villousness that possibly increase the contact surface between that area and the surrounding water. This would suggest a sensitive function; these white spots possibly detect chemical cues of the environment. I recognized six transformation series: the white spots may be present on the posterior and posterolateral part of the ventral area, near the vent tube and the body tail junction, as well as on the anterior and anterolateral part, around the branchial chamber. Additionally, I found in some hylodids with very similar structures on the dorsal and ventral fins, forming a line of spots, which I also individualized as different characters.

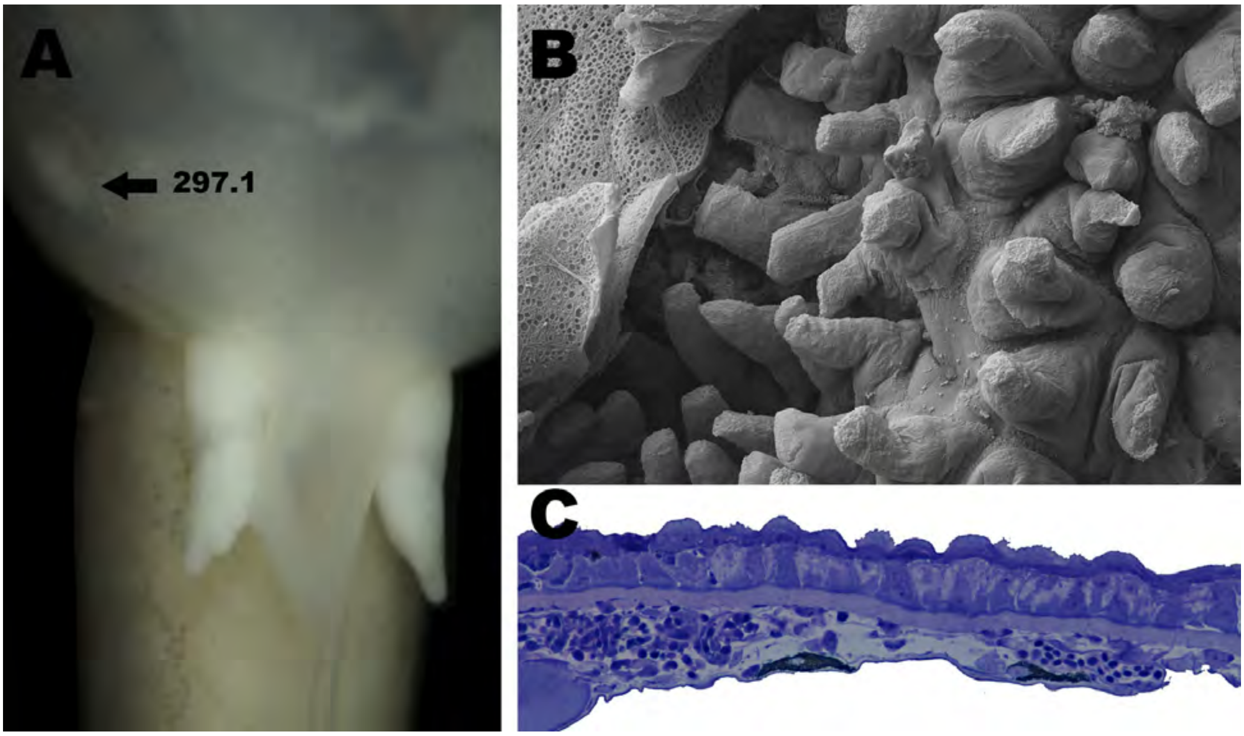

Figure 10. White spots on the ventrolateral surface of the tadpole of *Epipedobates darwinwallacei* (A); SEM images of the posterolateral white spots of *Rheobates palmatus* (B); cross section of the posterolateral white spots of *Hyloxalus subpunctatus* (C).

297. WHITE SPOTS ON POSTEROLATERAL BODY SURFACE: ABSENT (0); PRESENT (1).

298. WHITE SPOTS ON ANTEROLATERAL BODY SURFACE: ABSENT (0); PRESENT (1).

299. WHITE SPOTS ON ANTEROVENTRAL BODY SURFACE: ABSENT (0); PRESENT (1).

300. WHITE SPOTS ON POSTEROVENTRAL BODY SURFACE: ABSENT (0); PRESENT (1).

301. LINE OF WHITE SPOTS ON DORSAL FIN: ABSENT (0); PRESENT (1).

302. LINE OF WHITE SPOTS ON VENTRAL FIN: ABSENT (0); PRESENT (1).

303. LARVAL, BODY COLORATION: BROWNISH WITH PALE AREAS AND SCATTERED DARK DOTS (0); FULLY PIGMENTED, GREYISH OR BLACKISH (1); FEW, SCATTERED MELANOPHORES OR COMPLETELY UNPIGMENTED (2).

Tadpoles may present several different combinations of color pattern. However, given the different pigments and tissue layers involved, it is difficult to stablish relations of homology. I opted for a conservative approach and considered just the overall pattern of melanization (Fig. 11).

304. LARVAL, CAUDAL COLORATION: VERTICALLY STRIPED (0); SCATTERED, CLUMPED MELANOPHORES (1); EVENLY PIGMENTED (2); FEW, SCATTERED MELANOPHORES OR COMPLETELY UNPIGMENTED (3).

This character was used and discussed by Grant et al. (2006: 94).

Figure 11. Living tadpole of *Dendrobates auratus* showing the full pigmented body.

Labial tooth

Tadpoles labial teeth are the product of the keratinization and development of a single cell (Altig 2006x). These elements present significant importance in feeding mechanism (Veneski et al. 2010). Candioti and Altig (2010) demonstrated that the labial teeth can vary among different taxa. I coded three different characters for labial teeth, as below.

305. LABIAL TOOTH, SIZE: SHORT, HEAD LONGER THAN TOOTH BODY (0); REGULAR, BODY SLIGHTLY LONGER THAN HEAD (1); LARGE, BODY TWO OR MORE TIMES LONGER THAN HEAD (2).

306. LABIAL TOOTH, CUSPS: ABSENT (0); PRESENT (1).

307. LABIAL TOOTH HEAD: REGULAR, ABOUT THE SAME DIAMETER OF TOOTH BODY (0) EXPANDED, WIDER THAN BODY (1).

Buccopharyngeal morphological characters

PRENARIAL ARENA

The prenarial arena (Fig. 12) is the area between the internal nares and the mouth opening (Wassersug 1976). Its size may be variable according to the extension and position of the nares as well as the depth of the upper jaw sheaths. In anuran larvae there are a myriad of structures that may be found in the prenarial arena (e.g., crests, ridges, pustulations, etc.), although their functions are mostly unknown. Wassersug (1980) hypothesized that those features may be involved in assisting the lower jaw in holding and positioning food; this is most evident on some Scaphiopodidae larvae that present a keratinized knob in the prenarial arena (Wassersug 1980). Dart-poison frogs may present several characters on this particular region, such as ridges and crest, or pustulations.

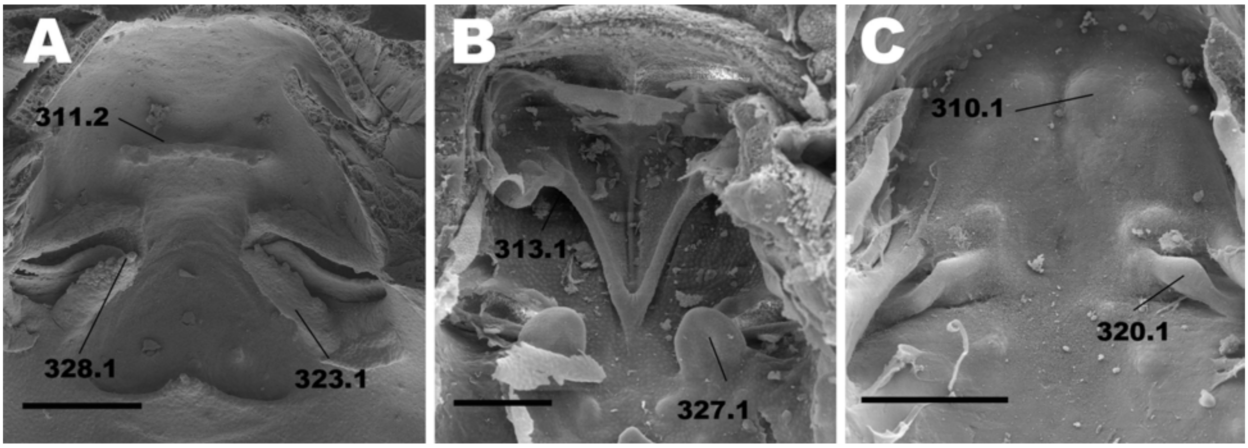

Figure 12. Variation observed in the prenarial arena of *Allobates olfersioides* (A), *Silverstoneia nubicola* (B), and *Oophaga pumilio* (C). Characters and their states are pointed. Scale bar = 200 µm.

308. LONGITUDINAL RIDGE ON THE PRENARIAL ARENA: ABSENT (0); PRESENT (1).

In some dendrobatoids there is a dermal crest on the prenarial arena parallel to the main axis (longitudinal) of the buccopharyngeal cavity. This crest may be quite distinct (e.g., *Ameerega hahneli*) or on moderate visible; it divides the prenarial arena in two halves.

309. RELIEF OF THE PRENARIAL ARENA: FLAT (0); CONCAVE (1).

The prenarial arena may vary in its relief. In several taxa it may be concave. Many studies (e.g., Weber and Caramaschi 2006; Candioti 2007) illustrated both conditions in several taxa but did not discuss this character. Among poison frogs, it was first illustrated by Wassersug (1980; Fig. 37; p.94) for *Silverstoneia nubicola* (as *Colostethus nubicola*).

310. DERMAL PAD ON PRENARIAL ARENA: ABSENT (0); PRESENT (1).

In *Oophaga* spp. there is a pad in the prenarial arena, a condition not observed in any other taxa in the present study, and as far as I know, it is the first report of this character is state described for anurans. The tadpoles of *Oophaga* are obligatory oophagus (Brust 1993; Pramuk and Hiler 1999) and it is possible that the presence of this pad may be associated with the egg consumption, given it was not observed in other facultative egg consumer larvae (Caldwell and Oliveira 1999; Bourne et al. 2001), such as *Ranitomeya vanzolinii* or *Anomaloglossus beebei*. Moreover, it was not observed in *Osteocephalus oophagous* (P.H. Dias unpublished data), an oophagous species, and an ecological correlation is still open to be tested by sampling more oophagous larvae. A possible function for this feature is to hold on slippery aliment (R. Wassersug pers.com), as is the case of trophic eggs.

311. TRANSVERSE DERMAL CREST ON THE PRENARIAL ARENA: ABSENT (0); PRESENT, FORMED BY THE SUPERPOSITION OF SEVERAL INDIVIDUAL PROJECTIONS (1); PRESENT, AS A CONTINUOUS DERMAL STRUCTURE (2). ADDITIVE.

In some poison frog tadpoles individual projections similar to enlarged pustulations may occur in the prenarial arena (state 1). Usually, these projections are joined, giving rise to a continuous dermal crest (state 2). Wassersug (1980: Fig.36: 92) illustrated it for *Hyloxalus subpunctatus* (as *Colostethus subpunctatus*). This transversal crest was present in several studies on tadpoles, as in many bufonids, hylodids, cycloramphids, among many others. In the literature, it has been illustrated in several other lineages as *Boana*, *Dryophytes*, *Leptodactylus*, *Platyplectron*, *Ptychohyla*, *Smilisca* among others (Wassersug 1980; Wassersug and Heyer 1983, 1988; Candioti 2007).

312. SIZE OF THE DERMAL CREST: SMALL, RESTRICTED TO MEDIALLY (0); LARGE, WELL-DEVELOPED (1).

When the transverse dermal crest is present on the prenarial arena (character 3), it may occupy different portions of it. In some species (e.g., *Allobates talamancae*) it is poorly developed and restricted to an area equivalent to a distance less than or equal to the distance between the inner margin of the internal nares. In other taxa, such as *Manophryne olmonae*, it may be larger, occupying an area of the prenarial arena equivalent to the area occupied by the internal nares.

313. DISTINCT V-SHAPED CREST IN THE PRENARIAL ARENA: ABSENT (0); PRESENT (1).

This particular character was observed in *Silverstoneia* species. Wassersug (1980) was the first to describe it. He noticed that a similar condition was observed in other funnel-mouthed larvae (viz., *Duellmanohyla schimdtorum* [as], *Microhyla hyemonsi*, and *Megophrys minor*). Further workers found the same structure in *Phasmahyla* larvae (Dias et al. in press) and *Megophrys stejnegeri* (P.H. Dias, unpublished data), but not in *Mantidactylus* (Grosjean et al. 2011). This V-shaped crest interlocks with the infralabial papillae and prevents large food particles entering the corners of the mouth (Wassersug 1980).

314. CILIATED EPITHELIUM ON THE PRENARIAL ARENA: ABSENT (0); PRESENT (1).

In some species of *Atelopus* a large portion of the prenarial arena is covered with small pores (Fig. 13 C, G and H). Detailed inspection of those pores revealed the presence of ciliated elements. The actual function of those remains unknown, but the most likely hypothesis is that they are chemoreceptive; i.e., the ciliated cells may act in conjunct with the vacuities (see character 13) to help those larvae to perceive chemical cues.

315. PUSTULATIONS ON THE PRENARIAL ARENA: ABSENT (0); PRESENT (1).

Pustulations are small, rounded projections that may be found at several different areas of buccal cavity, both in the floor and in the roof. In the prenarial arena of poison frogs and their relatives, pustulations may also be present (state 1).

316. PENDULUM-LIKE PAPILLA ON THE PRENARIAL ARENA: ABSENT (0); PRESENT (1).

The prenarial arena as discuss above, may present several features. The larvae of *Atelopus* present a pendulum-like papilla hanging on the prenarial (Fig. 13 C and D). Such feature is invariably present in *Atelopus*.

INTERNAL NARES

The internal nares are present and perforated in all anuran larvae, but the Microhylidae (Wassersug 1980). They frequently possess a sensory epithelium associated with its internal surface. The internal nares vary in orientation and in associated features such as valves and pustulations.

317. INTERNAL NARES OPENING: OPEN (0); CLOSED (1).

The large majority of dendrobatoids and their relatives possess perforated internal nares that permit water to be drawn into the buccopharyngeal cavity. Nevertheless, the internal nares are poorly developed and closed in some endotrophic forms, such as in the nidiculous tadpole of *Allobates masniger*.

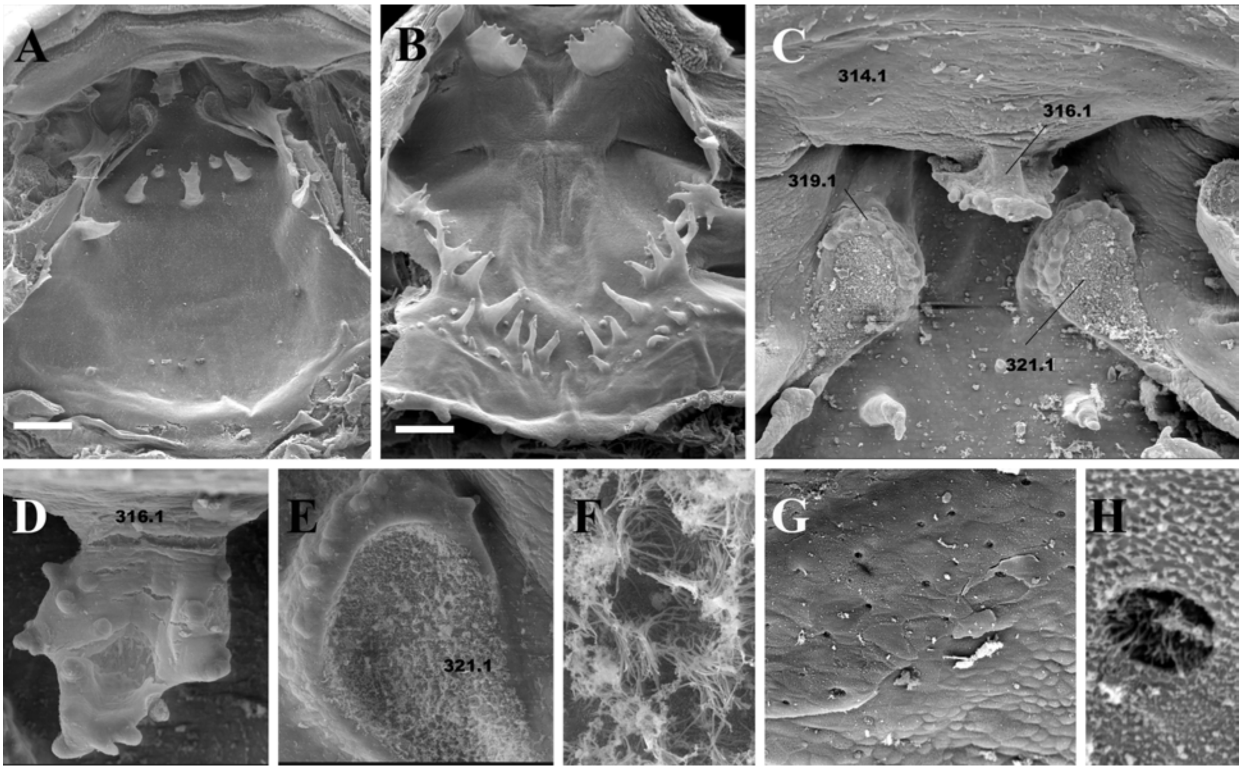

Figure 13. Buccopharyngeal anatomy of *Atelopus carrikeri* (same character states in *Atelopus zeteki*). Roof (A) and floor (B) of the buccopharynx. Detail of the prenarial arena (C); pendulum like papilla (D); vacuities (E) with details of the internal cilia (F); porus on the prenarial arena (G) with detail of the cilia inside a porus (H). Scale bar = 200 μm.

318. INTERNAL NARES ORIENTATION: PERPENDICULAR (0); INCLINED (1); PARALLEL (2).

The internal nares may assume different positions regarding the longitudinal axis of the buccopharyngeal cavity. In dendrobatoids, they can be perpendicular (state 0) or slightly inclined (generally in 30−45°; state 1). State 2, in which the internal nares are longitudinally oriented, is restricted to centrolenid larvae.

319. ORNAMENTATION ON THE ANTERIOR WALL ON THE INTERNAL NARES: ABSENT, SMOOTH (0); PRESENT, SMALL CONICAL TUBERCLE.

In many dendrobatoids, the anterior margin of the internal nares is ornamented with small conical or rounded tubercles. The presence of these tubercles may be associated with protection of the sensitive epithelia of the olfactory surface, possibly by preventing large particles from entering in the internal nares.

320. VALVE PROJECTION ON THE POSTERIOR WALL OF THE INTERNAL NARES: REDUCED OR ABSENT (0); PRESENT, WELL-DEVELOPED (1).

The posterior wall of the narial opening is quite flexible and developed, forming a valve that can close the internal nares (Wassersug 1976, 1980). Many taxa present, besides the valve, a valve projection that varies in size and degree of development. This is a variable character in dendrobatoids with many taxa, such as most of the *Allobates* having little or no projection, whereas others present a well-marked valve projection.

321. VACUITIES WITH CILIATE EPITHELIUM PROJECTING FROM THE MEDIAL WALL OF THE NARES: ABSENT (0); PRESENT (1).

Van Eeden (1951) found what he called "ciliated epithelium bands" in *Ascaphus truei* and suggested that the cilia could have some role in the feeding mechanism proposed by Noble (1927). Wassersug (1980) confirmed the presence of this feature in *Ascaphus truei* and said that *Boana rufitela* (as *Hyla rufitela*) and *Hyalinobatrachium fleischmanni* (as *Centrolenella fleischmanni*) presented such character-state, although with a different morphology forming a *cul de sac* (p.112) and suggest that it may have a chemosensory function. The presence of the vacuities was reported to several Cophomantinae species (e.g., d'Heursel and Haddad 2007; Kolenc et al. 2008; Magalhães et al. 2015; Pezzuti et al. 2015) and may be a putative synapomorphy for the subfamily (Faivovich et al. 2005; Kolenc et al. 2008). This feature was not seen in any dendrobatoids; however, it was constant in all *Atelopus* (Fig. 13 E and F) and centrolenid species examined.

322. CILIATED EPITHELIUM INSIDE NARES: ABSENT (0); PRESENT (1).

Van Eden (1951) reported the presence of ciliated bands on the internal nares, which Wassersug (1980) hypothesized as cleansing features, emphasizing the necessity of keeping large particles away from the nares. In many dendrobatoids, the internal nares are covered with a layer of ciliated tissue. This character was only visualized with SEM analysis.

POSTNARIAL ARENA

The postnarial arena is the dorsal area that occludes with the tongue anlage (and its papillae); it is defined anteriorly by the posterior margin of the internal nares and posteriorly by the median ridge. Wassersug (1980) drew attention to the fact that species with poorly developed tongue anlage frequently also possess a poorly developed postnarial arena. Very often, the postnarial arena is covered with postnarial papillae that are organized in inverted V rows. Each postnarial papillae was treated as an individual and coded in different transformation series.

323. FIRST PAIR OF POSTNARIAL PAPILLA: ABSENT (0); PRESENT (1).

324. SECOND PAIR OF POSTNARIAL PAPILLA: ABSENT (0); PRESENT (1).

325. THIRD PAIR OF POSTNARIAL PAPILLA: ABSENT (0); PRESENT (1).

326. FOURTH PAIR OF POSTNARIAL PAPILLA: ABSENT (0); PRESENT (1).

327. SHAPE OF THE FIRST POSTNARIAL PAPILLAE PAIR: CONICAL (0); OBLIQUE (1).

The first postnarial pair of papillae is the most variable among anuran larvae. In species that possess a funnel mouth, it is frequently modified into a large oblique structure (Wassersug 1980; Grosjean et al. 2011; Dias et al. in press). The funnel mouthed dendrobatoids, *Silverstoneia*, has an oblique (state 1) papillae. The same configuration was observed in the semi-terrestrial tadpoles of *Thoropa*. I did not observe any shape variation in the other pairs of postnarial papillae.

328 . ORNAMENTATION OF THE FIRST PAIR OF POSTNARIAL PAPILLAE: ABSENT (0); PRESENT AS CONICAL OR ROUNDED POSTULATION (1).

Two conditions were observed for the postnarial papillae when present. In some taxa they have smooth surfaces, whereas in others they are covered with small conical or rounded pustulations.

329. ORNAMENTATION OF THE SECOND PAIR OF POSTNARIAL PAPILLAE: ABSENT (0); PRESENT AS CONICAL OR ROUNDED POSTULATION (1).

330. ORNAMENTATION OF THE THIRD PAIR OF POSTNARIAL PAPILLAE: ABSENT (0); PRESENT AS CONICAL OR ROUNDED POSTULATION (1).

331. ORNAMENTATION OF THE FOURTH PAIR OF POSTNARIAL PAPILLAE: ABSENT (0); PRESENT AS CONICAL OR ROUNDED POSTULATION (1).

332. PUSTULATION IN THE POSTNARIAL ARENA: ABSENT (0); PRESENT (1).

As noted above (character 7), pustulations may be present in different areas of the buccopharyngeal cavity. Some tadpoles pustulations (state 1) are distinctly present in the postnarial arena.

333. SMALL PAPILLA ONLY ANTERIOR THE MEDIAN RIDGE: ABSENT (0); PRESENT (1).

In some tadpoles, there are a few small conical papillae right before the median ridge. These papillae are larger than pustulations but much smaller than other buccal roof papillae.

334. MEDIAN RIDGE: ABSENT (0); PRESENT (1).

The median ridge marks the end of the postnarial arena. It is a feature highly variable among tadpoles. According to Wassersug (1980), due to its central location, the median ridge may play a role in splitting the respiratory current into right and left ones. In the present study, I found the median ridge absent in several taxa, namely those with macrophagous feeding habits (e.g., *Oophaga* larvae) or ones that do not feed at all (e.g., *Allobates nidicola*).

335. SHAPE OF THE MEDIAN RIDGE: TRIANGULAR (0); ELLIPTICAL (1); QUADRANGULAR (2); CONCAVE (3); CONICAL (4); TRAPEZOID (5); OBLIQUE

336. MARGINAL STRUCTURE OF MEDIAN RIDGE: SMOOTH (0) SINGLE MEDIAL PROJECTION (1); MULTIPROJECTIONS (2); MEDIAL NOTCH, FORMING A BIFID STRUCTURE (3).

The margin of the median ridge varies greatly in shape among different taxa. In some taxa, the median ridge is smooth, devoid of any projections or notches (state 0). Other taxa have single, medial projections, (state 1) or several projections (state 2); in other cases, I observed a medial indentation that bifurcates the ridge (state 3).

337. LATERAL RIDGE PAPILLAE: ABSENT (0); PRESENT (1).

The lateral ridge papillae are interesting character found only in Orton Type IV tadpoles (e.g., Rabanal and Formas 2009; Dias et al. 2014). Wassersug (1980: 114) concluded that the lateral ridge papillae are developmentally associated with the postnarial and buccal roof arena. According to him, when the elements of the arenas are absent, the lateral ridge papillae are also absent. I found that both lateral ridge and postnarial and buccal roof arenas papillae are absent in the endotrophic larvae of *Allobates nidicola* and *Allobates masniger*, supporting Wassersug (1980) conjecture. However, those features seem to vary independently, given that I found cases in which the postnarial papillae are absent, but the lateral ridge is present, as in *Oophaga*. It is true, though, the lateral ridge papilla in that species is reduced in size (not coded). Moreover, when present, the lateral ridge papillae can vary in size, shape, ornamentation and branching pattern, without affecting the structure of the postnarial papillae. I thus, considered the lateral ridge and the postnarial papillae as distinct structures and have coded their presence/absence independently, as well as their variation in texture and structure. The lateral ridge papillae may vary regarding their shape, branching, and ornamentation, as below.

338. SHAPE OF THE LATERAL RIDGE PAPILLAE – CONICAL (0); FLAP-LIKE (1)

339. BRANCHING OF THE LATERAL RIDGE PAPILLAE: NOT BRANCHED (0); BIFURCATED (1); TRIFURCATED (2); MULTIPROJECTED (3).

340. ORNAMENTATION OF THE LATERAL RIDGE PAPILLAE: SMOOTH (0); CONICAL OR ROUNDED PUSTULATIONS (1).

341. LATERAL ROOF PAPILLAE: ABSENT (0); PRESENT (1).

Some taxa (e.g., *Ameerega flavopicta*) have papillae on the lateral buccal roof. Those are not the same as the lateral papillae of the buccal roof arena. The later delineate the buccal roof arena laterally, and very often surrounds a field of pustulations within the buccal roof arena. These are scattered laterally on the buccal roof with no association with other feature.

342. PUSTULATIONS ON THE BUCCAL ROOF ARENA: ABSENT (0); PRESENT (1)

343. DENSITY OF PUSTULATIONS ON THE BUCCAL ROOF ARENA: FEW, SCATTERED PUSTULATIONS (0); MODERATE (1); HIGHLY POSTULATED (2). ADDITIVE.

In state 0, few scattered pustulations can be seen in the buccal roof arena; they are spaced, distant from each other—the distance between pustulations is larger than two times de diameter of pustules. In state 1, there are a larger density of pustulations, however, there is still space between them—separated by a distance larger than a pustule's diameter. In state 2, there are so many pustules that they commonly contact each other or are separate by a distance smaller than pustules' diameter.

344. GLANDULAR ZONE IN THE BUCCAL ROOF: ABSENT OR INDISTINGUISHED (0); WELL-DEVELOPED WITH SECRETORY PITS WELL-MARKED (1).

The glandular zone is a band of secretory tissue that can be observed under microscope with secretory pits, which are pores through which the mucus is secreted (Wassersug 1980). Histological preparations confirmed the presence of glandular tissue (Kenny 1969a,b). Kenny (1969a) named the glandular zone as "dorsal food traps" (p.234). He hypothesized that the secretory pits would secret mucous that would entrap food particles in chords (see also Savage 1952; Kenny 1969b). According to this hypothesis, the secretory zone acts in concordance with the dorsal and ventral vela in order to capture particles that are then directed toward the esophagus. Wassersug (1980: 115) found that the area occupied by the glandular zone can vary among tadpoles, but failed to find any taxonomic, phylogenetic, or ecological correlation. However, he (p.115) stated the size of the secretory pit could be related to the maximum size of ingested particle. I coded the glandular zone as conspicuous or well-developed when the secretory pits could be identified (state 1).

345. DORSAL VELLUM: ABSENT (0); PRESENT, VESTIGIAL OR POORLY DEVELOPED (1); PRESENT, WELL-DEVELOPED (2).

The dorsal velum was named by Goethe (1785), but also called gill cover plates (Schulze 1892), filter valves (Kratochwill 1933), and branchio-pharyngeal tract (Weisz 1945). Wassersug (1980: 117) recognized two schools of thought about the function of the dorsal vellum. One school, represented by Kratochwill (1933) and Kenny (1969a) views that the dorsal velum, together with the pressure cushions (see below) as functioning to seal off the buccal cavity from the filter chambers, to prevent reverse flow during feeding and gill irrigation. The other school is represented by Savage (1962), who stated that the dorsal velum directing water toward the filter cavities. Despite accepting Savage (1962) view, Wassersug (1980) stress that both functions may occur in a non-exclusive manner. In dart poison frogs, the dorsal velum was present (state 1) in all species, accept the endotrophic larvae of *Anomaloglossus apiau*. Other endotrophic dendrobatoids species, such as *Allobates nidicola* and *Allobates masniger*, the dorsal velum was present reduced in size. I also found the dorsal velum absent (state 0) in the bufonid *Frostius pernambucensis*, another endotrophic species.

346. CONTINUITY OF DORSAL VELUM: MEDIALLY INTERRUPTED (0); MEDIALLY CONTINUOUS (1).

When present, the dorsal usually is discontinuous medially (state 0). Wassersug (1980) described this character for several anuran larvae; he found that few species—*Ascaphus truei*, *Boana rufitela*, *Dendropsophus leucophyllatus*, *Dendropsophus phlebodes*, *Dryophytes femoralis*, and *Hyalinobatrachium fleischimanni*—present the dorsal velum medially continuous. In dart poison frogs, I found the same pattern in which most species present the dorsal velum discontinuous medially, but a few taxa (e.g., *Silverstoneia erasmios*) have it medially continuous. Richard Wassersug (pers.com) told me that, as the medial notch on the ventral velum, such gap in the dorsal velum may provide more exposure to the glottis, and the possibly are correlated with the usage of lungs during larval life.

347. SHAPE OF DORSAL VELUM: SEMI-CIRCLE (0); V-SHAPED (1).

Most commonly, the dorsal vellum presents a V-shape arrangement, directed towards the esophagus (state 1). More rarely, the dorsal velum may present a semi-circle.

348. MARGIN OF DORSAL VELUM: SMOOTH (0); FRINGED OR PAPILLATED (1).

There are two conditions for the texture of the dorsal vellum. In some taxa, the border of the dorsal velum is fringed, with several projections that resembles buccal papillae. Wassersug (1980) described this character and suggested that these projections/papillae may have a sensory function, although he admitted that it was merely a speculation (p.116). However, he also pointed out that the presence of papillae on the inner medial margin of the dorsal velum could be correlated with suctorial, stream dwelling Orton type 4 tadpoles. Wassersug and Heyers (1988) described and used this character to diagnose different, then called leptodactyloid frogs, and found them present in several genera, for instance, *Leptodactylus*, *Odontophrynus*, *Hylodes* and others. I found both conditions within the dart poison frogs and their relatives.

349. PUSTULATIONS POST VELUM: ABSENT (0); PRESENT (1).

In some species, I found small pustulations caudally (distal) to the dorsal velum.

INFRALABIAL PAPILLAE

Infralabial papillae (Fig. 14) are the first features encountered on floor of the buccopharyngeal cavity. Usually, they are found immediately behind the mouth`s opening and present in two pairs. However, there is much variation in these structures, starting with their number. There may be a single pair as in *Cycloramphus stejnegeri* (Wassersug and Heyer 1983) or up to 12 in tadpoles of *Heleophryne natalensis* (Wassersug and Heyer 1988). Wassersug (1980: 98) suggested that infralabial papillae may function in three ways: as respiratory structures, as sensory structures, or as mechanical foils directing water flow. Wassersug was disinclined though to credit the infralabial papillae with a predominantly respiratory or sensory function given their small surface/volume relation. Instead, he noted that the infralabial papillae are commonlyaligned in front of the internal nares and could help direct large particles away from the nares. He also mentioned that some large infralabial papillae may prevent large particles from entering the buccal cavity or play some role in food selection (Wassersug 1980: 96). Infralabial papillae also vary in size, shape and branching pattern (e.g., Inger 1985; Viertel 1982; Chou and Li 1997; Fabrezi and Vera 1997; Candioti 2005; Dias et al. 2014; Dias 2018). I categorized infralabial papillae into three distinct groups. The first pair is located near the midline behind the mouth`s opening and below the infrarostral cartilages. The second pair, is adjacent to the first pair—on the processus ventromedialis of Meckel`s cartilage. The third pair is dorsomedially to the second pair. Each of these pairs may vary independently in their shape, branching and ornamentation. Thus, they were coded separately. Moreover, one or more pairs may be absent in some taxa.

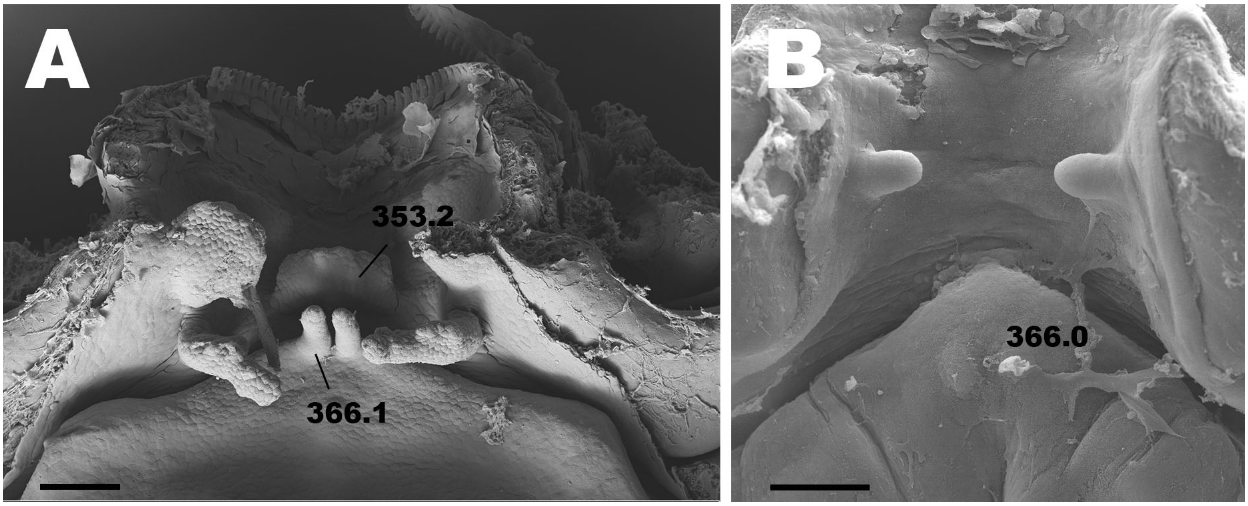

Figure 14. Some variation of the infralabial papillae in *Allobates olfersiodes* (A) and *Oophaga pumilio* (B). Scale bar = 100 µm.

350. FIRST PAIR OF INFRALABIAL PAPILLA: ABSENT (0); PRESENT (1)

As discussed above, the first pair of infralabial papillae is located right behind the mouth opening. This pair is absent in several taxa (Fig. 14 B); indeed, Wassersug and Heyer (1988), in their study of tadpoles from several different genera and families, found the the pair lacking but the second and the third pairs present. Dendrobatoids present a distinct pattern, with the majority of tadpoles of the major of species having all three pairs of infralabial papillae.

351. SECOND PAIR INFRALABIAL PAPILLA: ABSENT (0); PRESENT (1)

The second pair of infralabial papillae is the least variable; in many species in where the first and the third pairs are absent, the second pair is invariably present. In fact, for some taxa the only infralabial papillae pair present was second pair. This is similar to what is seen in bufonids buccopharyngeal anatomy (i.e., in *Atelopus*, *Amazophrynella*, *Dendrophyniscus*, *Frostius*, *Melanophryniscus*, *Incilius*, *Peltophryne*, *Rhaebo*, and *Rhinella.*

352. THIRD PAIR INFRALABIAL PAPILLA: ABSENT (0); PRESENT (1)

353. UNION OF THE FIRST PAIR OF INFRALABIAL: ABSENT, FREE PAPILLAE (0); PARTIAL, BOTH PAPILLAE CAN BE RECOGNIZED (1); COMPLETE, ORIGINATING A SINGLE STRUCTURE (2). ADDITIVE.

In many dendrobatoids the first pair of infralabial papillae, when present, are joined in together. In some taxa, the papillae are not completely joined (state 1) and it is possible to identify the free extremity of each individual papillae (e.g., *Aromobates saltuensis*, *Hyloxalus mystax*). In others (e.g., *Allobates olfersiodes*, *Phyllobates lugubris*) both papillae are joined, forming a single structure (state 2; Fig. 14 A). Assuming a function of mechanical function (see above), a single, burly midline structure could act to restrict large particles from entering the buccal cavity.

354. SHAPE OF THE FIRST PAIR OF INFRALABIAL: CONICAL (0); TRIANGULAR (1).

I found two different shapes for the infralabial papillae. In the first and more common one, the infralabial papillae are conical (state 0). In the second configuration, the papillae were triangular. This was observed only in the larvae of *Silverstoneia erasmios*.

355. BRANCHING OF THE FIRST PAIR OF INFRALABIAL: NOT BRANCHED (0); BIFURCATED (1).

Most commonly, the first pair of infralabial papillae are not branched, forming a compact structure. In some cases, as *Colostethus imbricolus* and *Colostethus inguinalis*, it was forked or bifurcated (state 1). I did not further divisions in the first pair as may occur in the second and third pairs.

356. ORNAMENTATION OF THE FIRST PAIR OF INFRALABIAL: SMOOTH (0); WITH ROUNDED OR CONICAL PUSTULATIONS.

357. SHAPE OF THE SECOND PAIR OF INFRALABIAL: CONICAL (0); FLAP-LIKE (1).

358. BRANCHING OF THE SECOND PAIR OF INFRALABIAL: NOT BRANCHED (0); BIFURCATED (1); TRIFURCATED (2).

359. ORNAMENTATION OF THE SECOND PAIR OF INFRALABIAL: SMOOTH (0); WITH ROUNDED OR CONICAL PUSTULATIONS.

360. SHAPE OF THE THIRD PAIR OF INFRALABIAL: CONICAL (0); FLAP-LIKE (1).

361. BRANCHING OF THE THIRD PAIR OF INFRALABIAL: NOT BRANCHED (0); BIFURCATED (1); TRIFURCATED (2); MULTI-BRANCHED (3).

362. ORNAMENTATION OF THE THIRD PAIR OF INFRALABIAL: SMOOTH (0); WITH ROUNDED OR CONICAL PUSTULATIONS.

363. DERMAL CONNECTION BETWEEN THE SECOND AND THIRD PAIRS: ABSENT (0); PRESENT (1).

In some taxa, in which the first and the second pairs of infralabial papillae are present, it is possible to identify a thin, dermal connection between both of them. Usually, they are clearly separated and it is possible to see the separate bases of each. However, in a few taxa, such as *Rheobates pseudopalmatus*, there is dermal connection between both papillae.

364. PUSTULATIONS BEFORE MOUTH OPENING: ABSENT (0); PRESENT (1).

LINGUAL PAPILLAE

Lingual papillae, or sensory papilla as named by Kenny (1969a), are papillae present on the anuran larvae tongue, or lingual bud. Hammerman and Thomas (1967) demonstrated that tadpoles have a gustatory sense, though they lack a differentiate taste epithelium. Thus, Hammerman and Thomas suggested that some other larval structure must play that role. The lingual papillae would be a likely candidate (Hammerman and Thomas 1967: 99). During metamorphosis, the lingual papillae are absorbed and incorporated into the true adult tongue, in which appear gustative papillae (Hammerman 1969; Paulson et al. 1995). Lingual papillae are present in most frogs, although absent by definition in the aglossal pipids, and in several othere lineages. These include the microhylids, *Rhinophrynus*, and *Dendropsophus*. Faivovich et al. (2005) however suggested their absence is a synapomorphy of Dendropsophini (=Dendropsophinae). When present, lingual papillae may vary from 1, as in *Anotheca spinulosa* (Wassersug 1980) to 11 as in *Paratelmatobius lutzii* (Wassersug and Heyer 1988). In one extreme cases, in *Ascaphus truei* larvae, several dozen blunt lingual papillae are found (Wassersug 1980).

365. MEDIAL, SINGLE LINGUAL PAPILLAE: ABSENT (0); PRESENT (1).

There is much variation in the lingual papillae of dart poison frogs and their relatives, where they may be none, one, or two of these structures. These papillae are located in different positions and may vary independently. When there is a single, long, blunt papilla, it is located medially on the lingual bud, forming a straight line with the mouth`s opening. When paired, these papillae are typically located more laterally than the single papilla. I observed a condition in which there were three papillae, a single medial one and a pair of lateral papillae in *Pseudopaludicola falcipes* (also described for *Pseudopaludicola* sp. by Wassersug and Heyer 1988), suggesting that these papillae may vary independently. Moreover, without further developmental, molecular and historical evidences, establishing homologies for these papillae is complicated, thus I opted for coding each of them (single medial, first and second lateral pairs) separately. Wassersug (1980: 99) also drew attention to the single medial lingual projection in *Anotheca* resembles that of *Isthmohyla zeteki*. Both are carnivorous arboreal tadpoles; that structure may be convergent and not homologous to the lingual papillae of other taxa. I refrained from creating a new terminology for that single medial papilla; instead, I discriminate it from the other oral structures on their topographical relationships.

366. FIRST PAIR OF LATERAL, LINGUAL PAPILLAE: ABSENT (0); PRESENT (1).
See discussion on character 59.

367. SECOND PAIR OF LATERAL, LINGUAL PAPILLAE: ABSENT (0); PRESENT (1).
This second pair of lingual papillae was observed a few times in the examined tadpoles—i.e., in all bufonids, centrolenids, and cycloramphids—but never in poison frogs.

368. ROUNDED PADS LATERAL TO LINGUAL BUDS: ABSENT (0); PRESENT (1).
In some taxa, the underlying Meckel`s cartilage is so prominent that it alters the relief of the buccal floor, giving rise to a pair of round pads to the sides the lingual bud (state 1).

369. DERMAL CRESTS ON ANTERIOR THIRD OF BUCCAL FLOOR: ABSENT (0); PRESENT (1).
In the *Silverstoneia* larvae, the ceratohyal are well-developed and marked on the relief of the buccal floor, forming a longitudinal, dermal crest on the anterior third of the floor.

370. ORIENTATION OF DERMAL CRESTS: PARALLEL (0); INVERTED V (1).
When the longitudinal dermal crests are present, they may be perpendicular to the longitudinal line that crosses the buccopharyngeal cavity, or may present a distinct angulation, forming and inverted-V relief (state 1).

BUCCAL POCKET

The buccal pockets are paired slits whose size vary according to the shape of the ceratohyal and the anterior margin of the branchial baskets (Wassersug 1980). The buccal pocket may or not be perforated, creating a pharyngeal by-pass (Gradwell and Paztor 1968). Just before the buccal pocket, there may be some papillae or pustulations, depending on the species.

371. Prepocket pustulations: absent (0); present (1).

In some taxa, it is possible to identify some pustulations on the prepocket region, located over the ceratohyal area.

372. Prepocket papillae: absent (0); present (1).

More common than the pustulations, are the prepocket papillae. Wassersug (1980) suggested that these papillae may function to block the entrance of large particles into the buccal pockets.

373. Perforation of buccal pocket: perforated (0); unperforated (1).

As discussed above, the perforation of the buccal pockets creates a connection between the buccal cavity and the branchial chambers (Wassersug 1976, 1980). Such character is difficult to score do to the occluded position in which the perforation may be found; in some taxa, as centrolenids, the perforation can be easily accessed, whereas in most tadpoles it is very occluded by the ceratobranchials. Wassersug (1980) reported that in tadpoles of *Silverstoneia nubicola*, the buccal pockets were perforated; I found that many other dendrobatoids tadpoles have the buccal pocket perforated.

374. Bifid papillae lateral to buccal pocket: absent (0); present, bifid (1); present, simple (2).

Almost all poison frog tadpoles presented a peculiar feature on the buccal floor. Medially, at the same line as the buccal pockets is a conspicuous, well-developed, often bifid papilla. Such papilla is clearly different from the buccal floor arena papilla due to its larger size and its bifid condition—buccal roof arena papillae are simple, long, conical papillae. In some taxa, this papilla may present further branching (not coded), whereas in some specimens, it was simple, although tall and large papilla (e.g., *Oophaga vicentei*). Nevertheless, this bifid papilla was absent in some poison frogs as *Phyllobates lugubris*. In some tadpoles with few buccal floor papillae, such as *Oophaga pumilio*, this papilla was still present, as single, simple element.

375. Supranumerary, posterior, floor arena papillae: 0 (0); 1 (1); 2 (2); 3 (3); 4 (4); 5 (5).

These are the buccal floor arena papillae that define the caudal border of the arena. I employed the same rationale as in the characters 65 and 66. When there were also papillae on the center of the arena (see character 68), I considered only the most external line of posterior papillae to score this character.

376. PAPILLAE ON CENTRAL AREA OF BUCCAL FLOOR ARENA: ABSENT (0); PRESENT (1).

Some tadpoles may present a wisp of conical, tall papillae in the central portion of the buccal floor arena. These papillae usually follow the midline in front of the glottis, and it has been suggested that their primary function is to prevent undesirable particles of entering the glottis (Wasssersug 1980: 102).

377. PUSTULATIONS ON BUCCAL FLOOR ARENA: ABSENT (0); PRESENT (1).

378. DENSITY OF PUSTULATIONS ON THE BUCCAL FLOOR ARENA: FEW, SCATTERED PUSTULATIONS (0); MODERATE (1); HIGHLY POSTULATED (2). ADDITIVE.

This character was scored the same way as character 37.

379. GLANDULAR ZONE IN THE BUCCAL FLOOR, IN GROSS INSPECTION: ABSENT OR UNDISTINGUISHED (0); WELL-DEVELOPED WITH SECRETORY PITS WELL-MARKED (1).

See comments on character 38. Most tadpoles that I observed lacked a differentiated, macroscopic glandular zone on the buccal floor. Several of them presented though with secretory pits on the velar margin and the secretory ridges on the ventral velar surface, however, evidence of a glandular zone was observed in only a few taxa (e.g., *Allobates trilineatus*).

380. SECRETORY RIDGES: ABSENT (0); PRESENT (1).

The secretory ridges (Kenny 1969a) are glandular features that help to form mucus strands to entrap food particles; they are part of the complex food trap system (Wassersug 1972). They are located on the ventral surface of ventral velum and are characterized by an irregular, concentric pattern of ridges. Histologically, the ridges resemble the epithelium of the dorsal glandular zone (Kenny 1969a). Wassersug (1980) found it absent in *Anotheca spinose* and *Denropsophus phlebodes*, both macrophagous larvae. Many dendrobatini, also macrophagous tadpoles, also lacked the secretory ridges. For further comments on secretory ridges and their morphology, see Wassersug and Rosenberg (1979).

381. FREE VENTRAL VELUM: INCONSPICUOUS (0); REGULAR, WELL-DEVELOPED (1).

The ventral vellum is, essentially, a valve which mechanically separates the anterior buccal cavity from the pharyngeal cavity (Wassersug 1976, 1980); several authors) have documented its function (e.g., Kenny 1969a; Gradwell 1971). The ventral velum plays an important role feeding; for instance, the secretory ridges on its ventral surface (see character 72) and the secretory pits along its free border can produce mucus to capture food particles (see characters 76). In dart poison frogs, I found a freely mobile ventral velum present in almost all dart poison tadpoles I examined, but inconspicuous, almost vestigial in some endotrophic tadpoles, as in *Allobates nicola* (state 0).

382. MARGINAL PROJECTIONS ON VENTRAL VELUM: ABSENT (0); PRESENT (1).

According to Wassersug (1980) in tadpoles that live in fast, moving water, the velar projections are more common and developed, whereas tadpoles from stand water tend to have arch shaped, smooth velar margin. Moreover, he attested that usually, the number of projections match the number of filter cavities. The projections may have the function of directing water flow toward the gill filters when the buccal floor is elevated. I found that most dendrobatoids have marginal projections on their ventral velum, but some taxa, such as *Hyloxalus bocagei* lack these projections.

383. MEDIAL NOTCH ON VENTRAL VELUM: ABSENT (0); PRESENT (1).

In general, the presence of the medial notch is associated with the presence of a large functional glottis, and therefore, large, functional lungs in tadpoles before metamorphosis (Wassersug 1980). I found a distinct medial notch present in most dendrobatoids tadpoles.

384. PITS ON THE MARGIN OF VENTRAL VELUM: ABSENT (0); PRESENT (1).

Kenny (1969b) demonstrated the secretory nture of these pits on the velar surface of *Pseudis paradoxa* and argued that they were unique to that species. Wassersug and Rosenberg (1979) though refuted Kenny`s (1969b) hypothesis, showing that pits were present in several other taxa. Both, Kenny (1969b) and Wassersug and Rosenberg (1979) suggested that these pits or pores may be associated food entrapment. They are present in several dendrobatoids; however, in some macrophagous, phytotelma dwellers, such as dendrobatini larvae, they are commonly absent (state 0).

385. SPICULAR SUPPORT: ABSENT OR POORLY EVIDENT (0); PRESENT, WELL-MARKED (1).

The velar surface receives support from the spicules of the ceratobranchials. Such support may be evident at first glance, and the marks of each spicules are well defined. In other cases, however, it is poorly developed, and no aspect of the underneath spicules can be observed. Large spicules possible strengthen the valve, preventing prolapse (Wassersug 1980: 104). It worth noting that spicules were not particularly evident in the phytotelma tadpoles I examined. Wassersug (1980) found the same pattern; i.e., *Anotheca spinosa* and *Bromeliohyla dendroscarta*, both phytotelma larvae, have little or no spicular support for their diminished velum.

386. GLOTTIS: EXPOSED (0); PARTIALLY OR FULLY COVERED BY THE VENTRAL VELUM (1).

Wassersug (1980) reported that the glottis was fully exposed in *Rhinophrynus*, microhylids, and pipids larvae. Notably all these tadpoles use their lungs before metamorphosis and have the ability to adjust their buoyancy in order to hold their position in the water column. Furthermore, as a generality he suggested that the glottis would be fully or partially covered by the ventral velum in taxa that did not develop functional lungs much before metamorphosis. When viewed from above, several tadpoles, including *Hyloxalus subpunctatus* (confirmed by me), the glottis could be seen as partially or completely exposed. In ventral view, I found the glottis completely exposed in several of the other taxa, such as *Allobates trilineatus* and *Anomaloglossus tepuyensis*.

387. FILTER PLATES: ABSENT (0); PRESENT (1).

The branchial baskets may vary in size in relation to feeding specializations. For instance, tadpoles adapted for microphaguous suspension feeding, such as those of *Phyllomedusa trinitatis*, have large dense branchial baskets. In contrast the macrophagous *Dendropsophus phlebodes* has very reduced ones. In each branchial cavity, there are filter plates, that connect the different cavities and bear filter rows. According to Wassersug (1980) there is correlation of the number of filter rows and the filtering ability. However, it is clear that both, basket size and filter row numbers are affected by tadpole size. Some researchers have undertaken a morphometrical and statistical analysis of this variation (e.g., Wassersug and Hoff 1979; Candioti 2006, 2007). In the present study I focused on the presence/absence of the filter rows, which are present in the large majority of dendrobatoids tadpoles, but absent in endotrophic and oophagous larvae.

Visceral characters

388. GUT COILING, AXIS: SWITCHBACK POSITIONED VENTRALLY, PERPENDICULAR TO BODY`S MAIN AXIS (0); SWITCHBACK LATERALLY DISLOCATED, OCCUPYING THE LEFT SIDE OF ABDOMINAL CAVITY (1).

Most tadpoles present a coiling axis in which the bowel lops curves ventrally at the center of the abdominal cavity (state 0). However, in dart-poison frogs, the coiling axis is laterally dislocated (Fig. 15) and positioned on the left side of the abdominal cavity (state 1). Lavilla and Vaira (1997: 23) described this character in the larvae of *Melanophryniscus rubriventris* and used it as a diagnostic character. Sánchez (2013) briefly mentioned this condition but did not discuss it further. This condition is present in almost all dendrobatoids herein examined. Other conditions for the intestine coiling have been described in the literature—for instance, Faivovich (2002: character 78: 386) mentioned that in tadpoles of *Scinax acuminate* and *Scinax garbei* the coiling axis is subparallel to the longitudinal axis of the body—but they have not been observed in poison frogs nor in their relatives.

389. GUT COILING, TYPE: LONG GUT, CONCEALING OTHER ORGANS (0); SHORT GUT, REVEALING OTHER ORGANS (1).

Sánchez 2013: 577) recognized two types of digestive tracts in dart-poison frog larvae. According to him, in some taxa, when observed perpendicularly, some of the internal organs may be concealed by the large, coiled intestines (state 0). And, in other taxa, the intestines are short and enlarged in a way that the internal organs are visible (state 1). Grant et al. (2017) used this character in their phylogeny of dart-poison frogs and their relatives.

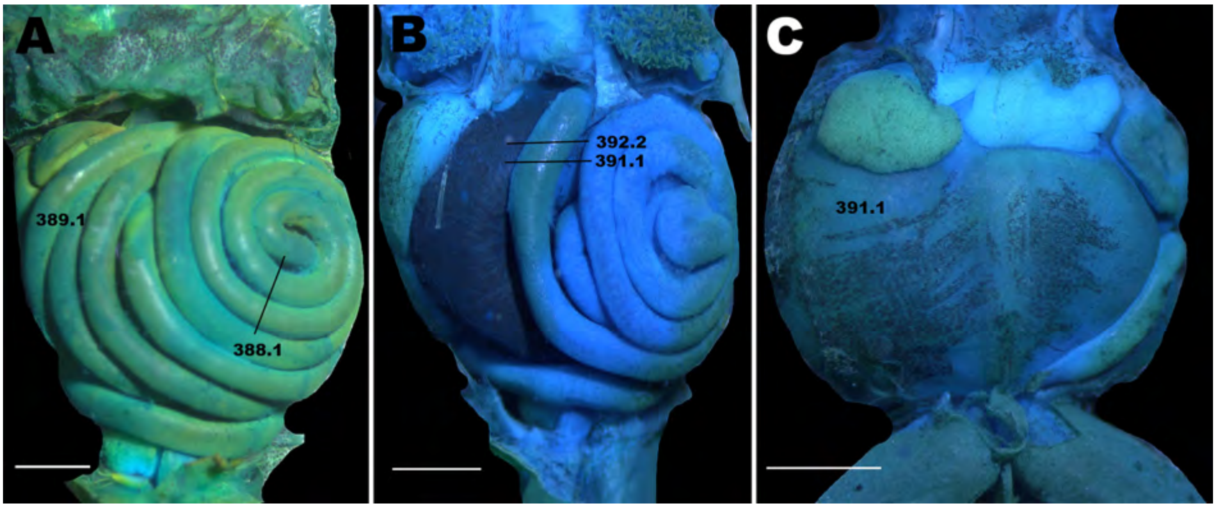

Figure 15. Digestive tract of three dendrobatoid species: *Colostethus brachyhistriatus* (A), *Andinobates* sp. Chocó1 (B), and *Oophaga vicentei* (C). Characters and their states are indicated. Scale bar = 5 mm.

390. DIGESTIVE TRACT, SIZE: REGULAR, LARGE WITH SEVERAL COILING (0); REDUCED, ABOUT THE TADPOLE`S TOTAL LENGTH (1).

The size of the digestive tract has been used as proxy for the diet type of tadpoles by several authors (e.g., Altig and Kelly 1974; Das 1995); long guts are very often associated with herbivory, whereas short stout guts would be characteristic of carnivores. Given that tadpoles are probably omnivores and that not everything present in the digestive tract is a food resource, that correlation has been questioned (Altig et al. 2007), and some authors (e.g., Naitoh et al. 1990) suggested the long digestive tract may be a possible compensation for the absence of peristalsis. Nevertheless, the variation in digestive tracts in anuran larvae exists and was herein considered to be a transformation series. Although it is more likely to be a continuum of size changing, we considered the guts to be long (state 0) if the entire tract when stretched is longer than the tadpole`s total length, while the opposite was considered as a short tract (state 1). In dart-poison frogs state 0 is the most common, with short digestive tract occurring mainly in dendrobatini larvae, but also in some phytotelm dwellers *Anomaloglossus* and *Hyloxalus*.

391. LARVAL STOMACH: ABSENT, FOREGUT OF REGULAR, UNIFORM DIAMETER (0); PRESENT, FORMED BY THE ENLARGEMENT OF THE FOREGUT REGION (1).

Lambertini (1928) proposed the term manicotto glandulare for the foregut swelling in tadpoles of *Rana temporaria*. The manicotto is a unique larval feature, located at the apex of the pancreatic loop and capable of secreting mucus (Griffiths 1961; Bloom et al. 2013). Histological sections have shown that the manicotto walls present reminiscent pancreatic tissue and developmental studies have demonstrated that the manicotto gives rise to at least part of the adult stomach (Griffiths 1961; Ishizua-Oka and Shimozowa 1987). Nevertheless, the manicotto is not a true stomach due to its inability of decreasing pH or of having pepsin activity (Haas et al. 2014; however, see comments of Altig et al. 1975 on the presence of pepsin in tadpoles). On the other hand, some taxa may present an enlarged foregut with enzymatic action and muscular walls, such as *Lepidobatrachus* (Ruibal and Thomas 1988; Carroll et al. 1991). The heterochronic stomach in this genus is associated with the lower concentration/activity of retinoic acid (Bloom et al. 2013). Haas et al. (2014) reported that tadpoles of *Occidozyga* presented an enlarged and muscular foregut as that of *Lepidobatrachus*, although the enzymatic action is unknown. We observed in tadpoles of *Oophaga* a great expansion of the foregut with muscular characteristics; we followed Haas et al. (2014) in calling it a larval stomach, although I only hypothesize enzymatic activity. In several dissected specimens of *Oophaga* (Fig. 15), the larval stomach was full of trophic eggs and occupied most of the abdominal cavity. Noble (1929) described the same condition in the facultative egg feeders *Hophlophryne regersi* and *Osteopilus brunneus*, who also may prey on small invertebrates or feed on vegetal debris.

392. TERMINAL PORTION OF THE ILEUM: REGULAR, UNIFORM IN DIAMETER (0); MODERATELY EXPANDED (1); GREATLY ENLARGED, FORMING A DIVERTICULE (2).

Many tadpoles, very often carnivorous and/or macrophagous, have a portion of the digestive system enlarged. For example, in carnivore tadpoles of *Hymenochirus*, the esophagus forms a diverticule (Viertel and Richter 1999), allowing the ingestion of entire large preys. In other cases, it is the manicotto that is enlarged, as in *Rana temporaria* (Lambertini 1928), or forming a larval stomach, as in *Oophaga*. Fabrezi (2011) demonstrated that in tadpoles of *Lepidobatrachus laevis*, besides the larval stomach (manicotto), the terminal segment of the ileum (which she called rectum) is also dilated. We observed the same condition in several tadpoles; in some larvae as *Silverstoneia* the ileum is moderately enlarged, wider than the adjacent digestive tract but not forming a caecum (state 1). In other taxa, as most of dendrobatini as well as bromeliad dwellers *Anomaloglossus*, the ileum is greatly enlarged, forming an expanded diverticule (state 2; Fig. 15). We considered this transformation series ordered.

393. ILEUM, PIGMENTATION: UNPIGMENTED (0); PIGMENTED (1).

Pigmentation of visceral components has been demonstrated to occur in several different taxa (e.g., Provete et al. 2012). Grant et al. (2006; 2017) used the pigmentation of tests and intestines in adult frogs as evidence to test the phylogenetic relationships of dendrobatoids. According to them, the presence of pigmentation evolved several times and it is an important character to delimite some groups – for instance, the presence of melanized tests is a synapomorphy for *Silverstoneia* + *Epipedobates* (Grant et al. 2017). We observed that the ileum of some larvae is highly melanized, particularly in dendrobatini.

394. LUNGS: RUDIMENTARY OR ABSENT (0); PRESENT (1).

Lungs are one of the organs that are present in both larvae and adult frogs. The primary function of the lungs is buoyancy (Wassersug and Seibert 1975; Viertel and Richards 1999); however, it is also involved in breathing atmospheric air, which may boost swimming ability and stamina (Wassersug and Feder 1983) and increase larval growth and development (Pronych and Wassersug 1987; Wassersug and Murphy 1987). Absence of lungs is very rare among tadpoles. Some benthic bufonids and some torrent tadpoles as *Ascaphus*, *Litoria* and *Nyctimystes*, for instance, lack lungs until they are very close to metamorphosis (Pronych and Wassersug 1994; Haas and Richards 1998). Haas (2003: character 133: 79) employed this character in his study of larval morphology. In our dataset, besides in bufonids, lungs were absent in some centrolenid larvae (e.g., *Ikakogi*).

395. LUNGS, SIZE: SMALL, OCCUPYING LESS THAN HALF THE PERITONEAL CAVITY (0); LARGE, REACHING CAUDALLY IN THE POSTERIOR HALF OF PERITONEAL CAVITY (1).

When present and functional, lungs may be short or poorly developed, occupying only a small fraction (less than half) of area of the peritoneal cavity in the sagittal plane (state 0). We observed a second condition in which the lungs are well-developed and extends posteriorly in the peritoneal cavity (state 1).

396. LUNGS, INFLATION: SHRUNKEN, NOT INFLATED (0); INFLATED, (1).

Some taxa have shrunken and winding lungs, whereas others have inflated lungs.

397. SKIN VASCULARIZATION: POORLY DEVELOPED, UNDETECTABLE UNDER STEREOSCOPIC MICROSCOPE (0); WELL-DEVELOPED, WITH SEVERAL VESSELS EVIDENT UNDER STEREOSCOPIC MICROSCOPE (1).

The larval anuran skin is highly vascularized (Saint-Aubain 1982) and is responsible for a large part of gas exchanges (Burggren and West 1982). Nevertheless, such vascularization is very often microscopic and cannot be observed under small magnifications (Jasisnki and Miodonski 1978). Observations on the skin of poison frogs and their relatives showed that, in some taxa, particularly in the phyototelma oophagic larvae of *Oophaga*, skin vascularization is well-developed and clearly observed under small magnifications. I this character, I consider skin vascularization well-developed (state 1) if it can be observed under stereoscopic microscope.

398. HYOBRANCHIAL SINUS: ABSENT (0); PRESENT (1).

The sinus hyobranchialis is formed by the circulatory system and lies ventrally to the hyobranchial apparatus (Hoffman 2004, 2010). Hoffmann (2004) was the first to mention it in a tadpole description, and later he described it for several centrolenid tadpoles (Hoffmann, 2010). This author recognized two basic features within the sinus: basic receptaculum disci oralisa and receptaculum lateralis et transversalis; he attributed great taxonomic value to this character. I also observed the presence of the sinus hyobranchial in the examined tadpoles of Centrolenidae.

Muscles Characters

399. RECTUS ABDOMINIS, NUMBER OF MYOTOMES: 4 (0); 5 (1); 6 (2); 7 (3).

The rectus abdominis (Fig. 16) is a paired muscle that runs through the vertebrate abdomen. It is invariably present in tadpoles throughout their development, usually originating in the posterior abdominal wall and inserting on the diaphragm. In sucker species such as *Aschaphus*, the rectus abdominis adducts trunk and tail during the snout retraction phase of sucker locomotion (Gradwell, 1971a). Gradwell (1975) suggests that in *Mixophyes balbus*, the rectus abdominis may help in the branchial constriction. Carr and Altig (1992) studied the rectus abdominis in a variety of tadpoles and concluded that the number of myotomes observed can vary among and within different taxa, including poison frogs – they analyzed *Ameerega flavopicta* and *Mannophryne herminae* tadpoles. Nevertheless, this character has been poorly studied and few works described the number of myotomes in the rectus abdominis (e.g., Manzano and Perotti 1999; Rowley et al.

2012). I observe the rectus abdominis varying from 4 to 7 myotomes in dart-poison frogs and their relatives.

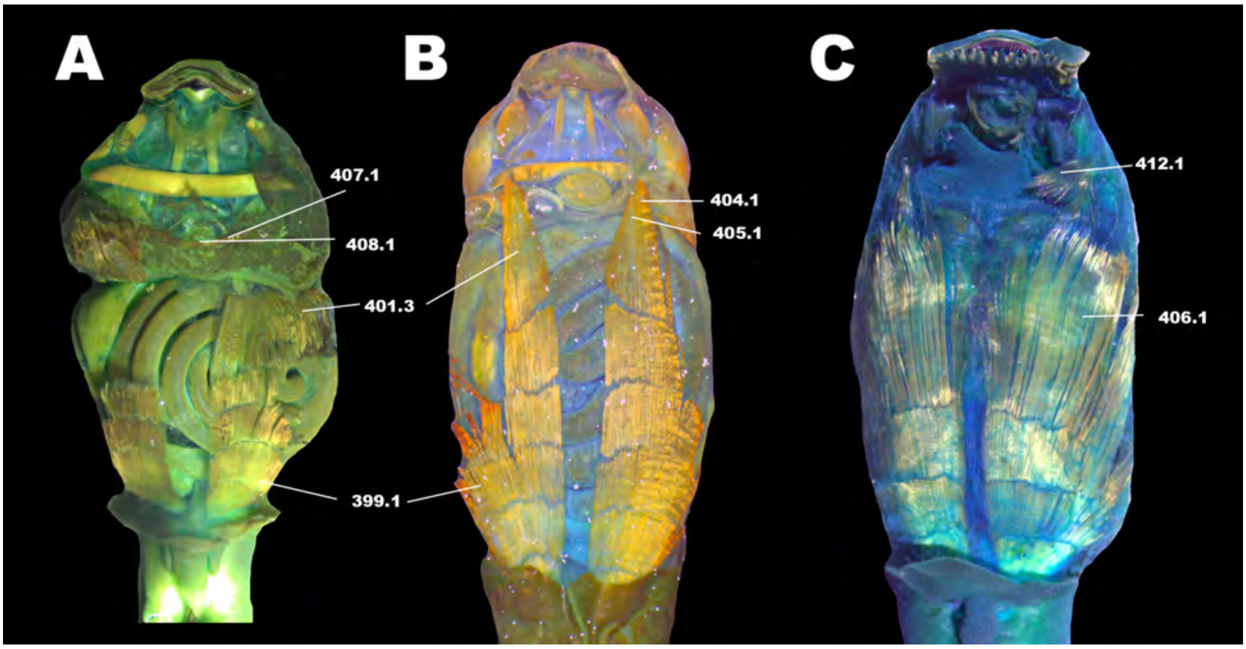

Figure 16. Variation in the rectus abdominis muscle in dart-poison frogs and their relatives; *Epipedobates machalilla* (A); *Hylodes fredi* (B); and *Vitreorana eurygnatha* (C). Characters and their states are indicated.

400. Myotomes: closed (0); open (1).

Myosepta are always closed in adult frogs, however, this condition can vary in tadpoles. Carr and Altig (1992) showed that closed myosepta are more common in species that live confined to small spaces (e.g., the arboreal *Bromeliohyla bromeliacea* [as *Hyla*]; the burrower *Vitreorana eurygnatha* [as *Centrolenella*]) or in suction feeders (planktonic *Xenopus*). They suggested that the action of the rectus abdominis is more important to larvae than to adults in those taxa, given that closed myoseptae surely are less elastic than open ones and probably possess stronger contraction action. They also hypothesized another function: maintenance of body shape in tadpoles, like those of *Osteopilus brunneus*, which eat large numbers of eggs. A more turgid, non-protruding abdomen (myosepta closed, higher fiber density) would aid in maneuvering in tight spaces (Noble 1929; Carr and Altig 1992). Manzano and Perotti (1999) questioned the hypothesis of Carr and Altig (1992) by showing that open/closed myotomes vary among larvae of different environments (ponds, streams), etc. However, Manzano and Perotti (1999) only examined 4 hylid and 1 hemiphractid tadpoles, and the ecological correlation between habitat and aperture of the myosepta is still unclear. In the present study, I coded variation in the aperture of the myosepta; state 1 (open) was scored in all individuals with a clear separation among different myotomes, state 0 (closed) were scored for individuals in which the myosepta was clearly filed with connective tissues, following do Carr and Altig (1992).

401. RECTUS ABDOMINIS, LARGER MYOTOME: SECOND (0); THIRD (1); FIFTH (2); SIXTH (3); SUBEQUAL (4).

Carr and Altig (1992) were the first to notice variation in myotome size. I used linear measurements to estimate the largest myotome, considering only the muscular fibers, and I counted their position from the insertion to the origin (Fig. 16). I also observed a different condition, in which all myotomes are approximately the same size (state 3).

402. RECTUS ABDOMINIS, WIDTH: RELATIVELY UNIFORM ALONG ITS WIDTH (0); THINNER ON THE ANTERIOR HALF OF ITS LENGTH (1).

Baldo et al. (2014: 432) reported that in tadpoles of *Melanophryniscus* the lateral fibers of the rectus abdominis originate at the mid-abdomen and the medial fibers can be tracked to the septum tranversum (diaphragm). I observed the same condition in several other bufonids and, rarely, on some dendrobatoids.

403. DEVELOPMENT OF THE RECTUS ABDOMINIS: POORLY DEVELOPED, RESTRICTED TO MEDIAL PORTION OF ABDOMINAL CAVITY (0); WELL-DEVELOPED, OCCUPYING ALMOST THE WHOLE VENTRAL AREA OF ABDOMINAL CAVITY (1).

In many tadpoles, when observed in ventral view, the rectus abdominis covers a small portion of the abdominal cavity revealing visceral components. On the other hand, some taxa present a well-developed rectus abdominis that covers almost entirely the visceral components, occupying a significant portion of the abdominal cavity, as in *Oophaga*. Noble (1929) suggested that the well-developed complex rectus abdominis and rectus cervicis of *Osteopilus brunneus* and *Hoplophryne* aids their locomotion in the confined spaces of banana leaves and bromeliads cisterns, pointing out that in pond dwellers those muscles are less developed. Jennings (1991) in an unpublished dissertation, noted that the degree of development of the rectus abdominis is variable in tadpoles of the same species that occupy streams and ponds. Regarding suctorial forms, Carr and Altig (1992) assumed that the higher density of fibers would help to stabilizing the abdomen and the spiracular wall during the locomotion via extension-retraction cycles of the oral disc, the same conclusion drawn by Gradwell (1971).

404. RECTUS ABDOMINIS ANTERIOR: ABSENT (0); PRESENT, INSERTING ON THE VENTRAL PROCESSUS ARTICULARIS QUADRATI (1).

The rectus abdominis usually presents a single slip that originates on some point of the abdominal wall, presumably in the pelvic girdle, and inserts on the peribranchial tissue or in the diaphragm (Gradwell 1971; Lynch 1984; Carr and Altig 1992). Nevertheless, a secondary slip of the rectus abdominis inserting on the ventral processus articularis quadrati, the rectus abdominis anterior (Fig. 16), may be present in some taxa. The first to describe this character was Noble (1929), and posteriorly it was described for many groups, mainly suctorial and burrowers forms—*Ascaphus truei* (Gradwell 1973), *Boophis*, *Hyloscirtus*, *Litoria* (Haas and Richards 1998), *Otophryne robusta* (Wassersug and Pyburn 1987), *Leptobrachella mjobergi* (Haas et al. 2006), *Telmatobius* (Candioti 2008), and *Occidozyga baluensis* (Haas et al. 2014). The first to refer to this secondary slip of the musculus rectus abdominis as rectus abdominis anterior were Haas et al. (2004). According to Haas et al. (2014: 335) the rectus abdominis anterior "extends the m. rectus abdominis (proper) anteriorly beyond the branchial diaphragm. It inserts to the ventral skin and with a tendon on the anteroventral face of the ceratohyale". Gradwell (1973) suggested that the rectus abdominis anterior (inserting on Meckel`s cartilage in *Ascaphus*) could pull the body towards the substrate after the adhesion of the sucker oral disc. Haas and Richards (1998) accepted that the same mechanism could work for *Litoria* tadpoles. I found the rectus abdominis anterior in several taxa; all Hylodidae larvae examined presented the character state 1, which was also present in several different bufonids (e.g., *Amazophrynella*). In those taxa, the rectus abdominis anterior has a tendinous insertion on the processus ventralis of palatoquadrate, but also present a concoctive connection to the ligamentum subhyoideus.

405. RECTUS ABDOMINIS ANTERIOR REGARDING PERIBRANCHIAL TISSUE: BELOW (0); ABOVE (1).

When present, the secondary slip of the rectus abdominis (rectus abdominis anterior) may run from the abdominal wall to the ventral palatoquadrate in two different ways—it may pass below the peribranchial tissue as occurs in bufonids (state 0), or above the peribrachial tissue, presenting some adherence to it, as occurs in hylodids (state 1).

406. INSERTION OF THE MAIN SLIP OF THE RECUTS ABDOMINIS (CENTRAL PORTION): PERITONEUM (DIAPHRAGM) (0); PERIBRANCHIAL TISSUE (1).

In most anurans, the main slip of the rectus abdominis inserts on the diaphragm (state 0). I observed a different pattern in some centrolenids (e.g., *Vitreorana eurygnatha*) in which the fibers of the rectus abdominis originate far more anteriorly, above the peribranchial tissue. As far as I know, this condition had never been previously reported.

407. INTERHYOIDEUS POSTERIOR: ABSENT (0); PRESENT (1).

Haas (2003: 57) defined the interhyoideus posterior as a more or less complete sheath of predominantly muscle fibers in the opercular fold. This muscle innervated by the nervo facialis (Gradwell and Walcot 1971; Gradwell 1972; Haas 2003) has been reported for several anuran larvae (e.g., Noble 1929; Gradwell 1972; Sokol 1975; Haas 2003) and received different names like constrictor coli (Edgeworth, 1935) or subbranchialis (Schuze, 1982). We observed the interhyoideus posterior in several lineages of poison frogs as well as in many outgroup taxa. This character is modified from Haas (2003; character 23) who attested that, due to the fragile nature of this muscle and its positioning externally to the opercular chamber, it is subject to damage during manual dissection of specimens, and that histological techniques should be employed to confirm its presence (p.57). Given the size of our matrix, histological preparations were not performed for many taxa; therefore, I stress that state 0 (absence) could represent an undetection of the muscle in our analysis.

408. INTERHYOIDEUS POSTERIOR, CONTINUITY: MEDIALLY INTERRUPTED (0); MEDIALLY CONTINUOUS (1).

When present, the interhyoideus posterior may be medially continuous or interrupted. I modified this character from Haas (2003: character 24) to recognize two distinct transformation series. One is related to the medial continuity (this character) and the other to the extent of muscle development. Hass (2003) recognized these two individuals as part of the same transformation series; however, given that I observed different configurations varying independently in several taxa, I hypothesize two different characters.

409. INTERHYOIDEUS POSTERIOR: THIN SHEATH (0); LOOSELY SPACED FIBERS IN RESTRICTED AREAS OF THE OPERCULUM (1); EXTENSIVE AND STRONGLY DEVELOPED (2).

This character is modified from Haas (2003: character 23). In state 0, the interhyoideus is very thin, represented by a small pack of fibers arranged as a beam, that may be continuous or not (see character 9). In state 1, some few scattered fibers are observed disorganized in the opercular fold. In state 2, the fibers are massive, occupying a significant portion of the opercular fold.

410. MUSCLE DIAPHRAGMATOPRAECORDALIS: ABSENT (0); PRESENT (1).

The muscle diaphragmatopraecordalis was described by Schulze (1892) and acts as a constrictor of the internal branchial chamber (Noble 1929; Haas 1997). Haas (1997: 190) considered it to be part of the interhyoideus posterior, an interpretation corrected by himself (2003: 58). Both interhyoideus posterior and diaphragmatopraecordalis are closely associated and usually converge to the same area on peribranchial chamber (Haas 2003).

411. MUSCLE SUBHYOIDEUS: ABSENT (0); PRESENT (1).

Baldo et al (2014) described the muscle sughyoideus as "a pair of [subhyoid] muscles that extended between the articular condyle of the ceratohyal and the skin ventral to the hyobranchial skeleton" (p.432). This muscle occupies the exact same position and trajectory as the ligamentum subhyoideus (Noble 1929), as noticed by Baldo et al. (2014: 437), and the homology between these two elements has yet to be investigated. Baldo et al. (2014) suggested that the muscle subhyodeus could be an exclusive synapomorphy for *Melanophryniscus*. Herein, I found it also in other bufonids lineages, such as *Amazophrynella*.

412. MUSCLE SUBQUADRATE: ABSENT (0); PRESENT (1).

Subquadrate muscle extends between the articular process and the ventral skin (Baldo et al. 2014). Noble (1929) was the first to describe this muscle for *Amolops ricketti*, but he interpreted it as a secondary slip of the interhyoideus posterior. Later, Candioti (2008) reported it for *Telmatobius* larvae and discussed its homology. Baldo et al. (2014) reported this muscle for many *Melanophryniscus*; they also call attention to the subquadrate ligamentum (see discussion on character 12). I found this muscle in different bufonids and centrolenids.

413. RECTUS CERVICIS, ANTERIOR INSERTION: PROCESSUS BRANCHIALIS II (0); PROCESSUS BRANCHIALIS III (1); CERATOBRANCHIAL III (2).

The rectus cervicis originates from the abdominal wall (peribranchial tissue), often as a continuation of the rectus abdominis (Haas 1997). This character is modified from Haas (2003, character 39, p.60).

414. ACCESSORY SLIP OF THE RECTUS CERVICIS: ABSENT (0); PRESENT, INSERTING ON THE CB IV (1).

This character is modified from Haas (2003: character 39: 60), who included this character as states of his character 39. I opt to individualize it as different transformation series, given that the insertion of the main slip of the rectus services can vary independently from the presence of the accessory slip. In some taxa, some fibers of the rectus cervicis (insertion on the processus branchialis II or III) extend to insert laterally to the ceratobranchial IV (state 1), forming an accessory slip. It is a very common state within dart-poison frogs and relatively uncommon within outgroup.

415. MUSCLE RECTUS CERVICIS, ORIGIN: ORIGINATING FROM THE DIAPHRAGM, BUT NOT PIERCING THE OPERCULUM (0); PIERCING THE OPERCULUM AND MEETING THE RECTUS ABDOMINIS (1).

The rectus cervicis usually originates at the diaphragm and can be tracked as an extension of the main slip of the rectus abdominis; both muscles are separated by a thin layer of tissue. Generally, the peribranchial tissue covers entirely the rectus cervicis origin and is fused to the diaphragm. However, in some taxa, particularly in dendrobatoids, the rectus cervicis pierces the diaphragm to meet the abdominal wall, where it originates (state 1).

416. MUSCLE DIAPHRAGMATOBRANCHIALIS: ABSENT (0); PRESENT, INSERTING ON DISTAL CB III (1).

The diaphragmatobranchialis originates on the peritoneum, very close to the origin of the rectus abdominis and the rectus cervicis and inserts on the distal, ventral margin of the ceratobranchial III. It was absent in some taxa, as in the endotrophic tadpole of *Anomaloglossus apiau*.

SUBARCUALIS OBLIQUUS

The subarcualis obliquus is muscle that usually inserts in the processus branchialis of either ceratobranchial II or III and originates on the processus urobranchialis of ceratohyal (Pussey 1943; Haas 1997, 2003). In some rare cases it may present three slips, like in *Aschaphus truei* (Haas 2003). In most dendrobatoids, a single slip can be observed inserting on the processus branchialis III. However, in some taxa (e.g., *Andinobates cassidyhornae*) it may present a secondary (ventral) slip. Besides Dendrobatoidea, the secondary slip has been reported in several lineages, especially in hylids (Candioti 2007; Haas 1997, 2003; Alcade et al. 2011). Among the umbelliform larvae of *Silverstoneia* another condition was observed, in which one slip of the subarcualis obliquus originates from a medial aponeurosis shared with some fibers of the subarcualis rectus I and with the rectus cervices. The possibility of presenting up to three different slips that may vary independently makes it very difficult to establish homology between each slip; for instance, when only one slip is present, it may originate in the ceratobranchial II or III, but when two are present, each slip originates on one ceratobranchial. Without further developmental studies, it is difficult to strongly support relationships of historical identity among these slips. Thus, I opt for a more conservative approach and code each slip independently, as absent and present, considering differences on its origin, when present.

417. SUBARCUALIS OBLIQUUS, CERATOBRANCHIAL II SLIP: ABSENT (0); PRESENT, INSERTING ON THE PROCESSUS BRANCHIALIS II (1); PRESENT, INSERTING ON THE DORSAL CERATOBRANCHIAL II.

Within dendrobatoids, the slip of the ceratobranchial II is not often present. When present, it is usually accompanied by the slip of the ceratobranchial III, as in some *Andinobates*. In the genus *Oophaga* and in some species of *Ranitomeya* it is present and alone.

418. SUBARCUALIS OBLIQUUS, CERATOBRANCHIAL III SLIP: ABSENT (0); PRESENT, INSERTING ON THE PROCESSUS BRANCHIALIS III (1); PRESENT, INSERTING ON THE DORSAL CERATOBRANCHIAL III.

The slip of the ceratobranchial III is very common in poison frogs and their relatives.

419. SUBARCUALIS OBLIQUUS, MEDIAL APONEUROSIS SLIP: ABSENT (0); PRESENT (1).

The presence of this slip is exclusive among anurans, found only in the genus *Silverstoneia*. Other anurans with the same disc configuration do not present this condition of the subarcualis obliquus (e.g., *Megophrys*). However, I found the same condition in the also umbelliform larvae of *Phasmahyla* (P.H.S. Dias in press). Data on other umbelliform larvae as *Duellmanohyla*, *Leptodactylodon*, *Mantidactylus*, and *Microhyla* are required to test the correlation between those characters.

420. MUSCLE SUBARCUALIS RECTUS II–IV: INSERTING ON THE PROCESSUS BRANCHIALIS III (0); INSERTING ON THE PROCESSUS BRANCHIALIS II (1); INSERTING ON THE CERATOBRANCHIAL I (2).

The subarcualis rectus II–IV is a small muscle originated at the ceratobranchial IV (Haas 2003). Usually, it extends to insert on the processus branchialis II, a configuration that named the muscle. Haas (2003) reported a large number of variations in this muscle. For instance, he reported the subarcualis rectus II–IV as discontinuous in *Pseudis* (see also Alcade and Barge 2006), and the presence of a lateralis slips in microhylids. In the present study, I observed less variation; I found differences only in the insertion of the subarcualis rectus II–IV, which in some species inserts as far as the ceratobranchial I, or anteriorly on the processus branchialis III. In some of the species presenting the insertion on the ceratobranchial I, a small set of fibers were weakly attached to the processus branchialis II as well, but we could not individualize this as a secondary slip and I recorded the variation for further studies.

421. INTERBRANCHIAL SEPTUM IV MUSCULATURE: ABSENT (0); LATERAL FIBERS OF THE M. SUBARCUALIS RECTUS II–IV INVADE THE SEMPTUM (1).

In some larvae, lateral fibers of the subarcualis rectus II–IV originate in a more lateral position and act as musculature of the interbranchial septum IV (Sokol 1977; Haas 2003; see also Haas 1997), which we scored as the state 1. State 1 is very common in bufonids (Haas 2003; Candioti 2007) and was proposed to be a synapomorphy for the family by Frost et al. (2006). Candioti (2008) also reported it for several *Telmatobius* larvae. Haas (2003: character 29: 58) used this character with the addition of a third state (origin of the m. subarcualis rectus II–IV completely far lateral), which I did not observe—in Haas` (2003) matrix, only pipoids presented that configuration.

CONSTRICTOR BRANCHIALIS MUSCLES

The constrictor branchialis are serial muscles inserting on the distal portion of the ceratobranchials (Haas 1997). I follow Haas (1997) in considering the constrictor branchialis I as missing in anurans. Salamanders, *Ascaphus truei*, *Spea bombifrons*, *Heleophryne natalensis*, *Pelodytes caucasicus* and Discoglossidae species possess the constrictor branchialis I, whereas in all other known anurans it is absent (Haas 2003). Haas (1996) and Cannatella (1999) discussed the homology assessment of the constrictor branchialis I in frogs. The constrictor branchialis II, III and IV are present in all dendrobatoids, except for some endotrophic species, in which it may be represented by a single almost undetectable fiber.

422. FUNCTIONAL CONSTRICTOR BRANCHIALIS II: PRESENT (0); ABSENT OR COMPOSED BY A SINGLE FIBER (1).

423. FUNCTIONAL CONSTRICTOR BRANCHIALIS III: PRESENT (0); ABSENT OR COMPOSED BY A SINGLE FIBER (1).

424. FUNCTIONAL CONSTRICTOR BRANCHIALIS IV: PRESENT (0); ABSENT OR COMPOSED BY A SINGLE FIBER (1).

425. MUSCLE CONSTRICTOR BRANCHIALIS II ORIGIN: PROCESSUS BRANCHIALIS II (0); PROCESSUS BRANCHIALIS III (1); CERATOBRANCHIAL II (2).

426. MUSCLE CONSTRICTOR BRANCHIALIS III ORIGIN: PROCESSUS BRANCHIALIS II (0); PROCESSUS BRANCHIALIS III (1); CERATOBRANCHIAL II (2).

427. MUSCLE CONSTRICTOR BRANCHIALIS IV ORIGIN: PROCESSUS BRANCHIALIS III (0); CERATOBRANCHIAL III (1); LATERAL EXTREMITY OF CERATOBRANCHIAL IV (2); PROCESSUS BRANCHIALIS II (3).

SUBARCUALIS RECTUS I COMPLEX

Haas (1997) reviewed the subarcualis rectus I complex. Caudate larvae present a single well-developed slip of the subarcualis rectus I, whereas anurans may present up to three slips (Haas 2003). Most anuran species, except for microhylids (see Haas 2003), present this muscle originating at the lateral base of the processus posterior hyalis (Haas 1997), but it may vary regarding its insertion. All dendrobatoids present three slips in the subarcualis rectus I—the dorsal slip, which invariably inserts on the dorsal ceratobranchial I, and the two (a and a`) portions of the ventral slip, which present the larger amount of variation, inserting on the ceratobranchialis II and III. Notwithstanding, there is a significant deviation from that standard condition in some outgroup taxa; in all studied cycloramphids I found a condition in which the dorsal slip is present in the ceratobranchial I, as expected, but the only ventral slip present is inserted on a medial raphe shared with an element of unknown homology, which I am calling the element Y. Such condition, as far as I know, has never been reported previously for any anuran larvae. Given the uncertain nature of that complex configuration, I followed the same reasoning applied to the subarcualis obliquus (see characters 18–20) and coded each ventral slip as an individual transformation series.

428. MUSCULUS SUBARCUALIS RECTUS I, VENTRAL SLIP AT THE CERATOBRANCHIAL II: ABSENT (0); PRESENT, AT PROCESSUS BRANCHIALIS II (1); PRESENT, AT CERATOBRANCHIAL II.

429. MUSCULUS SUBARCUALIS RECTUS I, VENTRAL SLIP AT THE CERATOBRANCHIAL III: ABSENT (0); PRESENT, AT PROCESSUS BRANCHIALIS III (1); PRESENT, AT CERATOBRANCHIAL III.

430. MUSCULUS SUBARCUALIS RECTUS I, VENTRAL AT THE MEDIAL RAPHE: ABSENT (0); PRESENT, ACCOMPANIED BY THE Y ELEMENT (1).

As discussed above, this condition was observed only in the cycloramphid tadpoles. In these tadpoles, the slips of the ceratobranchials II and III are absent and the Y element is invariably present. Such element has an uncertain homology relation; it originates on the diaphragm and inserts on the medial raphe shared with the ventral slip of the subarcualis rectus I. There are some possibilities that might be explored in further studies. The first possibility is that the Y element is a continuation of the rectus abdominis (rectus abdominis anterior); the topographic relation supports this hypothesis, given that the Y element originates in the diaphragm at the same point in which the rectus abdominis inserts—very close to the origin of the rectus cervicis as well. The second possibility is that the Y element is a second myotome of the subarcualis rectus I and the medial raphe represents a closed myosepta. The third possibility is that the Y element represents an unnamed muscle that evolved only in cycloramphid larvae. Unfortunately, there is no developmental data on this feature—to date, this is the first register of cranial muscles for the family—and I could not properly test these hypotheses. Nevertheless, it is interesting to note that all cycloramphid larvae examined in this study present semi-terrestrial tadpoles. I suggest that this Y element is correlated with such peculiar lifestyle; data on other non-semi-terrestrial cycloramphids (viz. some nidicolous *Cycloramphus* and *Zachaenus*) plus observations of other semi-terrestrial tadpoles as *Artholeptides*, *Indirana*, *Nannophrys* and *Petropaedes* will be essential to solve this question.

431. MUSCLE LEVATOR ARCUUM BRANCHIALIUM III, ORIGIN: SINGLE SLIP, ORIGINATING LATEROVENTRAL OTIC CAPSULE (0); TWO SLIPS, WITH THE SECONDARY ONE ORIGINATING AT THE DORSAL OTIC CAPSULE AND CROSSING THE AXIAL MUSCULATURE (1).

In its most common configuration, the levator arcuum branchialium III originates at the lateroventral otic capsule and inserts on the ceratobranchial III (Haas 2003). I observed a particular condition in centrolenids, in which the levator archum branchialium III has a secondary slip with dorsal origin in the otic capsule and extends towards the ceratobranchials crossing the axial musculature (Fig. 17). As far as I know, no other anuran larva presents this character state.

432. MUSCLE L. A. BRANCHIALIUM III, INSERTION: AT THE DISTAL CERATOBRANCHIAL III (0); AT PERITONEU (1).

In most known anuran larvae, the l. a. branchialium III inserts on the third ceratobranchial. We observed a highly modified condition in the cycloramphid larvae, in which this muscle is well-developed and extends ventrally to insert on the peritoneu, close to the origin of the rectus cervicis and insertion of the rectus abdominalis. No other anuran larva presents such condition as far as we know. See discussions on character 31, regarding the semiterrestrial tadpoles.

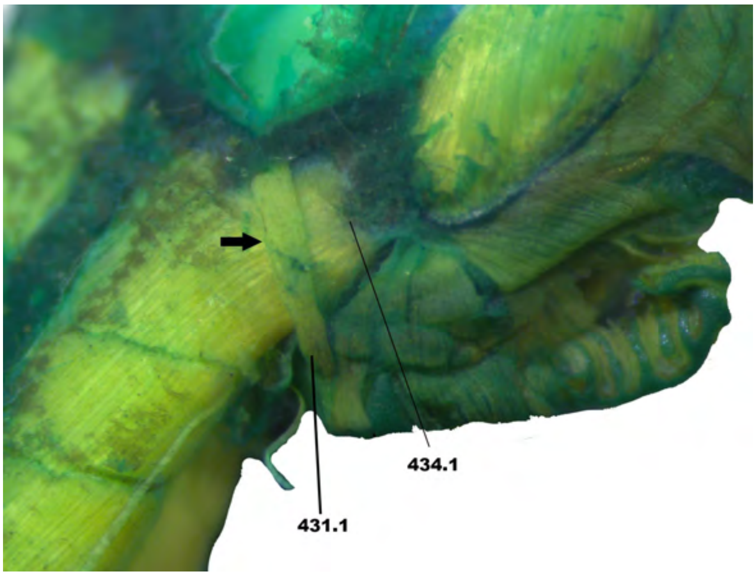

Figure 17. Detail of the levator archum branchialium in the tadpole of *Ikakogi tayrona*.

433. MUSCLE GENIOHYODEUS, ORIGIN: BETWEEN CB II AND CB III (0); BETWEEN CB III AND IV (1); AT THE LEVEL OF CB III (2); AT THE LEVEL OF CB IV (3); BETWEEN CB I AND II (4).

The ganiohyoideus is a long muscle observed ventrally in tadpoles. Usually, it originates on the hypobranchial plate and inserts on the infrarostral cartilages. It has been reported to vary regarding its origin, which may be at the ceratobranchial I as in *Ascaphus* or at the ceratobranchial III as in *Heleophryne* (Haas 1997). In all larvae studied here, the pattern of origin and insertion was invariable, however, the point in which this muscle originates at the hypobranchial plate (and therefore its longitude) may present variation. I used its position relative to the ceratobranchials as landmarks to delimit five character-states.

434. AXIAL MUSCLES (LAST MYOTOME), INSERTION EXTENSION: RESTRICTED TO THE POSTEROLATERAL OTIC CAPSULE (0); WELL DEVELOPED, EXTENDING OVER THE DORSAL OTIC CAPSULE (1).

The axial muscles are responsible for providing central support for the body; they are serially divided and cover the notochord and vertebral elements. Most tadpoles present the last myotome of the axial muscles inserted on the ventrolateral otic capsule (state 0), but I observed that in burrowing centrolenids and in the fast-flow dwellers *Atelopus* tadpoles, the last myotome insertion is anteriorly displaced, covering the dorsal surface of the otic capsules (state 1). Wassersug and Pyburn (1987) described this same condition in tadpoles of *Otophryne robusta*, also a burrowing tadpole. Haas et al. (2006) stated that this condition is very common in burrowing larvae.

435. SUSPENSORIOHYOIDEUS, INCLINATION: STRAIGHT, FORMING A 90^{o} ANGLE WITH THE SUBOCULAR BAR (0); POSTERIORLY ORIENTED (1).

The suspensoriohyoideus is a thin muscle partially covered by the orbitohyoideus. It originates at the posterior descending margin of the processus muscularis of palatoquadrate and inserts on the dorsolateral portion of the lateral porcessus of ceratohyal. In lateral view, the suspensoriohyoideus may form a straight pack of fibers (state 0) in some tadpoles, whereas, in other taxa, those fibers may be posteriorly oriented, towards the otic capsule (state 1).

436. SUSPENSORIOANGULARIS, ORIGIN: POSTERIOR MARGIN OF PROCESSUS MUSCULARIS (0); POSTERIOR MARGIN OF PROCESSUS MUSCULARIS, BUT ALSO AT VENTRAL PALATOQUADRATE (1); VENTRAL PALATOQUADRATE (2).

The suspensorioangularis is a jaw depressor muscle (Starrett 1973) that plays a role in both gill irrigation and feeding mechanism, being more active during the later (Larson and Reilly 2003). Generally, it originates at the posterior processus muscularis quadrati and inserts on Meckel`s cartilage. In the literature, it has been reported as originating on the anterior margin of the processus muscularis – as in *Dendropsophus* (Candioti 2007, P.H.S. Dias personal observation). In dart poison frogs and their relatives, I observed three different conditions: most dendrobatoids present the suspensorioangularis originating on the posterior descendent margin of the processus muscularis (state 0). In some dendrobatini and outgroup taxa, for instance, some *Hylodes*, *Crossodactylus* and centrolenids, the suspensorioangularis originates on the posterior processus muscularis, but also in the ventral palatoquadrate (state 1). In some aromobatids, as *Allobates nidicola* and other outgroup taxa (e.g., the harlequin tadpoles, *Atelopus*), there is a third condition in which the suspensorioangularis originates exclusively from the ventral surface of the palatoquadrate (state 2).

437. SUSPENSORIOANGULARIS, ORIGIN REGARDING ORBITAL POSITION: POST OR SUBORBITAL (0); EXCLUSIVELY PREORBITALLY (1).

Haas (2003: char. 44) stated two conditions for the relative position of the suspensorioangularis regarding the orbital position. In most anurans, that muscle originates postorbitally, i.e., anteriorly from the eyes in lateral view (state 0). Nevertheless, some taxa presented a plesiomorphic condition shared with urodels, in which the suspensorioangularis originates preorbitally—*Ascaphus truei*, *Alytes*, *Bombina*, and *Discoglossus*. Haas found that this character state re-evolved in some particular lineages of neobatrachians (viz. *Leptobatrachus* and *Atelopus*). In my observations, I corroborate Haas (2003) results in which *Atelopus* present a preorbital position.

438. ORBITOHYOIDEUS, ORIGIN: PROCESSUS MUSCULARIS QUADRATI (0); PROCESSUS MUSCULARIS QUADRATI, BUT ALSO EXTENDING INTO THE PROCESSUS ANTORBITALIS AND ORBITAL CARTILAGE (1).

The orbitohyoideus is responsible for lowering the buccal floor (Satel and Wassersug 1981); contraction of the orbitohyoideus rotates the ceratohyal cartilage, causing floor depression (Gradwell 1968, 1972; Larson and Reilly 2003) and resulting in the flux of water to the buccal cavity due to negative pressure. It is consistently active during the feeding kinematics of tadpoles (Larson and Reilly 2003). The orbitohyoideus originates on the processus muscularis quadrati and inserts on the lateral edge of ceratohyal. Generally, it is a thin muscle, but in most dendrobatini I found it hyperthorpied. In those species its origin sometimes extends further to reach the processus anthorbitalis (state 1). Well-developed orbitohyoideus have been reported in the literature of macrophagous larvae (Fig. 18); for instance, Candioti (2007) reported it as the largest muscle in tadpoles of *Dendropsophus microcephalus* and *Dendropsophus nanus*; she also reported that in the carnivore tadpole of *Lepidobatrachus*, the orbitohyoideus extends its insertion on the anterior margin of the commissura quadratocranialis. The orbitohyoideus is also well-developed in the carnivore larvae of *Ceratophrys* (Candioti 2005), *Occidozyga* (Haas et al. 2014), and *Leptobatrachus* (Ruibal and Thomas 1988), but such extended origin into the processus anthorbitalis seems to be an exclusive trait of dendrobatini.

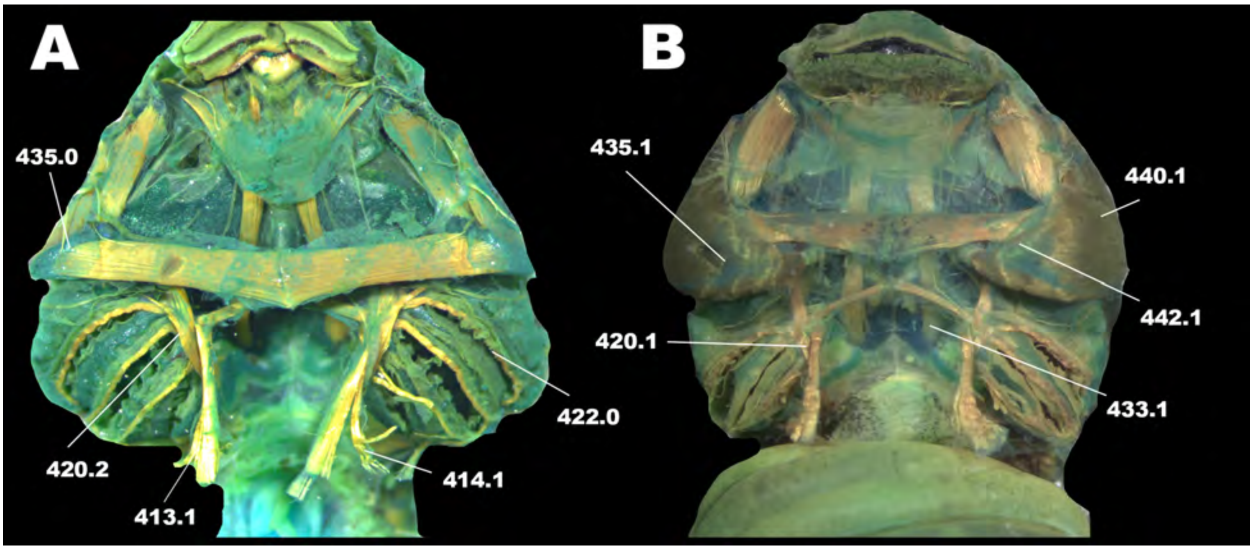

Figure 18. Ventral view of the cranial muscles of *Hyloxalus maculosus* (A) and *Adelphobates galactonotus* (B). Characters and their states are indicated.

439. ORBITOHYOIDEUS, INSERTION: LATERODORSAL CERATOHYAL (0); VENTROLATERAL CERATOHYAL (1).

Inserting on the laterodorsal portion of the ceratohyal is the most common configuration for the orbitohyoideus (state 0). As discussed above (see character 38), in some dendrobatini the orbitohyoideus is hypertrophied and extends its insertion towards the processus anthorbitalis; in those same taxa, the origin of the orbitohyoideus is also expanded, reaching the ventrolateral surface of the ceratohyal (Fig. 18).

440. ORBITOHYODEUS, LATERAL EXTENSION: RESTRICTED TO THE AREA OF PROCESSUS MUSCULARIS (0); LATERALLY EXPANDED, OCCUPYING AN EXTENSION WIDER THAN PROCESSUS MUSCULARIS (1).

The well-developed orbitohyoideus of some poison frogs is also expanded laterally. In those taxa, packs of muscular fibers extrapolate the edges of the processus muscularis laterally. In other words, in state 1, the width of the orbitohyoideus is larger than that of the processus muscularis.

441. ORBITOHYOIDEUS, INCLINATION: PERPENDICULAR (0); FORWARD INCLINED (1).

In lateral view, the fibers of the orbitohyoideus are usually directed anteriorly. In some taxa, like *Anomaloglossus praderioi*, they form a straight angle with the main axis of the chondrocranium (state 1).

442. ORBITOHYOIDEUS AND INTERHYODEUS: CLEARLY SEPARATED FROM EACH OTHER IN THEIR INSERTIONS (0); ORBITOHYODEUS OVERLAPS THE INTERHYOIDEUS IN THEIR INSERTIONS (1).

In some dendrobatids with a massive orbitohyoideus, the insertion of this muscle overlaps the interhyoideus (Fig. 18). In state 1, the orbitohyoideus possesses an area of insertion so broad that its fibers cover part of the terminal insertion of the interhyoideus on the lateroventral ceratohyal.

443. LARVAL MUSCULUS LEVATOR MANDIBULAE EXTERNUS: PRESENT AS A SINGLE MUSCLE BODY (0); TWO PORTIONS (PROFUNDUS AND SUPERFICIALIS) (1).

This character was used by Haas (2003: character 54). The levator mandibulae externus, also called m. adductor mandibulae externus superficialis, plays an important role in the systematic of poison frogs. Haas (2001) studied the cranial muscles of amphibians and stated that the m. levator mandibulae externus in the anuran larvae may present two slips: the profundus that usually inserts on suprarostral alae by sharing a tendon with the levator mandibulae longus profundus, and the superficialis, usually inserted on adrostral tissue or in the processus posterior dorsalis of suprarostral. Myers et al. (1991) suggested the absence of the m.a.m externus superficialis as a synapomorphy for all dendrobatids (Dendrobatoidea sensu Grant et al. 2006) but *Aromobates*, for which they reported the presence of the superficialis slip in 9 of 11 individuals (p. 8). Grant et al. (2006) with a broader taxonomic sample confirmed Myers et al.`s (1991) hypothesis by finding the superficialis slip absent in virtually all dendrobatoids. I found both slips in all examined dendrobatoids larvae. Whether the superficialis slip is lost or fused to the profundus during development remains unknown. I examined this muscle in developmental series of *Ameerega trivittata* and *Hyloxalus subpunctatus* and I observed that by Gosner (1960) stage 41/42 the superficialis slip cannot be found. Such ontogenetic variation explains why Krings et al. (2017), who used only stage 41 tadpoles, reported the superficialis slip absent in the five species of *Ranitomeya* studied by them (*R. amazonica*, *R. benedicta*, *R. imitator*, *R. reticulata*, and *R. vanzolinii*). I confirm the superficialis slip present in the *Ranitomeya imitator* and *Ranitomeya vanzolinii* examined. I also confirm the presence of the superficialis slip in *Dendrobates tinctorius*, *Epipedobates anthonyi*, *Epipedobates boulengeri*, *Epipedobates tricolor*, and *Phyllobates bicolor*, *contra* Krings et al. (2017, table 4, p. 24) who reported it missing in those species.

444. LEVATOR MANDIBULAE EXTERNUS SUPERFICIALIS, INSERTION: PROCESSUS POSTERIOR DORSALIS (0); ADROSTRAL TISSUE (1); DORSAL MECKEL`S CARTILAGE (2).

As discussed above, all dendrobatoids present the two slips of the levator mandibulae externus, and I found it inserted in the adrostral tissue invariably in poison frogs. Candioti (2007) reported the superficialis slip inserted in the processus posterior dorsalis of the suprarostral in *Telmatobius* cf. *atacamensis* (see also Candioti 2008) even when the adrostral cartilage was present; therefore, I hypothesized independence among the adrostral presence and the insertion of the superficialis slip on it. Furthermore, I found a third state in which this muscle is inserted in the dorsal portion of Meckel`s cartilage. This condition was observed in the cycloramphid larvae, but it was reported in the literature for pipoids (Haas 2003), in *Dendropsophus microcephalus* and *Dendropsophus nanus* (Candioti 2007).

445. FUNCTIONAL LARVAL M. MANDIBULAE LATERALIS: ABSENT (0); PRESENT (1).

This character was modified from Haas (2003: character 56). Haas (2001) showed that in some species this muscle develops only close to metamorphosis. Haas (2003) coded the presence of this muscle in terms of functionality, by using histological techniques; he considered the muscle functional when striated cells could be verified. I coded only presence and absence of this muscle, since I could not employ histological techniques for all the terminals in the matrix. Most dendrobatoids possess the m. mandibulae lateralis, although it is absent in some species, especially in outgroup taxa (e.g., *Melanophryniscus moreirae*).

446. MUSCLE MANDIBULAE LATERALIS, INSERTION: PROCESSUS POSTERIOR DORSALIS (0); ADROSTRAL TISSUE (1).

When present, I observed two distinct patterns of insertion of the mandibulae lateralis: at the adrostral tissue, as in most dendrobatoids (state 1), or in the processus posterior dorsalis (state 0), as in some hylodids, odontophrynids, among others.

447. PROFUNDUS AND SUPERFICIALIS PORTIONS OF M. LEVATOR MANDIBULAE LONGUS: BROADLY OVERLAPPING AT INSERTION (0); NOT OVERLAPPING (1).

Haas (2003: character 62) discussed some variations regarding the origin of the m. levator mandibulae profundus et superfcialis. These two muscles may overlap at their origins (usually on the posterior curvature of palaquadrate) or may present different points of origin. Haas (2003) states that in *Xenopus* and microhylids those two muscles are parallel. We did not find this state, however, in poison frogs and their relatives these two muscles can be completely overlapped (state 0) or slightly dislocated at their origins (state 1).

448. LEVATOR MANDIBULAE LONGUS, WIDTH: SUPERFICIALIS WIDER (0); EQUAL (1).

There is some degree of variation in the development of the longus group of levators of the mandibulae. In many species, the longus superficialis is wider than the longus profundus (state 0), whereas in other groups, they occupy the same area. I have not observed the profundus to be larger than the superficialis.

449. LEVATOR M. LEVATOR MANDIBULAE LONGUS GROUP, DEVELOPMENT: REGULAR, LEAVING SPACES IN THE FENESTRA SUBOCULAR (0); WELL-DEVELOPED, OCCUPYING ALL THE FENESTRA SUBOCULAR AND COVERING THE M. L. M. L. INTERNUS (1).

The levator longus group varies extensively regarding their development. Most tadpoles present this muscle occupying a significant portion of the fenestra subocular, but it is possible to see spaces in the fenestra subocular, and very often in the m. levator mandibulae longus internus (state 0). However, some frogs, particularly dendrobatini species, present these muscles massively developed, occupying the entire space of the fenestra subocular (state 1).

450. TENDON OF M. LEVATOR MANDIBULAE INTERNUS: PRESENT (0); ABSENT (1).

The m. levator mandibulae internus inserts on the Meckel`s cartilage via a long tendon. In some species (e.g., *Dendrobates auratus*) the tendon is absent, and the muscle has a fleshy insertion on the Meckel`s cartilage.

451. MUSCLE SUBMENTALIS (INTERMANDIBULARIS ANTERIOR): ABSENT (0); PRESENT (1).

The submentalis or intermandibularis anterior is a small muscle that connects both infrarostral cartilages. Haas (2001: 14) states that this muscle develops only in late developmental stages. However, I observed that in some taxa, particularly in Hylodidae larvae, it might appear even in young tadpoles. I scored its presence and absence.

452. INSERTION OF THE M. LEVATOR MANDIBULAE INTERNUS REGARDING JAW ARTICULATION: MEDIAL (0); LATERAL (1).

Haas (2001, 2003: character 59) discussed that in some taxa the muscle levator mandibulae internus possesses a medial insertion on the Meckel`s cartilage (state 0), but that most of the anuran larvae present an oblique orientation, and the muscle, therefore, inserts laterally on the Meckel`s cartilage (state 1). We observe the same kind of variation, although state 0 was less frequent—it was observed only in few taxa, such as *Atelopus* larvae.

453. RAMUS MANDIBULARIS (C.N.V3), REGARDING THE L. M. LONGUS GROUPS: BETWEEN PROFUNDUS AND SUPERFICIALIS (0); DORSAL TO BOTH MUSCLES (1).

This character is modified from Haas (2003: character 64: 64). The ramus mandibularis is a portion of the trigeminal nerve (Coghill 1916). The relationships between the c.n.V_3 and other elements have been explored in taxonomy (e.g., Lynch 1986) and in the establishment of homologies (e.g., Haas 2001) in anurans. Haas (2003) found that in caudates the mandibular branch of the trigeminus runs ventrally (posterior) to the levator longus group, whereas in most anurans it runs dorsally. He found an intermediate condition in which the c.n.V_3 runs between the longus superficialis and the longus profundus muscles in some taxa, as the microhylids *Kaloula pulchra* and *Dyscophus antongilii*. In dart poison frogs, the c.n.V_3 runs dorsally to the levator mandibulae longus group (state 1), with a single polymorphism (medially) in *Allobates olfersiodes* (*alagoanus*); however, I also observed a medial condition in the outgroup—both species of *Vitreorana* included in the present study present character state 0.

454. RAMUS MANDIBULARIS (C.N.V3), REGARDING THE M. L. M. EXTERNUS GROUP: BETWEEN EXTERNUS AND SUPERFICIALIS (0); DORSAL TO BOTH MUSCLES (1).

This character is modified from Haas (2003: character 65: 64). In salamanders, the c.n.V_3 runs ventrally to both muscles, whereas most anurans present it dorsally to the externus group (Haas 2003; see also character 53). However, some variation has been reported; Haas (2003) found that in some anurans the c.n.V_3 runs medially, between the externus and the superficialis slips. He also reported (p.65) that in some taxa, like *Agalychnis callidryas* and *Gastrotheca riobambae*, the c.n.V_3 runs medially and also pierces the profundus slip. I observed only two conditions—medial and dorsal—for this character. All examined dendrobatoids present the character state 1 (see also character 43), but some outgroup taxa—particularly bufonids and some hylodids—present the c.n.V_3 running medially, between the superficialis and profundus slips of the levator mandibulae externus (state 0).

Chondrocranium characters

(Fig. 19)

SUPRAROSTRAL CARTILAGE

The suprarostral cartilage provides support for the upper jaw sheath. The suprarostral cartilage usually comprises two elements, the lateral alae and the central corpus (Haas 1995). This cartilage forms the upper jaw of the tadpoles and represents a unique structure among vertebrates; they are powered by jaw muscles and are directly involved in the feeding habits of the tadpoles. There are several different combinations of character-states with suprarostrals (Fig. 20); corpora and alae may be completely free from each other, as in *Hylodes* (Bilate et al. 2012) or completely joined in a single, stout element, as in *Ceratophrys* (Candioti 2005). Adrostral elements may be present, as in some *Telmatobius* (Candioti 2008), and the suprarostral may even be located dorsally on the chondrocranium, as in *Phasmahyla* (Dias et al. 2018x). In dart-poison frogs there several variations in the suprarostral cartilages.

455. FUSION BETWEEN PAR CORPORIS: NOT FUSED (0); FUSED DISTALLY (1); FUSED PROXIMALLY (2); FUSED MEDIALLY (3); COMPLETELY FUSED (4); FUSED ALMOST DISTALLY (5).

Suprarostral corpora may present different degrees of fusion. For instance, in *Mannophryne olmonae* they are fused proximally (state 2), in *Dendrobates truncatus* they are fused distally (state 1), and in *Silverstoneia erasmios* they form a single, completely fused element (state 3). Some species present particular conditions in which the suprarostral corpora are fused almost distally (e.g., *Ameerega hehneli*). In dendrobatoids, however, the most common condition is to present both corpora free.

456. INCLINATION OF THE PAR CORPORIS IN FRONTAL VIEW: PARALLEL (0); CONVERGING DISTALLY TO THE MIDLINE, V-SHAPED (1).

In frontal view, both corpora may be parallel to each other, perpendicular to the longitudinal axis of the chondrocranium (state 0). In the other observed state, both corpora converge to a midpoint distally, assuming a V orientation (state 1).

457. STRUCTURE OF PROXIMAL INTERNAL MARGIN OF THE PARS CORPORIS: SMOOTH (0); WITH A PROCESS MEDIALLY DIRECT (1).

In some species of poison frogs, the inner margin of the suprarostral corpora may present a projection. The projections of both margins are pointed at each other.

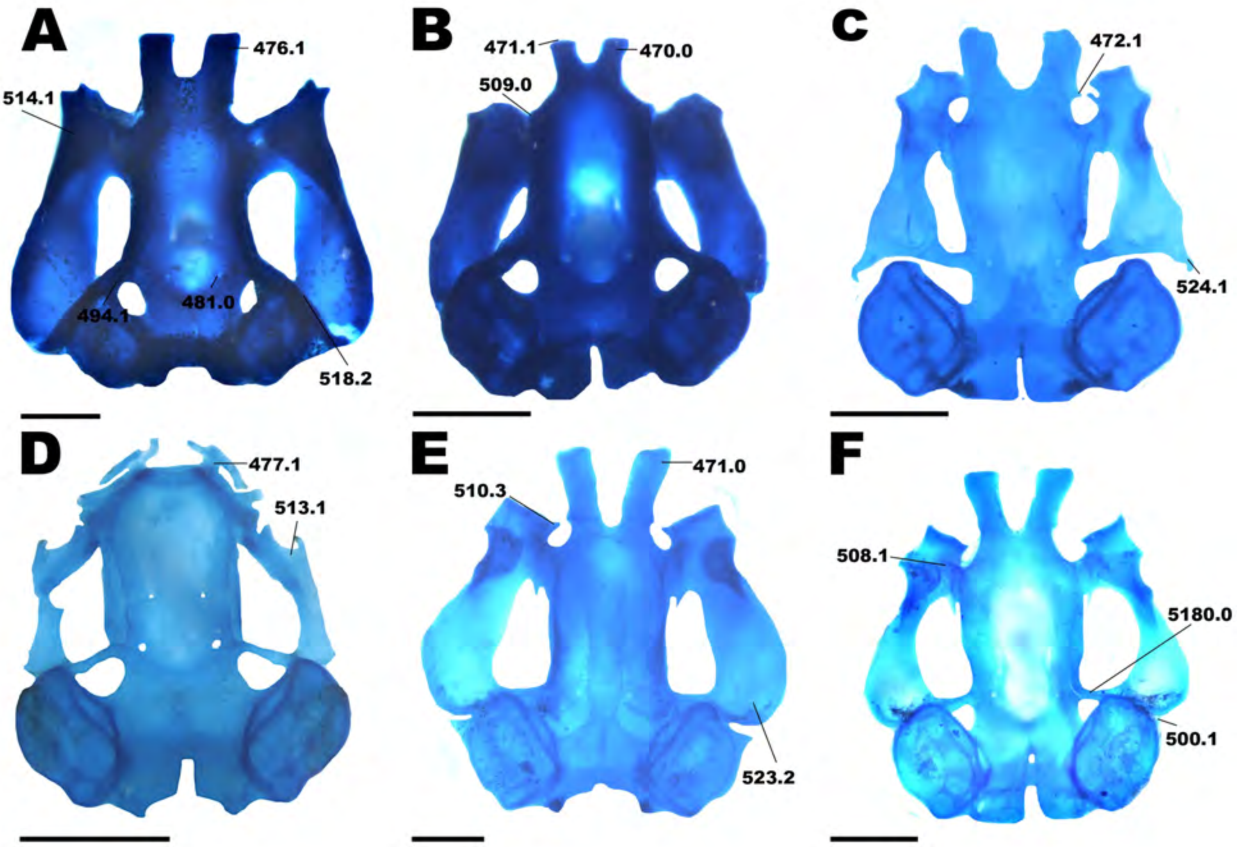

Figure 19. Chondrocranial diversity in Dendrobatoidea. *Ranitomeya amazonica* (A); *Oophaga pumilio* (B); *Silverstoneia flotator* (C); *Allobates nidicola* (D); *Rheobates pseudopalmatus* (E); and *Epipedobates boulengeri* (F). Characters and their states are indicated. Scale bar = 10 mm.

458. EXPANSION OF THE PARS CORPORIS ALONG ITS LENGTH: UNIFORM (0); DISTALLY EXPANDED (1).

In several poison frogs, the most distal portion of the suprarostrals are expanded. In those taxa, the width of terminal corpora is perceptively larger than the rest of the cartilage.

459. PARS CORPORIS WIDTH: THIN (0); LARGE (1).

I considered the corpora thin if their width in frontal view was smaller or similar to the width of the cornua trabeculae (state 0). In other taxa, particularly in Dendrobatini, their width surpasses the width of the cornua trabeculae. I considered the width of the cornua trabecula on its medial portion (see character 471).

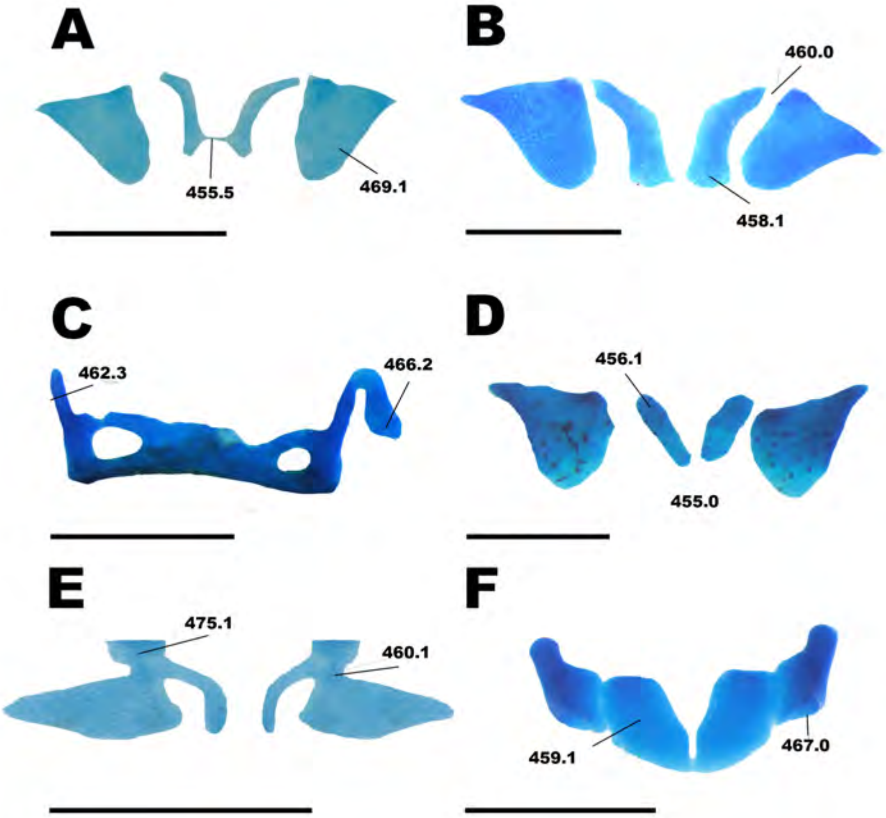

Figure 20. Phenotypic diversity in the suprarostral cartilage of dart-poison frogs. *Epipedobates anthonyi* (A); *Phyllobates auroteania* (B); *Silverstoneia nubicola* (C); *Hyloxalus maculosus* (D); *Allobates nidicola* (E); and *Dendrobates truncatus* (F). Characters and their states are indicated. Scale bar = 5 mm.

460. FUSION BETWEEN PARS CORPORIS AND PARS ALARIS: NOT FUSED (0); FUSED PROXIMALLY (1); FUSED DISTALLY (2); FUSED PROXIMALLY AND DISTALLY, WITH A SMALL CENTRAL FENESTRA (3); COMPLETELY FUSED (4).

The suprarostral corpora and pars alaris may present different degrees of fusion. They may be completely free from each other or fused at different portions, as distally or proximally. In some rare cases, both corpora and alae are completely fused, originating a single piece of cartilage. In the literature, almost all possible combinations have been reported (e.g., Larson and de Sá 1998; Candioti 2005, 2007), with large variations even among closely related taxa (e.g., Dias et al. 2013, 2014). I recognized five different states for dendrobatoids and their relatives.

461. PROCESSUS ANTERIOR DORSALIS: ABSENT (0); PRESENT, SHORT, WIDER THAN LONGER (1); PRESENT, MEDIAL, AS LONG AS WIDE (2); PRESENT, LARGE, LONGER THAN WIDER (3). ADDITIVE.

In frontal view, the superior medial corner of the suprarostral alae may present a protuberance, which is called the processus anterior dorsalis (Haas 1995), that articulates with the cornua trabeculae. I used the length and width of the processus anterior dorsalis to determine its size.

462. PROCESSUS POSTERIOR DORSALIS: ABSENT (0); PRESENT, SHORT, WIDER THAN LONGER (1); PRESENT, MEDIAL, AS LONG AS WIDE (2); PRESENT, LARGE, LONGER THAN WIDER (3). ADDITIVE.

In frontal view, the processus posterior dorsalis is located on the dorsal, external edge of the suprarostral alae. See character 461 for size estimation.

463. EXTREMITY OF PROCESSUS ANTERIOR DORSALIS: ACUMINATE (0); ROUNDED (1).

When present, the processus anterior dorsalis may present its extremity pointed, as a cone, or it may be rounded, smooth, like a bump.

464. EXTREMITY OF PROCESSUS POSTERIOR DORSALIS: ACUMINATE (0); ROUNDED (1).

See character 463.

465. PROXIMAL MARGIN OF THE PARS ALARIS: STRAIGHT (0); CONCAVE (1); CONVEX (2).

466. ADROSTRAL ELEMENT: ABSENT (0); PRESENT, WITHOUT CARTILAGINOUS CORE (1); PRESENT, WITH CARTILAGINOUS CORE (2). ADDITIVE.

Haas (1995: 242) defined the adrostral tissue mass as “a condensation of connective tissue rich in collagen fibers” located dorsolaterally to the suprarostral alae; the ligamentum mandibulosuprarostrali connects the adrostral to the Meckel`s cartilage. Haas (1995) suggested that the presence of this mass could be a synapomorphy of dart poison frogs. He also stated that in some species the adrostral mass presented a small cartilaginous core. I recognized a transformation series including both conditions of the adrostral element: with or without its cartilaginous core.

467. DISTAL MARGIN OF THE PARS ALARIS: STRAIGHT (0); ROUNDED (1); ACUMINATE (2).

468. PARS CORPORIS SHAPE: VERTICALLY RECTANGULAR (0); HORIZONTALLY RECTANGULAR (1); QUADRANGULAR (2).

In frontal view, the pars corporis could present different shapes; I considered it quadrangular if its height and width were similar (state 2). If it was wider than higher, I considered it horizontally rectangular, and the opposite was scored as vertically rectangular.

469. PARS ALARIS SHAPE: RECTANGULAR (0); SUBTRIANGULAR (1); QUADRANGULAR (2).

I considered the suprarostral alae to be rectangular when it was taller than wider (state 0). In state 1, if the proximal margin was wider than the distal one, the suprarostral alae assumed a subtriangular conformation. In state 2, height and width were approximately equal.

470. CORNUA TRABECULAE WIDTH: UNIFORM (0); DISTALLY EXPANDED (1).

471. DISTAL EXTREMITY OF THE CORNUA TRABECULAE: TRUNCATE (STRAIGHT) (0); SUBTRUNCATE (ROUNDED BORDERS) (1).

472. PLANE OF DISTAL MARGIN OF THE CORNUA TRABECULAE: STRAIGHT, PERPENDICULAR TO CHONDROCRANIUM LONGITUDINAL AXIS (0); INCLINED MEDIALLY (1).

473. PROCESSUS LATERALIS TRABECULAE: ABSENT (0); PRESENT (1).

474. SUPRAROSTRAL AND CORNUA TRABECULAE, ARTICULATION: SUPRAROSTRAL POSITIONED AT THE DISTAL EXTREMITY OF THE CORNUA TRABECULAE (0); CORNUA TRABECULAE EXTENDS FAR ANTERIORLY TO SUPRAROSTRAL (1).

475. FUSION BETWEEN SUPRAROSTRAL AND CORNUA TRABECULAE: ABSENT (0); PRESENT (1).

In some species, in dorsal view, the suprarostral corpora and the distal margin of the cornua trabeculae were connected by a small strip of cartilage. This condition was observed only in *Allobates nidicola* and *Allobates masniger*.

476. DIVERGENCE BETWEEN BOTH CORNUA TRABECULAE: DIVERGING DISTALLY, V-SHAPE (0); PARALLEL ALONG ITS LENGTH (1).

Considering its origin at the planum intratrabeculare anticum, the cornua trabeculae may extends rostrally parallel to each other or diverging, assuming a V-shape in dorsal view.

477. CORNUA TRABECULAE PLANE: PARALLEL TO MAIN AXIS (0); VENTRALLY DIRECTED (1).

In the endotrophic tadpoles, the entire rostral region is modified; the suprarostral cartilages are reduced and the cornua trabeculae assumes a peculiar conformation. Instead of being parallel to the chondrocranium`s longitudinal axis, the cornua trabeculae in these species is ventrally directed, almost in a straight angle with the chondrocranium axis. This condition is very rare and observed in direct developers as *Philautus* or *Eleutherodactylus* (Hanker et al. 1992; Kerney et al. 2007).

478. PROCESSUS ORBITONASALIS: ABSENT (0); PRESENT, SHORT (1); PRESENT, MODERATE (2); PRESENT, LARGE (3). ADDITIVE.

The processus orbitonasalis is a process of the anterior wall of the braincase, confluent with the cartilage orbitalis, located above the procesus antorbitalis and about the same level of the foramen orbitonasalis. I used its length and width to determine its relative size.

479. FENESTRA BASICRANIALIS: COMPLETELY OPEN (0); PARTIALLY COVERED (1); FULLY FUSED (2). ADDITIVE.

CRANIAL FLOOR FORAMINA

The cranial floor is usually pierced by two foramina, the formanen catoricum primatium, through which the arteria carotis enters the cavum cranii, and the craniopalatinum, which serves as an exit for the palatinus ramus of the arteria carotis interna (Haas 1995). The foramen caroticum primarium is located at the level of the processus ascendes, whereas the craniopalatium is more anterior, at the level of the eyes. When these foramina are present—sometimes the fenestra basicranialis is not completely occluded and it is impossible to identify these foramina—they may vary in their shape. In some taxa they must adopt a rounded conformation, whereas in other, they are oval or elliptical.

480. FORAMEN CAROTICUM PRIMARIUM: ABSENT (0); PRESENT (1)

481. SHAPE OF THE FORAMEN CAROTICUM PRIMARIUM: ROUNDED (0); OVAL (1).

482. FORAMEN CRANIOPALATINUM: ABSENT (0); PRESENT (1).

483. SHAPE OF FORAMEN CRANIOPALATINUM: ROUNDED (0); OVAL (1).

ORBITAL CARTILAGE FORAMINA

Four different foramina are recognized in the orbital cartilage. The prootic foramen is located between the otic capsule, planum basale, and the pila antotica. This foramen serves as an exit for the trigeminus nerve and the nervus facialis. The foramen oculomotorium is delimited by the pila antotica posteriorly and by pila metoptica anteriorly; the nervus oculomoturis runs through this foramen (as well as the arteria ophtalmica). The foramen opticum is the most anterior one and is delimited by the pila metoptica and peopitc. Additionally, there is a fourth foramina, the troclear; it may vary in its location on the lateral and dorsal axis of the orbital cartilage when present. In some cases, the orbital cartilage is not well-developed and the boundaries between these foramina becomes blurred and it is difficult to identify them. When they are present, they may vary in their shape.

484. FORAMEN OPTICUM: INCONSPICUOUS (0); WELL-MARKED (1).

485. SHAPE OF THE FORAMEN OPTICUM: ROUNDED (0); OVAL (1).

486. FORAMEN OCULOMOTORIUM: INCONSPICUOUS (0); WELL-MARKED (1).

487. SHAPE OF THE FORAMEN OCULOMOTORIUM: ROUNDED (0); OVAL (1).

488. FORAMEN PROOTICUM: INCONSPICUOUS (0); WELL-MARKED (1).

489. FORAMEN TROCHLEAR: ABSENT (0); PRESENT (1).

490. SHAPE OF THE FORAMEN TROCHLEAR: ROUNDED (0); OVAL (1).

491. LOCATION OF THE FORAMEN TROCHLEAR IN THE HORIZONTAL AXIS OF CARTILAGO ORBITALIS: AT POSTERIOR THIRD (0); AT MEDIAL THIRD (1); AT ANTERIOR THIRD (2).

492. LOCATION OF THE FORAMEN TROCHLEAR IN THE VERTICAL AXIS OF CARTILAGO ORBITALIS: AT SUPERIOR HALF (0); AT INFERIOR HALF (1).

493. CARTILAGO ORBITALIS, HEIGHT – LOW (0); MEDIAL (1); HIGH (2).

I considered the cartilage orbitalis to be high if its height is close to the dorsal margin of the otic capsule. If it was shorter than half of the otic capsule`s height I considered it low. The medial condition was reserved for taxa in which the orbital cartilage is approximately half of the height of the otic capsule.

494. POSTERIOR CONTACT BETWEEN THE CARTILAGE ORBITALIS AND THE OTIC CAPSULE: ABSENT, FORMING THE FENESTRA PROOTICA (0); IN CONTACT, FORMING THE DORSAL MARGIN OF THE FORAMEN PROOTICUM (1).

The orbital cartilage may or not contact the otic capsule. When it does, it forms the dorsal margin of the foramen prooticum; if not, then the foramen prooticum lacks dorsal margin and receives the name of fenestra prootica (Haas 1995). Haas (1995) reported that all dendrobatoids lack such contact, except *Dendrobates tinctorius*, in which the contact was present. Later, de Sá and Hill (1998) also found the contact in the chondrocranium of *Dendrobates auratus* and proposed that it would be a synapomorphy for the genus *Dendrobates* (equal to what we recognize as Dendrobatini). I confirm de Sá and Hill (1998) predictions; I found all Dendrobatini with this contact present.

495. SHAPE OF THE FENESTRA OVALIS: ROUNDED (0); OVAL (1).

496. ORIENTATION OF THE ARCHUS PRAEOCCIPITALIS: POSTEROLATERAL (INCLINED) (0); POSTERIOR (PARALLEL) (1).

The archus praeoccipitalis limits the foramen perilymphaticum and the foramen jugularis. This feature presents two different conditions within poison frogs. I found that in most frogs, the archus praeoccipitalis axis, from mouth to tail is posterolaterally directed, creating an angle with the chondrocranium`s longitudinal axis (state 0). In some cases, the archus praeoccipitalis is parallel to the main axis of the chondrocranium.

497. MEDIAL PROJECTION OF ARCHUS PRAEOCCIPTIALIS: ABSENT (0); PRESENT (1).

The internal medial margin of the archus praeoccipitalis presents a medial projection (state 1) in most poison frogs.

498. LARVAL CRISTA PAROTICA: INCONSPICUOUS (0); WELL-DEVELOPED (1).

Many frogs have a ledge on the anterolateral border of the otic capsule, lateral to the canalis semicircularis, the larval crista parotica (Haas 1995). In most tadpoles, such salience is well-developed and easily noticed. Some taxa, however, present it very short, almost as it was missing. That is the case of some dendrobatoids (e.g., *Silverstoneia flotator*) and some bufonids (e.g., *Amazophrynella*).

499. POSITION OF LARVAL CRISTA PAROTICA IN THE OTIC CAPSULE: LOW (0); MEDIAL (1); SUPERIOR (2).

Observing the otic capsule in lateral view it is possible to recognize that the crista parotica may occupy different portions of it; in most larvae it is located at the superior third of the otic capsule (state 2), but it also was observed at the medial (state 1) portion or in the lower third (state 0).

500. PROCESSUS ANTEROLATERALIS: ABSENT (0); PRESENT, SHORT (1); PRESENT, MODERATE (2); PRESENT, LARGE (3).

This character is modified from Haas (2003: character 66: 64). The crista parotica may present an anterolateral expansion, the processus anterolateralis. I recognize that, when present, this process presents differences in size. I considered small (state 1) if its width at the basis is longer than its length, and large (state 3) if the opposite; if both values were similar, I coded it as moderate (state 2).

501. EXTENSION OF THE PROCESSUS ANTEROLATERALIS: NOT REACHING THE POSTERIOR MARGIN OF PALATOQUADRATE (0); REACHING THE PALATOQUADRATE, FORMING THE LARVAL PROCESSUS OTICUS (1).

The processus anterolateralis may be well-developed and extend towards the posterior margin of the palatoquadrate, and in many taxa both structures are fused (state 1). Haas (2003) suggested that this condition is more common in ranoids, although it has been reported in several hyloids as well, as *Rhinoderma darwinii* (Lavilla 1987), *Hylorina sylvatica* (Cárdenas-Rojas et al. 2007), *Limnomedusa macroglossa* (Alcalde and Blotto 2006). No dart-poison frog presents the processus oticus, and its presence was restricted to outgroup taxa.

502. EXTREMITY OF PROCESSUS ANTEROLATERALIS: ACUMINATE (0); ROUNDED (1).

I observed that the distal extremity of the processus anterolateralis is often acuminated (state 0), but in some taxa, its border is rounded (state 1).

503. ORIENTATION OF THE PROCESSUS ANTEROLATERALIS IN DORSAL VIEW: ANTEROLATERAL (0); ANTERIOR (1).

When observed in dorsal view, the processus anterolateralis of the otic capsule may be oriented parallel to the longitudinal axis of the chondrocranium, which is a rare condition (state 1). Most species in fact present the processus directed anterolaterally (state 0).

504. PROCESSUS POSTEROLATERALIS OF CRISTA PAROTICA: ABSENT (0); PRESENT (1).

Haas (2003: character 67: 64) described that some pipoid, microhylids, and *Pseudis* species present an posterolateral expansion of the crista parotica (state 1). Larson and de Sá (1998) also reported this condition in several *Leptodactylus*. In dart-poison frogs this character state was observed only in few taxa, as *Allobates kingsburyi* and *Epipedobates narinensis*. Outgroup taxa also present this condition, *Proceratophrys bigibbosa*, for instance.

505. TAENIA TECTI MEDIALIS: ABSENT (0); PARTIALLY DEVELOPED (1); FULLY DEVELOPED (2). ADDITIVE.

The taenia tecti medialis is one of the components that may be involved in the covering of the cavum cranii roof, together with the taenia tecti transversalis (character 506). The taenia tecti medialis creates a bridge between the tectum synoticum and the taenia tecti transversalis. Haas (1995: 247) reported that *Silverstoneia nubicola* (as *Colostethus*), *Dendrobates tinctorius*, and *Epipedobates anthonyi* tadpoles possess rudimentary (state 1) taenia tecti medialis, which he (p. 255) suggested as a one of the diagnostic characters of Dendrobatoidea (as Dendrobatidae). I found a similar condition among several examined poison frogs. In outgroup species, as *Cycloramphus boraceiensis* for instance, the taenia tecti medialis is well-developed and reaches far anteriorly in the roof of cavum cranii (state 2). It is noteworthy, however, that caution must be taken when analyzing and coding this character, given that it has been demonstrated that this cartilage can vary along the development (de Jongh1968; Haas 1996). This character, together with characters 506 and 507 is a modification of Haas (2003) character 96.

506. TAENIA TECTI TRASNVERSALIS: ABSENT (0); PARTIALLY DEVELOPED (1); FULLY DEVELOPED (2). ADDITIVE.

The taenia tecti transversalis, as the medialis, is also involved in the covering the roof of cavum cranii. Haas (1995) suggested partially developed taenia tecti transversalis is another diagnostic of Dendrobatoidea. See comments on character 505. The taenia tecti medialis and transversalis may occur independently.

507. TECTUM PARIETALS: ABSENT (0); PRESENT (1).

The tectum parietal is a cartilage that covers a large portion of the cavum cranii. Most taxa do not present this condition (state 0). I found the presence of the tectum parietali only in outgroup taxa, as *Hylodes amnicola*.

508. PROCESSUS ANTORBITALIS: ABSENT (0); PRESENT (1).

The commissura quadratocranialis anterior connects the palatoquadrate to the braincase and has two portions, a proximal shallow, low portion and a distal, step high portion; in the transition between these two regions there may be a cartilaginous projection, the processus antorbitalis (Haas 1995). Although most species possess the procesuss antorbitalis, it is absent in some taxa (e.g., *Hylodes phyllodes*; *Cycloramphus boraceiensis*).

509. SIZE OF THE PROCESSUS ANTORBITALIS: SHORT (0); MODERATE (1); LARGE (2).

In dorsal view, it is possible to measure width and length of the processus antorbitalis. I considered it to be short (state 0) if it was wider than longer, and large (state 2) if the opposite was true. Moderate (state 1) condition was scored when both measures were approximately equal.

510. PROCESSUS QUADRATOETHMOIDALIS: ABSENT (0); PRESENT, SHORT (1); PRESENT, MODERATE (2); PRESENT, LARGE (3). ADDITIVE.

The processus quadratoethmoidalis arises from the steep margin of the commissura quadratocranialis anterior; it serves as a point of attachment for the ligamentum quadratoethmoidalis (Haas 1995). I used length and width to determine the size of the processus quadratoethmoidalis.

511. EXTREMITY OF THE PROCESSUS QUADRATETHMOIDALIS: ACUTE (0); ROUNDED (1).

512. PROCESSUS PSUEDOPTRIGOYDEUS: ABSENT (0); PRESENT, SHORT (1); PRESENT, MODERATE (2); PRESENT, LARGE (3). ADDITIVE.

The processus pseudpterygoideus projects from the posterior margin of the commissura quadrocranialis anterior towards the fenestra subocularis (Haas 1995). Haas (2003: character 77: 69) used this character in his study of larval morphology. The presence of the processus pseudopterygoideus has been used by several authors to diagnostic and delimit groups. Dias et al. (2013) used this character to comment on the relationships within *Proceratophrys* and other hyloids. I considered the relation between length and width to determine the size of processus pseudopterydoideus.

PROCESSUS MUSCULARIS QUADRATI

The processus muscularis quadrati extends dorsally from the lateral margin of the palatoquadrate (Haas 1995). The external face of the processus muscularis serves as an attachment point to some muscles, as the orbitohyoideus or the suspesoriangularis; the inner face is the point of origin of the levator mandibulae externus (Haas 2001). The processus muscularis is inclined towards the processus antorbitalis and both are connected via the ligamenti tecti superius et inferius. This triangular process may vary in size and orientation.

513. PROCESSUS MUSCULARIS QUADRATI, HEIGHT: HIGH (0); LOW (1).

In lateral view, the processus muscularis may be short, i.e., it is shorter than half of the otic capsule height, or tall, when it is higher than half of otic capsule.

514. PROCESSUS MUSCULARIS QUADRATI, WIDTH: REGULAR, SHORTER OR ABOUT THE SAME SIZE AS THE ATLAS (0); LARGER, MORE THAN 1.5 THE ATLAS LENGTH (1).

In most species the width of the processus muscularis is regular, although in most Dendrobatini (e.g., de Sá and Hill 1998) the processus muscularis is broad, which reflects a wide surface for the anchorage of the orbitohyoideus. Such variation has been associated with the buccal pump capacity (Wassersug and Hoff 1979). I used the length of the atlas—first presacral vertebra—to determine the relative width of the processus muscularis; to measure the width of the processus muscularis, I followed its descending margin until the point of merging with the palatoquadrate.

515. CONTACT BETWEEN PROCESSUS ANTHORBITALIS AND PROCESSUS MUSCULARIS: ABSENT (0); PRESENT (1).

Some taxa present the processus muscularis so inclined.

516. COMMISSURA QUADRATOORBITALIS: ABSENT (0); FORMED BY LIGAMENTOUS TISSUE (1); CHONDRIFIED (2). ADDITIVE.

The ligamnenti tecti superius et inferius connects the processus muscularis and antorbitalis as discussed above. In some frogs these ligamentous are replaced by chondrified structure, the commissura quadratoorbitalis. Haas (2003: character 78: 69) described a “high” condition, but it was unique for hyperoliids. No poison frog presented the commissura quadratoorbitalis, but several outgroup taxa, particularly bufonids, in which the commissura was invariably present.

517. PERFORATION OF THE ARCHUS SUBOCULAR: ABSENT (0); PRESENT (1).

In some tadpoles, as *Aromobates saltuensis*, it is possible to see a perforation on the archus subocular. When present, this character state was constant in multiple individuals of the same species.

518. ANGLE FORMED BY THE PROCESSUS ASCENDENS AND THE LONGITUDINAL AXIS OF THE CHONDROCRANIUM: STRAIGHT (0); ANTERIORLY INCLINED (1); POSTERIORLY INCLINED (2).

519. PROCESSUS ASCENDENS: LOW (0); INTERMEDIATE (1); HIGH (2).

Sokol (1981) was the first to discuss the possible phylogenetic implications of the different conditions of attachment of the palatoquadrate. Haas (2003: character 71: 66) used this character in his phylogenetic analysis. He recognized the same three conditions of Sokol (1981), who used the foramen oculomotorium as a landmark, and proposed a fourth condition—ultralow. The ultralow condition can only be precisely scored with histological cross sections, what was not practical given the size of my matrix. Moreover, previous evidence (Haas 1995, 2003) suggested that no poison frog has the ultralow condition, nor do most closely related outgroup taxa. Therefore, I coded only the three conditions of Sokol (1981): low (state 0), intermediate (state 1), and high (state 2).

520. POSTERIOR CURVATURE OF THE PALATOQUADRATE: POSTERIOR, AT THE LEVEL OF OTIC CAPSULE (0); AT THE LEVEL OF PROCESSUS ASCENDENS (1); ANTERIORLY, AT THE LEVEL OF PILA ANTOTICA (2).

I considered the point of maximum curvature of the posterior palatoquadrate to code this character.

521. POSTEROLATERAL MARGIN OF PALATOQUADRATE: FLAT (0); CONCAVE (1).

Depending on the attachment between the processus ascendens and the arcus subocular, the posterior margin may form a posterior edge, creating a clear concave aspect (Haas 2003: character 68: 64). Haas (2003) said that the state 1 was very perceptive in dendrobatoids. I found this state in most poison frogs and also in some outgroup species.

522. POSTERIOR REGION OF PALATOQUADRATE REGARDING THE ATLAS: REGULAR, SMALLER THEN ATLAS (0); BROAD, LARGER THAN THE ATLAS (1).

Dendrobatini larvae present a broad posterior region of the palatoquadrate, which serves as a surface for the origin of the levator mandibulae longus group.

523. GREATEST WIDTH OF SUBOCULAR BAR. ANTERIOR (0); MEDIAL (1); POSTERIOR (2).

524. POSTERIOR PROCESS OF PALATOQUADRATE: ABSENT (0); PRESENT (1).

In the posterior margin of the palatoquadrate, I found that *Silverstoneia* larvae present a pointed, large, posterior process (state 1). This condition was not observed in any other taxa, although in the literature it has been reported in some larvae, as *Pseudis* (Haas 2003).

525. ANGLE OF THE ARCUS SUBOCULARIS REGARDING THE CHONDROCRANIUM MAIN AXIS IN DORSAL VIEW: STRAIGHT ANGLE (0); ANTERIORLY DIRECTED (1).

I considered the main axis of the arco subocular to be the line that passes from its curvature to the distal border of the processus articularis quadrati. Then, I used the longitudinal axis of the chondrocranium together with the archus subocularis to code this character. In most species, I found an anteriorly directed archus subocularis.

526. ANGLE OF THE ARCUS SUBOCULARIS REGARDING THE CHONDROCRANIUM MAIN AXIS IN LATERAL VIEW: STRAIGHT ANGLE (0); INCLINED (1).

See comments on character 525; the differences between both characters is the view used to score the character (dorsal in character 525 and lateral in 526).

527. ORIENTATION OF THE INFRAROSTRAL CARTILAGE: PARALLEL (0); V-ORIENTED (1).

Infrarostral cartilage can be oriented in two different patterns; V-oriented, i.e., their medial extremities caudally directed, or parallel, forming and straight angle with the longitudinal axis.

528. THICKNESS OF THE INFRAROSTRAL CARTILAGE: UNIFORM (0); THIN AT THE EXTREMITIES (1); THIN MEDIALLY (2); THIN ON THE MEDIAL EXTREMITY (3).

529. FREE BASIHYAL: ABSENT (0); PRESENT (1).

Haas (2003: character 105: 75) employed this character in his study. The basihyal (Fig.21), or copula I as it is also known, is a cartilaginous element embedded in the ligamentum interhyale. Haas (1995) reported that in bufonids and dendrobatids this element is small and subject to individual variation. Haas (2003) used histological techniques to score this character. I coded present whenever any alcian blue positive element appeared between the ceratohyals.

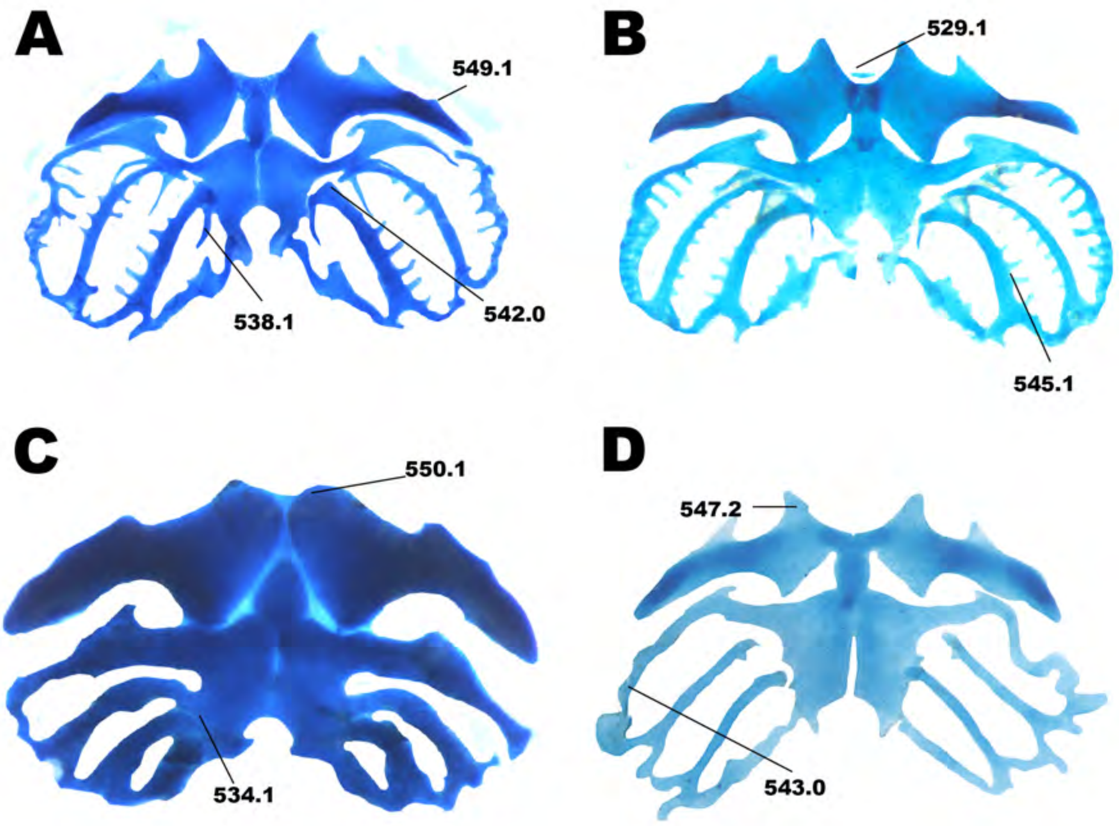

Figure 21. Diversity of hyobranchial morphology in Dendrobatoidea. *Allobates juani* (A); *Ameerega bilinguis* (B); *Oophaga pumilio* (C); *Allobates nidicola* (D). Characters and their states are indicated.

COMMISSURA PROXIMALIS

Haas (1995: 251) defined commissura proximalis as the proximal fusion between ceratobranchials. He suggested that the lack of commissura proximalis between the ceratobranchials was a putative synapomorphy for dendrobatids.

530. COMMISSURA PROXIMALIS I–II: ABSENT (0); PRESENT (1).

531. COMMISSURA PROXIMALIS II–III: ABSENT (0); PRESENT (1).

532. COMMISSURA PROXIMALIS III–IV: ABSENT (0); PRESENT (1).

CERATOBRANCHIAL AND HYPOBRANCHIAL PLATES

Each ceratobranchial may be free or fused to the hypobranchial plate. Usually, the ceratobranchial I is continuous with the planum hypobranchial and I found no other condition among poison frogs and their relatives. However, I found that the ceratobranchialia II–IV may vary; in most species the ceratobranchial II and III were free, but in some taxa, they were fused to the hypobranchial plate. The ceratobranchial IV is the opposite; the most common condition was the fusion between it and the hypobranchial plate.

533. FUSION OF THE CB II WITH HYPOBRANCHIAL: ABSENT (0); PRESENT (1).

534. FUSION OF THE CB III WITH HYPOBRANCHIAL: ABSENT (0); PRESENT (1).

535. FUSION OF THE CB IV WITH HYPOBRANCHIAL: ABSENT (0); PRESENT (1).

SPICULE

Spicula I–IV are horizontal cartilages that originate and project from the proximal margin of each ceratobranchial and provide support for the ventral velum (Haas 1995). Haas (2003) reported they are absent in caudates and in some frogs, as the carnivorous *Lepidobatrachus*. I found spicules missing in some dendrobatoids, particularly in some endotrophic and some oophagous larvae. When present, the fourth spicule is the most variable; it may be free or fused to the hypobranchial plate, and it may be thin or enlarged.

536. SPICULE I: ABSENT (0); PRESENT (1).

537. SPICULE II: ABSENT (0); PRESENT (1).

538. SPICULE III: ABSENT (0); PRESENT (1).

539. SPICULE IV: ABSENT (0); PRESENT (1).

540. FOURTH SPICULE, FUSION TO THE HYPOBRANCHIAL PLATE: FREE (0); FUSED (1).

541. SHAPE OF THE FOURTH SPICULE: NORMAL (0); ENLARGED (1).

542. PROCESSUS BRANCHIALIS: OPEN (0); CLOSED (1).

Larson and de Sá (1998) used this character in their phylogenetic analysis of larval *Leptodactylus*. According to them, when the processus branchialis of ceratobranchial II and III contact each other medially, they are closed (state 1). See also Haas (2003: character 114: 76).

CARTILAGINOUS PROJECTIONS OF THE CERATOBRANCHIALS

In most examined frogs, the ceratobranchials present some lateral, cartilaginous projections. These projections provide additional support for the filter plates and rows and to the branchial filaments. They were absent in oophagous and endotrophic larvae.

543. LATERAL CARTILAGENOUS PROJECTIONS OF THE CERATOBRANCHIAL I: ABSENT (0); PRESENT (1).

544. LATERAL CARTILAGENOUS PROJECTIONS OF THE CERATOBRANCHIAL II: ABSENT (0); PRESENT (1).

545. LATERAL CARTILAGENOUS PROJECTIONS OF THE CERATOBRANCHIAL III: ABSENT (0); PRESENT (1).

546. LATERAL CARTILAGENOUS PROJECTIONS OF THE CERATOBRANCHIAL IV: ABSENT (0); PRESENT (1).

PROCESSESS OF THE CERATOHYAL

The ceratohyal is the proximal component of the apparatus hyobranchial; the posterior component is the hypobranchial plate and the branchial basket. Several processes can be found in the dorsal margin of the ceratohyal. The processus anterior hyalis is the most medial one, followed laterally by the processus anterolateralis hyalis. A third process, the processus of the crista lateralis hyalis, may or may not be present; the crista lateralis hyalis is the lateral expansion of the ceratohyal, and on its dorsal margin, a triangular process may or not occur. I coded the presence and absence of each process, and for all of them, I used length and width to determine their size. Moreover, I found variation on the extremity of these processes. Whereas in most poison frogs they are acute, pointed and triangular, some specific taxa (e.g., *Oophaga*) may present more rounded, dome-like processes; variation regarding the extremity was coded as different characters.

547. PROCESSUS ANTERIOR HYALIS: ABSENT (0); PRESENT, SHORT (1); PRESENT, LARGE (2). ADDITIVE.

548. PROCESSUS ANTEROLATERALIS HYALIS: ABSENT (0); PRESENT, SHORT (1); PRESENT, LARGE (2). ADDITIVE.

549. PROCESSUS CRISTA LATERALIS HYALIS: ABSENT (0); PRESENT, SHORT (1); PRESENT, LARGE (2). ADDITIVE.

550. EXTREMITY OF THE PROCESSUS ANTERIOR HYALIS: ACUTE (0); ROUNDED (1).

551. EXTREMITY OF THE PROCESSUS ANTEROLATERALIS HYALIS: ACUTE (0); ROUNDED (1).

552. EXTREMITY OF THE PROCESSUS CRISTA LATERALIS HYALIS: ACUTE (0); ROUNDED (1).

553: PROCESSUS LATERALIS HYPOBRANCHIALIS: ABSENT (0); PRESENT, SHORT (1); PRESENT, LARGE (2).

Haas (1995: 251) defined this character as a posterior expansion of the outer margin of the hypobranchial plate, located distally to the ceratobranchial I origin. He found that this process was present in poison frogs. I also code this character; furthermore, I recognize variation in size structure.

554. EXTREMITY OF THE PROCESSUS LATERALIS HYPOBRANCHIALIS: ACUTE (0); ROUNDED (1).

See character 553.

555. CONDYLUS ARTICULARIS: SHORT, NOT VISIBLE IN FRONTAL VIEW (0); LARGE, EXTREMITY VISIBLE IN FRONTAL VIEW (1).

In frontal view, the condyles articularis, i.e., the point of articulation between the ceratohyal and the ventral palatoquadrate, may be well-developed or inconspicuous. In some taxa, the condylus is large, its dorsal margin is taller than the borders of the ceratohyal, and it is possible to see a bump above the ceratohyal line in frontal view (state 1).

556. PROCESSUS ANTERIOR BRANCHIALIS: ABSENT (0); PRESENT, SHORT (1); PRESENT, LARGE (2). ADDITIVE.

The processus anterior branchialis projects from the dorsal margin of the ceratobranchial I (Haas 1995). Most poison frogs present this character, however I found it missing in some taxa, as in the endotrophic *Allobates nidicola*.

557. EXTREMITY OF THE PROCESSUS ANTERIOR BRANCHIALIS: ACUTE (0); ROUNDED (1).

558. POSTERIOR MARGIN OF THE CERATOHYAL: CONCAVE (0); STRAIGHT (1).

In ventral view, the posterior margin of the ceratohyal usualy is concave, but in some tadpoles, such curvature is less accentuated, and the ventral margin is basically plain (state 1).

Natural History Characters

559. LARVAL HABITAT: GROUND-LEVEL POOL OR STREAM (0); PHYTOTELMATA (1); NIDICOLOUS (2); SEMI-TERRESTRIAL (3).

Tadpoles can be found in almost every water body in the world but at the poles. They can inhabit and develop in large and small streams of slow and fast waters (e.g., Downie et al. 2001; Strauß et al. 2013), in temporary or permanent ponds (e.g., Fabrezi 2011), or in large, lentic water bodies as lakes. Many species are specialized to live in phytotelma, as large or small bromeliads, nutshells, tree holes, banana leaves, or even bamboo pools (e.g., Lannoo et al. 1987; Lethinen et al. 2004). Tadpoles of different lineages adopt a semiterrestrial life-style (e.g., Bokermann 1965; Cocroft and Heyer 1988; Chaning et al. 2012), whereas others develop in terrestrial chambers or nests (e.g., Caldwell and Lima 2003; Nuñez et al. 2012). Some tadpoles can even tolerate estuarine brackish water and tidal pools (e.g., Gordon and Tucker 1965; Dunson 1977).

Within dart-poison frogs and their relatives, I observed the occupancy of ground-level pools or streams (state 0)—that include, for instance, fast-flowing water bodies and temporary pools—, the usage of phytotelma (state 1; without distinction between ground or high-level plant pools), and the development in terrestrial nests (state 2). Moreover, additionally to those three states, which are the same as in Grant et al. (2017), I coded the semi-terrestrial habitat (state 3), a characteristic of *Thoropa* and *Cycloramphus* larvae.

560. LARVAL TROPHIC GUILD: EXOTROPHIC (0); ENDOTROPHIC (1).

Grant et al. (2006) considered this character as part of their character 112, "Larval diet" (p.102), a rational altered by Grant et al. (2017: 6). The latter opt to distinguish trophic guild from larval diet. I agree with Grant et al. (2017) and herein I code the characters individually. Tadpoles may be divided into two ecomorphological groups regarding nutritional sources: endotrophic (state 1), if all required larval nutrients come exclusively from parents (some exceptions in facultative endotrophics, as *Incilius periglenes*; Crump 1989); and exotrophic (state 0), which obtain nutrients from the surrounding environment. Obviously, limits between these both extremes are quite blurred and much more variation exists. For instance, tadpoles of *Incilius periglenes* are facultative endotrophics (Crump 1989) and the nidiculous tadpoles of *Adenomera diptyx* require a feeding period in order to complete metamorphosis (de La Riva 1995).

Altig and Johnston (1989), on the basis of developmental modes, habitat, and external morphology characters, recognized six developmental guilds for endotrophic tadpoles and 18 for exotrophic tadpoles. Most dendrobatoids herein examined possess a free-living, exotrophic larva; the few endotrophic species fit the nidiculous guild of Altig and Johnston (1989), which is characterized by the seldom association with parent`s body and by presenting a free-living, non-feeding tadpole that may present characters states of exotrophic larvae. Nidiculous larvae very often present reduced body pigmentation, mouthparts, spiracle, closed vent tube, reduced or close nares, large hind limbs (Cruz and Peixoto 1982; Duellman and Grey 1983; Kaiser and Altig 1994; Thibaudeau and Altig 1999; Altig and McDiarmid 1999; Caldwell and Lima 2003; Cárdenas-Rojas et al. 2007b; Candioti et al. 2011). Besides personal observation and external and internal morphology characters observed, I also took data from natural history habits in the original descriptions of tadpoles.

561.EXOTROPHIC DIET: DETRITIVOROUS (0); PREDACEOUS (1); OOPHAGOUS (2).

Tadpole diet is a controversial issue. For a long time, tadpoles were believed to be herbivorous due to the large amount of vegetal items in their digestive tract. However, with the advent of new evidence and technologies such as the usage of stable isotopes (e.g., Schiesari 2004, 2009) this view has been questioned (Altig et al. 2007). Currently, the available evidence suggests that in most cases tadpoles are at least omnivorous (e.g., Vassilieva et al. 2017). In some particular cases, as in some Panamanian centrolenids that feed basically on microbes (Verbug et al. 2007), there may be some specificity in food resource; however, in general, tadpoles vary considerably in their feeding preferences.

Tadpoles can, in fact, have some trophic plasticity (Caut et al. 2012) and they can shift their role in the aquatic communities because of predators, competitors or even as part of their development (Arribas et al. 2015; Glos et al. 2016). So far, little is known on tadpole dietary habits, but future researches may demonstrate the differences in the ingested and absorbed nutrients (Altig et al. 2007). Nevertheless, some tadpoles are currently less controversial regarding their diets, as in the case of the carnivorous larvae of *Lepidobatrachus* or *Spea* (Ruibal and Thomas 1988; Crump 1992) that ingest large preys entirely. It is known that many dendrobatini are predators, carnivorous, and oftenly cannibalistic tadpoles (Myers and Daly 1976; Summers 1990; Caldwell and Araújo 1998; Brown et al. 2011; pers. observation). There is a strong correlation between predaceous habits and the usage of phytotelma occupancy, although some dendrobatoids that inhabit phytotelma present a completely distinct diet (oophagy, which can be obligatory, as in *Oophaga* [Weygoldt 1980; Brust 1993] or facultative, as in some *Ranitomeya* and *Anomaloglossus* [Caldwell and Oliveira 1999; Bourne et al. 2001]).

Given the above and the absence of further evidence, I considered that the term detritivorous applies for omnivores tadpoles that feed on filter particles, grasp of periphyton or ingest large portions of organic and inorganic matters (state 0). I followed Grant et al. (2006: 102) in considering that all tadpoles found in ground-level pools or streams (or other water bodies) should be treated as detritivorous in the absence of contradictory evidence. All species reported or personally observed to attack and consume invertebrates, other tadpoles or even siblings were coded as state 1; I also used gut content in some cases (e.g., *Minyobates steyermarki*) to determine this state. I considered oophagous (state 2) the tadpoles that depend exclusively on maternal egg provisioning to develop; and I considered polymorphic those species in which egg deposition occurs facultative, in order to complement or accelerate development (as *Ranitomeya imitator* [Brown et al. 2008b; Yoshika and Summers 2016]).

Continuous characters

Some of the observed characters presented a large variation. For example, the absolute number of marginal papillae on the oral disc may vary from 0 (none) to 40 in a same region. Moreover, these papillae are subject to large intraspecific variation. Therefore, I opt to treat these characters as continuous (see Goloboff et al. 2006). Below, I list the continuous characters and the range of variation in each of them.

562. MARGINAL PAPILLA, DORSOLATERAL REGION, UPPER LIP: 0 TO 26.

563. MARGINAL PAPILLA, VENTROLATERAL REGION, LOWER LIP: 0 TO 39.

564. MARGINAL PAPILLA, MEDIAL REGION, LOWER LIP: 0 TO 28.

565. SUPRANUMERARY, LATERAL, ROOF ARENA PAPILLAE: 0 (0); 1 (1); 2 (2); 3 (3); 4 (4); 5 (5); 6 (6); 7 (7); 8 (8); 9 (9); 10 (10); 11 (11); 12 (12).

The lateral roof arena papillae usually are conical, long, simple not ornamented papillae, curved inwards in the direction of the buccal roof arena (Wassersug 1976). They delineate the buccal roof arena laterally and posteriorly (see character 35). Wassersug (1980: 115) mentioned that the overall number of lateral roof papillae is correlated with the number of buccal floor arena papillae; however, the number of the first is always smaller than the later. Suggested functions for the lateral roof arena papillae were gas exchange, chemical sensitive, and mechanical regulation of water flow in the buccal cavity (Kenny 1969a; Wassersug 1980). For each species, I coded the number of supranumerary papillae by counting the total number of papillae on each side, recording the largest number of papillae that I observed. Variation in the number were treated as polymorphic states.

566. SUPRANUMERARY, LATERAL, FLOOR ARENA PAPILLAE, SUPERIOR TO THE BIFID PAPILLAE: 0 (0); 1 (1); 2 (2); 3 (3); 4 (4); 5 (5); 6 (6); 7 (7); 8 (8); 9 (9); 10 (10); 11 (11); 12 (12); 13 (13); 14 (14); 15 (15); 16 (16); 17 (17); 18 (18); 19 (19); 20 (20); 21 (21); 22 (22); 23 (23); 24 (24); 25 (25). The buccal floor arena is defined laterally and posteriorly by a series of conical, tall, simple papillae. Different functions for the buccal floor arena papillae have been proposed, ranging from respiration to mechanical effectors of flow, just as for the infralabial papillae (Kratochwill 1933; Kenny 1969a; Gradwell 1972; Wassersug 1980; see also comments above about the infralabial papillae). These papillae often are numerous and oriented towards the center of the buccal floor arena (Wassersug 1976). The bifid papilla observed at the same level as the buccal pocket (see character 64) is present almost invariably, and I used it to delimit superior and inferior portions of the buccal floor arena; i.e., I consider the supranumerarial papillae rostrally to the bifid floor papilla as "superior" and those caudally to it, "inferior".

567. SUPRANUMERARY, POSTERIOR, ROOF ARENA PAPILLAE, INFERIOR TO THE BIFID PAPILLAE: 0 (0); 1 (1); 2 (2); 3 (3); 4 (4); 5 (5); 6 (6); 7 (7); 8 (8); 9 (9); 10 (10); 11 (11); 12 (12); 13 (13); 14 (14); 15 (15); 16 (16); 17 (17); 18 (18); 19 (19); 20 (20); 21 (21); 22 (22); 23 (23); 24 (24); 25 (25). These are the buccal floor arena papillae located below (posteriorly) to the bifid lateral floor arena papillae, which is adjacent to the buccal pockets.

Phylogenetic Analysis

I performed a total evidence analysis under parsimony as optimality criteria. A six-step approach was used for heuristic searches:

1) Using the standard direct optimization algorithm (Wheeler, 1996), run one 40 h search using 256 CPUs (= 10,240 CPU-hours), one 40 h search using 512 CPUs (= 20,480 CPU-hours), and two 96 h searches using 512 CPUs (= 98,304 CPU-hours) using the command "search", which implements a driven search composed of random addition sequence Wagner builds, Subtree Pruning and Regrafting (SPR) and Tree Bisection and Reconnection (TBR) branch swapping (RAS + swapping; Goloboff, 1996), Parsimony Ratcheting (Nixon 1999), and Tree Fusing (Goloboff 1999), and alternates between the specified optimization algorithm (standard direct optimization in this case) and static-approximation, which searches using the implied alignment of the best tree in memory. To accelerate searches, treat equal-length loci (viz., BDNF, H3F3C, SLC8A1, RHO, and SIAH1) as pre-aligned.

2) Remove pre-aligned constraints and perform 6,000 rounds of Tree Fusing of all optimal trees saved in Step 1.

3) Perform approximation of Goloboff's (1999) consensus-based sectorial search method. Specifically, assuming the clades shared by the optimal trees of the previous analyses are probably present in the global optimum, perform one 8 h driven search using the strict consensus of the optimal trees from Steps 1–2 as the constraint topology and the standard direct optimization algorithm run on 512 CPUs (4,096 CPU-hours).

4) Remove topological constraint and swap best trees from Steps 1–3 using standard direct optimization algorithm, storing up to two minimum-length trees per starting tree.

5) Calculate cost of optimal tree from all previous analyses using approximate iterative pass algorithm (Wheeler 2003a) and generate matrix version of tree- alignment (i.e., implied alignment; Wheeler 2003b).

6) To verify the length reported by POY v.5.1.1 and search for better and/or additional trees given the implied alignment, perform aggressive search of the implied alignment in TNT v.1.5 (Goloboff et al. 2008; Goloboff and Catalano 2016; equal costs for all transformations, gaps treated as fifth state), stopping when stable consensus reached five times (tnt command: xmult= replications 10 rss css xss ratchet 10 drift 10 fuse 5 consense 5).

I used YBIRÁ (Machado 2015) to visualize and list synapomorphies. All compute-intensive analyses were run on Ace, a high-performance computing cluster housed at the Museum of Zoology of the University of São Paulo composed of 12 quad-socket AMD Opteron 6376 16-core 2.3-GHz CPU, 16 MB cache, 6.4 GT/s compute nodes (= 768 cores total), eight with 128 GB RAM DDR3 1600 MHz (16 × 8 GB), two with 256GB (16×16GB), and two with 512 GB (32×16GB), and QDR 4x InfiniBand (32 GB/s) networking.

RESULTS

Phylogenetic Analysis

The driven search performed 702 RAS + swapping, 622 rounds of Tree Fusing, and 134 rounds of Ratcheting. The final unconstrained swap of all optimal trees resulted in a single tree of 97,624 steps, which was further reduced to 97,522 steps by approximate iterative pass optimization.

Ingroup monophyly and Outgroup relationships

In the optimal hypothesis, Dendrobatoidea was monophyletic, supported by molecular and phenotypic synapomorphies (Fig. 22). Additionally, the data also supports the monophyly of several families as proposed in other studies (e.g., Frost et al. 2006; Pyron and Wiens; Pyron 2014). Notwithstanding, I did not recover Leptodactylidae with its three subfamilies as proposed by Pyron and Wiens (2011). *Leptodactylus fuscus*, the only representative of Leptodactilinae, was recovered as the sister of all studied taxa but *Boana boans* that was the root of the tree. The monophyletic Paratelmatobiinae containing *Rupirana* + (*Scythrops* + *Paratelmatobius*) was recovered as sister to Allophrynidae plus Centrolenidae. Leiuperinae was not monophyletic—*Pseudopaludicola falcipes* was the sister a large clade containing all species but *Leptodactylus fuscus* and *Boana boans*, whereas the other representatives of the subfamily were sister to Bufonidae.

The monophyletic Bufonidae was composed by three clades; the most basal was represented by the genus *Melanophryniscus*, sister to all other bufonids. The second clade comprises the species of the former Atelopodidae: *Dendrophryniscus* as sister to *Atelopus* + (*Frostius* + *Amazophrynella*). In the last clade, *Nanophryne variegata*, *Peltophryne peltocephala*, *Rhaebo*, and *Rhinella* formed successive less inclusive clades; *Rhinella marina* was sister to the paraphyletic *Incilius*—*Incilius boucorti* was sister to *Anaxyrus*.

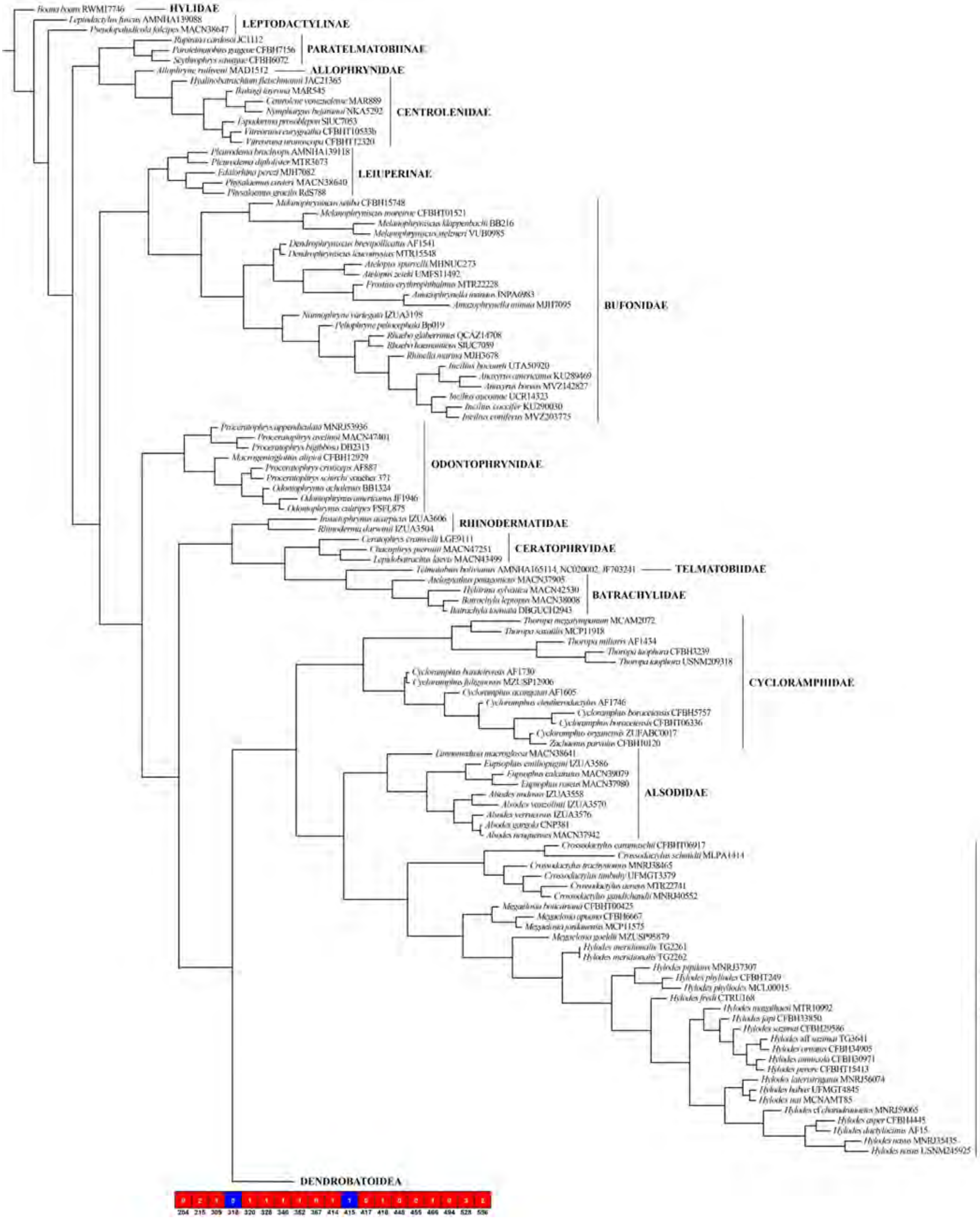

Figure 22. Optimal hypothesis of outgroup relationships. Tree shows branch-lengths (from the most parsimonious trees), and selected nodes labeled with unambiguous larval synapomorphies (red square = unique, homoplastic; blue square non-unique, homoplastic; characters below the square and synapomorphic state inside the square.

Despite monophyletic, the internal relationships within Odontophrynidae are controversial given that *Proceratophrys* was recovered polyphyletic. The *Proceratophrys bigibbosa* species groups was monophyletic and sister to *Proceratophrys appendiculata*. This clade was sister to a clade composed by the monotypic *Macrogenioglotus* + (*Proceratophrys cristiceps* group + the monophyletic *Odontophrynus*). Odontophrynidae was the sister clade to a large clade containing the remaining Hyloides lineages, including Dendrobatoidea.

Batrachylidae formed a monophyletic clade; *Atelognathus* was sister to *Hylorina* + *Batrachyla*. *Batrachylidae* was sister to *Telmatobius bolivianus*, the sole representative of Telmabtobiidae. Ceratophryidae was recovered monophyletic; *Ceratophrys* is sister to a clade of *Lepidobatrachus* + *Chacophrys*. The relationships within Ceratophryidae are exactly the same as hypothesized by Faivovich et al. (2014). *Rhinoderma* and *Insuetophrynus* are sister taxa, corroborating the monophyly of Rhinodermatidae. This family is sister to the clade containing Ceratophryidae + (Telmatobiidae + Batrachylidae) and both clades are sister to a large assamblage containing Cycloramphidae + (Alsodidae + Hylodidae) plus Dendrobatoidea.

My results refute the hypothesis of Grant et al. (2017) that recovered *Thoropa* as sister to all Dendrobatoidea. In my optimal solution, *Thoropa*, *Zachaenus* and *Cycloramphus* formed a monophyletic clade, the family Cycloramphidae. While *Thoropa* was monophyletic, *Zachaenus parvulus* is nested within *Cycloramphus*. Alsodidae was monophyletic, presenting the monotypic *Limnomedusa* as sister to *Alsodes* + *Eupsophus*. The optimal topology is greatly in accordance with that of Blotto et al. (2013), including the internal relationships. Hylodidae was recovered monophyletic, although *Megalosia goeldi* was recovered as sister to all *Hylodes*, rendering it paraphyletic. The remaining *Megaelosia* species were recovered as sister to *Hylodes* + *Megaelosia goeldi* and this clade was sister to the monophyletic *Crossodactylus*.

Ingroup relationships—general results

The internal relationships agree with Grant et al.`s (2017) hypothesis, and all Dendrobatoidea higher level taxa were recovered monophyletic. Dendrobatoidea contains two clades, corresponding to the families Dendrobatidae and Aromobatidae.

Aromobatidae is composed two clades: Allobatinae + (Aromobatinae + Anomaloglossinae). Allobatinae is a monotypic subfamily that includes the genus *Allobates*; Aromobatinae comprises *Aromobates* and *Mannophryne*, whereas Anomaloglossinae contains *Anomaloglossus* and *Rheobates*—all monophyletic.

Dendrobatidae contains three major clades: Colostethinae + (Dendrobainae + Hyloxalinae). Colostethinae includes (*Silverstoneia* + *Epipedobates*) + *Colostethus* + (*Leucostethus* + *Ameerega*).

Dendrobatinae contains *Phyllobates*, "*Colostethus*" *ruthveni* group, *Minyobates*, *Oophaga*, *Adelphobates*, *Dendrobates*, *Excidobates*, Andinobates, and *Ranitomeya*. Hyloxalinae is composed by *Paruwrobates*, *Ectopoglossus*, and *Hyloxalus*. All genera within Dendrobatidae were recovered monophyletic.

Systematics of dart-poison frogs and larval morphology

Dendrobatoidea Cope, 1865.

Type genus: *Phyllobates* Bibron in La Sagra, 1840.

Immediate more inclusive taxon: Athesphatanura

Sister group: Unnamed clade composed by Alsodidae, Cycloramphidae, and Hylodidae.

Content: Aromobatidae and Dendrobatidae.

Characterization: Unambiguous optimized synapomorphies are: **1)** Gap on P1 absent (character 240.0); **2)** upper jaw sheath with a medial notch (character 215.2); **3)** Relief of the prenarial arena concave (character 309.1); **4)** internal nares perpendicular orientation (character 318.0); **5)** valve projection on the posterior wall of the internal nares present, well-developed (character 320.1); **6)** first pair of postnarial papillae with conical or rounded pustulations (character 328.1); **7)** lateral ridge papillae with conical or rounded pustulations (character 340.1); **8)** third pair of infralabial papillae present (character 352.1); **9)** second pair of lateral, lingual papillae absent (character 367.0); **10)** accessory slip of the rectus cervicis present, inserting on CB IV (character 414.1); **11)** muscle rectus cervicis origin, piercing the operculum and meeting the rectus abdominis (character 415.1); **12)** subarcualis obliquus, CB II slipe absent (chracter 417.0); **13)** subarcualis obliquus, CB III slipe present, inserting on the processus branchialis III (character 418.1); **14)** levator mandibulae longus superficialis wider than profundus (character 448.0); **15)** pars corporis not fused (character 455.0); **16)** adrostral element present, without cartilaginous core (character 466.1); **17)** posterior contact between the cartilago orbitalis and the otic capsule absent (character 494.0); **18)** infrarostral cartilage thinner medially (character 528.3); **19)** processus anterior branchialis present, large (character 556.2).

Comments: The superfamily Dendrobatoidea is distributed throughout Central and South America, occupying streams in dense forests, open fields, lowland rainforests, 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). The monophyly of Dendrobatoidea is well-supported since Noble (1926) and consistently recovered in several studies (e.g., Frost et al. 2006; Grant et al. 2006, 2017; Santos et al. 2009; Pyron and Wiens 2011; Pyron 2014).

Aromobatidae Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel, and Wheeler, 2006.

Type genus: *Aromobates* Myers, Paolillo-O, and Daly 1991.
Immediate more inclusive taxon: Dendrobatoidea.
Sister group: Dendrobatidae.
Content: Aromobatinae, Allobatinae, Anomaloglossinae.
Characterization: Unambiguous optimized larval synapomorphies are: **1)** second pair of postnarial papillae with conical or rounded pustulations (character 329.1); **2)** pars corporis distally expanded (character 458.1).

Allobatinae

Allobates Zimmermann and Zimmermann, 1988

Type species: *Prostherapis femoralis* Boulenger, 1884
Immediate more inclusive taxon: Aromobatidae
Sister group: Unnamed clade composed by Anomaloglossinae and Aromobatinae.
Content: 52 recognized species.
Characterization: **1)** Gap on A2 present, large (character 203.2).
Comments: *Allobates* (Fig. 23) is the second largest genus within Dendrobatoidea with 51 recognized species (Frost 2018)—*Hyloxalus* is the largest genus with 58 nominal species. My results are greatly in accordance with those of Grant et al. (2007). I also found the Atlantic Forest species *Allobates olfersiodes* as the sister of the remaining *Allobates*. Subsequently, two Venezuelan species form successive lineages sister to the rest of *Allobates*—an undescribed species from the Neblina Base Camp, Rio Mawarinuma and *Allobates undulatus*, from Cerro Yutajé. Less inclusive clades included a group of Peruvian and Ecuadorian species: *Allobates kingsburyi*, *Allobates peruvianus*, *Allobates fratiscenscus*, and an undescribed species of Mendez, Ecuador.

The trans-Andean species formed a monophyletic group; *Allobates niputidea* was sister to two clades of *Allobates talamancae*. I included for the first time DNA sequences and phenotypic data for the Colombian (Quibdo, Chocó) populations assigned to *Allobates talamancae*. Previous studies (e.g., Grant et al. 2006, 2017) included specimens from Nicaragua, Panamá and Ecuador; they found that Central America populations diverged largely from Ecuadorian samples—Ecuador individuals differ from those of Nicaragua by 9.6% and from those of Panama by 8.2% in the cytochrome b sequences (Grant et al. 2017). The first clade that I recovered was composed by Panamanian and Costa Rican specimens, and the second clade contained the Colombian and Ecuadorian individuals.

Grant et al. (2017: 30) claimed that the South America clade might not be conspecific with the Central America clade, a hypothesis supported by my results. I also found several differences in larval morphology between tadpoles from Colombia and Panama, which provides further evidences to recognize the Colombia-Ecuador clade as a distinct historical individual. Other taxa might be included in this trans-Andean clade, although their phylogenetic position is unknown; these species are *Allobates ignotus* and *Allobates wayuu*. This trans-Andean clade is the sister to the remaining Amazonian *Allobates*.

The greatest difference between my results and those of Grant et al. (2017) concerns the *femoralis* group. Grant et al. (2017) proposed the *femoralis* groups and the 22-chromossoome groups as sister taxa. I failed in recovering that relationships because *Allobates flaviventris* + *Allobates magnussoni* were sister to *Allobates crombiei* + (*Allobates nidicola* + *Allobates masniger*), which in turn, were recovered as sister to the *femoralis* group—in Grant et al. (2017) those taxa were nested within the 22-chromossome group. Other topological differences are related with the positioning of some species. For instance, Grant et al. (2017) found *Allobates granti* as sister to *Allobates caeruleodactylus*, whereas I found it as sister to *Allobates chalcopis*.

The Atlantic Forest clade deserves further attention in future studies. Recent evidence from acoustic data suggested a cryptic diversity hidden under the single species *Allobates olversiodes* (Forti et al. 2017). Larval morphology also provides differences among populations of *Allobates olfersiodes*. Additionally, this clade is supported by 37 phenotypic synapomorphies from adult and tadpoles. I suggest that this clade should be recognized as a separated genus, which will be described elsewhere.

Tadpoles: Tadpoles of *Allobates* usually develop in temporary, small ponds or in pools formed near the margins of streams (e.g., Duellman 1978; Lima et al. 2009, 2010), although some taxa use phytotelmata—as fallen palm petioles—opportunistically, as *Allobates femoralis* (Silverstone 1976; Caldwell and Araújo 2004). Nevertheless, the biology of these tadpoles is poorly known—many of their descriptions were based on captivity reared specimens obtained from egg clutches (e.g., Simões et al. 2010, 2013; Castillo-Trenn 2004; Lima et al. 2007, 2015)—and only c.a 50% of the species have their tadpoles described (e.g., Dunn 1924; Bokermann 1975; Myers and Donnelly 2001; Kok et al. 2006b).

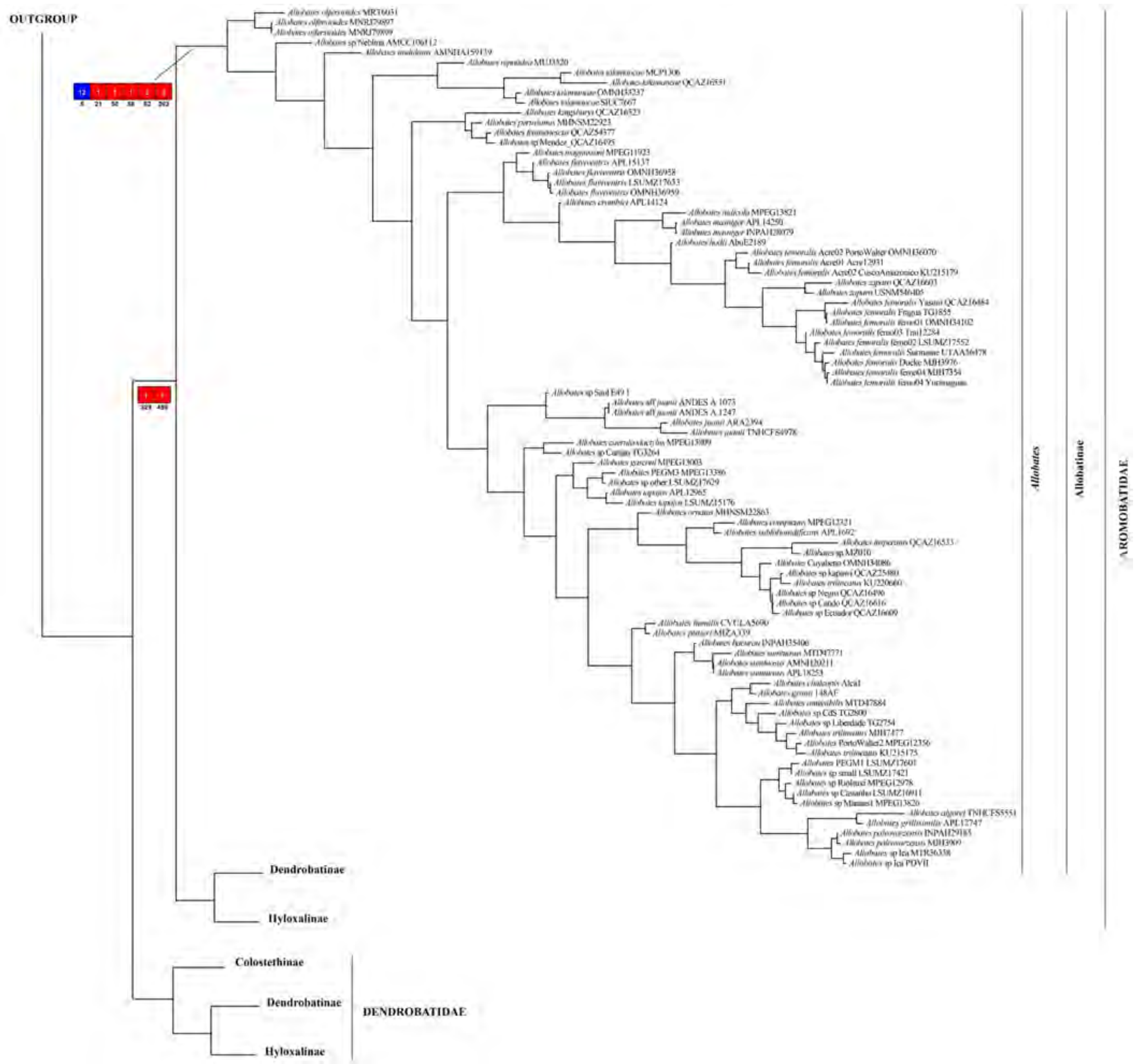

Figure 23. Optimal hypothesis of relationships within Allobatinae. Tree shows the branch-lengths (from the most parsimonious trees) and selected nodes labeled with unambiguous larval synapomorphies (red square = unique, homoplastic; blue square non-unique, homoplastic; characters below the square and synapomorphic state inside the square.

Other characters: Despite the phenotypic synapomorphies, several interesting characters evolved within these tadpoles. For instance, given the combination of characters, there are four patterns in marginal papillae size and configuration:

1) regular sized, conical, well-distributed papillae: this is the case of species of the *femoralis* group (*Allobates femoralis*, *Allobates hodli*), but also the condition present in the trans-

Andean *Allobates* (*Allobates niputidea*, *Allobates talamancae*) and in some other species (e.g., *Allobates undulatus* and *Allobates trilineatus*).

2) few, conical or rounded, reduced but large papillae on the upper lip, with regular, large numbered papillae in the lower lip: this condition is observed in some few species, as *Allobates granti* and *Allobates sumtuosus*.
3) few, conical or rounded, reduced but large papillae on the upper lip, with large, conical, reduced in number, papillae on the lower lip: condition observed in *Allobates brunneus*, *Allobates paleovarzensis*, and *Allobates subfolinidificans*, for example.
4) reduced, conical papillae on the upper lip, with very large, conical, reduced in number, barbell like, papillae on the lower lip.

The fourth condition is the most strikingly different configuration of marginal papillae in Dendrobatoidea, and given my optima hypothesis, it evolved at least three times: in *Allobates caeruleodactylus*, *Allobates grillisimilis*, and *Allobates tapajos*. *Allobates marchesianus* also present this condition, however its phylogenetic placement is unknown, which may represent a fourth independently acquisition of such large papillae.

Another interesting character not coded in the present study due to the absence of data for most species is the dark line in the snout between the eye and the nostril. This character state can be observed clearly in the pictures of the tadpole of *Allobates paleovarzensis* (Lima et al. 2010: Fig.7: 13) but is also present in tadpoles of *Allobates sumtuosus* (Simões and Lima 2012) and *Allobates subfolinidificans* (Lima et al. 2007). I found it also in the sister species of *Allobates paleovarzensis*, and undescribed (currently in process of description by P.H.S Dias and M.A. Anganoy-Criollo) from the Icá River, Amazon. Nevertheless, this character can be properly scored in living individuals and it is likely to occur in other *Allobates* larvae.

Other tadpoles: *Allobates wayuu* is an endemic species of the isolated Serranía de La Macuira, at La Guajira departament, Colombia. Acosta et al. (1999) concluded that this species would be closely related to *Colostethus inguinalis*. Grant et al. (2006), however, transferred it to *Allobates*. The tadpoles of *Allobates wayuu* were poorly described by Acosta et al. (1999). Examined tadpoles of *Allobates wayuu* shared several characters with other *Allobates* species, and also with other genera, as *Hyloxalus* and *Colostethus*. The most conspicuous character-state presented by the larvae of *Allobates wayuu* is the shelf on the upper jaw sheath (Dias et al. in press). This character state is present in all *Allobates* from Atlantic forest, in the *Colostethus fraterdanieli* complex, *Rheobates palmatus*, *Hyloxalus italoi*, and in all *Epipedobates* (see character 223).

Given the combination of characters of both adults and tadpoles, it unlikely that *Allobates wayuu* is closely related to any of these species. For example, despite sharing the shelf with the Atlantic Forest species, *Allobates wayuu* differ from those tadpoles in several other characters, including the fusion of the first pair of infralabial papillae, a synapomorphy of the Atlantic Forest frogs. Additionally, this species is geographically isolated, occurring in the extreme North of South America. As happened to other isolated taxa (e.g., "*Colostethus*" *ruthveni*) I predict that *Allobates wayuu* will represent a different, unnamed lineage among poison frogs.

Tadpoles of *Allobates mandelorum* present several character-states that are also present in several lineages of Dendrobatoidea (e.g., *Colostethus*, *Anomaloglossus*, *Hyloxalus*). Some of these characters suggested that this species is not closely related to *Allobates*. Despite some few *Allobates* presenting a medial notch on the upper jaw sheath, this character-state is more common in other lineages as Aromobatinae, for instance. Furthermore, the jaw sheaths of *Allobates mandelorum* are strongly keratinized and they lack a gap on P-1.

The other *Allobates* species that resembles *Allobates mandelorum* is *Allobates undulatus*. *Allobates undulatus* also present the medial notch (although polymorphic), well-keratinized jaw sheaths, an also lack the gap on P-1. Additionally, they share several other characters from external morphology, cranial muscles and buccopharyngeal cavity. Nevertheless, these two species are separated by a large geographical distance, in which there are dry lands and the large Orinoco River. Moreover; no other *Allobates* species occurs so north in Venezuela as *Allobates mandelorum*.

Most of the character-states present by *Allobates mandelorum* and *Allobates undulatus* are also found in Aromotidae larvae; all Aromobatidae (except *Aromobates nocturnus* and *Manophryne neblinae*) present well-keratinized jaw sheaths with a medial notch on the upper jaw sheath and several species (e.g., *Aromobates nocturnus*, *Aromobates saltuensis*) lack a gap on P-1, which suggest *that Allobates mandelorum* could be part of the family Aromobatidae. La Marca (1993) suggested that *Allobates mandelorum* were not closely related to the collared species (= *Mannophryne*). Based on larval characters and adult phenotypic evidence; for example, *Allobates mandelorum* have extensive toe webbing, a common character in *Aromobates* and *Mannophryne* frogs (Rivero 1978; La Marca 1993, 1994; Grant et al. 2006). I suggest that *Allobates mandelorum* should be transferred to *Aromobates*: *Aromobates mandelorum* **com. nov.**.

La Marca and Mijares-Urrutia (1997) described two tadpoles found in the axils of a bromeliad together with adults of *Allobates bromelicola*. This tadpole presented a depressed body, rounded tail tip, ventral mouth, large A-2 gap, low fins, well-keratinized jaw sheaths, with a medial notch, and low spiracle. Those characters are common in phytotelmata larvae of *Anomaloglossus* and Dendrobatidae. No other *Allobates* occupies bromeliads, however this is a common trait in some *Anomaloglossus* species. In fact, the character-states of *Allobates bromelicola* are the same of those of *Anomaloglossus beebei* or *Anomaloglossus roraima*. Nevertheless, several characters evolved convergently in phytotelm dwellers (see comments on “Character Evolution section) and there is no reason to reject the possibility of a *Allobates* species becoming specialized for phytotelm usage. More evidence is required to positioned precisely this species.

Allobates goianus is a poorly known species that inhabits the Brazilian Cerrado. This species has been reported from Goiás states in at least four different localities (Carvalho et al. 2016; Frost 2018). Its tadpole was described by Bokermann (1975) and since then received no further attention. Carvalho et al. (2016) provided a new account on the species, expanding the geographical distribution, and providing new data on the morphology and advertisement call. According to them (p. 24, 25 and 27), no morphological or acoustic character distinguish this species from *Allobates brunneus* and *Allobates olfersiodes* (although they mention that the dorsal color pattern might be diagnostic in relation to *Allobates olfersiodes*: p.27).

The tadpoles of *Allobates goianus* can be promptly differentiated from those of *Allobates olfersiodes* by lacking the medial notch and the shelf on the upper jaw sheath and they are more similar to the tadpoles of *Allobates brunneus*. *Allobates goianus* tadpoles can be distinguished from those of *Allobates brunneus* by the anteroventral mouth (ventral), alternated marginal papillae on the lower lip (straight), the extensive keratinization of the jaw sheaths (only the border keratinized), arch-shaped upper jaw sheath (trapezoid), rounded narial opening (elliptical). Given the above, I predict that *Allobates goianus* will be closely related to *Allobates brunneus* and reject any close relationships with *Allobates olfersiodes*.

Aromobatinae Myers, Paolillo-O and Daly, 1991

Type genus: *Aromobates* Myers, Paolillo-O and Daly, 1991

Immediate more inclusive taxon: Aromobatidae

Sister group: Anomaloglossinae

Content: *Aromobates* and *Mannophryne*.

Characterization: Unambiguous optimized larval synapomorphies are: **1)** labial teeth on P-1 discontinuous, with medial interruption (characters 209.1); **2)** interhyodeus posterior, medially interrupted (character 408.); **3)** adrostral element present, with cartilaginous core (character 466.2); **4)** fenestra basicranialis completely closed (character 479.2); **5)** foramen trochlear present (character 489.1); **6)** angle formed by the processus ascendens and the main axis of the chondrocranium posteriorly oriented (character 518.2).

***Aromobates* Myers, Paolillo-O and Daly, 1991**

Type species: *Aromobates nocturnus* Myers, Paolillo-O and Daly, 1991

Immediate more inclusive taxon: Aromobatinae

Sister group: *Mannophryne*

Content: 18 recognized species.

Characterization: No unambiguous optimized larval synapomorphy for this taxon.

Comments: *Aromobates* (Fig. 24) comprises 18 species of Andean frogs, distributed mainly in Venezuela, but also in adjacent Cordillera Oriental of Colombia (Frost 2018; Grant et al. 2017). My optimal topology is almost identical to that of Grant et al. (2017), with exception of the position of *Aromobates nocturnus*. In Grant et al. (2017) it was the sister to a clade comprising an undescribed species of Los Alcaravanes, *Aromobates meridensis*, *Aromobates ericksonae*, *Aromobates saltuensis* and *Aromobates cannatellai*. In my tree, *Aromobates nocturnuss* is the sister to all *Aromobates* but *Aromobates ornatissimus*.

Tadpoles: Only ten tadpoles of Aromobates have been described so far (La Marca 1985; La Marca and Mijares-Urrutia 1988; Myers et al. 1991; Mijares-Urrutia 1991; Mijares-Urrutia and La Marca 1997) and they are poorly known; no aspect of their internal morphology has been described and the last tadpole description is from more than 20 years ago. Tadpoles of *Aromobates* inhabit quiet pools of Andean mountains streams (Mijares-Urrutia and La Marca 1997). Larvae of *Aromobates alboguttatus*, *Aromobates duranti*, *Aromobates mayorgay*, *Aromobates nocturnus*, and *Aromobates meridensis* are usually found among rocks in shallow, flowing streams; these streams are usually of sandy bottom and present scarce vegetation (Myers et all 1991; Mijares-Urrutia and La Marca 1997). Larvae of *Aromobates molinari*, however, usually occur in cascade streams pools (La Marca 1985). Many character-states observed in *Aromobates* larvae are the same as those of several *Colostethus*, *Hyloxalus* and *Mannophryne*. Mijares-Urrutia and La Marca (1997: 140) pointed out these similarities. The same authors provided a set of phenotypic traits that would characterize the genus:

Body depressed-oval, between postero-trinagular and rounded-oval; naris rounded with protuberant smooth rim; interorbital distance wider than internarial distance, spiracle sinistral, not forming a free tube; cloacal opening dextral; caudal musculature does not reach the tail tip; tip of tail oval; caudal fins with origin on the body-tail junction; narrower than caudal musculature at mid-length of tail; oral disc intra-angular with rostral gap; lacking intra-marginal papillae; keratodonts with small serrations; rostrodonts with small serrations; supra-rostrodonts with *rounded medial notch; keratodonts formula 2(2)/3(1), uniserial. Caudal musculature and tail present a dark spotted pattern of coloration.*

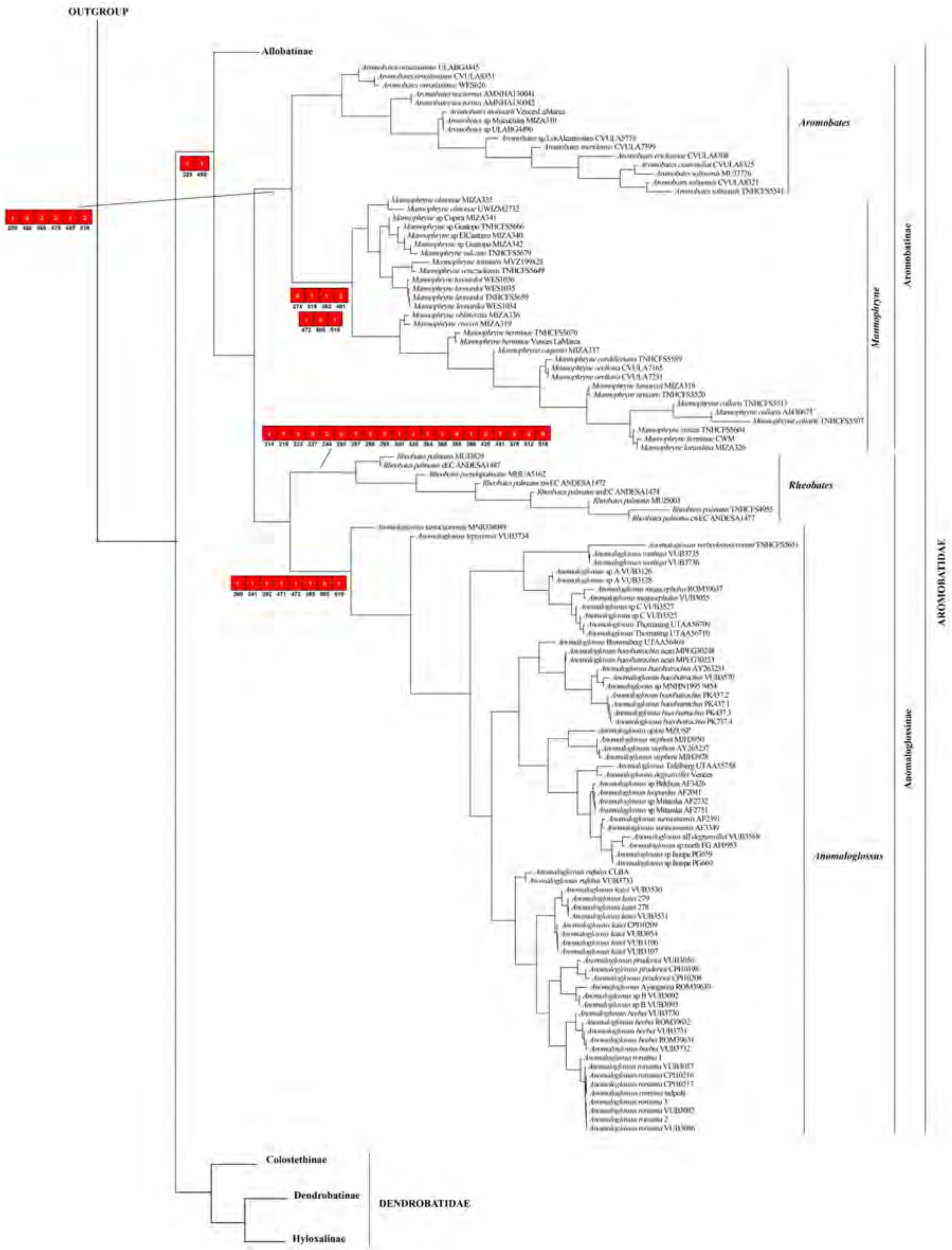

Figure 24. Optimal hypothesis of relationships within Aromobatinae and Anomaloglossinae. Tree shows the branch-lengths (from the most parsimonious trees), and selected nodes labeled with unambiguous larval synapomorphies (red square = unique, homoplastic; blue square non-unique, homoplastic; characters below the square and synapomorphic state inside the square.

With terminological changes, I agree with most of these characters. The internarial/interorbital distance is highly variable, even within the same lot of tadpoles, and, in most larvae, they are quite the opposite of what was described by La Marca (1994) and Mijares-Urrutia and La Marca (1997).

The most strikingly different tadpole within *Aromobates* is the one of *Aromobates nocturnus*. As Myers et al. (1991: 12) described, this is a large tadpole (> 60mm in total length); in fact, the largest Dendrobatoid tadpole. *Aromobates nocturnus* is a stream-dweller species, and the adult frogs are strongly associated with streams, never being caught out of them. This tadpole is also hard-to-catch according to the authors (p.12), and they stated it presents low abundance. The larvae of this species resemble those of Hylodidae—large, robust tadpoles, with well-keratinized mouth-parts and evident lateral line system (Faivovich 1998; Pombal et al. 2002, 2003; Costa et al. 2012; Silva-Soares et al. 2015). Another interesting character shared by *Aromobates nocturnus* and most hylodids is the presence of submarginal papillae. Submarginal papillae have been reported in very few dendrobatoids: *Silverstoneia* (Dunn 1924; Savage 1968; Ibáñez and Smith 1995; Savage 2002; Gran and Myers 2013), *Hyloxalus edwardsi* (Lynch 1982) and *Ameerega flavopicta* from Goiás state population (Costa et al. 2006).

Other tadpoles: In the present study, only the tadpoles of *Aromobates molinari*, *Aromobates nocturnos*, and *Aromobates saltuensis*, and those of an undescribed species were included in the analysis. However, I also examined tadpoles of *Aromobatas mayorgai* and seven other tadpole descriptions are available in the literature (Mijares-Urrútia 1991; Mijares-Urrútia and La Marca 1997). Generally, tadpoles of *Aromobates* (and *Mannophryne*) are very similar and share most of their character states. Based on available evidence it is not possible to make any predictions or further comments on internal relationships.

Mannophryne La Marca, 1992

Type species: *Colostethus yustizi* Myers, Paolillo-O and Daly, 1991

Immediate more inclusive taxon: Aromobatinae

Sister group: *Aromobates*

Content: 19 valid species.

Characterization: Unambiguous optimized larval synapomorphies are: **1)** Origin of the dorsal fin at the junction body/tail (character 274.0); **2)** internal nares inclined towards mouth (character 318.1); **3)** third infralabial papillae with rounded or conical (character 362.1); **4)** processus anterior dorsalis present, medial (character 461.2); **5)** distal margin of the cornua trabeculae oriented medially (character 472.1); **6)** taenia tecti medialis absent (character 505.0); **7)** processus ascendens attachment low (character 519.1).

Comments: *Mannophryne* currently comprises 19 species distributed in Andean mountains and lowlands of Venezuela, and in the islands of Trinidad and Tobago (Frost 2018); these frogs are characterized by the presence of a dermal collar (Grant et al. 2006), among other synapomorphies. I recovered a monophyletic *Mannophryne* containing two clades: A and B, named by Manzanilla et al. (2009). Although the composition of these clades is the same as that proposed by Grant et al. (2017), the internal relationships are different. For example, in one of these clades, I found *Mannophryne olbliterata* and *Mannophryne riveroi* as sister of all other taxa, whereas Grant et al. (2017) found *Mannophryne riveroi* in that position. These two clades have also been recovered by Manzanilla et al. (2009).

Tadpoles: History of the larval morphology of *Mannophryne* is old. Boulenger (1895) described the tadpoles of *Mannophryne trinitatis*, one of the oldest descriptions of a dendrobatoid larva. Unfortunately, the morphology, ecology and biology of *Mannophryne* tadpoles have been poorly studied. To date, only ten tadpoles have been described (e.g., La Marca 1994; Dixon and Rivero-Blanco 1985; Manzanilla et al. 2007) and no aspect of their internal anatomy is known. La Marca (1994) reviewed the collared frogs of the genus *Mannophryne* and described several tadpoles. According to him, the larvae of Venezuelan *Mannophryne* inhabit mountain rivers and pools. The larvae of some species, as *Mannophryne yustizi*, can tolerate low water temperatures, as 11.5ºC, which was 6ºC below the air temperature (La Marca 1989). *Mannophryne olmonae* and *Mannophryne trinitatis* also develop in stream side pools (Lehtinen and Hailey 2008), which parent frogs choose carefully in order to avoid predators (Downie et al. 2001; Jowers and Downie 2005). Lehtinen and Hailey (2008) reported high densities (>50 individuals) of tadpoles of *Mannophryne olmonae*, even in small pools—less the 1 meter long and 10 cm deep.

Other tadpoles: The only tadpole examined but not included in the phylogenetic analysis of the present study was that of *Mannophryne neblinae*. This tadpole was originally described by La Marca (1994). The larval morphology of this tadpole is in agreement with the character-states present in other *Mannophryne* larvae, although, these shared characters does not strongly support any hypothesis of relationships. Tadpoles of *Mannophryne neblinae* and *Mannophryne herminae* are the only two species of the genus that present the dorsal fin originating on the posterior third of the body, which may suggest a close relationship. Nevertheless, the tadpoles of *Mannophryne neblinae* are unique within the genus in lacking the medial notch on the upper jaw. Moreover, La

Marca (1994) attested that this is the only species in the genus presenting uniform colored dorsum, and that their tadpoles are “unique in having [larvae with] large labial papillae” (p. 62).

Anomaloglossinae Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel, and Wheeler, 2006

Type genus: *Anomaloglossus*
Immediate more inclusive taxon: Aromobatidae
Sister group: Aromobatinae
Content: *Anomaloglossus* and *Rheobates*.
Characterization: No unambiguous optimized larval synapomorphies for this taxon.

Anomaloglossus Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel, and Wheeler, 2006

Type species: *Colostethus beebei* Noble, 1923
Immediate more inclusive taxon: Anomaloglossinae
Sister group: *Rheobates*
Content: 28 species.
Characterization: Unambiguous optimized larval synapomorphies are: **1)** vent tube parallel to the main axis of the body in lateral view (character 269.1); **2)** lateral roof papillae present (character 341.1); **3)** terminal portion of the ileum moderately expanded (character 392.1); **4)** distal extremity of the cornua trabeculae subtruncated (rounded borders) (character 471.1); **5)** plane of the distal margin of the cornua trabeculae inclined medially (character 472.1); **6)** foramen opticum oval (character 485.1); **7)** taenia tecti medialis absent (character 505.0); **8)** processus ascendens attachment low (character 519.1).
Comments: *Anomaloglossus* (Fig. 24) comprises 28 species distributed in North and Northeastern South America (Frost 2018). My optimal hypothesis is largely in agreement with that of Grant et al. (2017). *Anomaloglossus tamacuarensis* is the sister to all *Anomaloglossus*, followed by *Anomaloglossus tepuyensis*. Subsequently, I found three major clades that correspond to the *Anomaloglossus stepheni* group, *Anomaloglossus megacephalus* group, and *Anomaloglossus beebei* group, in which the *megacephalus* and *beebei* groups are sister taxa.

Tadpoles: *Anomaloglossus* is a very interesting genus regarding the biology of their larvae. There are pond and river dwellers, phytotelmata specialized tadpoles and even non-feeding, nidiculous, phoretic tadpoles (Lescure 1984; Kok et al. 2006a,b; Bourne et al. 2001; Grant et al. 2006; Myers and Donnelly 2008; Vacher et al. 2017). Vacher et al. (2017) reported that endotrophy evolved several times independently in the genus.

Several species of the *Anomaloglossus stepheni* group present endotrophic larvae, that share several characteristics, as reduction or loss of mouth parts, spiracle, vent tube, among others (see "Character Evolution" section). These endotrophic larvae might be nidiculous, as those of *Anomaloglossus stepheni*, or phoretic as *Anomaloglossus degranvillei*, whose tadpole develops in the back of the parent frog (Lescure 1984; Juncá et al. 1994; Vacher et al. 2017).

The exclusively bromeliad dweller (Kok et al. 2006a) *Anomaloglossus beebei* presents a very plastic diet. Bourne et al. (2001) reported that tadpoles of this species feeds on trophic eggs laid by female, but also from detritus, insect larvae, and also from other tadpoles, con and heterospecific.

Anomaloglossus kaiei lives in small pools and feeds (at least facultatively) on trophic eggs laid by female (Kok et al. 2006a). Kok et al. (2006a) found that tadpoles survive in the absence of trophic eggs. The analysis of gut content suggested that these larvae also feed on detritus. This is the sole example within Dendrobatoidea of trophic egg deposition in a non phytotelmata species. Kok et al. (2006a) noted that the habitat in which tadpoles were found present different sources of food and the egg deposition was performed by the female without any courtship behavior.

Anomaloglossus wothuja lives in small pools at the side of streams (Barrios-Amóros and Rivas 2004). According to its original description, this tadpole presents an interruption on the first posterior row of keratodonts. This is a unique condition within *Anomaloglossus* (Fig. 24) all species examined lack the P-1 gap.

Other tadpoles: *Anomaloglossus parkerae* is found in small ponds and streams (Duellman 1997). This tadpole shares several characters with other *Anomaloglossus* larvae, as ventral mouth, absence of P-1 gap, and the presence of a medial notch on the upper jaw sheath. Duellman (1997) described the oral disc as not emarginated, however, all *Anomaloglossus* present a lateral emargination. Moreover, Duellman (1997: Fig. 12: 13) illustration of the oral disc clearly shows an emargination. Character-state inferred from Duellman (1997) allows the assignation into *Anomaloglossus*, but no further comments on its placement can be made.

***Rheobates* Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel, and Wheeler, 2006**

Type species: *Phyllobates palmatus* Werner, 1899

Immediate more inclusive taxon: Anomaloglossinae

Sister group: *Anomaloglossus*

Content:

Characterization: Unambiguous optimized larval synapomorphies are: **1)** upper jaw sheathes keratinized only in the border (character 214.1); **2)** lower jaw sheathes keratinized only in the border (character 219.1); **3)** shelth present (character 223.1); **4)** spiracle, only the border free (character 237.3); **5)** spiracle with melanocytes scattered and white border (character 244.2); **6)** fleshy rim flat (character 255.0); **7)** lateral projection on the inner margin of the nares present (character 257.1); **8)** left wall of the vent tube fused medially (character 266.1); **9)** white spot on the anterolateral portion of the body, present (character 298.1); **10)** white spot on the posteroventral region present (character 300.1); **11)** median ridge elliptical (character 335.1); **12)** pustulations anterior to mouth opening present (character 364.1); **13)** medial, single, lingual papillae present (character 365.1); **14)** first pair of lateral, lingual papillae absent (character 366.0); **15)** glottis partially or fully covered by the velum (character 386.1); **16)** muscle subarcualis rectus II-IV inserting on the ceratobranchial I (character 420.2); **17)** muscle submentalis present (character 451.1); **18)** processus orbitonasalis present, large (character 378.3) **19)** processus pseudopterygoideus present, moderate (character 512.2); **20)** pprocessus ascendens forming a straight angle with the chondrocranium.

Comments: *Rheobates* (Fig. 24) is a small genus with only two recognized species that are endemic of Colombia (Frost 2018). However, it is likely that it hides a larger cryptic diversity waiting to be discovered. My optimal hypothesis is almost identical to that of Grant et al. (2017). which is in turn very similar to that of Muñoz-Ortiz et al. (2015). Individuals of Villavicencio, Meta and Puente Nacional, Santander, are sister to all *Rheobates*, followed by *Rheobates pseudopalpatus*. Although molecular evidence points to the existence of more than one taxa, I was not able to find any significant difference in the tadpoles of several populations of *Rheobates palmatus* and *Rheobates pseudopalmatus*.

Tadpoles: The tadpoles of *Rheobates* are poorly known. Dunn (1944) provided the first description; he and colleagues found an egg clutch on a rock and raised it in laboratory, providing interesting formation on the initial development of *Rheobates palmatus* (*Hyloxalus grnuliventris* on the original paper). Then, he described briefly the free-living tadpole based on collected individuals as well as those raised in captivity. Edwards (1974), in an unpublished Ph.D. dissertation, also described the tadpole of *Rheobates palmatus*. Rivero and Serna (1995) described *Rheobates pseudopalmatus* from surroundings of Antioquia, Medellín, Colombia; in the same paper, they briefly commented the morphology of the larvae, but did not provide any illustrations. The last work dealing with tadpoles of *Rheobates* is that of Lynch (2006) who described the tadpoles found in lowlands of Northern Colombia.

Dendrobatidae Cope, 1865

Type genus: *Phyllobates* Bibron in la Sagra, 1840

Immediate more inclusive taxon:

Sister group: Unnamed clade composed by Alsodidae, Cycloramphidae, and Hylodidae.

Content: Dendrobatinae, Colostethinae, and Hyloxalinae

Characterization: Unambiguous optimized larval synapomorphies are: **1)** processus anterior dorsalis present, medial (character 461.2).

Colostethinae Cope, 1867

Type genus: *Colostethus* Cope, 1866

Immediate more inclusive taxon: Colostethinae

Sister group: Unnamed clade composed of Dendrobatinae and Hyloxalinae.

Content: *Ameerega*, *Colostethus*, *Epipedobates*, *Leucostethus*, and *Silverstoneia*.

Characterization: Unambiguous optimized larval synapomorphies are: **1)** Stitches of the anterior pit line present (character 283.1).

Silverstoneia **Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel, and Wheeler, 2006**

Type species: *Phyllobates nubicola* Dunn, 1924

Immediate more inclusive taxon: Colostethinae

Sister group: *Epipedobates*.

Content: 8 valid species.

Characterization: Unambiguous optimized larval synapomorphies are: **1)** lower labium umbelliform (character 173.1); **2)** upper labium umbelliform (character 174.1); **3)** central emargination of the lower lip present (character 176.1); **4)** submarginal papillae spread among the inner surface of the lower lip present (character 195.1); **5)** submarginal papillae spread among the inner surface of the upper lip present (character 196.1); **6)** labial dermal ridge on P-2 absent (character 200.0); **7)** labial dermal ridge on P-3 absent (character 201.0); **8)** Gap on P-1 present (character 204.1); **9)** margin of the upper jaw sheath smooth (character 215.0); **10)** dorsal margin of the upper crenellated (character 224.1); **11)** snout rhomboid (character 227.1); **12)** left wall of the vent tube fused medially (character 266.1); **13)** margin of the vent tube irregular (character 273.1); **14)** transversal crest on the prenarial arena absent (character 311.0); **15)** V-shaped crest on prenarial arena present (character 313.1); **16)** ornamentation of the anterior wall of the internal nares absent (character 319.0); **17)** first postnarial papillae oblique (character 327.1); **18)** first pair of postnarial papillae smooth (character 328.0); **19)** medial projection of the median ridge absent (character 336.0); **20)** lateral ridge papillae keel-like (character 338.2); **21)** lateral ridge papillae not branched (character 339.0); **22)** second pair of infralabial flap-like (character 357.1); **23)** second pair of infralabial papillae not branched (character 358.0); **24)** ridge on the first third of the buccal floor, present (character 369.1); **25)** subarcualis obliquus, central aponeurosis slipe present (character 419.1); **26)** suspensorioangularis, origin posterior processus muscularis, but also ventral palatoquadrate (character 437.1); **27)** pars corporis parallel in frontal view (character 456.0); **28)** pars corporis large, wider than longer (character 459.1); **29)** proximal margin of the pars alaris concave (character 465.1); **30)** adrostral element present, with cartilaginous core (character 466.2); **31)** cornua trabeculae parallel along their length (character 476.1); 31) cartilago orbitalis high (character 493.2); **32)** fenestra ovalis rounded (character 495.0); **33)** larval crista parotica inconspicuous (character 498.0); **34)** processus muscularis low (character 513.1); **35)** processus ascendens forming a straight angle with the chondrocranium (character 518.0); **36)** infrarostral cartilage thiner at the extremities (character 528.1); **37)** free basihyal present (character 529.1); **38)** processus anterolateralis hyalis present, short (character 548.0); **39)** processus anterior branchialis present, short (character 556.1).

Comments: *Silverstoneia* (Fig. 25) currently comprises 8 species that occur from Southweastern Costa Rica to Southwestern Colombia, below 1600 m. (Grant and Myers 2013; Frost 2018). This genus has been recovered monophyletic constantly and it is supported by several phenotypic synapomorphies, most of which came from larval morphology (Grant et al. 2006, 2017). My optimal hypothesis is almost identical to that of Grant et al. (2017), with some small differences; I also found *Silverstoneia punctiventris* as sister to *Silverstonea flotator* and this clade as sister to *Silverstoneia nubicloa* + *Silverstoneia erasmios*. Differences regarding Grant et al. (2017) are in some internal relationships. For instance, while I found *Silverstoneia erasmios* (LSB218) as sister to all other "*erasmios*", Grant et al. (2017) found the same individual as sister to *Silverstoneia* aff. *nubicola* (THNCF9442).

Tadpoles: Tadpoles of *Silverstoneia* are unique among Dendrobatoids in possessing a funnel-mouth, or umbelliform, oral disc (e.g., Dunn 1944; Ibáñez and Smith 1995; Grant and Myers 2013). This peculiar phenotype evolved independently at least seven times in anurans (Dias et al. 2018). In *Silverstoneia*, several character-states are associated with this phenotype, as the expanded oral lips, reduction of labial teeth, dorsal emargination, expanded postnarial papillae, presence of v-shaped crest in the prenarial arena, presence of a medial aponeurosis shared by the subarcualis obliquus, subarcualis rectus I, and rectus cervicis, among others. These tadpoles can be found in small streams, where adult frogs are concentrated during the reproductive period (Savage 1968; Ibáñez and Smith 1995), although is some occasions they can occupy small ponds, as in *Silverstoneia erasmios* (Gustavo González pers.com). Tadpoles of *Silverstoneia* usually feed on the water surface (Savage 2002), and despite the mouth often being upwards, they can move it down to adhere to rocks and other substrates when resting (Savage 2002).

Other tadpoles: Grant and Myers (2013) described the tadpole of *Silverstoneia minima*. The character-states presented by the authors suggests a close relationship with *Silverstoneia flotator*: both species lack lateral emargination, lack labial teeth in most of their ridges (*Silverstoneia minima* preset teeth on A-1), and lack keratinization on the jaw sheaths. I expect that future work to recover these species as closely related.

I examined an additional tadpole housed at Instituto de Ciencias Naturales, Universidad Nacional de Colombia that could not be assigned to any species precisely. This tadpole was collected at the type locality of *Silverstoneia punctiventris*. Nevertheless, the character-states present in such tadpoles are in accordance with Grant and Myers (2013) description of *Silverstoneia dalyi*: both share the ventral mouth, lateral and central (lower lip) emarginations, absence of labial teeth and keratinization on jaw sheaths, and the caudal muscles reach the tail tip. The only difference is that I found the labial ridge of the first superior row, A-1, and Grant and Myers (2013) did not illustrated these features. There are some hypotheses to explain these shared characters: 1) this tadpole in fact is that of *Silverstoneia punctiventris*, which has never been described, and this species is closely related to *Silverstoneia dalyi*; 2) this tadpole is of *Silverstoneia dalyi*, whose distribution reaches the type locality of *Silverstoneia punctiventris*; sympatry is very common in *Silverstoneia* species (see Ibáñez and Smith 1995; Grant and Myers 2013). Further evidence is necessary to test which hypothesis better explains the evidences.

Figure 25. Optimal hypothesis of relationships within Colostethinae and Anomaloglossinae. Tree shows the branch-lengths (from the most parsimonious trees), and selected nodes labeled with unambiguous larval synapomorphies (red square = unique, homoplastic; blue square non-unique, homoplastic; characters below the square and synapomorphic state inside the square.

***Epipedobates* Myers, 1987**

Type species: *Prostherapis tricolor* Boulenger, 1899

Immediate more inclusive taxon: Colostethinae

Sister group: *Silverstoneia*

Content: 8 recognized species.

Characterization: Unambiguous optimized larval synapomorphies are: **1)** shelf present (character 223.1); **2)** dark throat collar present (character 233.1); **3)** white spots on anteroventral surface of the body present (character 299.1); **4)** white spot on the posteroventral region present (character 300.1); **5)** relief of the prenarial arena flat (character 309.0); **6)** lungs shrunken, not inflated (character 396.0); **7)** interhyodeus posterior, extensive and strongly developed (character 409.2); **8)** pars corporis fused almost distally (character 455.5); **9)** distal margin of the cornua trabeculae inclined medially (character 472.1).

Comments: *Epipedobates* (Fig. 25) currently comprises 8 species of frogs distributed from Panama to Ecuador (Frost 2018). Recently, Grant et al. (2017) transferred *Ameerega maculata* to *Epipedobates*. In 2006, Grant et al. (2006) refrained to transfer the so called *Dendrobates maculatus* to *Epipedobates* because that former has spotted body, and they opted to transfer it to *Ameerega,* given that spotted pattern was missing in *Epipedobates*. However, after the description of *Epipedobates darwinawallacei*, which also possess spotted ventral coloration (Cisneros-Heredia and Yánez-Muñoz 2011), Grant et al. (2017) transferred *Ameerega maculata* to *Epipedobates*. *Epipedobates*, in Grant et al. (2017) was a monophyletic group, sister to *Silverstoneia*. I recovered similar results—I confirm the monophyly of the genus and its close relationships with *Silverstoneia*, however, I found differences in the internal relations of the genus. Whereas Grant et al. (2017) found both lineages of *Epipedobates boulengeri* (Gorgona Island and continental populations) as sister to all other species, I found that the mainland *Epipedobates* was sister to a clade containing *Epipedobates anthonyi* + (*Epipedobates tricolor* + *Epipedobates machalilla*) and *Epipedobates espinosai* plus *Epipedobates darwinwallacei* occupied the place of the *boulengeri* lineages as sister to all species but Gorgona Island`s *boulengeri*.

Tadpoles: Of the eight species of *Epipedobates*, six have their tadpoles described (Funkhouser 1965; Silverstone 1976; Coloma 1995; Mueses-Cisnero et al. 2008; Anganoy-Criollo and Cepeda-Quilindo 2017; Dias in press). Tadpoles played an important role in the systematics of the genus; Silverstone (1976: 7) used the character "dark brown transverse band on the posterior portion of the throat" as a diagnostic character for his *Phyllobates femoralis* group—*Epipedobates* (*sensu* Grant et al. 2006) minus *Allobates femoralis*. Haas (1995) studied the chondrocranium of *Epipedobates anthonyi* and *Epipedobates tricolor*. Later, Anganoy-Criollo and Cepeda-Quilindo (2017) suggested four putative synapomorphies for the genus *Epipedobates* based on larval morphology: a moderate gap of A-2, presence of the shelf on the upper jaw sheath, moderate notch on the upper jaw sheath, and the size of the external nares. Simultaneously, Dias et al. (in press) also suggested the presence of the shelf as a putative synapomorphy for the genus and said that the subcutaneous dark bands of Silverstone (1976) would represent other synapomorphies for *Epipedobates*. Moreover, Dias et al. discussed the occurrence of white spots in the larvae of *Epipedobates* and other dendrobatoids, stressing the possibility of this character also optimize as synapomorphy for the genus.

Other tadpoles: The tadpole of *Epipedobates narinensis* was described by Mueses-Cisneros et al. (2008) and redescribed by Anganoy-Criollo and Cepeda-Quilindo (2017). Tadpoles of *Epipedobates* are very conservative in their morphology; the larvae of *Epipedobates* narinensis share most of its characters with all other *Epipedobates*.

Colostethus Cope, 1866

Type species: *Phyllobates latinasus* Cope, 1866
Immediate more inclusive taxon: Colostethinae
Sister group: Unnamed clade composed by *Ameerega* and *Leucostethus*
Content: 17 species.
Characterization: Unambiguous optimized larval synapomorphies are: **1)** anterior depression present (character 231.1); **2)** white spots at the posterolateral portion of the body, present (character 297.1); **3)** white spots on anteroventral surface of the body present (character 299.1); **4)** second pair of postnarial papillae present (character 324.1); **5)** second pair of postnarial papillae with conical or rounded pustulations (character 329.1); **6)** pre pocket pustulations absent (character 371.0).
Comments: *Colostethus* (Fig. 25) comprises 17 species distributed in Colombia and Panama (Grant et al. 2017). The taxonomic history of Colostethus is extensive and complicated; for detailed history see Grant et al. (2006). Recently, Grant et al. (2017) confirmed previous studies (e.g., Santos et al. 2009; Pyron and Wiens) in finding *Colostethus* paraphyletic to *Ameerega*. They solved the paraphyly erecting the genus *Leucostethus* to *argyriogaster* and *fugax*. They also found that the endemic rocket frog of Sierra de Santa Marta, *Colostethus ruthveni,* was nested within Dendrobatinae and, therefore, would represent a new genus that is in process of description. Grant et al. (2017) recovered two groups within *Colostethus*: *Colostethus latinasus* and *Colostethus fraterdanieli* groups. The *latinasus* group, which carries the type species, is distributed from northern Colombia to Costa Rica. The *fraterdanieli* group comprises three nominal species: *Colostethus fraterdanieli*, *Colostethus brachyhistriatus*, and *Colostethus ramirezi*—which occur in

northern Colombia, Valle del Cauca and slopes of the Cordillera Central and Occidental from Cauca to Quindío (Frost 2018)—plus an undescribed species of the Gorgona Island (in process of description by T. Grant and W. Bolivar).

My results largely agree with Grant et al. (2017) in showing both clades but with some differences in the internal relations. Within the *latinasus* group I also recovered two clades, with the same composition as Grant et al. (2017) but with some small changes in relations, but nothing that would affect the monophyly of any Grant et al.`s (2017) clade. In the *fraterdanieli* group, there were larger differences. Whereas Grant et al. (2017) found a monophyletic *Colostethus fraterdanieli*, I found the Cordillera Occidental populations to be sister of all species of the clade but the unnamed species of Gorgona Island. I also found *Colostethus brachyhistriatus* to be sister of *Colostethus ramirezi*, contrasting with Grant et al. (2017) that recover it as sister to all species but those of Gorgona Island. Grant et al. (2917: 43) pointed out that two names are available for the Cordillera Occidental clade: *Colostethus yaguar*a and *Colostethus alacris*, but further evidence, including samples from the type localities of these species, are still needed for solving taxonomic problems within these lineages.

Grant et al. (2017) proposed that the entirely pigmented testis is a synapomorphy for the fraterdanieli clade. I found that the shelf in the upper jaw sheath is present in *Colostethus fraterdanieli*, *Colostethus ramirezi*, *Colostethus brachyhistriatus*, and also in some tadpoles that could be assigned to the Cordillera Occidental populations. This character-state is likely to be another synapomorphy for the fraterdanieli group, however, it is pending on the description of the tadpoles from Gorgona Island for an unambiguous optimization.

Tadpoles: Only seven tadpoles of *Colostethus* have been described so far (Dunn 1924; Savage 1968; Rivero and Serna 1995; Grant and Castro 1998; Grant 2007), however, most of these descriptions possibly employed tadpoles of other species. The taxonomy of species of the *Colostethus latinasus* group is complex (Grant 2004; Grant et al. 2006, 217), not only for adult frogs, but also for tadpoles. Dunn (1924) described the tadpoles of *Colostethus latinasus*, however, Breder (1946) clarified that the tadpoles referred by Dunn as *latinaus* were in fact those of *pratti*. Savage (1968) followed Breder (1946) comments, however, Savage himself did not provide voucher numbers for his specimens and it is likely that the tadpoles described by him as *latinasus* belong to a different species (T. Grant pers. com). Grant (2004) restricted *Colostethus inguinalis* to the northern Chocó, Colombia; thus, the tadpoles described as *inguinalis* by Savage (1968) are more likely to be *panamansis*.

Problems in assignment of tadpoles to the correct species are not exclusivity of the *latinasus* group but are also common in the *fraterdanieli* group. For instance, the tadpole of *Colostethus* *fraterdanieli* was described two times, and yet it remains undescribed. Grant and Castro (1998) described the tadpole of *Colostethus fraterdanieli* from the Valle del Cauca, in a locality that in fact is inhabited by *Colostethus brachyhistriatus*. Rivero and Serna (1995) described the tadpoles of *Colostethus fraterdanieli* from Urrao, and, in fact, these tadpoles are those of *Colostethus ramirezi*. Thus, the tadpoles of *Colostethus fraterdanieli* had never been formally described.

Grant et al. (2017: 41) stated that species of the fraterdanieli group, with exception of the Gorgona Island population, cannot be distinguished morphologically based on adult morphology. My results, however, suggest that there are some larval characters that allow the identification of some these species. For instance, *Colostethus ramirezi* and *Colostethus brachyhistriatus* differ from *Colostethus fraterdanieli* by the spiracle more attached to the body (free distally) and lateral oriented eyes (anterolateral). *Colostethus ramirezi* have acute tail tip (rounded in *fraterdanieli* and polymorphic in *brachyhistriatus*), and the suprarostral corpora fused almost distally (free in *fraterdanieli* and *brachyhistriatus*). *Colostethus brachyhistriatus* have the cornua trabeculae parallel (diverging in *ramirezi* and *fraterdanieli*). I stress, however, that more populations of *Colostethus brachyhistriatus* and *Colostethus ramirezi* should be sampled in order to investigate for further intraspecific variation.

Other tadpoles: Grant (2007) described briefly the tadpole of *Colostethus ucumari*, although he did not provide any illustration of the tadpole. Examination of the sole specimen available, that was collected from the back of a parent frog, show several character-states uncommon, which may be consequence of its developmental stage or life-style. This tadpole presented the labial ridges 1/3 but no labial teeth on them, poorly keratinized jaw sheaths, with a medial notch on the upper jaw (contra Grant 2007: 48) and lacked the inner wall of spiracle and stitches of the lateral lines. In the literature there are examples of back-riding tadpoles with a similar set of characters (e.g., Anganoy-Criollo 2013), although some species in the same developmental stage (Gosner 25) are well-developed and present many character-states as free-living larvae. One fact drew my attention: in this particular tadpole, the short guts were full of yolk. It is common for young tadpoles to present large amount of yolk that will be rapidly consumed before the parent frog releases the larvae (e.g., Whymann 1859), however, it is common for endotrophic tadpoles to present reduction of the mouthparts and spiracle and to have guts with a large amount of yolk. Unfortunately, I could not examine the internal morphology of these tadpoles to search for further evidences, and given the very limited number of individuals, it is impossible to make further predictions, although some degree of endotrophy (there are facultative endotrophic tadpoles; see De La Riva 1995) should not be discarded.

Cochran and Goin (1964) described *Colostethus mertensi* from Quintana, near Popayán, department of Cauca, Colombia. This species is poorly studied and has never been included in any phylogenetic study. I examined tadpoles assigned to this species and they share several characters with all *Colostethus* tadpoles studied herein. It resembles most *Colostethus panamasis*, with which *merstensi* shares the presence of the crest on the floor of buccopharyngeal cavity, small and shrunken lungs. Nevertheless, this tapole presents other character states, as the absence of musculo interhyoideus posterior, present in all *Colostethus*, but absent in some *Hyloxalus* tadpoles (e.g., *vertebralis*, *italoi* [from Colombia], and *yasui*); moreover, the crest on buccal floor is also present in some *Hyloxalus* (e.g., *bocagei*). Additionally, *Colostethus mertensi* have a large number (19–22) of supranumerary papillae, whereas other *Colostethus* present inferior number (ranging from 4 in *panamansis* to 12 in *brachyhistriatus*); several *Hyloxalus* species present a large number of such papillae (e.g., 18–23 in Peruvian *elachyhistus*).

In general, *Colostethus mertensi* share more character-states with *Hyloxalus* larvae than with *Colostethus*. Adult males have the finger IV swollen, which led Grant et al. (2006) to place the species within *Colostethus*; however, under new findings of Grant et al. (2017), it is known that several *Hyloxalus* species may also present this character-state, "so it is conceivable that [*C. agilis* and] *C. mertensi* is [are] misplaced" (Grant et al. 2017: 69). I herein suggest the transference of *mertensi* from *Colostethus* to genus *Hyloxalus*, *Hyloxalus mentensi* com. **nov.**, until further evidence allows a more severe test. *Colostethus agilis*—that is phenotypically almost non-differentiable from *mertensi*—is also likely to be an *Hyloxalus*, although I did not examine any tadpoles of this species and I refrain from transfering it.

***Leucostethus* Grant, Rada, Anganoy-Criollo, Batista, Dias, Jeckel, Machado, and Rueda-Almonocid, 2017**

Type species: *Colostethus argyrogaster* Morales and Schulte, 1993

Immediate more inclusive taxon: Colostethinae

Sister group: *Ameerega*

Content: 2 species.

Characterization: No unambiguous optimized larval synapomorphies for this taxon.

Comments: Grant et al. (2017) erected the genus *Leucostethus* to solve the paraphyly of *Colostethus* due to the position of *argyrogaster* and *fugax*, which were recovered as sister to *Ameerega*. I corroborate the results of Grant et al. (2017) in finding *Leucostethus* as sister to *Ameerega*.

Tadpoles: Tadpoles of *Leucostethus* are unknown.

***Ameerega* Bauer, 1986**

Type species: *Hyla trivittata* Spix, 1824

Immediate more inclusive taxon: Colostethinae

Sister group: *Leucostethus*

Content: 31 recognized species.

Characterization: No unambiguous optimized larval synapomorphies for this taxon.

Comments: The 31 species assigned to *Ameerega* (Fig. 25) are distributed through all the Amazon basin, in foot hills of the Andes and in the Brazilian savannas known as Cerrado (Grant et al. 2017; Frost 2018). Grant et al. (2017) recognized four species groups within *Ameerega*: *bassleri*, *braccata*, *rubriventris*, and *petersi* groups. I found similar results regarding some groups and species, although, with some important differences.

I recovered the same *rubriventris* group, containing *macero*, *rubriventris*, *altamazonica*, and the unnamed species from Porto Walter. Also, I recovered the *bassleri* group with almost the same composition and relationships as Grant et al. (2017), with exception of *berohoka*, which I found closely related to *flavopicta* and *braccata*. I found a similar *braccata* group, with *braccata* and *flavopicta* a sister to *berohoka*; *Ameerega bohemei* was sister to all *Ameerega* (it is worth to note that the braccata group is the following clade to *boehmei*). Phenotypically, *Ameerega boehmei* is very similar to *Ameerega flavopicta* and *Ameerega braccata* (Lotters et al. 2009). Grant et al. (2017) found *berohoka* nested within the *bassleri* group.

In Grant et al. (2017), *Ameerga bilinguis* was the sister to all *Ameerega*, followed by a clade containing *zaparo* and *parvula*. I found that *bilinguis* is the sister to pongoensis, and that clade is sister to *zaparo* + *parvula*; this clade is sister to the *bassleri* group. Grant et al. (2017) found *pongoensis* as sister to *smaragdina*.

I recovered the *petersi* group containing *petersi*, *cainarachi*, *pulchripecta*, *simulans*, and *smaragdina*. The *petersi* group of Grant et al. (2017) was very similar in composition, but *pongoensis* was the sister to *smaragdina* and *pulchripecta* was the sister to all terminals of *hahneli*.

I found *picta* and *yungicola* as sister, identical to Grant et al. (2017) but with a different position in the tree. In my results, the pica clade was sister to all *Ameerega* minus *braccata* group and *boehmei*, whereas to Grant et al. (2017) it was the sister to *braccata*, *rubriventris*, and *petersi* groups plus the *hahneli* clade. I found that *Ameerega trivittata* was the sister to *hahneli* clade.

Tadpoles: The history of tadpoles in the genus *Ameerega* in ancient. The first dart-poison frog tadpole described was that of *Ameerega trivittata* by Whyman (1859). Yet in the 19th century, Cope (1887) described briefly the larvae of *Ameerega braccata*. Since then, few efforts have been made regarding tadpoles of the genus. Currently, only 14 tadpoles have been described and no aspect of the internal morphology is known. Whereas some larvae received many attention, as *Ameerega picta*, mentioned in six publications (Lescure 1976; Silverstone 1976; Haddad and Martins 1994; Lamotte and Lescure 1997; Duellman 2005; Schulze et al. 2015), or *Ameerega hahneli,* described five times (Lescure 1976; Haddad and Martins 1994; Rodríguez and Duellman 1994; Duellman 2005; Menin et al. 2017), most tadpoles of the genus remain unknown.

The little information in the literature confirms that these larvae live in temporary/permanent ponds or slow flow streams (Poelman et al. 2010; Menin et al. 2017). Silverstone (1976: 47) cited that M. Hoogmoed found tadpoles of *Ameerega trivittata* in fallen palm petioles, but as far as I know, there are no other report of phytotelmata usage by these tadpoles.

Dendrobatinae Cope, 1865

Type genus: *Phyllobayes* Bibron in la Sagra, 1840

Immediate more inclusive taxon: Dendrobatidae

Sister group: Hyloxalinae

Content: *Adelphobates*, *Andinobates*, *"Colostethus" ruthveni* group, *Dendrobates*, *Excidobates*, *Oophaga*, *Minyobates*, *Phyllobates*, and *Ranitomeya*

Characterization: No unambiguous optimized larval synapomorphies for this taxon.

Phyllobates Bibron in la Sagra, 1840

Type species: *Phyllobates bicolor* Bibron, 1840

Immediate more inclusive taxon: Dendrobatinae

Sister group: Unnamed clade composed by "*Colostethus*" *ruthveni* group and Dendrobatini

Content: 5 species.

Characterization: Unambiguous optimized larval synapomorphies are: **1)** vent tube short, near of the body wall (character 271.0); **2)** origin of the dorsal fin at the junction body/tail (character 274.0) **3)** pre pocket pustulations absent (character 371.0).

Comments: *Phyllobates* (Fig. 26) currently comprises five species distributed from Nicaragua to Colombia (Frost 2018). This genus is well-supported by both, phenotypic and genotypic characters and its taxonomy is the same as proposed by Myers et al. (1978). I further corroborate the monophyly of *Pyllobates*, and within the genus there are two clades: a Central America clade that contains *Phyllobates lugubris* and *Phyllobates vittatus*, and a South America Clade, which includes *Phyllobates aurotaenia*, *Phyllobates bicolor*, and *Phyllobates terribilis*. Nevertheless, my optimal tree differs from previous studies (Santos et al. 2009; Grant et al. 2017) regarding the monophyly of *Phyllobates aurotaenia*. Whereas those studies found a paraphyletic *Phyllobates aurotaenia* regarding both *Phyllobates terribilis* and *Phyllobates bicolor*, I found the four terminals to form a monophyletic clade, sister to *Phyllobates bicolor* + *Phyllobates terribilis*.

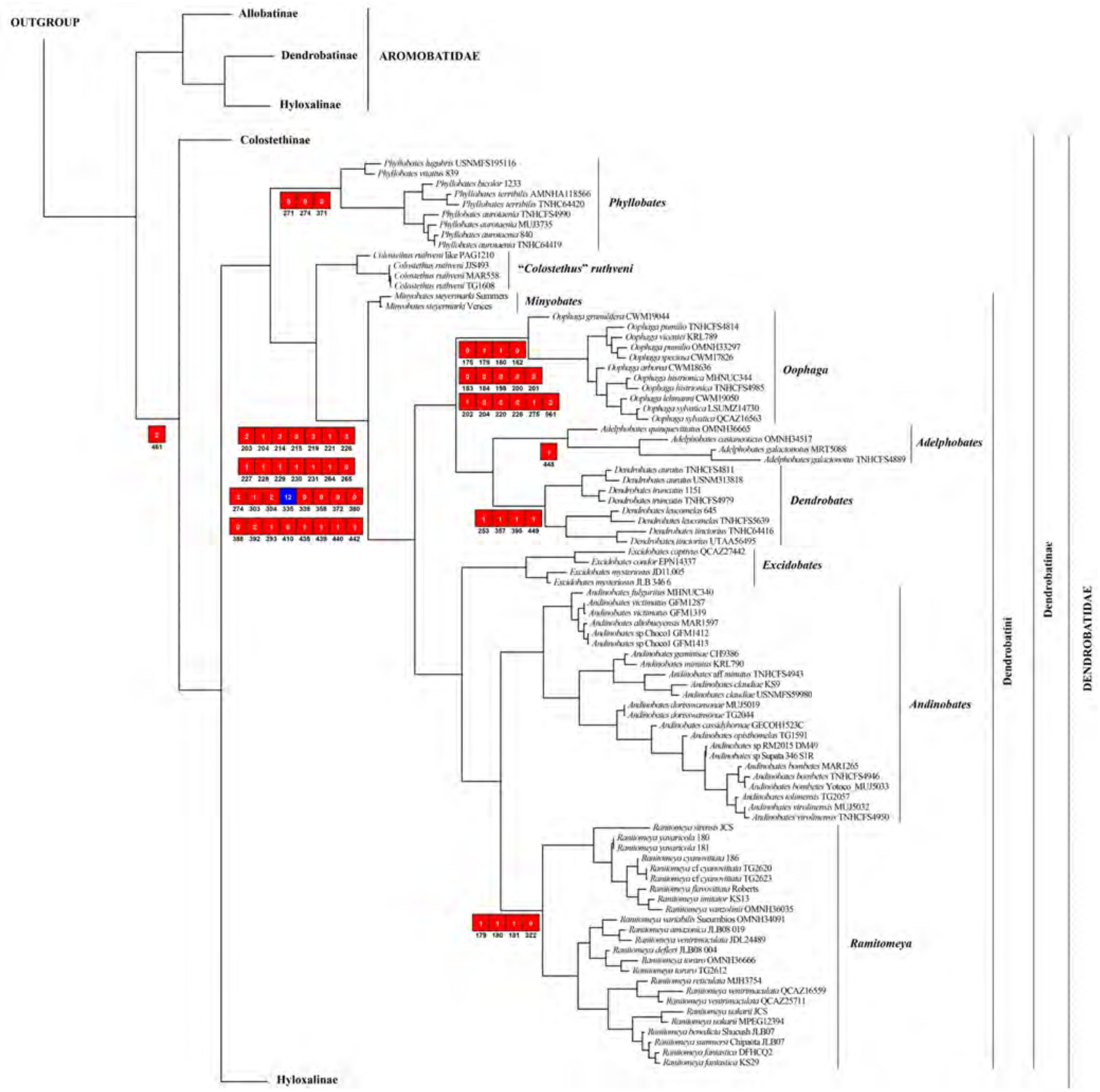

Figure 26. Optimal hypothesis of relationships within Dendrobatinae and Anomaloglossinae. Tree shows the branch-lengths (from the most parsimonious trees), and selected nodes labeled with unambiguous larval synapomorphies (red square = unique, homoplastic; blue square non-unique, homoplastic; characters below the square and synapomorphic state inside the square.

Tadpoles: Only three of the five species of *Phyllobates* have their tadpoles described (Savage 1968; Silverstone 1976; Myers et al. 1978; Donnelly et al. 1990; Savage 2002), which is shocking, given these frogs are commonly found as pets. This probably reflects the general disinterest that many herpetologists have for tadpoles. The ecology of *Phyllobates* larvae is poorly known. Savage reported that larvae of *Phyllobates lugubris* and *Phyllobates vittatus* can be found in small pool of phytotelmata, as a fallen palm petiole or in tree holes (Savage 1968, 2002; Silverstone 1976). *Phyllobates terribilis* also have been found in fallen leaves (M. Gómez-Díaz, pers. com) and the tadpoles of *Phyllobates aurotaenia* have been found in a temporary pond in an open area (M. Anganoy-Criollo pers. com.) or in river side pools, and sometimes in fallen palm bracts (Amézquita 2016). Castro-Herrera and Kahn (2016) and Kahn and Castro-Herrera (2016) said that tadpoles of *Phyllobates bicolor* and *Phyllobates terribilis* are deposited in standing water bodies in the forest, but they did not specify in which water bodies (ponds or phytotelmata). Regarding larval diet, Amézquita (2016: 425) suggests that tadpoles of *Phyllobates aurotaenia* seem to be omnivorous.

Dendrobatinae

"Colostethus" ruthveni group

Type species: *Colostethus ruthveni* Kaplan, 1997

Immediate more inclusive taxon: Dendrobatinae

Sister group: Dendrobatini

Content: 2 species

Characterization: No unambiguous optimized larval synapomorphies for this taxon.

Comments: The Santa Marta rocket frog, "*Colostethus*" *ruthveni* as a *Colostethus* species. Grant et al. (2006) did not include this species in their study but positioned it as member of the new defined *Colostethus*. Recently, Grant et al. (2017) included representatives of "*Colostethus*" *ruthveni* from Santa Marta and *Colostethus* sp ruthveni-like, an undescribed species from Valledupar, Colombia. Surprisingly, these species were found nested within Dendrobatidae, as sister to Dendrobatini. Given the morphological similarity, it was expected that "*Colostethus*" *ruthveni* would be recovered as member of *Colostethus*, *Hyloxalus* or *Allobates*. I corroborate Grant et al.`s (2017) results (Fig. 26); I also found "*Colostethus*" *ruthveni* and its sister species as sister to all Dendrobatini. The positioning of these species as sister to Dendrobaini raises several questions on the evolution of several characters, as aposematic coloration, phytotelmata usage and predaceous tadpoles.

Tadpoles: The tadpoles of "*Colostethus*" *ruthveni* were first described by Ruthven and Gaige (1915), that considered it *Hyloxalus* (*Prostherapis*) *subpunctatus*. Later, Kaplan (1997), based on the data of Ruthven and Gaige (1915), provides some comments on the larva. The tadpoles of "*Colostethus*" *ruthveni* inhabit pools (Ruthven and Gaige 1915) or small streams (J. Ospina-Sarria, pers.com.) in high elevations of the Sierra Nevada de Santa Marta, Colombia. Ruthven and Gaige (1915) noticed a particular interesting character; they attested that "in life small tadpoles were uniform black, the heads of the older specimens conspicuously golden" (p.5). Such golden coloration observed in tadpoles is unique in this larvae among dendrobatoids.

"*Colostethus*" *ruthveni* share several character-states with *Colostethus* and *Hyloxalus* tadpoles, as the presence of a simple, moderately keratinized jaw sheath, with a medial notch on upper jaw, elements of the filtering apparatus (as the secretory ridges and pits), and a long gut that conceals other organs; larvae of "*Colostethus*" *ruthveni* are very distinct from those of Dendrobatini frogs.

Dendrobatini Cope, 1865

Type genus: *Phyllobates* Bibron in la Sagra, 1840

Immediate more inclusive taxon: Dendrobatinae

Sister group: "*Colostethus*" *ruthveni* group

Content: *Adelphobates*, *Andinobates*, *Dendrobates*, *Excidobates*, *Oophaga*, *Minyobates*, and *Ranitomeya*

Characterization: Unambiguous optimized larval synapomorphies are: **1)** gap on A-2 present, large (character 203.2); **2)** gap on P-1 present (character 204.1); **3)** upper jaw sheathes fully keratinized (character 214.3); **4)** margin of the upper jaw sheath smooth (character 215.0); **5)** lower jaw sheathes fully keratinized (character 219.3); **6)** jaw sheaths massive, corresponding to more than 50% of the oral disc height (character 221.1); **7)** body globular on dorsal view (character 226.3); **8)** snout rhomboid on dorsal view (character 227.1); **9)** body depressed on lateral view (character 228.1); **10)** snout profile truncated (character 229.1); **11)** presence of bumps on the ventral surface of the body (character 230.1); **12)** presence of bumps on the laterodorsal surface of the body (character 231.1); **13)** left wall of the vent tube free (character 264.1); **14)** dorsal wall of the vent tube fused (character 265.0); **15)**; origin of the dorsal fin at second half of the tail (character 274.3); **16)** larval coloration, fully pigmented, grey or black (character 303.1); **17)** larval caudal coloration, evenly pigmented (character 304.2); **18)** lateral ridge papillae not branched (character 339.0); **19)** second pair of infralabial papillae not branched (character 358.0); **20)** pre pocket papillae absent (character 372.0); **21)** secretory ridges absent (character 380.0); **22)** visceral mass forming a straight angle with body`s axis in ventral view (character 388.0); **23)** terminal portion of the ileum greatly enlarged, forming a diverticule (character 392.2); **24)** ileum, pigmentation pigmented (character 393.1); **25)** muscle diaphragmatopraecordialis absent (character 410.0); **26)** orbitohyoideus inserting ventrolateral ceratohyal (character 435.1); **27)** orbitohyiodeus, originating at processus muscularis quadrati, but also extending into the processus antorbitalis and orbital cartilage (character 439.1); **28)** orbitohyodeus, laterally expanded, occupying an extension wider than processus muscularis (character 440.1); **29)** orbitohyodeus overlaping the interhyoideus at their insertions (character 442.1).

Minyobates Myers, 1987

Type species: *Dendrobates steyermarki* Rivero, 1971

Immediate more inclusive taxon: Dendrobatini

Sister group: Unnamed clade composed by *Adelphobates*, *Andinobates*, *Dendrobates*, *Excidobates*, *Oophaga*, and *Ranitomeya*

Content: 1 species.

Characterization: Unambiguous optimized larval synapomorphies are: **1)** spiracle free medially and distally (character 237.1); **2)** spiracle with melanocytes scattered (character 244.3); **3)** narial opening rounded (character 252.1); **4)** dorsal wall of the vent tube fused at the base (character 267.2); **5)** stitches of the supraorbital lateral line absent (character 282.0); **6)** stitches of the infraorbital lateral line absent (character 284.0); **7)** transversal crest on the prenarial arena absent (character 311.0); **8)** internal nares inclined towards mouth (character 318.1); **9)** first postnarial papillae oblique (character 327.1); **10)** medial projection of the median ridge absent (character 336.0); **11)** lateral ridge papillae smooth (character 340.0); **12)** medial notch on the vellum`s margin absent (character 383.0); **13)** lungs, reduced, smaller than esophagous (character 395.1); **14)** myotomes closed (character 400.0); **15)** levator mandibulae longus superficialis, width equal to profundus (character 448.1).

Comments: *Minyobates* (Fig. 26) was proposed by Myers (1987) to accommodate small-sized dendrobatoids, or basically what today is recognized as *Andinobates*. Nowadays, *Minyobates* is a monotypic genus, whose phylogenetic positioning is controversial. Recently, it has been recovered as sister to *Adelphobates* (Twomey and Brown 2008b; Santos et al. 2009; Pyron and Wiens 2011; Pyron 2014) or to a larger clade containing *Adelphobates*, *Dendrobates*, and *Oophaga* (Pérez-Peña 2010; Brown et al. 2011). Grant et al. (2017) included two individuals in their study and found them as sister to the whole large clade that contains *Adelphobates*, *Andinobates*, *Dendrobates*, *Excidobates*, *Oophaga*, and *Ranitomeya*, corroborating Grant et al. (2006). My results are in agreement with both studies, and I found *Minyobates steyermarki* as the sister to all other lineages of Dendrobatini.

Tadpoles: The tadpoles of *Minyobates steyermraki* had never been described. Grant et al. (2006: 171) reported several larval characters as complementary diagnoses for the genus *Minyobates*. Kahn (2016) provided a comparative board of larval morphology of Andean poison frogs, in which he reports some characters for the tadpoles of *Minyobates steyermraki*; it is worth to note that Kahn`s board is full of errors in characters assignation. For instance, he affirms that larvae of *Adelphobates*, *Ameerega*, *Andinobates*, *Dendrobates*, *Excidobates*, and *Ranitomeya* possess submarginal papillae, which is wrong; submarginal papillae occur only in *Silverstoneia* (Grant and Myers 2013), *Hyloxalus edwardsi* (Lynch 1982), and *Aromobates nocturnus* (this work). I found several tadpoles of *Minyobates seyermarki* housed at the herpetological collection of the American Museum of Natural History; those tadpoles were collected by Charles W. Myers and John Daly in 1978 at the Cerro Yapaca, about 900 m.a.s.l., the type locality of the species, with no further data.

These tadpoles can be promptly associated with Dendrobatini by the depressed body, massive, well-keratinized, arch-shaped jaw sheaths, low tail fins with rounded tip, very low spiracle and short guts, among other charcateristics.

Adult frogs can be found in bromeliads (Gorzula and Señaris 1999). La Marca (2016: 389) attested that parent frogs deposit tadpoles in the axis of bromeliads and that "leaf litter detritus accumulations and algae growing within the bromeliad axils likely comprises the bulk of these poison frog`s larval diet".

Oophaga Bauer, 1994

Type species: *Dendrobates pumilio* Schmidt, 1857

Immediate more inclusive taxon: Dendrobatini

Sister group: Unnamed clade composed by *Adelphobates* and *Dendrobates*

Content: 9 species.

Characterization: Unambiguous optimized larval synapomorphies are: **1)** lateral emargination of the oral disc absent (character 175.0); **2)** marginal papillae on the medial region of the lower lip rounded (character 179.1); **3)** marginal papillae on the ventrolateral region of the lower lip rounded (character 180.1); **4)** marginal papillae of the medial region of the lower lip straight (character 182.0); **5)** the marginal papillae of the ventrolateral region of the lower lip straight (character 283.0); **6)** marginal papillae of the dorsolateral region of the upper lip straight (character 184.0); **7)** labial dermal ridge on A-2 absent (character 198.0); **8)** labial dermal ridge on P-2 absent (character 200.0); **9)** labial dermal ridge on P-3 absent (character 201.0); **10)** gap on A1 present (character 202.1); **11)** gap on P-1 absent (character 204.0); **12)** lower jaw sheath arch shaped (character 220.0); **13)** body elliptical on dorsal view (character 226.0); **14)** tail tip acute (character 275.1); **15)** exotrophic diet oophagous (character 561.2).

Comments: *Oophaga* (Fig. 26) is a monophyletic genus well-supported by larval and adult morphology, behaviors, and DNA synapomorphies (Myers and Daly 1976; Grant et al. 2006, 2017). Currently, it comprises nine recognized species distributed from Caribbean Nicaragua to Colombian Chocó and western Ades slopes in Ecuador (Frost 2018). My results are largely congruent with previous studies (e.g., Grant et al. 2006, 2017), but differ in the positioning of *Oophaga arborea*. Grant et al. (2017) found *Oophaga arborea* to be sister of Oophaga_pumilio_THNCFS4814 and this clade sister to all other *Oophaga* but *granulifera*, which was the most basal species. I found *Oophaga arborea* to be sister of a clade containing *Oophaga histrionica* as sister to *Oophaga lehmani* + *Oophaga sylvatica*. As Grant et al. (2017), I also found that the South American species (*histrionica*, *lehmani*, and *sylvatica*) formed a monophyletic group.

Tadpoles: Five of the nine *Oophaga* have their tadpoles described (Starret 1960; Savager 1968, 2002; Silverstone 1975; Jungder 1985; Hersek et al. 1992; Van Wijingaarden and Bolaños 1992). The evolution of *Oophaga* tadpoles is an interesting matter. The female deposits the tadpoles in small-sized phytotelmata and keep visiting them to provide a trophic egg for their development (Weygoldt 1980; Stynoski 2009). During the visitation, hungry tadpoles signalize to their mother by vigorously moving their bodies against the mother (Weygoldt 1980; Stynoski and Noble 2012) that, in turn, responds with egg deposition. Apparently, the begging behavior is a strong, indirect, signaling of tadpole quality, and non-begging tadpoles are likely to be less fed by the mothers (Dugas et al. 2017). The oophagic diet of *Oophaga* is obligatory (Brust 1993), and in the absence of the mother, tadpoles starve to death. Given the presence of alkaloids in the eggs, tadpoles of *Oophaga* possess chemical defense, and this is possibly the only case of provisioning of post-hatched offspring with chemical defense (Stynoski et al. 2014). All tadpoles of *Oophaga* have depressed bodies, rounded tail tips, massive jaws but reduced labial teeth and few, enlarged marginal papillae on the un-emarginated oral disc. For further information, see comments in “Character Evolution” section.

Adelphobates Grant, Rada, Anganoy-Criollo, Batista, Dias, Jeckel, Machado, and Rueda-Almonocid, 2017

Type species: *Dendrobates castaneoticus* Caldwell and Myers, 1990

Immediate more inclusive taxon: Dendrobatini

Sister group: *Dendrobates*

Content: 3 recognized species.

Characterization: Unambiguous optimized larval synapomorphies are: **1)** levator mandibulae longus superficialis, width equal to profundus (character 448.1).

Comments: The three species belonging to *Adelphobates* (Fig. 26) can be found along Amazon drainage (Frost 2008). My results are identical to previous studies (e.g., Grant et al. 2006, 2017), in which *Adelphobates quinquevittatus* is sister to *Adelphobates castaneoticus* plus *Adelphobates galactunotus*. This genus was previously recognized solely on the basis of molecular synapomorphies, but Grant et al. (2017) reported that the long gut, concealing other organs and the absence of 1,4-disubstituted quinolizidines were the first phenotypic synapomorphies for de the genus.

Tadpoles: Two of the tree species have their tadpoles described (Caldwell and Myers 1990), but the tadpole of *Adelophobates galactonutus* still pends on a formal description. *Adelophobates* larvae can be found in small, ground level phytotelmata, such as nutshells or fallen palm leaves (Caldwell and Myers 1990), in which they act as predators of insect larvae and other tadpoles (Caldwell 1993), including siblings (Caldwell and Araújo 1998).

***Dendrobates* Wagler, 1830**

Type species: *Rana tinctoria* Cuvier, 1797
Immediate more inclusive taxon: Dendrobatini
Sister group: *Adelphobates*
Content: 5 recognized species.
Characterization: Unambiguous optimized larval synapomorphies are: **1)** plane of narial opening bellow surrounding area (character 253.1); **2)** second pair of infralabial flap-like (character 357.1); **3)** lungs, small, occupying less than half peritoneal cavity (character 395.0); **4)** levator mandibulae longus group, well-developed, occupying all the fenestra subocular and covering the m. l. m. l. internus (character 449.1).
Comments: *Dendrobates* (Fig. 26) was a large genus including most of the bright colored poison frogs, but Grant et al. (2006) restricted the genus to six nominal taxa—*Dendrobates azureus* was subsequently considered a synonym of *Dendrobates tinctorius* (Wollenberg et al. 2006). These species can be found from Southern Nicaragua to North of South America, including Brazil, Colombia, and Guianas (Frost 2018). Nevertheless, some authors (e.g., Santos et al. 2009; Pyron and Wiens 2011) insisted in recognizing the Dendrobates *lato sensu*, even without any objective, scientific reason. This position was criticized by Brown et al. (2011) and also addressed by Grant et al. (2017). In the present study, I included five of the six species of *Dendrobates*; *Dendrobates nubeculosus* is known only by the holotype and no tissues or tadpoles were available. My results are identical to those of previous studies (e.g., Grant et al. 2006, 2017; Pyron and Wiens 2011). I found two clades, one containing the very similar trans-Andean species *Dendrobates auratus* and *Dendrobates truncates*, and the other with the *Dendrobates leucomelas* and *Dendrobates tinctorius*.

Tadpoles: Of the five species, only three tadpoles have been formally described. As mentioned above, only the holotype of *Dendrobates nubeculosus* is known and the tadpoles of *Dendrobates* *leucomelas* have never been described. Tadpoles of *Dendrobates* can be found in tree holes, fallen palm petioles and even in standing water in the hollow of a flattish rock (Dunn 1941; Eaton 1941; Savage 1968). Tadpoles of *Dendrobates* are usually aggressive and cannibalistic (Caldwell and Araújo 1998; Gray et al. 2009). These larvae present a well-developed, massive jaw sheaths (Silverstone 1975), and a modified chondrocranial anatomy when compared to other dendrobatoids (Haas 1995; de Sá and Hill 1998), with robust, posteriorly expanded palatoquadrate, robust processus muscularis and reduced hyobranchial apparatus.

Excidobates Twomey and Brown, 2008

Type species: *Dendrobates mysteriosus* Myers, 1982

Immediate more inclusive taxon: Dendrobatini

Sister group: Unnamed clade composed by *Andinobates* and *Ranitomeya*

Content: 3 valid species.

Characterization: No unambiguous optimized larval synapomorphies for this taxon.

Comments: *Excidobates* is a small genus that contains three species restricted to Peru and Ecuador (Frost 2018). Herein, I included the three species of *Excidobates* and my results are largely congruent with that of Grant et al. (2017) in recovering *Excidobates condor* as sister to *Excidobates captivus* and both as sister to *Excidobates mysteriosus* (Fig. 26). This result is quite different to that of Almendaríz et al. (2012), who found *Excidobates mysteriosus* as the sister of *Excidobates condor*. Grant et al. (2017) and my results differ from Almedaríz et al. (2012) in several aspects, as source of evidence (total evidence x small amount of DNA data), optimality criteria (parsimony x likelihood) and alignment (tree alignment x static alignment), which may justify the different results.

Tadpoles: The tadpoles of the three species have been described (Schulte 1990; Twomey and Brown 2008b; Almendaríz et al. 2012), but several characters were not properly described or illustrated. Larvae of *Excidobates condor* develop in bromeliads (Almendaríz et al. 2012), and it is likely that the other two species also use phytotelmata to breed. Twomey and Brown (2008b: 134) said that, although they could not find any free-living tadpole, they found adult frogs carrying tadpoles near *Heliconia* plants, which is often used by poison frogs to deposit their larvae. Schulte (1990) reported that the tadpoles of *Excidobates mysteriosus* possess an omnivorous diet, and he also hypothesized that *Excidobates mysteriosus* females might lay trophic eggs to supplement the diet of the tadpoles (p.64). I was able to examine tadpoles of *Excidobates condor*, but data from the other two species (very limited for *captivus*) were taken from the literature.

***Andinobates* Twomey, Brown, Amézquita, and Mejía-Varga, 2011**

Type species: *Dendrobates bombetes* Myers and Daly, 1980

Immediate more inclusive taxon: Dendrobatini

Sister group: *Ranitomeya*

Content: 15 species.

Characterization: Unambiguous optimized larval synapomorphies are: **1)** dorsal wall of the vent tube medially fused (character 267.1); **2)** vent tube opening rounded (character 272.1); **3)** median ridge concave (character 335.3); **4)** dorsal vellum arch shaped (character 347.0); **5)** pars corporis distally expanded (character 458.1); **6)** extremity of the processus posterior dorsalis rounded (character 464.1); **7)** processus quadratoethmoidalis absent (character 510.0); **8)** processus ascendens anteriorly directed (character 518.1); **9)** arcus subocularis forming straight angle with the chondrocranium longitudinal axis in lateral view (character 526.0); **10)** extremity of the processus anterior hyalis rounded (character 550.1); **11)** extremity of the processus anterolateralis hyalis rounded (character 551.1).

Comments: *Andinobates* (Fig. 26) currently comprises 15 species of small-sized frogs, distributed from Panama to Ecuador. Brown et al. (2011) proposed three species group based primarily in the previous works of Silverstone (1975), and Myers and Daly (1980): 1) *Andinobates minutus* group, for *minutus* and *claudiae*; 2) *Andinobates fulguritus* group, for *altobuyensis*, *fulguruitus*, and *viridis*; and 3) *Andinobates bombestes* group, for *abditus*, *bombetes*, *daleswansoni*, *dorisswansoni*, *opisthomelas*, *tolimensis*, and *virolinensis*. Grant et al. (2017) corroborated these three groups and confirmed the inclusion of *cassidyhornae* in the *bombetes* group and *geminasae* in the *minutus* group. Additionally, they included *victimatus* in the *fulguritus* group.

My results are in agreement with Brown et al. (2011) and Grant et al. (2017), with few differences in the internal relationships. I also recovered the three species groups: the *bombetes* and *fulguritus* groups form sister clades, and both are sister to the *minutus* group. Biogeographically, these results are interesting, given that the lowland and the Andean species formed monophyletic assemblages.

The *fulguritus* group presents some issues to be addressed. In Grant et al. (2017), *Andinobates fulguritus* was sister to all other species and both *victimatus* terminals were sister to a clade containing the non-monopyletic *Andinobates* sp. Chocó1 and *Andinobates altobuyensis*. Grant et al. (2017: 53) drew attention to the fact that those species are very similar. For instance, *Andinobates* sp. Chocó1 and *Andinobates altobuyensis* differ in coloration, but *Altobuyensis* is nested within the two *Andinobates* sp. Chocó1. This is important, because the only character supporting *victimatus* were the different coloration—pairwise distance of the cyt b was only 2.1% between *victimatus* and other terminals and SVL was only 0.5 mm larger. This evidence suggested that *victimatus* could be a synonym of *altobuyensis*. However, in my hypothesis, I recovered *Andinobates* sp. Chocó1 as monophyletic and some characters that could support *victimatus* as a different species. Notwithstanding, when only the larval characters are analyzed separately (not showed), there is no parsimonious solution for the relationships among the members of the *fulguritus* group, and a large politomy is created. My results support the maintenance of the *victimatus* status, but I stress that further studies are necessary to clarify the taxonomy and the phylogeny of the *fulguritus* group.

Tadpoles: Eight tadpoles are known for the genus (Silverstone 1975; Myers and Daly 1976x, 1980; Ruiz-Carranza and Pinilla 1992; Bernal et al. 2007). *Andinobates* are phytotelmata dwellers, usually occupying bromeliads (Silverstone 1975). Larval characters have been important in the systematic of the genus. Silverstone (1975) used several larval traits to diagnose his species groups and Myers and Daly (1980) explicitly considered the absence of papilla in the central region of the lower lip to be a synapomorphy for the *bombetes* group.

Brown et al. (2011) described the genus *Andinobates* and in the same study, provided some information on larval morphology. Unfortunately, there are many errors in character descriptions and scoring in Brown et al. (2011). For instance, they describe the tadpoles of *Andinobates minutus* and *Andinobates virolinensis* as lacking the gap in P-1, when in fact, both species have this feature.

Within the *Andinobates bombetes* group, I included a Panamanian specimen assigned to *Andinobates minutus* and a second one from Colombia, morphologically similar, that was named *Andinobates* aff. *minutus*. Those two specimens did not form a monophyletic group—*Andinobates geminisae* was the sister to Panamanian *minutus*. Tadpoles of these taxa are also different. Colombian tadpoles of *Andinobates minutus* differ from those of Panama in many characters, as having P-3 smaller than P-2 (equal), medial, small projection on upper jaw (smooth), presenting a lateral, marginal rim projection on nostril (absent), long vent tube (short), dorsal fins originating posterior to body/tail junction (at the body/tail junction), stitches of lateral line evident (undetected). This supports the existence of two species under the name *Andinobates minutus*. Differently from *Allobates talamancae*, there are few larvae of *Andinobates minutus* in scientific collections, so the sample size analyzed was too small, which refrain me of taking further decisions.

Other tadpoles: Besides the eight known tadpoles, I also included in the analysis larvae of *cassidyhornae*, *victimatus*, and of the unnamed species from Chocó (Andinobates_sp_Choco). Additionally, I also analyzed tadpoles of *Andinobates viridis* that were not included in the analysis. The tadpoles of *Andinobates viridis* are phenotypically very similar to other *Andinobates*. The most striking character is that some specimens possess a small, medial projection on the upper jaw sheath.

Besides that, the marginal papillae of the medial region of the lower lip are more spaced than in other species of the *fulguritus* group, but do not form the gap observed in tadpoles of the *bombetes* group.

Ranitomeya **Bauer, 1986**

Type species: *Dendrobates reticulatus* Boulenger, 1884 "1883"

Immediate more inclusive taxon: Dendrobatini

Sister group: *Andinibates*

Content: 16 valid species.

Characterization: Unambiguous optimized larval synapomorphies are: **1)** marginal papillae on the medial region of the lower lip rounded (character 179.1); **2)** marginal papillae on the ventrolateral region of the lower rounded (character 180.1); **3)** marginal papillae on the dorsolateral region of the upper lip rounded (character 181.1); **4)** ciliated epithelium inside internal nares absent (character 322.0).

Comments: *Ranitomeya* comprises 16 species of bright-colored, small-sized frogs that occurs in west slopes of the Andes and through the Amazon basin, from Peru to French Guiana (Frost 2018). Brown et al. (2011) recognized four species groups, the *Ranitomeya defleri*, *Ranitomeya reticulata*, *Ranitomeya vanzolinii*, and *Ranitomeya variabilis* groups. Later, Grant et al. (2017) confirmed those groups and point some inconsistences in the identifications of some DNA sequences used by other investigators (e.g., Brown et al. 2011; Santos et al. 2014).

My optimal hypothesis (Fig. 26) is identical to that of Grant et al. (2017). I found the four species groups monophyletic, with the *defleri* and *variabilis* groups as sister clades to the *reticulata* group. This large clade was sister to the *vanzolinii* group.

Tadpoles: So far, 14 of the 16 species of *Ranitomeya* have their tadpoles described. Descriptions are pending for *Ranitomeya cyanovittata* and *Ranitomeya ventrimaculata*. Aspects of the internal morphology are also known. Krings et al. (2017) described and compared the cranial muscles, visceral components, and chondrocranium for five species of *Ranitomeya* (viz. *amazonica*, *benedicta*, *imitator*, *reticulata*, and *vanzolinii*). Despite several errors in character delimitation and structure identification (see discussion in cranial muscles and visceral components characters), this was the first study of internal morphology for the genus.

Brown et al. (2011) revised the taxonomy of *Ranitomeya* and described very briefly aspects of the morphology of several tadpoles. Unfortunately, Brown et al. (2011) did not illustrate those tadpoles nor provide voucher numbers and collection information for the analyzed material. Some of the larval characters were used by Brown et al. (2011) to diagnostic and/or delimitated groups within *Andinobates* and *Ranitomeya*.

Brown et al. (2011) tentatively reported the diet of several *Ranitomeya* tadpoles. They recognized three different kinds of diet. Following Brown et al. (2011), tadpoles of *Ranitomeya* could be arranged as (but see also Lehtinen et al. 2004):

1) Detritivouros: *amazonica*, *benedicta*, *defleri*, *fantastica*, *flavovitata*, *imitator*, *reticulate*, *sirensis*, *summersi*, *toraro*, *uakari*, *vanzolinii*, *variabilis*, *yavaricola*.
2) Predaceous: *amazonica*, *benedicta*, *defleri*, *flavovittata*, *imitator*, *reticulata*, *sirensis*, *summersi*, *toraro*, *uakari*, *vanzolinii*, *variabilis*, and *yavaricola*.
3) Oophagous: *amazonica*, *vanzolinii*, *variabilis*.

All *Ranitomeya* larvae are phytotelmata dwellers (e.g., Poelman and Dicke 2007; Brown et al. 2008b). In species that lay trophic eggs, parents periodically visit the phytotelm with the larvae, and the egg deposition occurs after tadpoles signalize their needs by begging for food (Yoshika and Summers 2016).

Hyloxalinae Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel, and Wheeler, 2006.

Type genus: *Hyloxalus* Jiménez de la Espada, 1870

Immediate more inclusive taxon: Dendrobatidae

Sister group: Dendrobatinae

Content: *Ectopoglossus*, *Hyloxalus*, and *Paruwrobates*

Characterization: Unambiguous optimized larval synapomorphies are: **1)** lungs not inflated (character 396.0); **2)** muscle subarcualis rectus II–IV inserting on ceratobranchial I (character 420.2); **3)** distal margin of the cornua trabeculae oriented medially (character 472.1).

Hyloxalus Jiménez de la Espada, 1870

Type species: *Hyloxalus fuliginosus* Jiménez de la Espada, 1870

Immediate more inclusive taxon: Hyloxalinae

Sister group: Unnamed clade composed by *Ectopoglossus* and *Paruwrobates*

Content: 58 recognized species.

Characterization: Unambiguous optimized larval synapomorphies are: 1) dorsal fin sigmoid (character 279.2); 2) foramen trochlear present (character 489.1).

Comments: *Hyloxalus* is the largest genus of poison frogs, with 58 recognized species, occurring in Colombia, Ecuador, Peru, and reaching the Amazon basin in Brazil (Frost 2018). Grant et al. (2006) removed *Hyloxalus* from the synonym with *Colostethus*. Grant et al. (2017) provided a new phylogenetic hypothesis and found interesting results, as the position of *Hyloxalus picachos* and *Hyloxalus cepedai*, who were previously considered to be part of *Allobates*.

My results (Fig. 27) largely in agreement with those of Grant et al. (2017). I also found the group *Hyloxalus bocagei* as monophyletic and sister to *Hyloxalus vergeli*. But contrary to Grant et a. (2017), the clade containing *cepedai*, *subpunctatus*, *picachos*, and an undescribed species from Agua Azul (*subpunctatus* clade) was not recovered as sister to *bocagei* group plus *vergeli*, but as sister to a clade containing the remaining species of *Hyloxalus*.

In this large clade, I found very similar results to Grant et al. (2017), but with some few internal rearrangements. For example, Grant et al. (2017) found *Hyloxalus pulcherrimus* and *Hyloxalus sylvaticus*, whereas I found it to be Immediate more inclusive to *Hyloxalus pulcherrimus* and *Hyloxalus sylvaticus*. Nevertheless, most of the relationships are similar between my results and those of Grant et al. (2017). I also found *Hyloxalus elachyhistus* and *Hyloxalus delatorre* non-monophyletic, which was discussed by Grant et al. (2017: 57).

The most interesting result is that, by changing the position of *subpunctatus* clade, I recovered all the webbed species as a monophyletic group. Both clades, the webbed and the not webbed, are supported by phenotypic and molecular synapomorphies. It is noteworthy to point that there is a generic name available for the poorly webbed clade—*Phyllodromus*. I stress, however, that the unwebbed clade, which could be recognized as *Phyllodromus*, is supported by a single phenotypic synapomorphy: the presence of labial dark stripe; Therefore, further evidences may refute the *Phyllodromus* hypothesis. Additional work is required to propose an taxonomic change within *Hyloxalus*.

Tadpoles: Despite its long history—the first tadpole of *Hyloxalus* was described by Barbour and Noble in 1920—, only 28 tadpoles of *Hyloxalus* have been described formally so far (e.g., Lynch 1982; Coloma 1995; Duellman 2004; Caldwell 2005; Páez-Vacas et al. 2010). Additionally, Edwards (1974), in a unpublished Ph.D. dissertation, briefly described the tadpoles of *Hyloxalus fuliginosus*, *Hyloxalus jacobuspetersi*, and *Hyloxalus shuar*. Most descriptions of *Hyloxalus* larvae are superficial and/or made based on back-riding tadpoles (Anganoy-Criollo 2013). Aspects of the internal morphology are known only for *Hyloxalus subpunctatus*; Wassersug (1980) described its buccopharyngeal cavity and Haas (1995) described chondrocranium morphology.

Tadpoles of *Hyloxalus* inhabit pools near streams (e.g., *Hyloxalys nexipus*), muddy pools (e.g., *Hyloxalus sylvaticus*), or even marshy streams (e.g., *Hyloxalus idiomelus*) (Duellman 2004; Páez-Vacas et al. 2010). A single species has been found exclusively in phytotelm, *Hyloxalus chlorocraspedus,* collected in a pool formed in a fallen tree (Caldwell 2005). They are presumably filter-feeding larvae (Wassersug 1980), except for *Hyloxalus chlorocraspedus*, which is at least omnivorous, given that Caldwell (2005) reported predation on mosquito larvae.

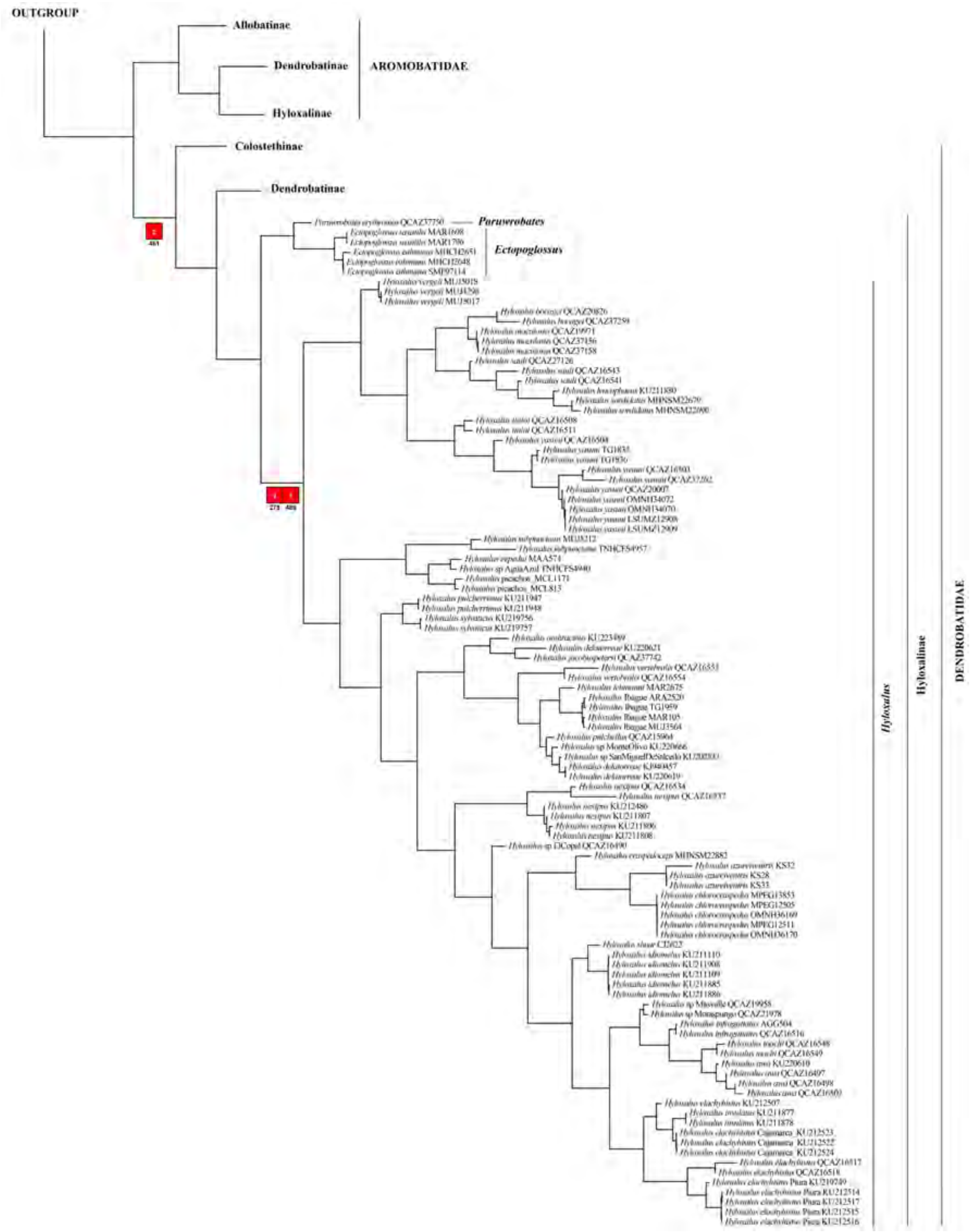

Figure 27. Optimal hypothesis of relationships within Dendrobatinae and Anomaloglossinae. Tree shows the branch-lengths (from the most parsimonious trees), and selected nodes labeled with unambiguous larval synapomorphies (red square = unique, homoplastic; blue square non-unique, homoplastic; characters below the square and synapomorphic state inside the square.

DISCUSSION

Phylogenetic relationships and larval morphology

My optimal hypothesis of phylogenetic (Fig. 28) relationships of dart-poison frogs is very similar to those presented in previous studies (e.g., Grant et al. 2006, 2017; Santos et al. 2009; Brown et al. 2011; Pyron and Wiens 2011; Pyron 2014). Within Dendrobatoidea, I recovered all families, subfamilies, and genera as monophyletic, as well as most species groups. This suggested that larval morphology is largely in agreement with other evidences and was not able to refute major relationships in Dendrobatoidea.

Nevertheless, regarding internal relationships, I had several different results, many of which are quite interesting. For example, in my hypothesis I found *Phyllobates aurtoatenia* monophyletic. This species was recovered paraphyletic by previous studies (e.g., Santos et al. 209; Grant et al. 2017), but with the inclusion of larval phenotypic characters the internal relationships changed. It is interest to point that I coded larval character for only two terminals of *Phyllobates auroteania*, and the other two had only genotypic characters. However, I coded phenotypic characters for *Phyllobates bicolor* and *Phyllobates lugubris*, which supported their relationships and changed the overall optimization of characters, rendering *auroteania* monophyletic.

The incorporation of larval morphology also supports the division of *Hyloxalus* in two distinct clades, characterized by different degrees of toe webbing. Interestingly, there is an available name for one of these taxa (*Phyllodromus*), and future studies on the taxonomy of this group will benefit from tadpole characters. Other examples can be found across the tree and my results corroborate what other researches (e.g., de Sá et al. 2014; Sánchez-Pacheco et al. 2017) have demonstrated. Phenotypic characters can have an impact in datasets composed primarily by DNA sequences. This demonstrated the cladistic principle that stated that regarding the dataset, structure is more important than quantity.

Additionally, larval morphology provided synapomorphies for several poorly known groups and allow discussions on the evolution of several lifestyles and behaviors. I comment some of these aspects.

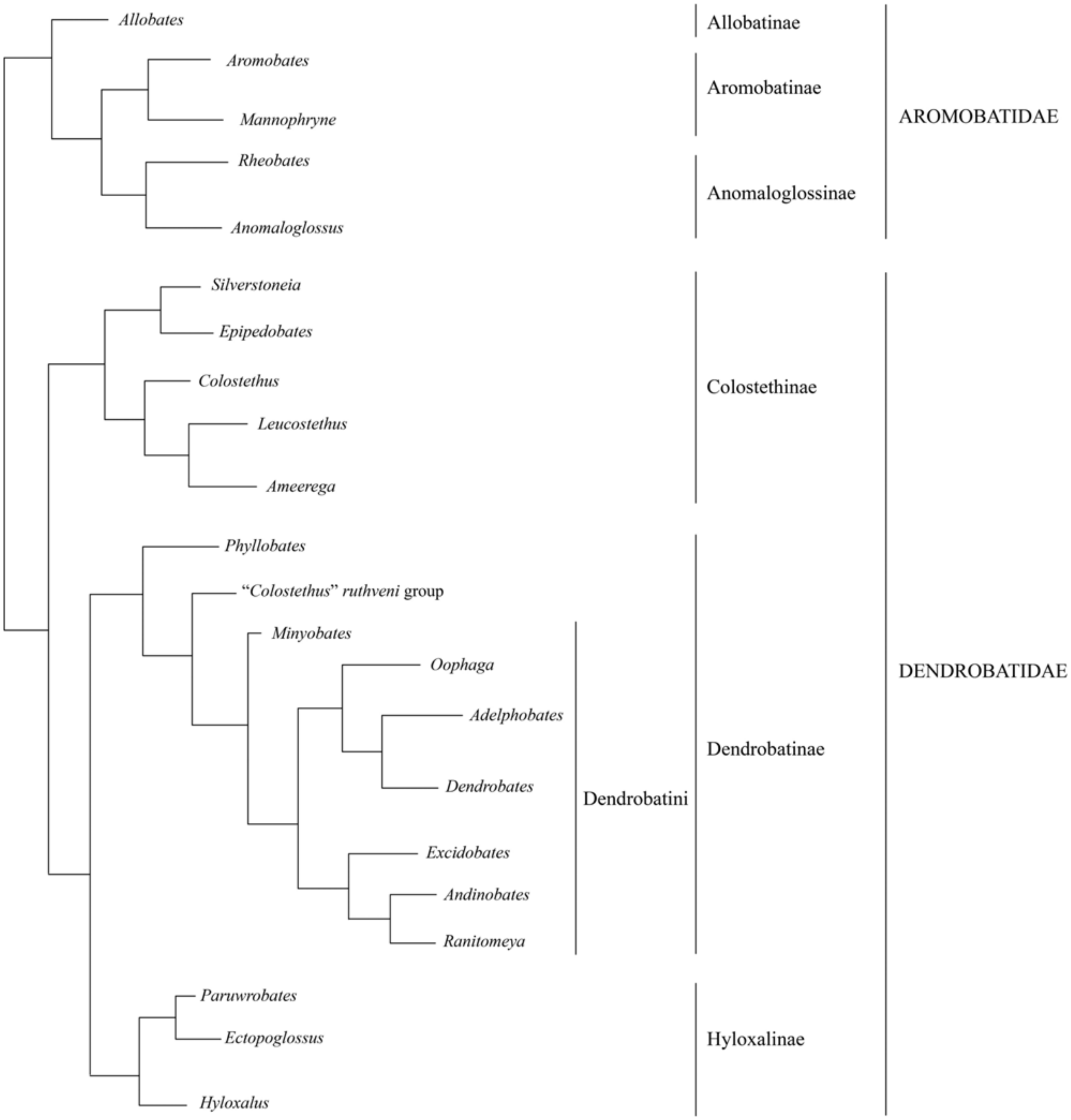

Figure 28. Summary of the higher-level taxonomy of Dendrobatoidea.

Lifestyle and Character Evolution

Evolution of nidicolous tadpoles

Amphibians present the greatest reproductive and developmental diversity among all tetrapods (Crump 2015), including the complete loss of a tadpole stage and the occurrence of nidicolous tadpoles, which are, essentially, non-feeding larvae (Altig and Johnston 1989; Altig and McDiarmid 1999x). Nidicoly evolved several times in anurans and have been reported in at least 11 families (e.g., Altig and Johnston 1989; Thibaudeau and Altig 1999).

Nidicolous development usually occurs in an isolated nest on the ground (e.g., Heyer 1969) or in various phytotelmata (e.g., Leong and Teo 2009); parental care is common and may involve egg attendance and transportation (Duellman and Grey 1983) or transportation of hatched tadpoles on the back (Lescure 1984) or gular region (Burge 1904) of the parent frog. In many cases, larvae will develop solely by feeding on the yolk retained in the egg, but this yolk reserve is rarely supplemented with oviducal (*Nectophynoides*) or pseudo-oviducal (e.g., *Rhinoderma*) secretions (Goicoecha et al. 1986; Altig and Crother 2006). Some taxa may be facultative endotrophic (Randrianiania et al. 2011), as *Incilius periglenes* (Crump 1989).

In my optimal hypothesis, nidicoly evolved in at least two independent events in Dendrobatoidea. The first event was in the ancestor of *Allobates masniger* and *Allobates nidicola* and the second is the *Anomaloglossus stepheni* group, as *Anomaloglossus apiau* (Fig. 29). The actual number of independent times that nidicoly appeared in the latter is unknown. Larvae of several species of this clade are unknown, and there is a large amount of missing data. Additionally, the larvae of *Anomaloglossus baeobatrachus* examined by me are exotrophic. Edwards (1974) also reported an exotrophic tadpole for this species. Nevertheless, according to Vacher et al. (2017), nidicoly evolved several times within the *baeobatrachus* complex. There are examples of the same phenomena in other lineages—see Castroviejo-Fisher et al. (2015) for the evolution of direct development independently in *Gastrotheca*—, however, more data is necessary to properly test this scenario. Herein, I address the questions and hypothesis raised by the known larvae of nidicolous dendrobatoids.

The nidicolous tadpoles of dendrobatoids have great ecological—*Allobates* tadpoles develop in terrestrial nests (Caldwell and Lima 2003), whereas some *Anomaloglossus* are phoretic and spend their entire larval life on the dorsum of an adult frog (Lescure 1984; Vacher et al. 2017)—and phenotypic diversity—tadpoles can be very similar to exotrophic larvae, as *Allobates chalcopis* (Kaiser and Altig 1994), or devoid of many tadpoles characters, as *Anomaloglossus degranvillei* (Lescure 1984). Interestingly, they share some peculiar character-states.

Most nidicolous larvae present a great reduction in mouthparts: the upper and lower lips are greatly reduced, basically absent; lower lip is absent in all *Anomaloglossus* (character 171.0), and the lower lip is absent (character 171.0) in all nidicolous tadpoles but *Anomaloglossus degranvillei*. When present, the lips are reduced and form a flap (characters 173.4 and 174.4), completely devoid of marginal papillae.

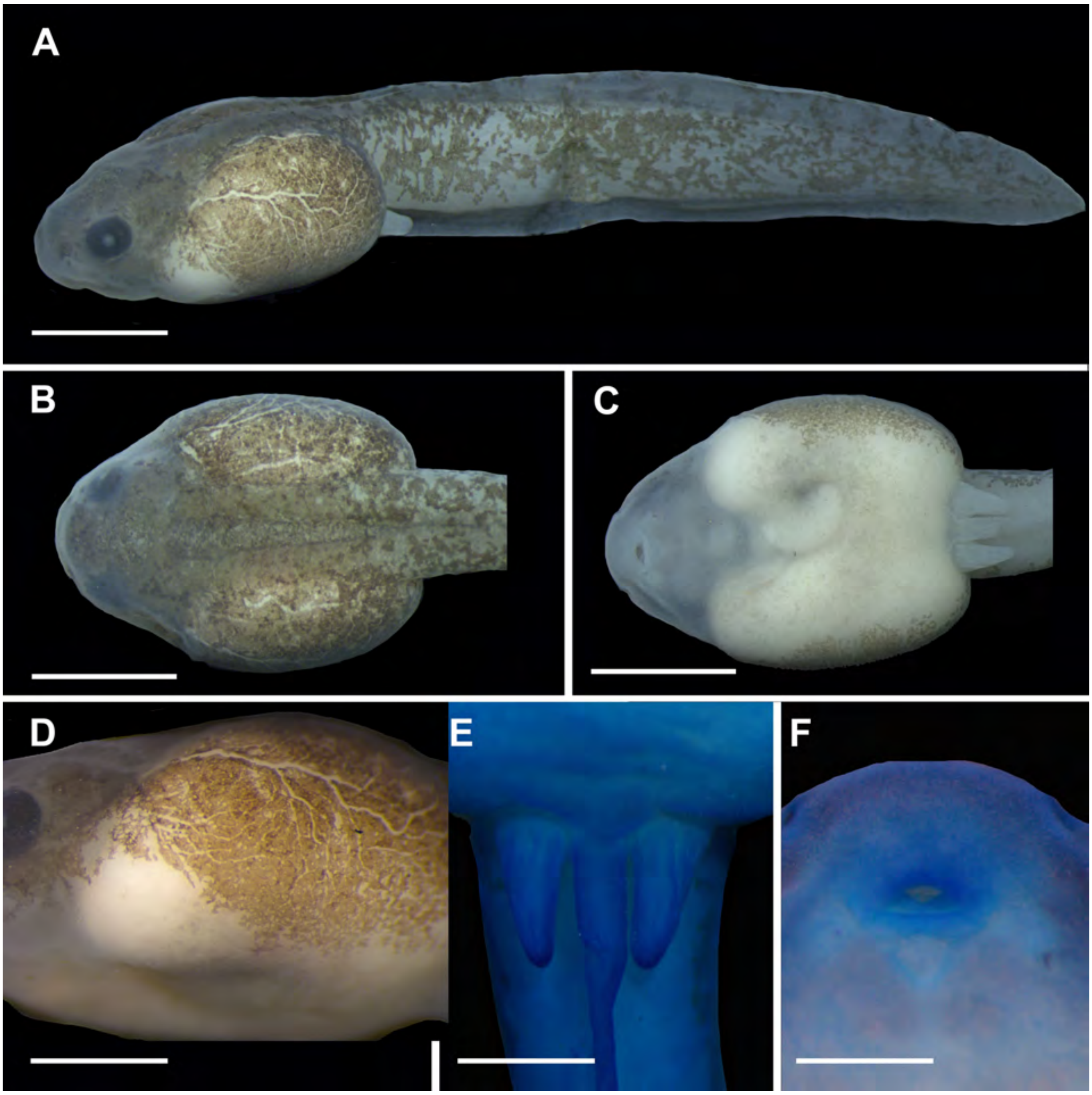

Figure 29. The tadpole of *Anomaloglossus apiau* in lateral (A), dorsal (B), and ventral (C) views. Detail of the missing spiracle (D), vent tube (E), and oral disc (F). Scale bar 1 mm.

Keratinized elements are also missing; examined tadpoles tadpoles lacked tooth ridges (characters 197.0 to 201.0) which make impossible the presence of labial tooth. The jaw sheaths are also absent (character 213.0 and 218.0), although *Allobates nidicola* and *Anomaloglossus apiau* present the bud of the lower jaw but lacking any keratinization (character. 219.0). While some endotrophic larvae that develop in larval environments may forage for food and ingest some detritus (e.g., *Pelophryne signata*; Leong and Teo 2009), dendrobatoids are either phoretic or develop in terrestrial nests. The absence of mouthparts is expected, because the development of those features would be a unnecessary energy cost.

Controversially, tadpoles of *Allobates chalcopis* present fully developed oral discs with all its mouthparts. Kaiser and Altig (1994) state that, in captivity, tadpoles of this species never move towards the water, and that in an aquarium 8 cm deep, tadpoles were often seen climbing the walls. When put in the water, these larvae did not present an effective swimming behavior. Kaiser and Altig (1994) hypothesized that tadpoles of *Allobates chalcopis* are part of a continuum of variation presented by nidicolous larvae that retain the plesiomorphic character-states but are no longer functional in tadpoles` typical environment.

Other structure that never develops in nidicolous tadpoles of poison frogs is the spiracle, absent in all examined species (character 234.0). These tadpoles spend their entire lives in a non-aquatic habitat. Gas exchanges are performed exclusively through the skin, given the complete reduction of internal gills and the rudimentary lungs (character 394.0). Stitches of the lateral line system are absent (characters 282.0 to 296.0)—the larvae have no need to perceive the surrounding environment.

These character-states related to external morphology are highly variable in anurans. Some taxa will present the same pattern as most dendrobatoids, with reduction or loss of several features; for instance, *Adenomera* and *Geocrina* larvae also lack mouthparts and spiracle (Heyer et al. 1990; Anstis 2010; Menin and Rodrigues 2013). Others are more similar to *Allobates chalcopis* in presenting external characters identical to exotrophic tadpoles; examples are *Eupsophus*, *Cycloramphus*, and *Frostius* (Formas 1992; Candioti et al. 2005, 2011; Nuñez et al. 2012; personal observation).

The buccopharyngeal anatomy (Fig. 30) also reflects endotrophy. Nidicolous tadpoles of *Allobates* and *Anomaloglossus* lack most papillae of the buccal roof and floor; no feature can be observed in the buccal roof and the internal nares are closed (character 317.1); the dorsal velum is absent in *apiau* (character 345.0) and vestigial in *nidicola* and *masniger*.

The infralabial papillae are extremely reduced and the lingual papillae are nothing but bumps in the lingual bud (Fig. 31). No element of the filtering system is present, and secretory ridges (character 380.0) and pits (character 344.0 and 379.0) could not be observed in any tadpole. The branchial basked is reduced, lacking filter plates (character 387.0) and rows.

Literature on the buccopharyngeal morphology of nidicolous larvae is scarce. According to the little available information, it is possible to observe two distinct patterns:

1) Nidicolous tadpoles that present external phenotypic characters resembling free-living larvae also present internal anatomy similar to free-living exotrophic tadpoles: the papillation of buccal roof and floor are present and well-developed. Within this group are the larvae of *Eupsophus* (Candioti et al. 2011) and *Rhinoderma darwinii* (Wassersug and Heyer 1988).

2) Nidicolous tadpoles that lack most tadpoles-specific characters: the larvae lack most papillae, secretory pits and ridges, glandular zone, and the internal nares are often close. In this group are the larvae of *Adenomera* (Wassersug and Heyer 1988), *Cycloramphus* (Wassersug and Heyer 1988), *Fritziana* (this study), *Frostius* (this study), and *Leipelma* (Bell and Wassersug 2003).

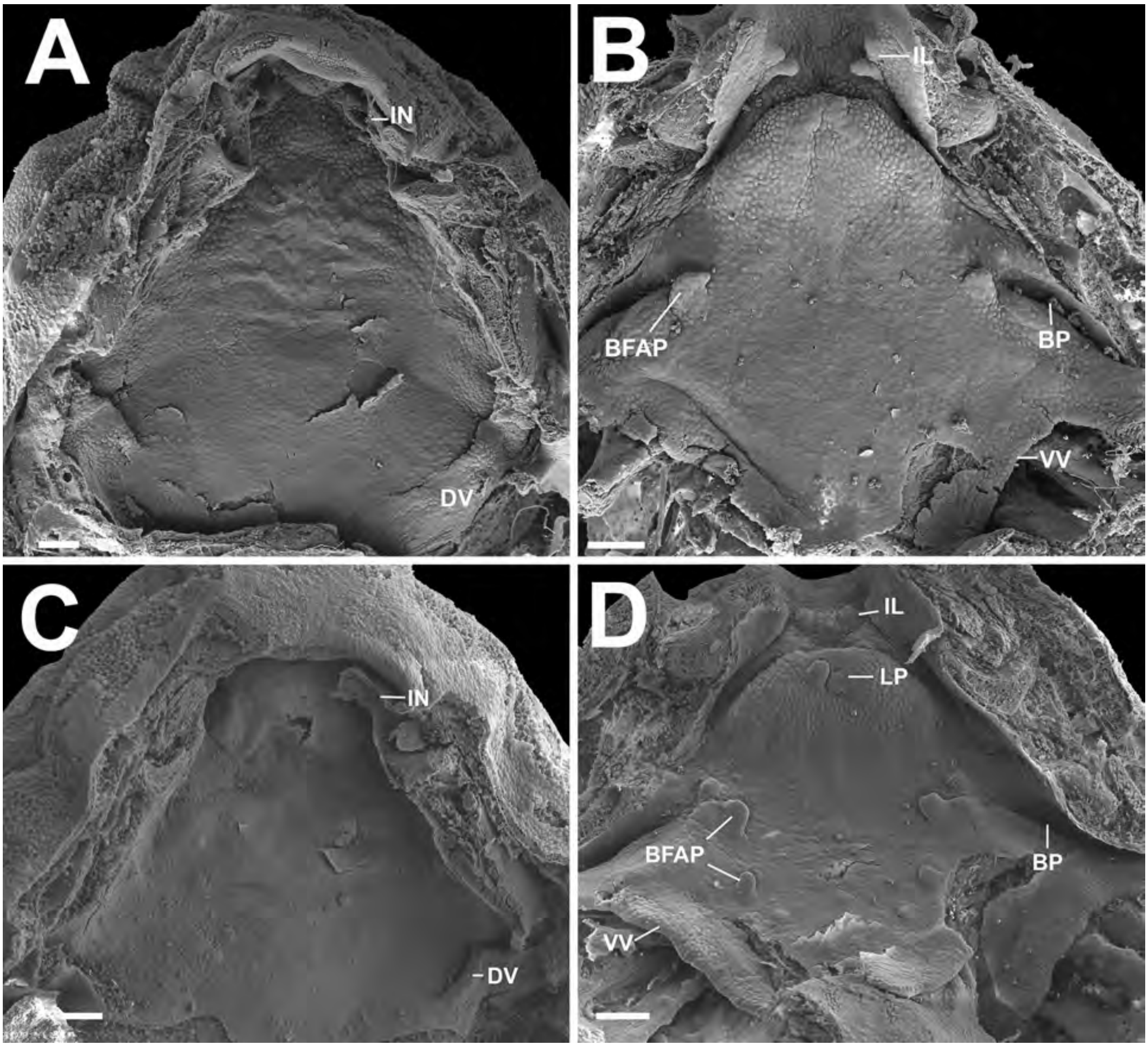

Figure 30. Buccopharyngeal morphology of *Allobates masniger* (A and B), and *Allobates nidicola* (C and D). BFAP, buccal floor arena papillae; BP, buccal pocket; DV, dorsal velum; IL, infralabial papillae; VV, ventral velum. Scale bar = 100 µm.

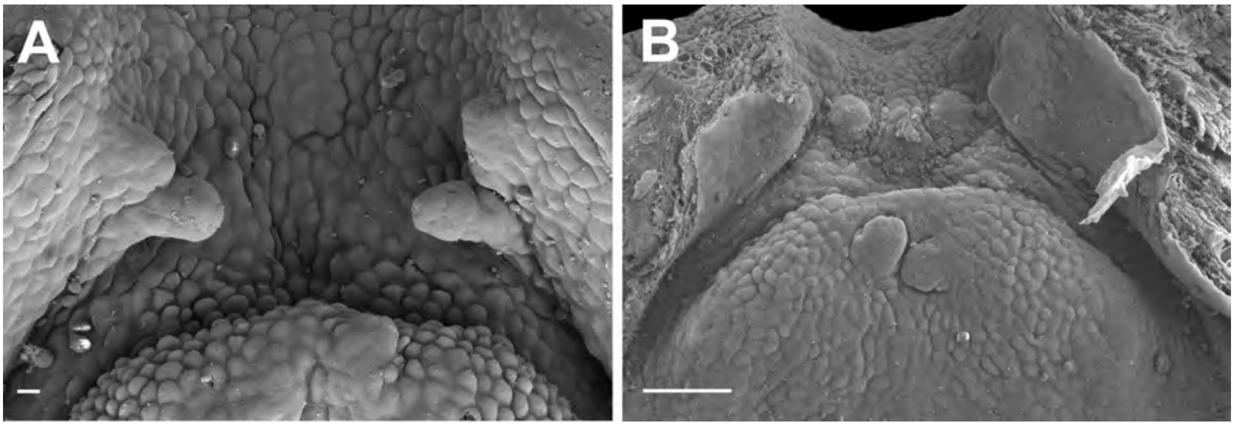

Figure 31. Detail of the infralabial and lingual papillae in *Allobates masniger* (A) and *Allobates nidicola* (B). Scale bar = 10 µm.

Allobates masniner, *Allobates nidicola*, and *Allobates apiau* fit in the second groups. I could not examine tadpoles of *chalcopis* and there is no information on its buccopharyngeal anatomy. However, I predict that they will present internal oral features similar as those of exotrophic tadpoles, given they possess several external morphology characters compatible with free-living exotrophic tadpoles (Kaiser and Altig 1994).

The second group larvae are more similar to direct-developers regarding their buccopharyngeal cavity. Duellman and Wassersug (1984) described the buccopharyngeal cavity for several direct-developing Hyphractidae frogs. Their overall morphology is quite in agreement with my findings in poison frogs (see also Wassersug and Heyer 1988 for data on *Eleutherodactylus coqui*).

The cranial muscles are also reduced (Fig. 32); both *Allobates* and *Anomaloglossus* present only five myotomes (character 399.1), in contrast with exotrophic dendrobatoids that present six. Muscles involved in branchial contraction and water movement are either absent or reduced—the interhyoideus posterior and diaphragmatobranchialis are missing (characters 407.0 and 410.0) and the three constrictor branchialis could not be detected (characters 422.1 to 424.1). Some muscles associated with feeding mechanisms are also reduced or missing; the levator longus group is very thin and the levator lateralis is absent.

The only other nidicolous tadpoles with cranial muscles studied are *Eupsophus calcaratus* (Candioti et al. 2005), *Eupsophus emiliopugini* (Candioti et al. 2011) and *Fritziana goeldi* (Haas 1996). The *Eupsophus* tadpoles present very similar patterns of insertion and origin of muscles as any exotrophic Hyloides. *Fritziana ohausi*, on the other hand, is more similar to dendrobatoids: it lacks the interhyoideus posterior, the superficialis slip of the levator externus, and the constrictor branchialis are poorly developed.

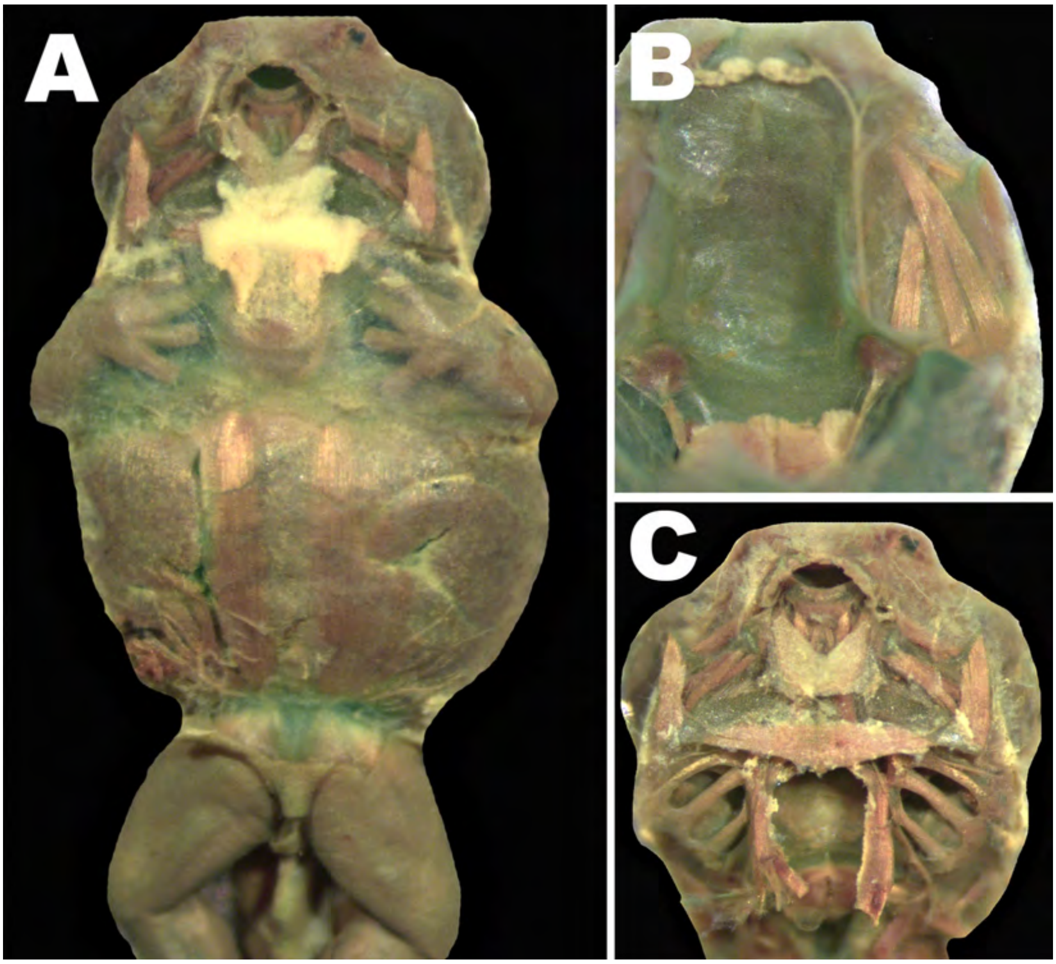

Figure 32. Images of the cranial muscles of *Allobates masniger*, showing the general ventral aspect (A), dorsal (B), and ventral (C) muscles.

The cartilaginous skeleton of nidicolous *Allobates* and *Anomaloglossus* is the most distinct among dart-poison frogs (Fig. 33), as they present very reduced suprarostral cartilages that are fused to the cornua trabeculae (character 475.1). The cornua trabeculae is unique among poison frogs; it is ventrally directed, forming a straight angle with the longitudinal axis of the chondrocranium. As far as I know, this condition had never been reported for any species with a larval stage—similar condition can be observed in the direct developer *Philautus silus* (Kerney et al. 2007) and *Eletherodactylus coqui* (Hanken et al. 1992). The branchial basket is reduced and the ceratobranchials lack spicules (characters 536.0 to 539.0) and cartilaginous projections (characters 543.0 to 546.0).

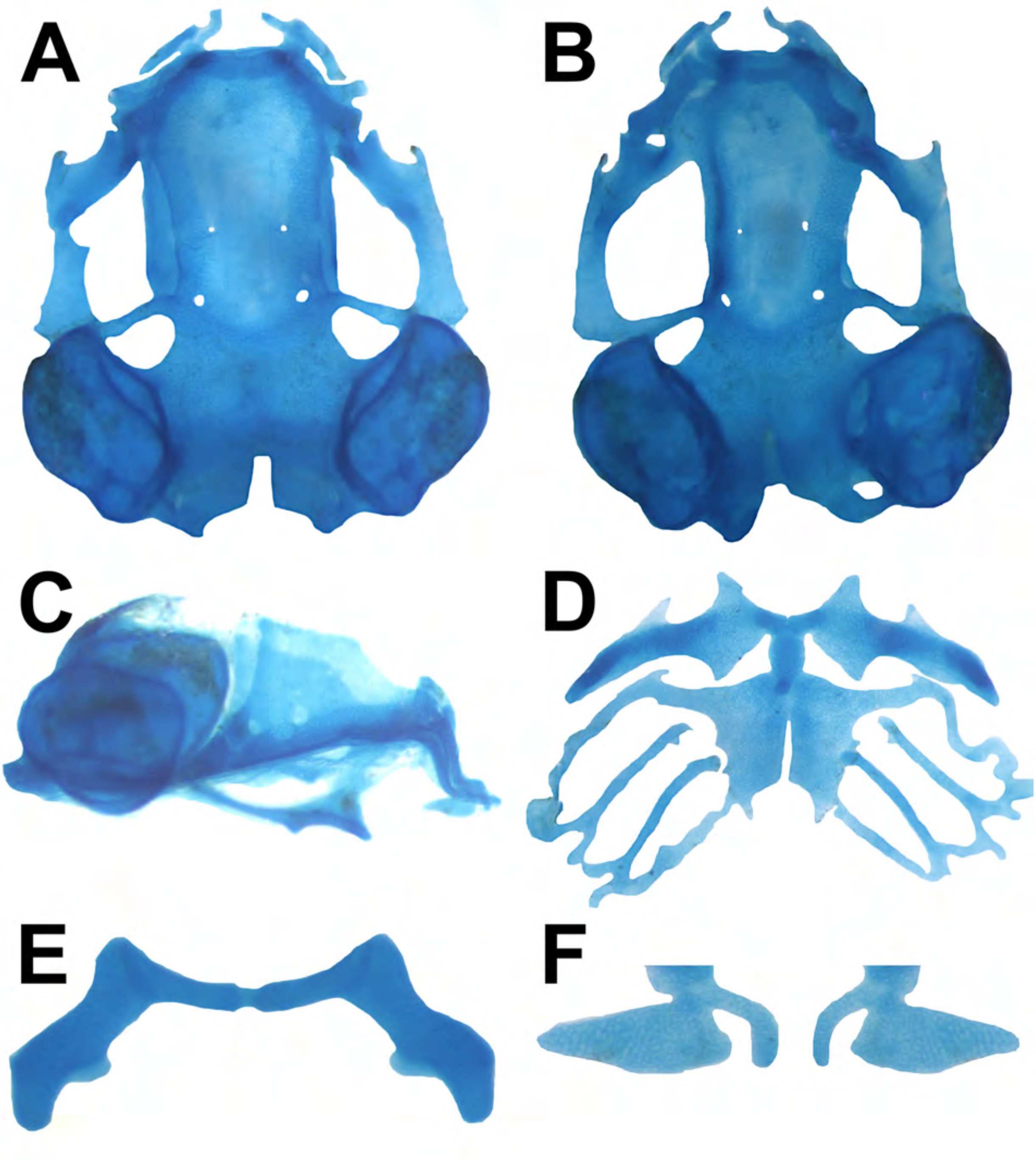

Figure 33. Chondrocranial skeleton of *Allobates nidicola* in dorsal (A), ventral (B), and lateral (C) views. Detail of the hyobranchial apparatus (D), lower jaw (E), and suprarostral (F) cartilages.

Chondrocranium data is available for few nidicolous tadpoles: *Cycloramphus stejnegeri* (Lavilla 1991), *Eupsophus calcaratus* (Candioti et al. 2005) *Eupsopohus emiliopugini* (Candioti et al. 2011), *Eupsophus nahuelbutensis* (Nuñez and Úbeda 2009), *Eupsophus queulensis* (Cárdenas-Rojas et al. 2007b*), Rhinoderma darwinii* (Lavilla 1987), *Fritziana goeldi* (Haas 1996). Some character-states are present in most of these larvae, as the short processus muscularis, large otic capsule, short cornua trabecular, tall orbital cartilage, reduced hyobranchial apparatus. With the exception of the large otic capsule, the other characters are in accordance with a non-feeding lifestyle.

My results under a broad comparison with available data on the literature shows that many characters evolved very similarly among unrelated taxa that present nidicolous tadpoles. However, there seems to not exist a general pattern of loss and gains of characters and nidicolous species may have tadpoles very similar to exotrophic species, as in *Eupsophus* (Cárdenas-Rojas et al. 2007; Candioti et al. 2011), or highly modified tadpoles lacking mouthparts, spiracle and/or other characters, as in *Phynobatrachus* (Rödel and Ernst 2002). Nidicolous larvae from several different families are available, however, the lack of details on anatomical character and uniform coverage of variation is a deterrent to a thorough understanding.

The evolution of endotrophic larvae possibly involves two different mechanism: the loss of some specific tadpole characters, and the acceleration in the development of some adult characters (Elinson 2001). For instance, it has been demonstrated that endotrophy is associated with the remodeling and/or loss of cartilaginous elements typical of tadpoles, as the suprarostral cartilages and palatoquadrate, and with changes in the onset of some skeletal elements (Hanken et al. 1992; Yeh 2002; Kerney et al. 2007).

It has been suggested that nidicoly would be an intermediate step towards the completely direct development (e.g., Lutz 1947; Magnussom and Hero 1991), although empirical evidences suggest the opposite. Gomez-Mestre et al. (2012) demonstrated that direct development arose almost as frequently directly from aquatic larvae as from terrestrial eggs with aquatic larvae. Furthermore, endotrophic free-living larvae did not originate direct developers. These findings are consistent with Altig and Crother`s (2006) hypothesis that endotrophic larvae did not evolved as the product of selective pressure to avoid predators or competitors of aquatic environments, but as results of developmental reppartening via changes in some gene family responsible for the development of tadpole specific traits (see also Altig 2006). Assuming that nidicolous tadpoles evolved under similar conditions or by similar mechanisms with different degrees of intensity, an interesting scenario rises.

Available evidences support Altig and Crother`s (2006) hypothesis partially. Wassersug and Duellman (1984) provided descriptions and illustrations of the buccopharyngeal anatomy of embryos of exotrophic tadpoles of *Gastrotheca riobambae* (fig.7: 11). The presence/absence of several papillae, its organization and overall morphology are very similar to those observed in nidicolous and direct-developers species. Wassersug and Duellman (1984: 35) also recognized that and state that “patterns seen among direct-developing species can be accounted by simple truncation of normal tadpole development”.

From my direct observations and compilation of literature information, the evidences support that nidicolous tadpoles are basically paedomorphic individuals and the occurrence of this lifestyle is due to the truncation of the regular larval development. From a developmental perspective, Altig and Crother (2006) suggested that simple changes in a family of genes that control the tadpole development should be enough to generate endotrophic larvae. The losses and gains of free-living, feeding tadpoles during the evolution of some lineages (e.g., Castroviejo-Fisher et al. 2015) suggests that some developmental program can be switched relatively easily among some species (see Altig and Crother 2006).

The second aspect of Altig and Crother (2006) hypothesis states that the rapid evolution of non-feeding terrestrial larvae/embryo had nothing to do with pressures to escape the dangerous aquatic habitats. According to Altig and Crother (2006), the rapid transition from exotrophic to endotrophic by developmental reppaterning was advantageous because it would allow tadpoles to rapidly occupy a different niche, and no pressure towards the terrestrial reproduction needs to be evocate as the causation. The results of Gomez-Mestre (2012) showing that direct development not always followed from aquatic larvae are consistent with Altig and Crother`s (2006) hypothesis, and it seems that evolution of direct development is not a response to selective pressures towards a terrestrial development.

More data, especially molecular and developmental, are necessary to expand Altig and Crother`s (2006) conjectures further. If the truncation of development is responsible for eliminating partially (as in nidicolous) or completely the tadpole semaphoronts from a given species` life-cycle, it is possible that, transitively, the opposite phenomena would be responsible for the insertion of such semaphoronts in the ontogenetic pathway of frogs. This scenario is consistent with Altig`s (2006a) hypothesis that "tadpoles evolved and frogs are the default". The field of molecular developmental biology is growing fast, and exciting times of new discoveries are coming.

Revisiting the nidicolous ecomorphological guild

Altig and Johnston (1989: 106) described the nidicolous guild as follows:

"Egg or larva seldom intimately associated with parent`s body; eggs often small and numerous; normal embryology results in free-living, non-feeding tadpole, continuum from those having morphological traits of exotrophic tadpoles, to those that have fins, oral apparatus, pigment

and/or spiracle variously reduced to absent; tadpole remains in or near nest site until metamorphosis."

Altig and Johnston (1989) recognized that there is continuum of variation within nidicolous tadpoles. However, their definition only employed external morphology characters. With the analysis of internal morphology, including buccopharyngeal morphology, cranial muscles, and chondrocranium, I propose that two different sub-guilds may be recognized within nidicolous larvae:

Nidicolous: Egg or larva seldom intimately associated with parent`s body; eggs often small and numerous; normal embryology results in free-living, non-feeding tadpole

> *Nidicolous type 1.* mouthparts present, usually with reduced number of rows; oral disc present, bordered by marginal papillae; jaw sheaths present, keratinized or not; spiracle absent or present; buccal roof and floor papillae present; ventral and dorsal vela regularly formed; filter plates and filter rows present, although seldom reduced; cranial muscles well-developed and following general patterns of origin and insertion; trabecular horns parallel to longitudinal axis; suprarostral cartilage present, not reduced; frequently, developing (at least in part) in aquatic environment and capable to feed on external sources. Examples: *Allobates chalcopis*; *Eupsophus* spp; *Rhinoderma darwinii*; *Cycloramphus stejnegeri*; *Pelophryne signata*.
>
> *Nidicolous type 2.* Mouthparts absent; spiracle absent; oral disc absent or reduced into a flap; marginal papillae absent; tooth ridges and rows absent; jaws absent, or when present, not keratinized; lateral line system absent or undetected; buccopharyngeal papillae completely absent or very reduced in number and size; internal nares closed; ventral and dorsal vela absent or vestigial; no filter rows or plates; secretory ridges and pits absent; cranial muscle with few fibers, with reduced or absent jaw muscles and constrictor branchialis muscles; trabecular horns ventrally directed; suprarostral cartilages reduced; often developing in terrestrial nests and unable of feeding. Examples: *Allobates masniger*, *Allobates nidicola*, *Anomaloglossus apiau*, *Anomaloglossus stepheni*; *Anomaloglossus degranvillei*, *Fritziana* spp; *Altiphrynoides malcomi*.

I stress, however, that the assignation of some larvae to one of this two subgroups should be made with caution and based on evidences of external and internal morphology. In the absence of internal morphology characters, it is possible to wrongly assign a species. In those cases of absence of evidences, I suggest the usage of nidicolous, without further divisions.

Life in plants—the evolution of phytotelmata tadpoles

Phytotelm (from Greek—*phytos* = plant; *telm* = plant; phytotelmata, plural) can be defined as a water body contained in or on plants or parts of plants, either living or dead (Thienemann 1934; Lehtinen et al. 2004), such as bromeliads tanks, bamboo stumps, tree holes, nut shells, and palm leaves. Phytotelmata water, which may be a mixture of rain water and plant secretion, usually presents very different physicochemical properties, as low dissolved oxygen, low pH—usually ranging from 4.0 to 6.0, reaching higher values of 7.0 in some extreme cases—and is very viscous (Laessle 1961; Maguire Jr. 1971; Richardson 1999).

Despite the absence of regular flow, small size, and little illumination to support primary productivity, phytotelmata habitats are highly diverse environments. A variety of life forms inhabit phytotelmata, such as bacteria, fungi, algae (blue-green, greens, englenoids, diatoms, etc.), protozoa (amoeba, ciliates, etc.), plathyhelminthes, rotifers, gastrotrichs, nematods, oligochaetes, crustaceans (otracods, copepods, cladocera, isopods, decapods), aracnids (acari), many insect larvae and adults, and even vertebrates, as anuran tadpoles (Maguire Jr. 1971; Kitching 2001; Richardson 1999). Besides its residents, phytotelmata may also provide shelter for several species during the day or during the dry season (Dunn 1937; Whittaker et al. 2015), as in *Bokermannohyla circundata*. Some animals do not live in the phytotelma, but use it as an egg deposition site, as occurs in the anole lizards of the *Anolis pentaprion* species group (P.H.S Dias, unpublished data).

Phytotelmata are safe habitats for tadpole development when compared to ponds and streams that present many predators and/or competitors (Summers and McKeon 2004), which led several lineages of frogs to colonize and use these habitats for breading. Whereas some taxa are opportunistic/occasional users of such habitat (e.g., *Boana pardalis*, Moura et al. 2011), many anuran species are obligate phytotelmata breeders—in 2004, Lehtinen et al. reported phytotelmata tadpoles in 102 species (44 genera and 9 families). To those species, phytotelmata may present a valuable and limiting resource (Donnelly 1989; Sabagh et al. 2017), limiting abundance and populational size. Phytotelmata dwellers tend to exhibit elaborated parental care features to compensate the constrains imposed by that habitat; Lehtinen and Nassbaum (2003) reported at least six different parental behaviors in phytotelamata species (*viz*., nest construction, egg attendance, egg transport, tadpole attendance, tadpole transport, and tadpole feeding).

In my optimal hypothesis, the Dendrobatoids colonized phytotelmata habitats several times (Fig. 34). In aromobatids, I found that was the condition of the ancestor of the *Anomaloglossus beebei* and *Anomaloglossus roraima* in agreement with Grant et al. (2006, 2017). Caldwell and Araújo (2004) and Silverstone (1976) reported tadpoles of *Allobates femoralis* in phytotelmata, although it seems to be an opportunistic usage, since tadpoles of this species are often found in small, terrestrial pools (e.g., Duellman 2005). Nevertheless, phytotelmata usage evolved a second time in aromobatids; La Marca and Mijares-Urrutia (1997) reported tadpoles of *Allobates bromelicoa* living in bromeliads.

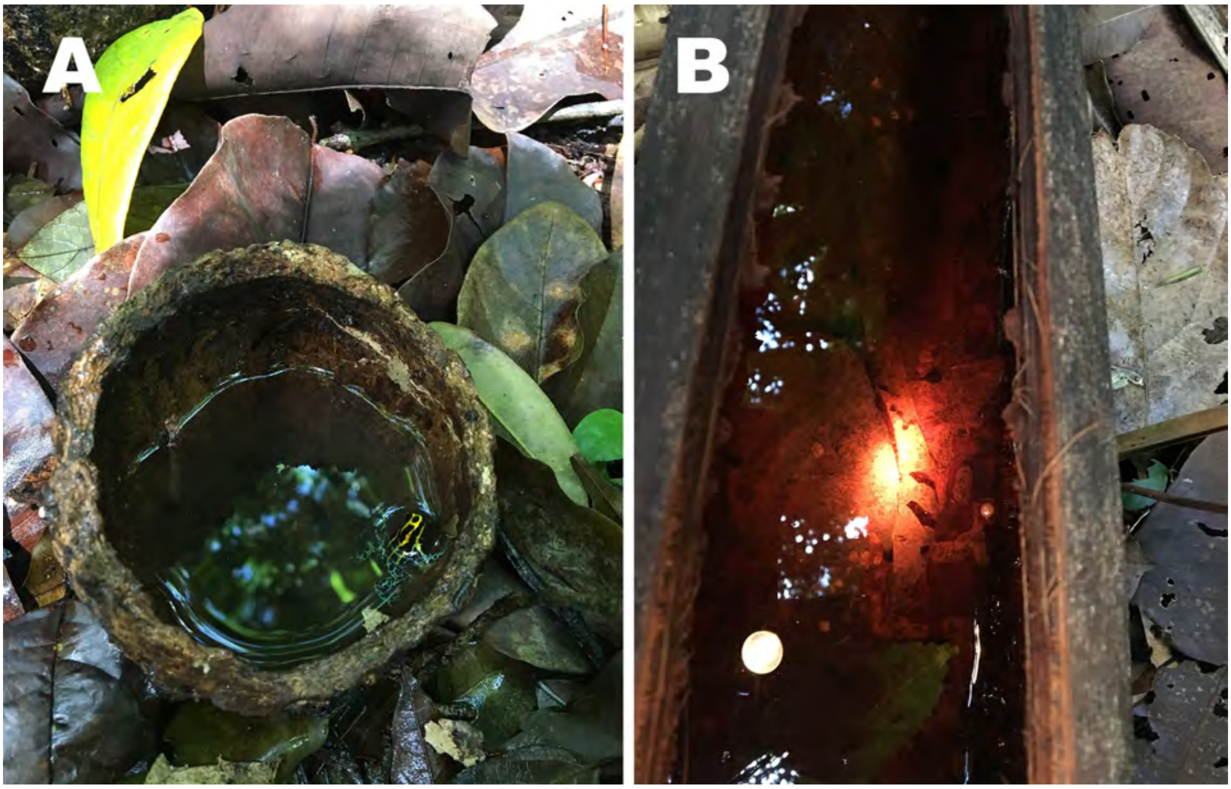

Figure 34. Examples of phytotelmata used by dart-poison frogs. *Ranitomeya amazonica* adults on a nutshell (A). Tadpoles of *Adelphobates galactonotus* on a fallen palm leaf. Photos by Taran Grant.

In Dendrobatidae, the evolution of phytotelmata usage is more complex and may have evolved two or three times. Tadpoles of *Hyloxalus chlorocraspedus* are exclusively phytotelmata dwellers (Caldwell 2005) and the only species in the genus *Hyloxalus* to present this lifestyle. Regarding the aposematic species, Grant et al. (2006) suggested that the usage of phytotelmata for breeding and development evolved in the most recent ancestor of the subfamily Dendrobatinae. However, the findings of Grant et al. (2017) challenged this hypothesis with the placement of the controversial Santa Marta rocket-frog, "*Colostethus*" *ruthveni* as sister to all Dendrobatini.

I recovered the same relationships as Grant et al. (2017): *Phyllobates* as sister to a clade composed by the "*Colostethus*" *ruthveni* group plus Dendrobatini. "*Colostethus*" *ruthveni* is known to use small ponds for tadpole development (Ruthven and Gaige 1915; Kaplan 1997; Jhon. Sarria-Ospina pers.com), whereas *Phyllobates* and all other Dendrobatinae are phytotelmata dwellers (e.g., Eaton 1941; Silverstone 1975, 1976; Myers and Daly 1980; Savage 2002; Brown et al. 2011; Almendaríz et al. 2012), with the sole exception of *Phyllobates aurotaenia*, that may be collected in small, ground, temporary ponds (M.A. Anganoy-Criollo pers.com.) or in side river puddles (Amézquita 2016). This leads to an ambiguous optimization of the usage of phytotelmata with two equally parsimonious scenarios: 1) the ancestor of all Dendrobatinae used phytotelmata for breeding and in the "*Colostethus*" *ruthveni* group there was a reversion for pond/stream usage; 2) the usage of phytotelmata evolved twice, one in the ancestor of *Phyllobates*, and independently in the ancestor of Dendrobatini, whereas "*Colostethus*" *ruthveni* group retained the plesiomorphic condition. No matter the scenario, larval morphology tells us interesting stories.

The tadpoles of "*Colostethus*" *ruthveni* share several character-states with other pond/stream larvae of Dendrobatidae, as a small gap on A-2 (character 203.0), jaw sheaths moderately keratinized (characters 214.1 and 219.1), the presence of a medial notch on upper jaw sheath (character 215.2), elliptical body (character 226.0), acute tail tip (275.1), color pattern originated from scattered melanophores (character 303.0), among many others. They present a functional, well-developed filtering apparatus, with secretory pits (character 344.1 and 379.1) and ridges (character 380.1), and its muscles and cartilages do not present any striking deviation from some *Colostethus* or *Hyloxalus* larvae.

The tadpoles of Dendrobatini, however, present several distinct characters. Most species present a globular (character 226.2), depressed (character 61.1) body with a rhomboid (character 228.1), truncated (character 229.1) snout; their spiracle is short, and almost ventrally located (character 240.2). In many species, the low, straight (characters 279.1 and 280.1) tail fins originate posteriorly to the body/tail junction (character 274.3) and the tail tip is rounded (character 107.0). Body and tails are often evenly pigmented (characters 303.1 and 304.2), presenting a dark coloration. The lungs are often large (character 395.1) and inflated (character 396.1), the glottis exposed and both vela are poorly developed and medially interrupted.

Lannoo et al. (1987), in a large study on larval morphology and ecology of the bromeliad tadpole of *Osteopilus brunneus*, realized that these tadpoles presented a set of phenotypic characters very different from other hylids. They followed Noble (1929) and Jones (1967) in considering that the long tails of *Osteopilus brunneus* would aid in swimming through the viscous waters of bromeliad tanks, which is full of egg capsule remains and debris; according to that view, these larvae were more likely to burrow than swim.

Several characters of the Dendrobatini larvae are consistent with Lannoo et al.`s (1987) hypothesis; the snout shape, which may be interpreted as a shovel, could increase the penetration capacity for tadpoles to "dig" into the viscous liquid. The rounded tail tip provides s stronger propulsion and more thrust (see Wassersug and Hoff 1985). The depressed body is ideal for maneuvering in reduced spaces of phytotelmata, especially in the tight space between leaves (Noble 1929).

The large, inflated lungs are a requirement for aerial respiration, given that phytotelmata present little dissolved oxygen (Laessle 1961). Phytotelm dwellers can be observed frequently coming to the surface to gulf atmospheric air (Noble 1929; Lannoo et al. 1987). I observed larvae of *Dendrobates auratus* and *Oophaga pumilio* repeating this behavior several times. The exposed glottis with a medial interruption of dorsal and ventral vela may facilitate the air entrance (R. Wassersug pers.com.). Another evidence that branchial breathing plays little or no part in these phytotelmata tadpoles is the absence of the muscle diaphragmatopraecordalis (character 410.0); this muscle acts as a constrictor of the branchial chamber (Noble 1929; Haas 1997), increasing brachial circulation.

Strong melanization resulting in dark tadpoles is another common character among Dendrobatini larvae. This uniform color pattern is commonly observed in social tadpoles (Thibaudeau and Altig 2012) that form schools (e.g., *Rhinella icterica*, *Boana semilineata*). Santos et al. (2017) hypothesized that the dark coloration allied to the low incidence of light inside phytotelms (bromeliads in their discussion) could offer some protection against external predators.

The same character-states commented above can also be observed in the dendrobatoids *Hyloxalus chlorocraspedus*, *Anomaloglossus roraima* and *Anomaloglossus beebei*, all of which are phytotelm dwellers. These character-states are also present in many phytotelmata tadpoles of different, unrelated taxa as *Theloderma* (e.g., Wassersug et al. 1981; Rauhaus et al. 2012), *Ololygon* (e.g., Silva and Alves-Silva 2011; Lacerda et al. 2015), *Osteopilus* (e.g., Noble 1929; Lannoo et al. 1987), *Anotheca* (e.g., Duellman 1970; Savage 2002), *Crossodactylodes* (e.g., Santos et al. 2017), *Mantella* (e.g., Jovanovic et al. 2009), *Ramanella* (e.g., Bowatte and Meegaskumbura 2011), among others. This strongly suggests specializations for living and develop in phytotelm.

Phyllobates larvae, in contrast with other phytotelm larvae, share only part of these character-states with Dendrobatini and, in some aspects, as suggested by Silverstone (1976: 7), "resembles those [tadpoles] of *Colostethus*"*. Some *Phyllobates* present the depressed body and rhomboid snout, as *Phyllobates bicolor* and *Phyllobates terribilis,* whereas others possess the elliptical body with rounded snout just like other Dendrobatidae non-phytotelmata larvae.

Phyllobates auroteania is the species that shares more characters with pond or stream dwellers. Not by coincidence, these larvae have been found in side stream puddles (Amézquita 2016) and temporary ground ponds (M.A. Anganoy-Criollo pers.com). Nevertheless, according to my optimal solution, this condition would be secondary within *Phyllobates*.

Jaws: the evolution of predaceous tadpoles

The colonization of phytotelmata involves a tradeoff between security and food resources. Whereas phytotelma is a safe environment due to the reduced number of predator and competitors, it also presents low abundance of food items. Makeon and Summers (2013: 727) emphasized this:

> "*If dendrobatid fitness were affected by larval predation in aquatic habitats, then a shift to direct development, as in some Anomaloglossus, or the utilization of extremely small water bodies may reflect selection pressure towards the derived reproductive strategies of the more toxic genera, such as Dendrobates and Ranitomeya. A complementary group of patterns in which clutch size is reduced and parental care is increased may be viewed as a tradeoff between lowered predation rates of smaller water bodies and lower food availability.*"

In dart-poison frogs, several adult behaviors were hypothesized as having evolved to overcome the difficulties imposed by phytotelmata (e.g., Summers 1999; Brown et al. 2008). I will argue that larval morphology also responded to the pressures imposed, especially regarding the feeding habits of tadpoles. I suggest two specializations in feeding habits of poison frogs within the phytotelmata environment: predatory behavior and oophagy. The habits are directly correlated with changes in mouthparts, muscles, viscera, and chondrocranium.

Predation may represent an alternative to augment calorie—especially from proteins—ingestions of the larvae. Predaceous and cannibalistic behaviors have been reported in several

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* Note that, to Silverstone (1976), *Colostethus* would include species now assigned to several genera as *Allobates*, *Hyloxalus*, and *Anomaloglossus*. For further comments on historical review of Dendrobatoidea systematics, see Grant et al. (2006).

unrelated taxa, for example: *Ceratophrys carwelli* (Candioti 2005), *Duttaphrynus stomaticus* (Saba et al. 2013), *Hoplobatrachus tigrinus* (Khan 2004; Grosjean et al. 2004), *Lepidobatrachus laevis* (Ruibal and Thomas 1989), *Leptodactylus pentadactylus* (Heyer et all 1975), *Occidozyga baluensis* (Haas et al. 2014), *Spea multiplicata* (Pfennig 1990, 1992a), and *Rhinella acutirostris* (pers.obser). Most of these species inhabit temporary ponds that are subjected to desiccation and "carnivory" is a form to accelerate larval development via the extra input of energy. Within poison frogs, however, it may represent the better option of getting any alimentary resource, given that phytotelmata tend to have less diversity than ponds.

Several authors reported that tadpoles of Dendrobatini, *Hyloxalus chlorocraspedus* and *Anomaloglossus beebei* ate invertebrates, other tadpoles, and even their own species; for example, *Adelphobates castaneoticus* is a predaceous larva that feeds on invertebrates and other tadpoles, including smaller conspecific individuals (Caldwell 1993). If co-occurring, tadpoles of *Dendrobates auratus* always preyed on *Oophaga granulifera* (Ryand and Barry 2011), and in the presence of conspecific tadpoles they are indiscriminate predators that cannibalize their siblings (Gray et al. 2009). Poelman and Dicke (2007) reported that tadpoles of *Ranitomeya amazonica* are cannibals and attack smaller tadpoles and eggs (see also Summers 1999). Rojas (2014) demonstrated that *Dendrobates tinctorius* prey on conspecific larvae. Caldwell (2005) reported that tadpoles of *Hyloxalus chlorocraspedus* feed on mosquito larvae. *Ranitomeya defleri* predate on two siblings few hours after hatch (pers. observation). Schulte (1990) affirms that tadpoles of *Excidobates mysteriosus* feed on insect larvae. Bourne et al. (2001) reported that tadpoles of *Anomaloglossus beebei* preyed on insect larvae and other tadpoles, con and heterospecific. Brown et al. (2011) reported that several *Ranitomeya* are predaceous tadpoles.

Tadpoles of *Dendrobates galactonotus* and *Dendrobates auratus*, in captivity, burst their swimming speed and invest on mosquito larvae (Fig. 35). They bited repeatedly and on every bite, more larvae were ingested (pers.obser.). However, dilacerations of the prey is not the only possible way of ingesting the pray; I found a large undamaged insect larva in the foregut of a *Minyobates steyermarki* tadpole, indicating that it was swallowed whole (Fig. 36).

The larval characters of phytotelma poison frogs are in accordance with that scenario. Together with the predatory behavior, several characters evolved within these lineages and ecomorphological considerations can be made. For example, the jaw sheaths generally act as the primary food removal surface (Altig 2006), however, cuspate sheaths of some carnivorous species may allow more efficient cutting of animal tissues (Altig and Johnston 1989: 94). All phytotelmata poison frogs presented massive jaw sheaths, fully keratinized jaw sheaths. These robust jaws are powered by large, massive levators.

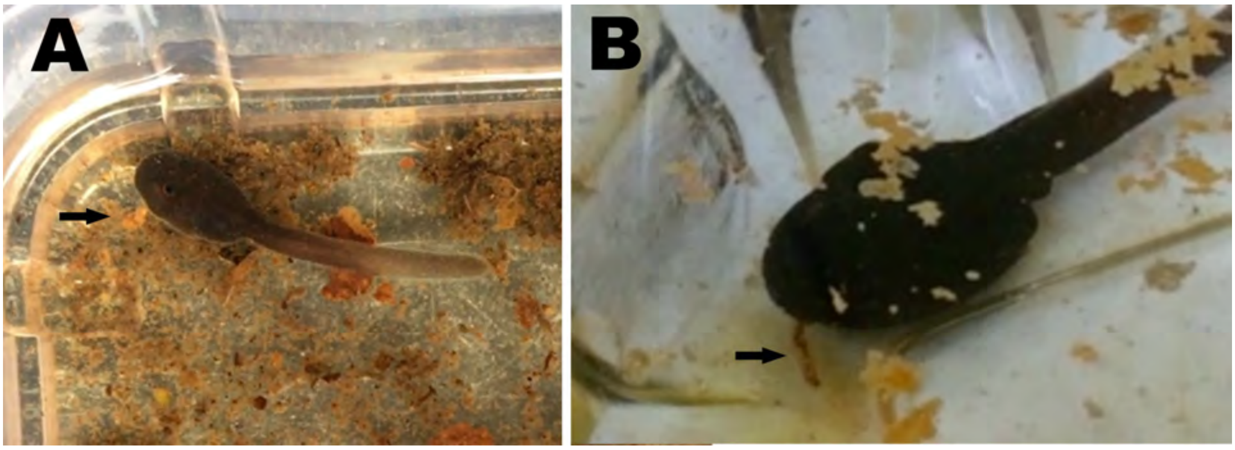

Figure 35. Images of the tadpoles of *Adelphobates galactonotus* (A) and *Dendrobates auratus* (B) preying on mosquito larvae in captivity. Arrows show mosquito larvae. Images by Taran Grant (A) and Madian Pamela (B).

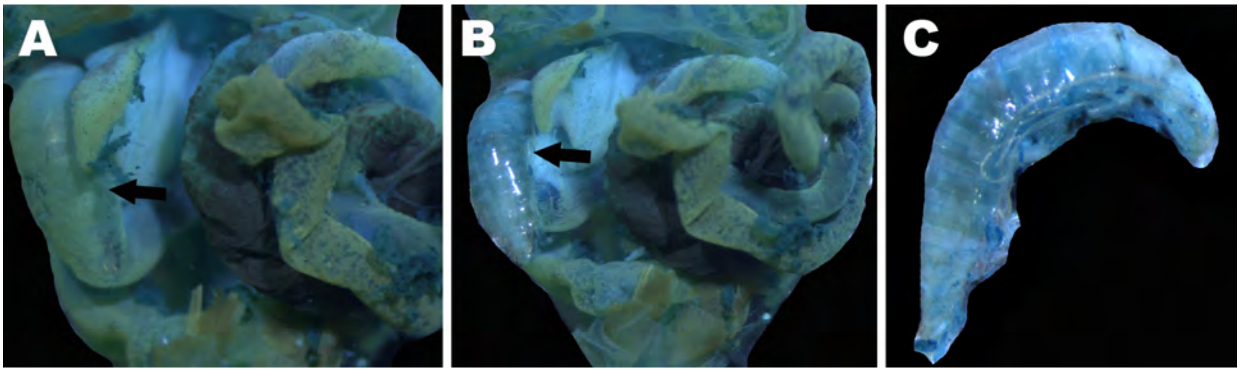

Figure 36. Digestive tract of tadpoles of *Minyobates steyermarki* showing a large insect larva found intact.

Predaceous larvae of dendrobatoids present a reduction in the papillae of the buccopharyngeal cavity: prepocket papillae are absent (character 372.0.), lateral ridge and infralabial papillae are not branched (character 339.0; character 358.0). Given that these tadpoles ingest large particles, such loss or reduction of features in the buccopharyngeal cavity can be explained by their feeding habits. The feeding habits of these tadpoles can also explain the absence of secretory ridges (character 380.0), which would be responsible for the production of the mucous that aids in the transportation of small particles obtained during filtering (Kenny 1969a,b). Wassersug and Rosenberg (1979) state that the absence of secretory ridges in carnivores larvae would not be unexpected, a hypothesis supported by my results.

Instead of filtering feeding larvae, predaceous tadpoles ingest larger food particles and generate large suction power into their mouths. Ruibal and Thomas (1989) reported that *Lepidobatrachus laevis* lacks keratinized jaw sheaths and relies solely on suction potency to capture their prey. According to Satel and Wassersug (1981), tadpoles of that species may present up to 4 times the buccal cavity size of “regular” tadpoles. Predaceous dendrobatoids also may swallow preys as a whole. Satel and Wassersug (1981) demonstrated that macrophagous (which includes predaceous) tadpoles have small values of IH/OH, which is directly proportional to the size of the orbitohyoideus. The orbitohyoideus in predaceous dendrobatoids is large, well-developed, originating at processus muscularis quadrati, but also extending into the processus antorbitalis and orbital cartilage (character 439.1) and inserting ventrolateral ceratohyal (character 435.1); this muscle is massive, expands laterally beyond the borders of the processus muscularis quadrati (character 440.1) and overlaps the interhyoideus at its insertions (character 442.1). This massive orbitohyoideus generates a great suction power.

The posterior region of the guts is greatly enlarged (character 392.2) and often pigmented (character 393.1) in predaceous tadpoles of dendrobatoids. In some anuran larvae, the foregut—also known as manicoto—is enlarged, forming a "larval stomach" (Noble 1929; Haas et al. 2014) that in some species—as *Lepidobatrachus*—in fact has enzymatic activity (Bloom et al. 2013; see also comments on character 391), responsible for chemical digestion; the terminal portion of the gut is responsible for absorption. Cross section analysis that reveled several folds, villi, and microvilli (Fig. 37). I hypothesize that the enlargement of the ileum observed in predaceous poison frogs is a specialization for absorbing the nutrients of large prays of slow digestion. The final portion of the ileum is close to the rectum and represents the final area in which absorption is possible prior to defecation.

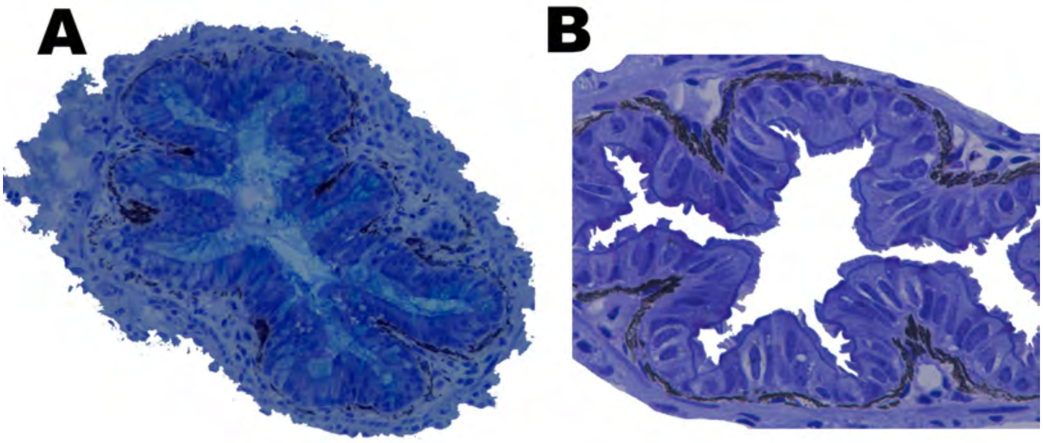

Figure 37. Cross section of the terminal portion of the ileum showing the presence of folds, villi (A) and microvilli (B), suggesting absorption function.

The combination of characters present in some dendrobatoids tadpoles, including Dendrobatini, *Anomaloglossus* and *Hyloxalus*, can be explained as specializations for the predaceous lifestyle. The combination of massive jaw sheaths and powerful suction ability allows these tadpoles to explore a wide range of preys, including small organisms that are swallowed entirely and large insect larvae or other tadpoles that need to be bitten. Given their ecological importance and phylogenetic distribution, it is arguable that these characters may have played a key role in evolution and diversification of phytotelm dwellers.

What do Phyllobate*s really eat?*

In the previous section, I demonstrated that tadpoles of *Phyllobates* do not share several characters with the phytotelm-specialized tadpoles of Dendrobatini. Here, I provide further comments on the possible feeding habits of the larvae of this genus.

Although access to the real diet of a tadpole is very difficult (Altig et al. 2007), on the basis of larval characters distribution I hypothesize that tadpoles of *Phyllobates* are not specialized for the predaceous lifestyle and are more likely to be filterers. Most character-states previously discussed are absent in *Phyllobates* larvae. These larvae may ingest some insect larvae or even other tadpoes, but not as their primary food resource. Mónica Goméz-Diaz (pers.comm.) often found several tadpoles of *Phyllobates terribilis* at different development stages co-existing in palm leaves, without demonstrating any aggressive behavior towards other tadpoles. There is no reference to cannibalism or predation among *Phyllobates*, as far as I know. Moreover, Donnelly et al. (1991) raised tadpoles of *Phyllobates lugubris* until metamorphosis with a diet based on algae. All this suggests that *Phyllobates* larvae may not require as much animal protein as Dendrobatini tadpoles do, and these needs are reflected in larval morphology.

Cannibalism and aggregation in Dendrobates larvae

Dendrobates tadpoles are often found in aggregations: Silverstone (1975) found 25 tadpoles of *Dendrobates tinctorius* in a rusty oil drum in an anthropomorphically changed environment. Eaton (1941) reported one to ten tadpoles of *Dendrobates auratus* on tree holes, and they were often of different developmental stages; see also Dunn (1941), who reported six tadpoles of *Dendrobates auratus* in the same water body. John. D. Lynch (pers. comm.) said that he collected several *Dendrobates truncatus* tadpoles of different developmental stages in the same tree hole.

At a first glance, these aggregations seem odd, especially given the several reports of cannibalism in this genus (e.g., Summers and McKeon 2004; Gray et al. 2009; Rojas 2014), but it may present some evolutionary advantage for these frogs. For example, some species of *Ranitomeya* increase the developmental rate of a tadpole by depositing eggs or newly-hatched younger tadpoles as an additional food resource during the dry season (Poelman and Dicke 2007; Shulte and Lotters 2013). It has been demonstrated that, in some cases, cannibalism increases larval development beyond simple predation; Nagai et al. (1971), for instance, reported a better efficiency in amino acid conversion in tadpoles of *Bufo japonicus* that preyed and fed on their conspecific, and Crump (1990) found that tadpoles of *Isthmohyla pseudopoma* became larger when fed on conspecific over heterospecific tadpoles.

The significance of these aggregations within *Dendrobates* are still open for investigation. Maybe the deposition of more than one tadpole in the same pool increases the chances of some of them reaching adult life. Another possibility is that, in the aforementioned cases, there were few available phytotelm tanks, and parents used the same plants for their offspring. Futher captivity and field studies may shed some light on these questions.

The evolution of oophagy

If predation on insect larvae and other tadpoles evolved as a mechanism of nutrition compensation in the sterile phytotelm environment, some species adopted a different strategy—the deposition of a trophic egg for larval consumption. Within dendrobatoids, oophagy evolved independently in several lineages. Tadpoles of *Oophaga* are obligatory oophagous and other phytotelm dwellers, as *Anomaloglossus beebei* (Bourne et al. 2001) and several *Ranitomeya* (Brown et al. 2011), are facultative oophagous.

Trophic eggs, also known as nurse eggs, are non-developing eggs or egg-like elements produced for offspring nutrition; this peculiar trait evolved in different animal groups, such as insects, polychaetes, spiders, fishes, salamanders, and frogs (Perry 2006). It noteworthy that trophic eggs do not necessarily need to be externalized and may be consumed intrauterine. Some authors (e.g., Jungfer and Wyegoldt 1999) argue that fertilized eggs could also be considered trophic eggs, contrasting with the general consensus that feeding on fertilized eggs would constitute cannibalism.

The deposition of trophic eggs evolved independently in several anuran families. Mandatory oophagy have been reported in *Oophaga* (Brust 2003), *Osteopilus brunneus* (Lannoo et al., 1987), *Osteocephalus oophagous* (Jungfer and Weygoldt 1999), *Leptodactylus fallax* (Gibson and Buley, 2004) and *Kurixalus eiffingeri* (Kam et al., 1996), for example. Egg consumption, however, has been reported in many other frogs, as *Mantella laevigata* (Heying, 2001), *Hoplophryne rogersi* (Noble 1929), *Trachycephalus resinifictrix* (Schiesari et al. 2003), *Anotheca spinosa* (Jungfer 1996), *Nasutixalus jerdonii* (Biju et al. 2016), *Aparasphenodon* *arapapa* (Lantyer-Silva et al. 2014), *Phyllodytes gyrinaetes* (Candioti et al. 2017a), *Rhacophorous vampyrus* (Rowley et al. 2012; Vasilieva et al. 2013), among others. I will argue below that both aforementioned strategies have different impacts on larval morphology of poison frogs, and that tadpoles of *Oophaga* present unique character-states not observed in facultative oophagous within Dendrobatoidea.

In *Oophaga* larvae, the oral disc is reduced, lacks emargination (character 175.0) and most labial ridges; their teeth, by consequence, are also absent (characters 198.0, 200.0, and 201.0). The only ridges present were A-1 and P-1, in which each tooth is very reduced (character 305.0) and almost occluded by the surrounding tissue. The jaw sheaths, on the other hand, are massive (character 221.1) and fully keratinized (characters 214.3 and 219.3). Those character-states are in accordance with the specialized diet of these larvae; trophic eggs are a very delicate, soft alimentary item and easy to ingest. The strong jaw sheaths are necessary to bite the eggs, but the labial teeth play no role in the feeding habits. In many cases, the eggs are swallowed entirely; this led Jungfer and Weygoldt (1999) to suggest that small sized eggs would be an adaptation in oophagous species.

The eggs entering the buccopharyx face little or no resistance, given the absence of the first (character 350.0) and third (character 352.0) pairs of infralabial papillae and all pairs of lingual papillae (characters. 365.0 and 366.0). Both buccal roof and floor papillae are absent or reduced; for instance, the bifid papilla adjacent to buccal pocket is present as a simple (character 374.1) and reduced element. All the glandular tissues are lacking (as in Dendrobatini), corroborating that these larvae are incapable of filter- feeding, or at least of feeding efficiently in this manner. In the prenarial arena, all *Oophaga* species present an elevation of tissue forming a pad (character 310.1). Richard Wassersug (pers.com) suggested that such pad may aid in holding the slippery eggs. The eggs pass directly through the buccopharynx to the esophagus, and then to the larval "stomach", due to potent suction generated by the well-developed orbitohyoideus that overlaps the interhyoideus in their origins (character 442.1).

I found that the foregut of *Oophaga* is greatly enlarged with muscular characteristics, forming a pouch (character 391.1). This poach is well-developed and occupies a large portion of the abdominal cavity. In *Oophaga arborea* tadpoles, the stomach was not filled with eggs[*], even though it was significantly larger than other digestive portions. Noble (1929) was the first to describe similar condition in tadpoles of *Osteopilus brunneus* and *Hophlophryne regersi*, two

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[*] The tadpoles of *Oophaga arborea* examined by me were those described by Myers et al. (1984), AMNH 117643, and the only *Oophaga* larvae I saw with empty intestines. These larvae were obtained from an egg clutch and raised in the lab. According to Myers et al. (1984: 9) these "larvae were never seen to feed ...; growth apparently was due entirely or mainly to their own yolk reserves..".

species known by their oophagic habits. Gross dissection of this structure in *Oophaga* larvae revealed a large amount of eggs, some of which were intact, while others were partially destroyed.

A cross section of the stomach (Fig. 38) evidenced that it is coated internally by a cylindrical, stratified epithelium and is covered externally by a thin, transversal muscle layer. Between these two layers it is possible to recognize some large, rounded cells with a central nucleolus. These are the characteristics of the oxyntic cells, responsible for secreting hydrochloric acid. The number of these cells were reduced, which suggests low production of the acid. Haas et al. (2014) suggested that a true stomach would have the ability of decreasing pH and presenting enzymatic activity of pepsin. The "stomach" of *Oophaga* larvae surely can decrease the pH, but further studies are pending to test the enzymatic activity. Posteriorly to the stomach, there is a small portion of intestines before another chamber is formed. This second diverticule is the terminal portion of the ilium, which is expanded in all Dendrobatini larvae (character. 392.2).

As in other phytotelmata dwelling Dendrobatini, the gas exchange in *Oophaga* is not performed by branchial filaments; the branchial basket is reduced, lacking filter plates and rows, the constrictor branchialis are nonfunctional (when detected), and other auxiliary muscles as the interhyoideus posterior (character 407.0) and diaphragmatopraecordialis (character 410.0) are absent. The ceratobranchials of *Oophaga* are reduced, fused to the hypobranchial plate (characters 533.1 to 535.1), and lack spicules (characters 536.0 to 539.0). Instead of branchial respiration, the small lungs (character 395.0) are always inflated (character 396.1), and I observed tadpoles of *Oophaga pumilio* engulfing atmospheric air several times.

Additionally to lung usage, I hypothesize that the skin is responsible for a significant portion of the gas exchange in *Oophaga* tadpoles; in these tadpoles, the larval skin is highly vascularized, with several vessels observed in gross dissection (character 397.1). A possible explanation for the increment of skin respiration can be found in the developmental sites used by oophagous species. *Oophaga* parents tend to seek for small sized phytotelmata for tadpole deposition, as *Dieffenbachia* and *Heliconia* axils (Fig. 39) and spaces between banana leaves (e.g., Van Wijingaarden and Bolaños 1992). Brown et al. (2008b,c) hypothesized that there is an inverted relationship between the amount of parental care and phytotelmata size. Small size phytotelmata surely will have less alimentary resources but, given that the parents provide trophic eggs for tadpole nutrition, such small pools are more attractive because of the reduced risk of predation and/or competition. Nevertheless, in these small pools, tadpole movements are restricted (pers.obser.) and swimming across reduced spaces to engulf atmospheric air possibly demands too much energy, so skin exchange becomes a more affordable mechanism for respiration.

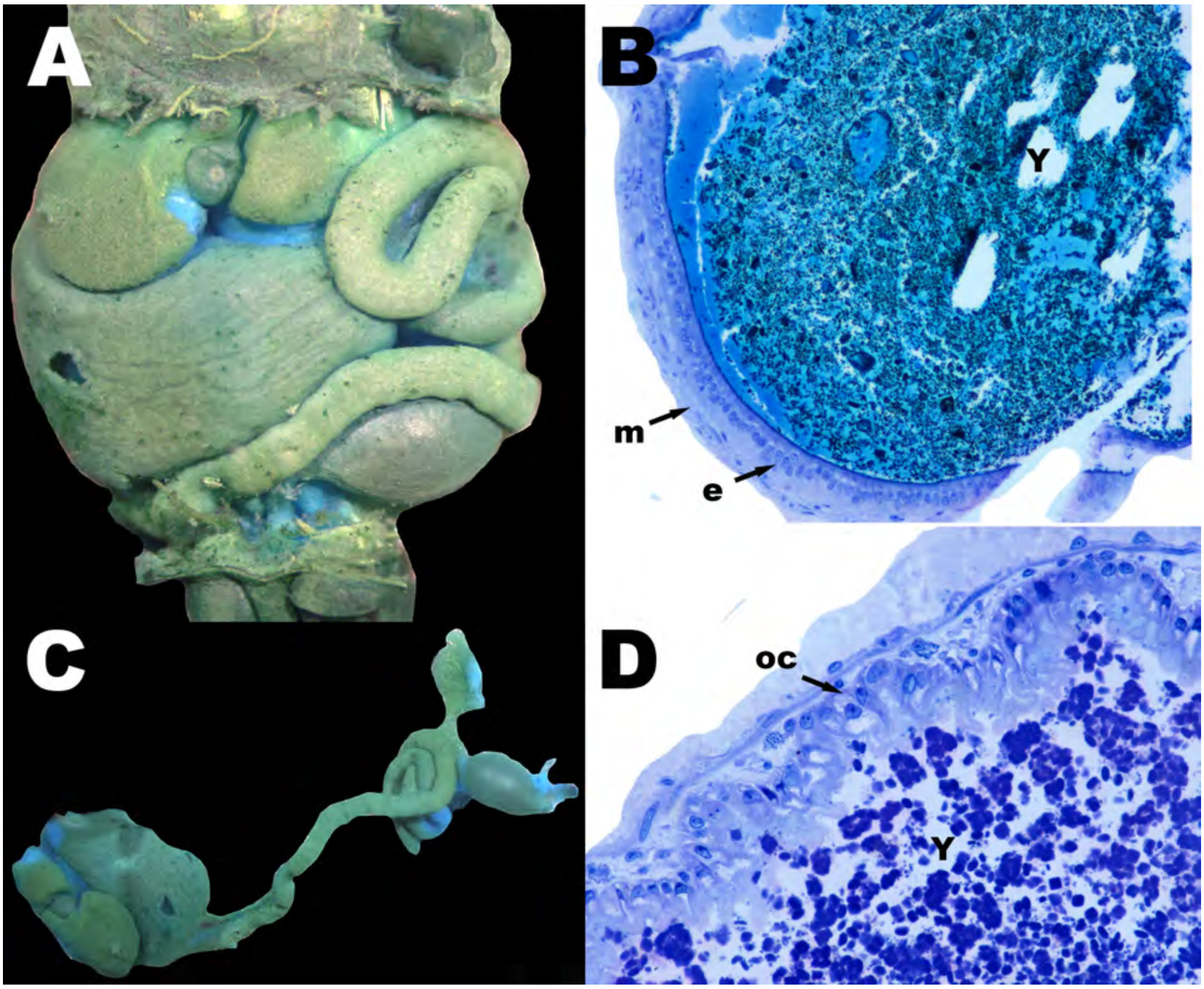

Figure 38. Images of the larval stomach of *Oophaga pumilio* (A and B). Cross section images of the stomach, in general view, showing the epithelial cells and the coat of muscles around it (B). Detail of the cross section showing the oxcyntic cells, responsible for hydrochloric acid (D). E, epithelial cells; M, muscle fibers; OC, oxcyntic cell; Y, yolk.

Several species of *Ranitomeya* (e.g., *amazonica*, *variabilis*, *vanzolinii*, *ventrimaculata*) and *Anomaloglossus beebei* are facultative oophagous. These larvae present a macrophagous diet and can pray on invertebrate larvae (see discussion of the evolution of predaceous larvae) but have trophic eggs as a complementary nutritional source (Caldwell 197; Bourne et al. 2001; Lehtinen et al. 2004; Brown et al. 2011). It is likely that facultative oophagy also occurs in other dendrobatini; for example, Schulte (1990) speculated that *Excidobates mysteriosus* would also be fed with trophic eggs.

Interestingly, these facultative species do not present the same character-states as the obligatory oophagous *Oophaga*. Their mouthparts are always present and, besides some reduction in number, the buccopharyngeal papillae are present. There are only two shared characteristics between these larvae: their poor ability of filtering (secretory ridges and pits are absent) and the enlargement of the posterior region of the ileum for nutrient absorption. This suggests that the complementary oophagy in *Ranitomeya* and *Anomaloglossus* is less or at most as important as the predaceous habits.

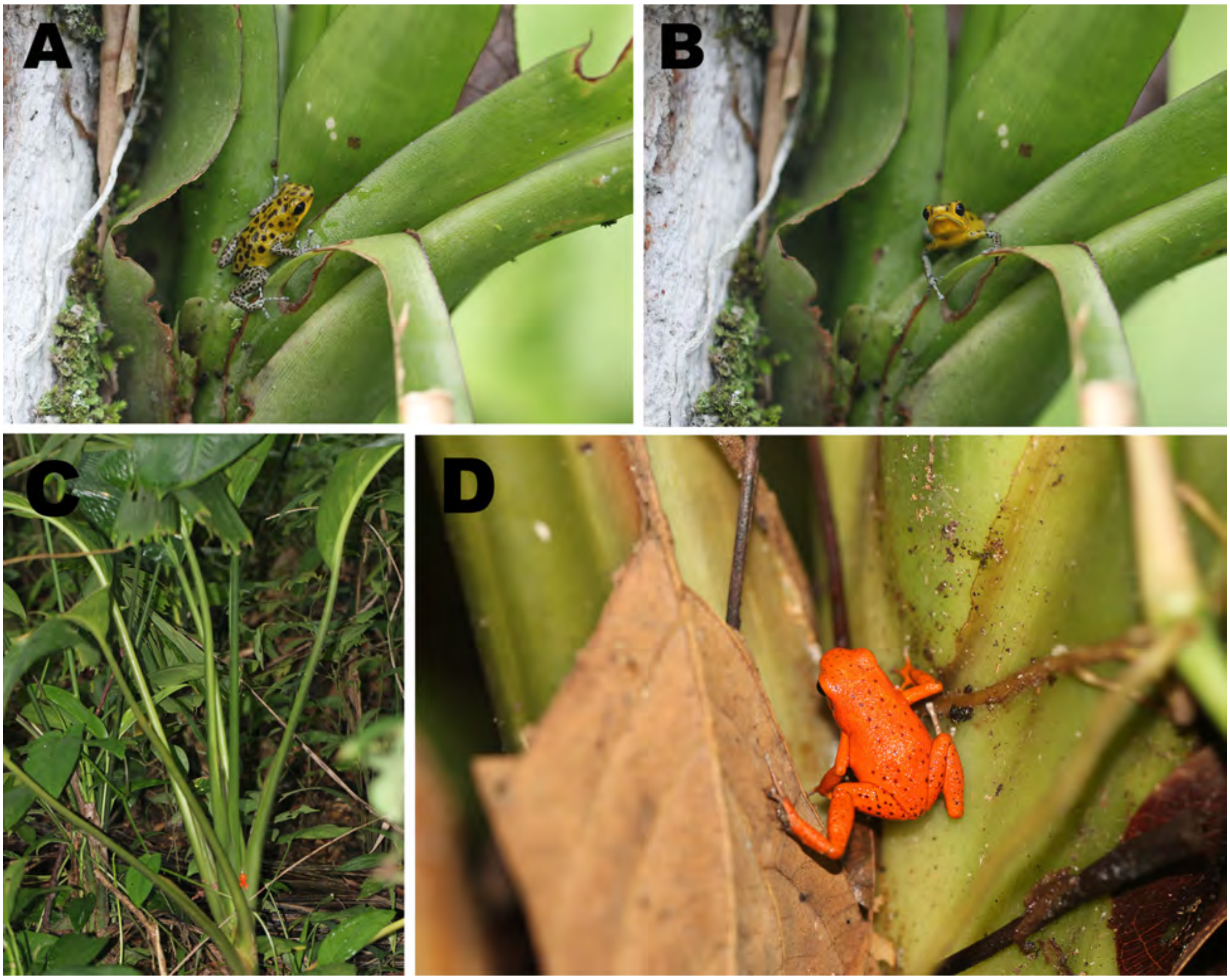

Figure 39. Individuals of *Oophaga pumilio* exploring two different phytotelmata, including a small bromeliad at El Crudo, Chiriqui Grande (A), and axils of *Dieffenbachia* leaves at Isla Solarte, Bocas del Troro (B), Panama. Note the polymorphism in color pattern.

As a comparison, I analyzed the obligatory oophagous larvae of the unrelated hylid *Osteocephalus oophagous* (Jungfer and Schiesari 1995); if deprived of trophic eggs laid by the female, tadpoles of this species would die in few days. Controversially, these tadpoles do not present similar changes in their character-states associated with phytotelm lifestyle and oophagous diet. The mouthparts were not reduced, buccopharyngeal elements were present, including secretory structures, and the cranial muscles and chondrocranium is very similar to other hylids. The lungs were reduced and shrunken, and the species present several gill filaments, suggesting branchial respiration. The only character present in *Osteocephalous oophagous* similar to *Oophaga* is the expansion of the foregut, forming a pouch, containing eggs.

As previously exposed, during their evolution, larvae of *Oophaga* experienced a great reduction in mouthparts, buccopharyngeal components, cranial muscles, and chondrocranium. Affected parts are mostly related to feeding, suggesting that oophagy demands few specialized characters. Oophaga larvae are different from all other dendrobatoids, and even other obligatory egg eaters as *Osteocephalus oophagous* do not present the same specialized character-states as *Oophaga*.

Larval behavior and future studies

Not only morphological characters are differentiated in oophagous larvae, but behaviors as well. *Oophaga* and *Ranitomeya* present particular behaviors to interact with their parents. Parental care and egg deposition behaviors are highly complex and may involve a single (Brust 1993) or both parents (Caldwell 1997) besides the participation of the tadpoles. Both *Oophaga* and *Ranitomeya* tadpoles signalize to their parents that they are hungry by vibrating their bodies and tails against the parents, a behavior known as begging that involves a complex combination of visual, tactile and chemical components (Stynoski and Noble 2012). A similar begging behavior has been reported in several oophagous species, as *Anotheca spinosa* (Jungfer 1996) and *Osteocephalus oophagous* (Jungfer and Weygoldt 1999).

Begging has been postulated as an honest signaling of the tadpole`s nutritional needs (Yoshika et al. 2016) and female are unlikely to feed non-begging tadpoles (Dugas et al. 2017). Begging has a high metabolic cost, and tadpoles experimentally induced to beg excessively presented lower growth rates then controled tadpoles (Stynoski et al. 2018).

Dugas et al. (2017) showed that tadpoles that were fed hours before their experiments begged less, suggesting that the tradeoff between displaying the costly behavior and receiving more food was play some part in the tadpole`s decision. Moreover, Stynoski and Noble (2012) demonstrated that tadpoles of *Oophaga pumilio* reduced the intensity of begging in the presence of predators. Those evidence suggest that begging is a far more complex behavior than perceived at first glance.

On the other hand, other empirical data challenge that view. More than once, I found several unfertilized eggs in the same pools as tadpoles of *Oophaga pumilio*, which, in turn, when studied, revealed to have several eggs in their stomachs, evidencing an abundance of food resources. The number of eggs/volume of eggs found in tadpoles was elevated, suggesting that these tadpoles had eaten a disproportional amount of food. It is possible that tadpoles in fact signalize for more food even when they are already satisfied. Parents take several days between visits to provide food— Brown et al. (2008) counted 7 to 10 days between visits of *Ranitomeya imitator*—and it is too risky for the tadpole to eat a low volume of eggs given that, if something happened to the parent frog in the interval between visits (e.g., predation, disease, etc.), the tadpole could starve to death. Nevertheless, the available evidences are not sufficient to test those conjectures and future studies are necessary.

The evolution of the funnel-mouth larvae

Silverstoneia is arguable the most astonishing genus among poison frogs regarding their tadpoles. The funnel-mouth larvae of *Silverstoneia* (Fig. 40) present several derived character-states not observed in any other lineages of dendrobatoids. In my optimal solution, *Silverstoneia* was recovered monophyletic and supported by 39 larval synapomorphies! Such impressive amount of character-states supporting the monophyly of this genus is due to its umbelliform oral disc and all changes associated with the neustonic lifestyle.

The umbelliform oral disc characterizes the neustonic ecomorphological guild of Altig and Johnston (1989). Such peculiar phenotype evolved independently in six frog lineages; besides *Silverstoneia*, umbelliform larvae are present in the megophryid *Megophrys* (Leong and Chou 1998; Grosjean 2003; Stuart et al. 2006; Li et al. 2001; Oberhummer et al. 2014), in the hylid *Phasmahyla* (Cruz 1982; Faivovich et al. 2005), in the microhylid *Microhyla* (Chou and Li 1997), in the manteillid *Mantidactylus* (Grosjean et al. 2011), and in the arthroleptid *Leptodactylodon* (Channing et al. 2012; Mapoyat et al. 2014). All these tadpoles share the reduction of the labial tooth rows and jaw sheaths, the presence of rounded or ridge-like submarginal papillae and the reduced or absent marginal papillae; however, detailed comparisons are scarce (Altig and McDiamird 1999), especially regarding internal morphology.

It was speculated that the funnel-mouth is a specialization for surface feeding, in which the tadpole would ingest small particles, such as pollen (Hora 1927; Smith 1926). If tadpoles of *Silverstoneia* present such feeding habit, then labial teeth would not be necessary, which is consistent with empirical observations: most *Silverstoneia* larvae completely lack labial teeth (characters 206.0 to 211.0), although the A-1 (character197.1) and P-1 (character 199.1) labial ridges are present in all examined species. Among other umbelliform larvae, labial teeth are present only in *Phasmahyla*, that may present LTRF from 0/1(1) to 1/2(1) (Cruz 1980, 1982; Cruz et al. 2008; Carvalho-e-Silva et al. 2009). *Leptodactylodon* (e.g., Mapouyat et al. 2014), *Mantidcatylus* (e.g., Grosjean et al. 2011), *Megophrys* (e.g., Leong and Chou 1985), and

Microhyla (e.g., Chou and Li 1997) completely lack labial teeth. When present, the labial teeth of *Silverstonia* are reduced and lack cups (character 306.0).

Figure 40. Tadpoles of *Silverstoneia flotator* (A), *Silverstoneia erasmios* (B), and *Silverstoneia nubicola* (C).

Silverstoneia are among the few dendrobatoids to present submarginal papillae, although they are very different in morphology and distribution when compared to those of other frogs (Fig. 41). The submarginal papillae of *Silverstoneia* are rounded and scattered on the central area of the oral disc (character 195.0 and 196.0). They possibly aid in directing particles to the mouth opening. All other umbelliform tadpoles present these submarginal papillae. Moreover, this character-state also evolved independently in some Central American hylids, such as *Duellmanohya* (Duellman 1970; pers.obs.).

The prenarial arena of *Silverstoneia* tadpoles is marked by the presence of a V-shaped crest (Fig.42). Wassersug (1980) was the first to describe this character in tadpoles of *Silverstoneia nubicola* and attested that this crest interlocks with the infralabial papillae, which would prevent large particles from entering the buccopharyx. This character-state evolved convergently in other funnel-mouth tadpoles (Fig. 43). Dias et al. (in press) reviewed the occurrence of this character in those larvae and found it present in all species for which buccopharyngeal descriptions are available, viz. *Microhyla heymonsi* (Chou and Lin 1997), *Megophrys* spp. (Wassersug 1980; Inger 1985; pers.obs.), *Mantidactylus* spp. (Grosjean et al. 2011). The buccopharyx of these larvae also present similar character-states, as the oblique postnarial papillae (character 327.1).

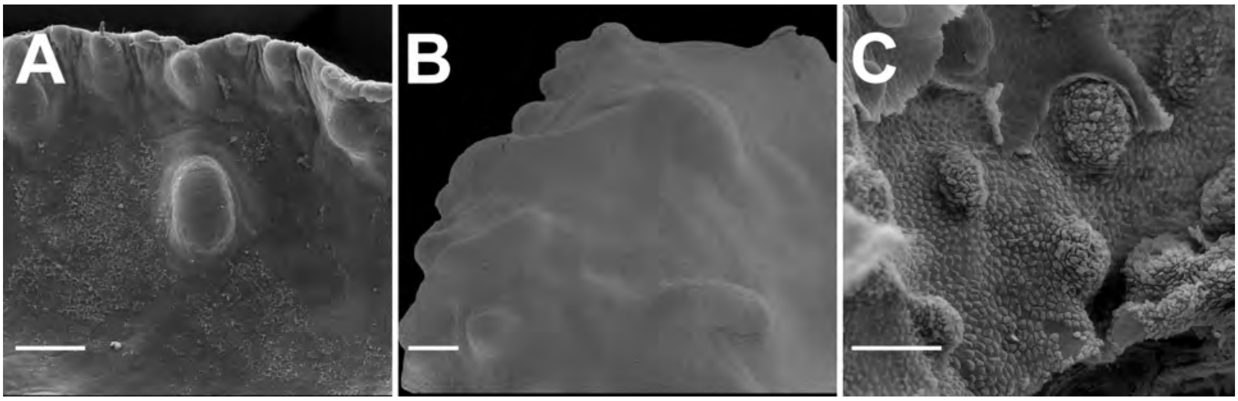

Figure 41. Submarginal papillae in tadpoles of *Silverstoneia erasmios* (A), *Silverstoneia flotator* (B), and *Silverstoneia nubicola* (C). Scale bar = 200 µm.

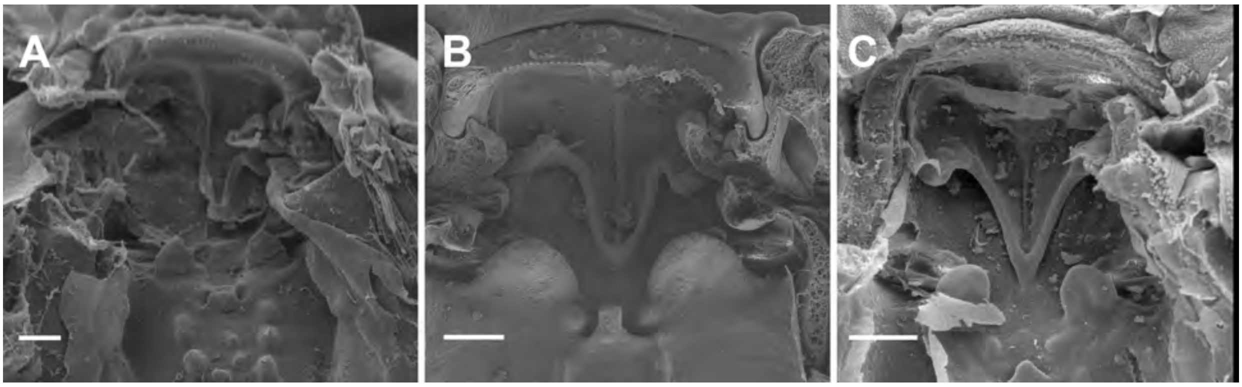

Figure 42. Detail of the prenarial arena of the tadpoles of *Silverstoneia erasmios*, *Silverstoneia flotator*, and *Silverstoneia nubicola* (C) showing the V-shaped crest. Scale bar = 100µm.

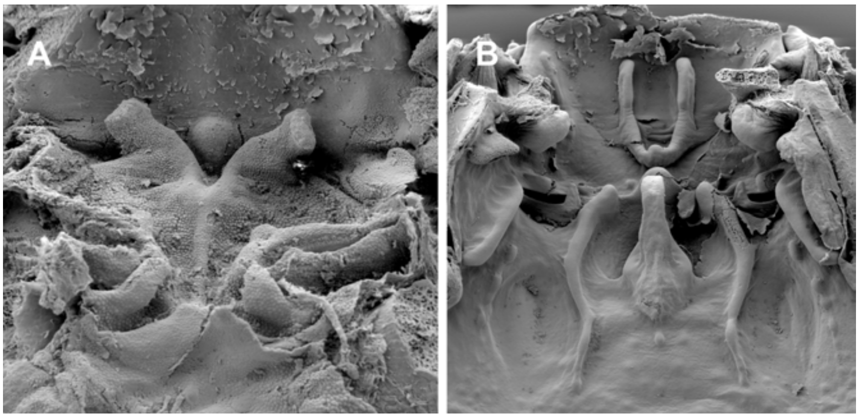

Figure 43. V-shaped crest on the prenarial arena of the umbelliform larvae of *Phasmahyla guttata* (A) and *Megophrys stejnegeri* (B).

Smith (1926) affirmed that tadpoles of *Megophrys* in captivity spend most of their time anchored to rocks, with their mouth unfolded in the surface, forming a parallel angle with the film of water. He also commented that in deeper waters in nature tadpoles are seldom observed in the surface, forming a 45° angle with the water film. The same position and behavior is exhibited by other umbelliform tadpoles, including *Silverstoneia* (Savage 1968), *Phasmahyla* (Costa and Carvalho-e-Silva 2008), and *Leptodactylodon* (Mapouyat et al. 2014). In all examined *Silverstoneia*, the lungs are always inflated (character. 396.1), which probably contributes for such buoyancy (Wassersug and Seibert 1975; Viertel and Richards 1999).

Savage (1968: 757) claimed that tadpoles of *Silverstoneia nubicola* in aquarium could rotate the oral disc to attach to rocks or other substrates, and that the tadpole could create a water flow with "slight movements of the edge of the oral disc". Such movements of the oral disc are made possible by the extensive, well-developed mandibulolabialis. In all *Silverstoneia* examined, the manibulolabialis can be observed spread amidst the lower lip. I predict that *Phasmahyla* tadpoles will present even greater capacity of movement in oral disc; hylids present the mandibulolabialis divided into two slips (Haas 2003), and in *Phasmahyla* both slips are present in most of the lower and upper lips.

Synergic contraction of some muscles may provide additional strength and amplify the resulting movement (Gradwell 1972). In *Silverstoneia* tadpoles I observed a case in which contraction of different muscles would necessarily interfere with the others. This is due to the presence of a medial aponeurosis shared by the subarcualis obliquus, subarcualis rectus I, and rectus cervicis (characters 419.1). The ventral fibers of those muscles are inserted directly into this aponeurosis in a way that contraction of any of these muscles will have an effect on the others. Functional implications of this character-state are not known. Given the feeding habits of these neustonic tadpoles, it is possible that it would contribute to the pumping mechanism. In the literature there are no reports of this condition, as far as I know. I observed a similar condition in tadpoles of *Phasmahyla cruzi* and *Phasmahyla guttata* (unpublished data). The presence of this condition in such unrelated taxa suggest that it may have some importance for neustonic tadpoles.

Development and evolution of the oral disc

Thibaudeau and Altig (1988) studied the ontogeny of the oral apparatus in some anuran larvae and demonstrated that the differentiation of some features follows a specific order. The oral disc develops from the oral pads, a slightly elevated tissue surrounding the mouth opening. By the end of differentiation of the oral disc, the labial teeth ridges start to develop. I hypothesize that the evolution of the umbelliform oral disc occurs due to developmental alterations on this transition. The period between the extension of the oral pad and the formation of the tooth ridges is possibly extended in *Silverstoneia* larvae, which would explain the very enlarged oral disc and the reduced number of ridges. Additional evidence for this hypothesis is the fact that *Silverstoneia* lack the marginal papillae that also develop after the differentiation of the oral pad.

I studied the oral disc of back-riding tadpoles of *Silverstoneia erasmios* with SEM preparation and the results are in accordance with that hypothesis. For most of their characters, back-riding tadpoles won`t usually be a semaphoront comparable with free-living tadpoles (see comments on semaphoronts definition in the "Materials and Methods" section), as characters haven`t yet gone through ontogenetic transformation. The oral disc in back-riders of *Silverstoneia erasmios* is already enlarged, but the labial ridges are not completely developed, labial teeth are not differentiated, and submarginal papillae are not formed. Free-living larvae of *Silverstoneia erasmios* present well-developed A-1 and P-1 ridges, with labial teeth in the former and several scattered submarginal papillae. If my hypothesis is correct, the oral pad differentiated early, possibly prior to hatching, but the labial teeth ridge and submarginal papillae didn`t, giving rise to the enlarged oral disc, with few labial ridges and teeth.

I also had the chance to examine back-riding tadpoles of *Silverstoneia dalyi* and *Silverstoneia nubicola* under stereoscopic microscope. I found exactly the same pattern—oral disc enlarged and labial ridges and submarginal papillae poorly developed. Observations were limited due to the small size of the samples.

Candioti et al. (2017b) studied the cement gland in Phyllomedusidae frogs. In their figure of a *Phasmahyla cochranae* embryo (5E and 5F; p.126), it is possible to see the well-developed buds of the oral disc, including their dorsal emargination, P-1 ridge poorly developed, and only few submarginal papillae buds.

The available empirical evidence provides support to my hypothesis. Nevertheless, it seems that this is a local event of heterochrony, given that other parts of the tadpole`s body were not affected. In other words, the oral disc presents positive allometric growth due to developmental truncation. It is possible that the same genes or genetic pathways were modified the same way in other umbelliform species. Data on development, including large series of embryos and molecular developmental data of other species are still necessary to properly test this hypothesis.

Comments on the evolution of fossorial larvae—the glass frogs tadpoles

Altig and Johnston (1989) proposed a ecomorphological guild for fossorial tadpoles and recognized two subcategories. In subcategory 1, they placed tadpoles that live on rocks of stream bottom, but more commonly buried in leaves; these tadpoles presented LTRF 2/3, reduced eyes and often, presented reddish ventral coloration due to a well-developed vascular system. In subcategory 2, they included tadpoles with reduced or absent labial teeth, and that were found among interstices of small stones. Many fossorial larvae can be found hiding below dead leaves and between/under rocks (e.g., Hirshchfeld et al. 2012), but many others have been found as deep as 40 cm deep in the sandy soil (Senevirathne et al. 2016).

Wassersug and Pyburn (1987) suggested a series of specializations of burrowing tadpoles, including dorsoventrally flattened and dorsolaterally expanded cranium, laterally expanded cornua, enlarged and inverted processus muscularis, ventral mouth, reduced fins, external nates unperforated, small eyes, thick skin, posterior expansion of ventral velum, enlarged jaw abductor, long spiracle tube. Many fossorial larvae present specializations for maneuvering in the interstitial space or between rocks and debris. For instance, Haas et al. (2006) described a specific kind of articulation between the chondrocranium and the vertebral column that would allow tadpoles of *Leptobrachella mjobergi* to move their bodies/heads more easily. Handrigan et al. (2007) reported the presence of supernumerary vertebra in the tail of several Megophryiidae tadpoles that would provide better anchorage of the caudal and axial musculature. Besides lacking some of these characters, the tadpoles of glass-frogs present several character-states that may be associated with their fossorial lifestyle.

Centrolenidae tadpoles (Fig. 44) have been reported as fossorial (e.g., Villa and Valerio 1982; Mijarres-Urrutia 1990; Rada et al., 2007; Terán-Valdez et al., 2009; Hoffmann 2010; Ospina-Sarria et al., 2011), although this condition has been poorly studied. Savage (2002) reported centrolenid tadpoles buried as deep as 20 cm in the debris. Besides centrolenids, this peculiar lifestyle evolved at least seven more times in anurans; fossorial tadpoles have been reported in the Arthroleptidae *Cardioglossa* (Blackburn 2008; Hirshchfeld et al. 2012), in the Microhylidae *Otophryne* (Pyburn 1980; Wassersug and Pyburn 1987; MacChuloch et al. 2008) and *Scaphiophryne* (Mercurio and Andreone 2006), in the Megophryidae *Leptobrachella* (Haas et al. 2006; Handrigan et al. 2007) and *Leptolalax* (Inger 1985; Handrigan et al. 2007), in the Micrixalidae *Micrixalus* (Senevirathne et al. 2016), and in the Ranidae *Staurois* (Inger and Wassersug 1990; Preininger et al. 2012).

The reduced nares of centrolenids (Fig. 44) are dorsally directed (character 250.0), rounded (character 252.1), bordered by a prominent (character 255.1) marginal rim. The combination of these characters may possibly help to prevent the entry of sand grains and other large particles from the substrate while tadpoles are buried. Reduced narial openings have been described in *Staourois* (Inger and Wassersug 1999) and in several *Cardioglossa* (Blackburn 2008; Hirshchfeld et al. 2012); Blackburn (2008: 618) states that it is probably unperforated, at least in tadpoles of *Cardioglossa monengouba*. Unperforated external nares were reported for *Otophryne* and *Scaphiophryne* tadpoles. Wassersug (1980) suggested that the unperforated internal nares could be a synapomorphy of Microhylidae, although Senevirathne et al. (2016) also reported unperforated nares in *Micrixalus*, suggesting that it may be a specialization of fossorial larvae. The internal nares of centrolenids were perforated, but how the small nares are related to the sensorial vacuities (character 321.1) present in all centrolenids is unknown (Fig. 45).

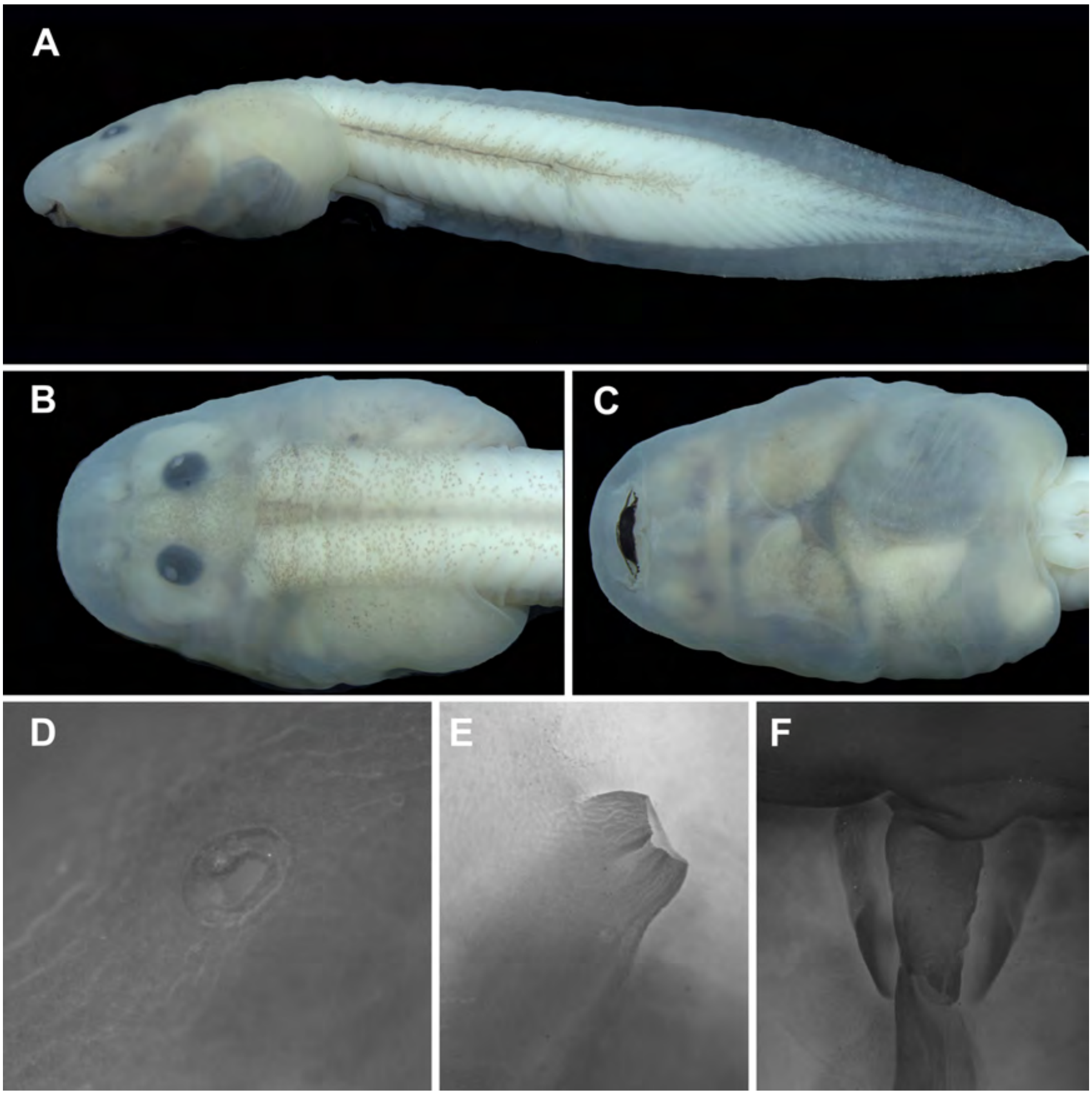

Figure 44. Tadpole of *Ikakogi tayrona* (MAR field series) in lateral (A), dorsal (B), and ventral (C) views. Details of the nostril (D), spiracle (E), and vent tube (F).

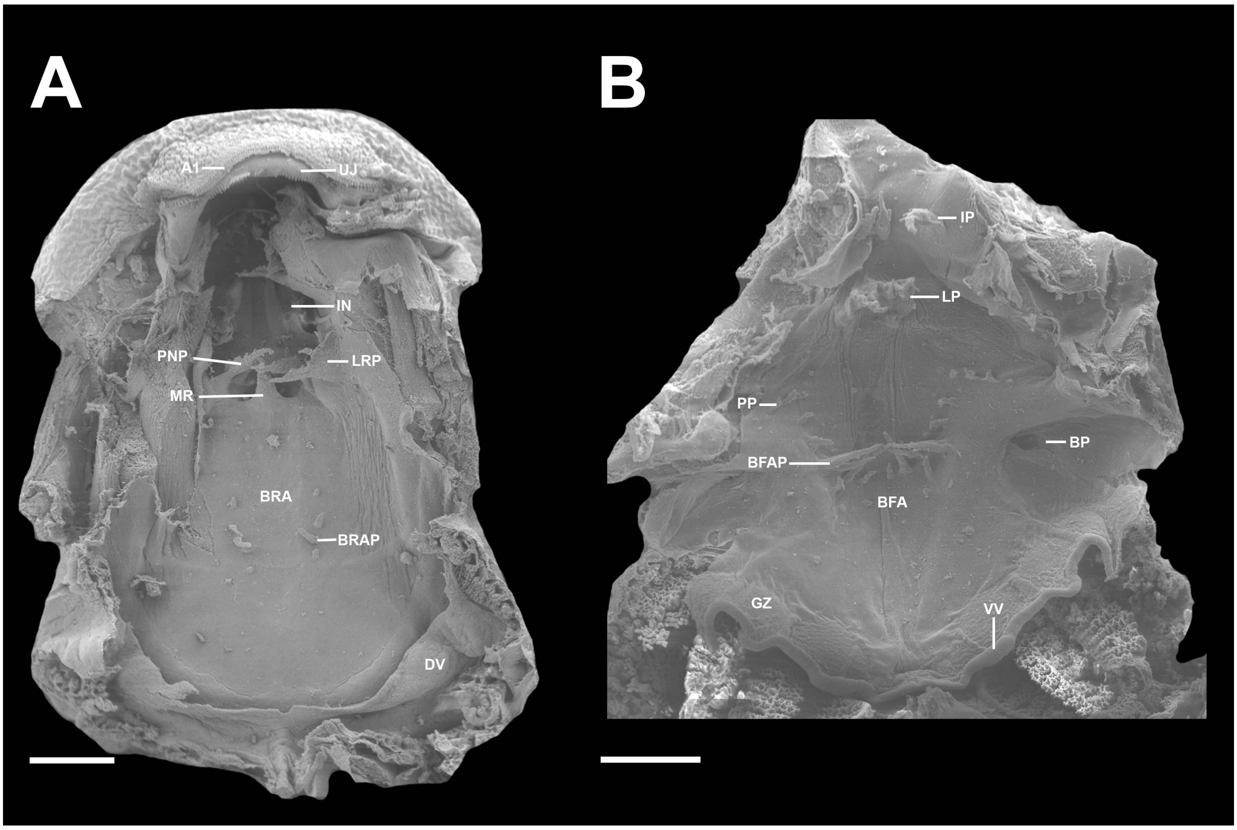

Figure 45. Buccal roof (A) and floor (B) of the tadpoles of *Ikakogi tayrona*. Scale bar = 500 µc. BFA, buccal floor arena; BFAP, buccal floor arena papillae; BP, buccal pocket; BRA, buccal roof arena; BRAP, buccal roof arena papillae; IN, internal nares; IP, infralabial papillae; LRP, lateral roof papillae; MR, median ridge; PNP, postnarial papilla; PP, prepocket papillae.

Centrolenid larvae eyes are reduced (character 248.1) and covered by a thick skin. Visual acuity is not a prerogative for living amidst detritus and sand. Eye reduction in these larva is analogous to the eye reduction and/or blindness in several cave-dwelling animals as the salamander *Proteus anguinus* (Kos et al. 2001). The same can be said on the pigmentation; all centrolenid lack pigmentation on their skins just as the leucistic *Proteus* (Lunghi et al. 2017) and other cave dwellers.

Lungs were absent in all examined tadpoles of centrolenid (character 394.0) and in all inspected developmental stages (up to Gosner 37). Lungs have been pointed as important features for larval buoyancy (e.g., Wassersug and Feder 1983; Wassersug and Murphy 1987; Pronych and Wassersug 1994). Wassersug and Pyburn (1987) reported the lungs to be absent in *Otophryne robusta*, even in late developmental stages (Gosner 33+). Haas (2003) suggested that reduced, non-functioning lungs was a synapomorphy for Bufonidae; it is noteworthy that most bufonids are benthic dwellers (Altig and McDiarmid 1999b). Functional inflated lungs may provoke a buoyancy which would have an effect of dragging tadpoles upward when they are trying to bury themselves into the substrate; several fossorial tadpoles bury themselves in substrate as a quick escaping mechanism (e.g., Senevirathne et al., 2016: 6). The reduction and even the absence of lungs may represent an advantage for fossorial larvae.

The presence of the sinus hyobranchialis (character 398.1) may serve as a compensation in gas exchange due to the absence of lungs (Fig. 46). Hoffman reviewed the morphology and taxonomic distribution of the sinus branchialis in Costa Rican centrolenids (see also Hoffmann 2004). The circulatory system of centrolenids is well-developed—the sinus hyobranchialis are a paired feature that collects and stores blood from peripheral system. A possible function for the sinus hyobranchialis is to help absorption and distribution of the oxygen removed from the highly oxygenated, fast flowing, surrounding water (most centrolenid larvae are lotic dwellers; e.g., Ospina-Sarria et al. 2011). The extensive interhyoideus posterior (character 409.2), the peculiar levator arcuum branchialium III that inserts on the dorsal otic capsule (character 431.1), and the subquadrate muscle (character 412.1) possibly aid in maintaining blood circulation in the sinus hyobranchialis, given that the contraction of all of them acts upon the brachial basket and peribranchial tissues.

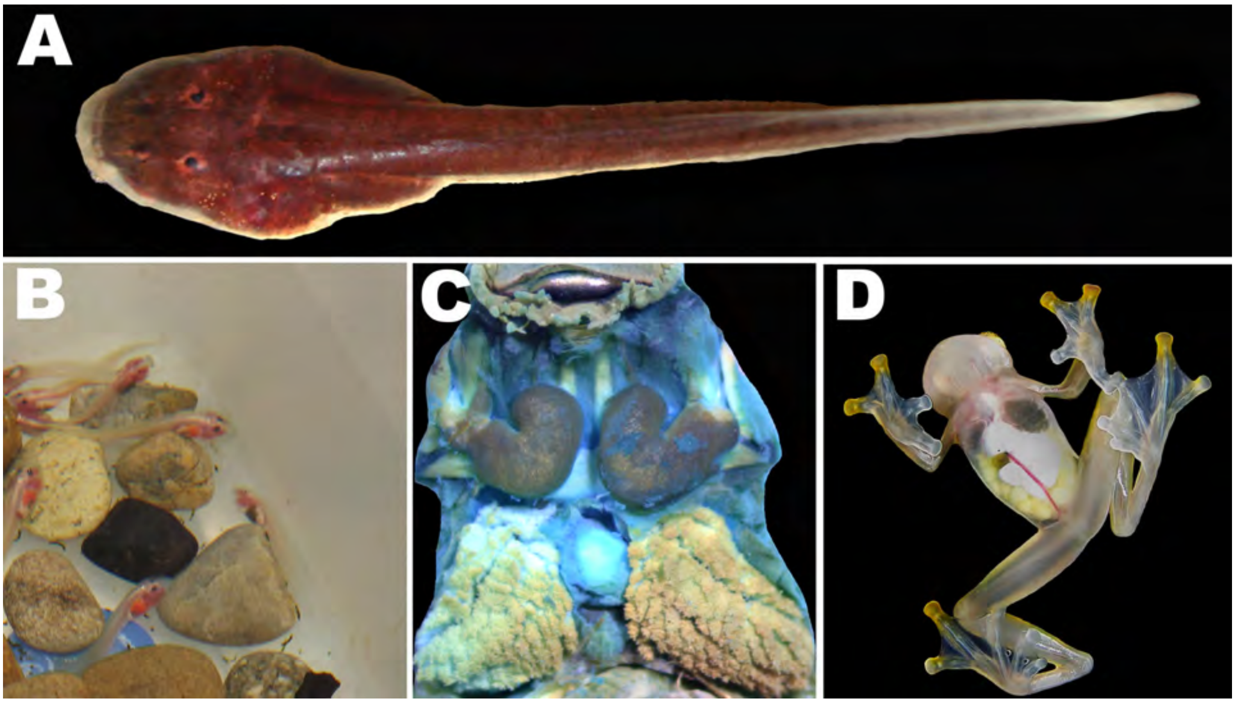

Figure 46. Red coloration in living specimens of *Centrolene venezuelensis* (A) and *Espadrana prosoblepon*. Detail of the sinus hyobranchialis in tadpoles of *Centrolene venezuelensis* (C); ventral view of adult glass frog of *Espadarana andina*; note the translucent skin and the absence of reddish coloration. Photos A and D by Marco A. Rada.

The presence of the sinus hyobranchialis confers a reddish coloration to the tadpole, especially in the branchial area, and—despite never having been formally described for taxa other than Centrolenidae—it is likely to occur in other fossorial larvae; the intense red color in tadpoles of *Micrixalus herrei* (Senevirathne et al., 2016: fig.3: 8), *Staurois parvus* (Preininger et al. 2012: fig.5 and 7: 50–51), and *Staurois guttatus* (Preininger et al. 2012: fig.11: 53) suggest that the sinus hyobranchialis may have evolved in those lineages as well.

Several cranial muscle character-states are possibly related to the burrowing habits of these larvae. For example, the myosepta of centrolenids are closed (character 400.0) and the axial musculature expands towards the otic capsule (character 434.1), which provide the strength for digging deep and maneuvering in the tight spaces of soil.

Haas (2006) compared the chondrocranium of *Leptobrachella mjobergi* with that of *Otophryne robusta* in the search for shared characters, but he only found a few of them. However, the chondrocranium of *Leptobrachella mjobergi* is very similar to that of centrolenids (Fig. 47); they share a low and wide chondrocranium, with a thin palatoquadrate (posteriorly) (character 522.0), with a posteriorly directed curvature (character 520.0) and expanded anteriorly (character 523.0). Although there are no mechanical studies on how that combination of characters would be related to burrowing habits, it is possible to suggest that the anteriorly robustness of the chondrocranium would be interesting to support the strength generated by tail and axial muscles to propel tadpole downwards during burrowing.

Several character-states can be associated to this particular lifestyle of centrolenids. Unfortunately, there are few studies on the ecology of these tadpoles, and my sample was very reduced compared to the true diversity of the group—currently the family comprises 155 species distributed in 11 genera (Frost 2018). In future researches, the analysis of more taxa will greatly contribute to a broader view of the evolution of burrowing in glass frogs.

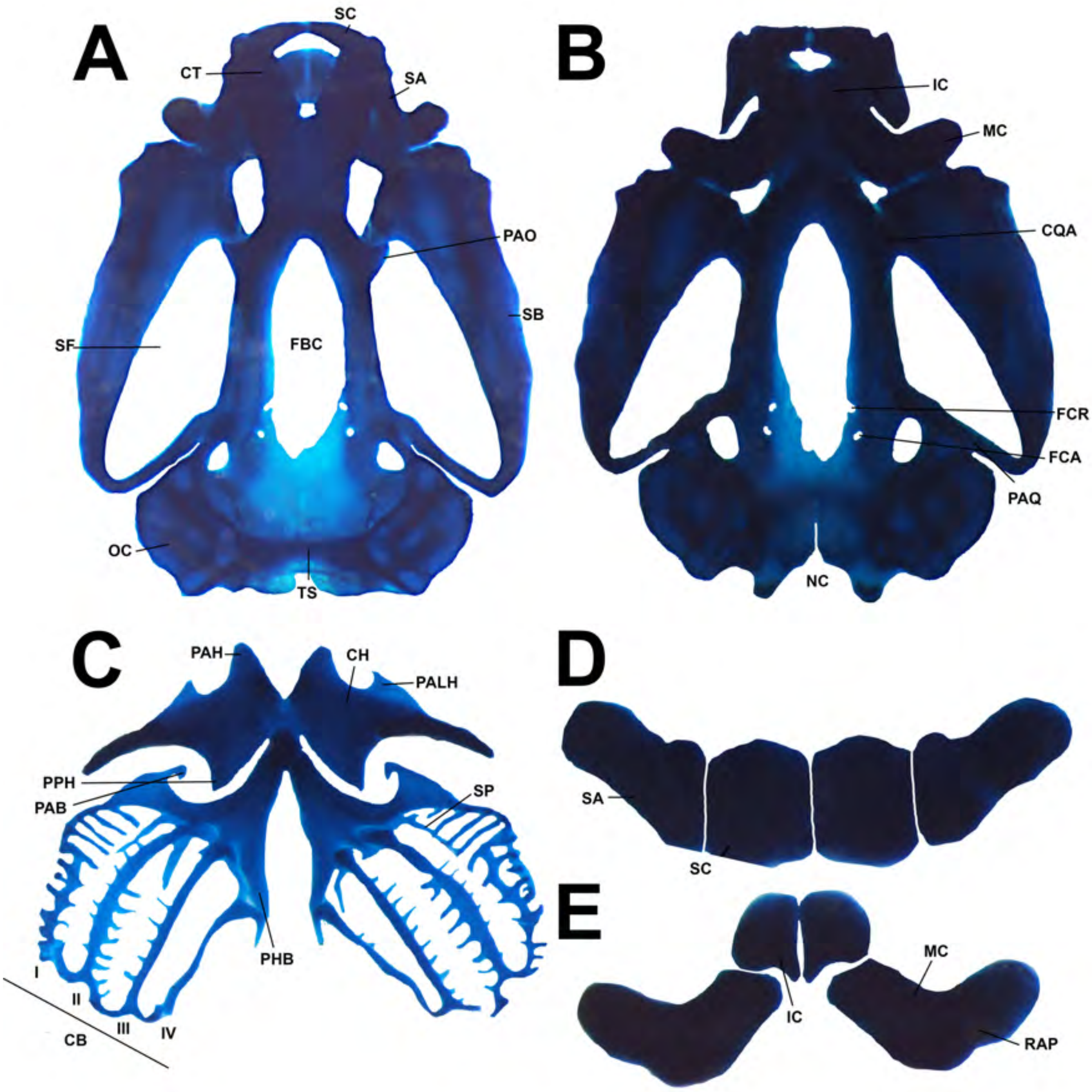

Figure 47. Chondrocranium of *Ikakogi tayrona* tadpoles in dorsal (A), and ventral view (B); hyobranchial apparatus (C), suprarostral cartilage (D), and lower jaw (E). CB, ceratobranchial; CH, ceratohyal; CQA, commissura quadratocranialis anterior; CT, cornua trabeculae; FCA, foramen caroticum primarium; FBC, fenestra basicranialis; FCR, foramen craniopalatinum; IC, infrarostral cartilage; MC, Meckel`s cartilage; OC, otic capsule; PAH, processus anterior hyalis; PALH, processus anterolateralis hyalis; PAO, processus antorbitalis; PAQ, processus articularis quadrati; PHB, processus hypobranchialis; PPH, processus posterior hyalis; SA, suprarostral alae; SB, subocular bar; SC, suprarostral corpora.

Living out of water: the evolution of semi-terrestrial tadpoles in Cycloramphidae

Semi-terrestrial tadpoles are rare among anurans. Despite the fact some authors reported that some suctorial tadpoles—as *Ascaphus* (Noble 1927), *Nasikabatrachus* (Zachariah et al. 2012), or *Meristogenys* (Gan et al. 2015)—could be found outside of water for some periods, few are the species that adopted this uncommon lifestyle along their entire development. This condition evolved at least five times in anurans; semi-terrestrial tadpoles have been reported in the South American Cycloramphidae tadpoles of *Thoropa* and *Cycloramphus* (Bokermann 1965; Heyer and Crombie 1979; Heyer 1983a,b; Caramaschi and Sazima 1984; Cocroft and Heyer 1988; Lima *et al*. 2010; Silva and Overnay 2012), in the African *Arthroleptides* (Drewes *et al.* 1999) and *Petropedetes* (Lawson 1993; Channing et al. 2012), and in the Asian *Nannophrys ceylonensis* (Kirstinghe 1958) and *Indirana beddomei* (Annandale 1918). These tadpoles share a set of phenotypic characters (Fig. 48), such as a flattened body, ventral mouth, massive, well-keratinized and laterally compressed jaw sheaths, low fins, usually restricted to the tail, and hind limbs with often early development (Altig and Johnston 1989).

Besides having those characters, the tadpoles of *Thoropa* and *Cycloramphus* herein examined presented some interesting apomorphic character-states, possibly associated with the semi-terrestrial lifestyle. The expansion of the posterolateral surface of the body into flattened skin expansions (character 259.1) possibly plays an important role in body adhesion to the substrate and it is present in all *Cycloramphus* and most *Thoropa* species. Wassersug and Heyer (1983) suggested that superficial tension was a vital mechanism to keep these tadpoles adhered to the rock surface. Superficial tension increases with the augmentation of the area in contact with the rock surface, provided by the dermal expansion.

Besides the body`s dermal expansion, tadpoles of *Thoropa* present a further possible specialization to increase adhesion by superficial tension. In these larvae, the ventral tail fin is expanded and marked by the presence of a medial groove (character 281.1), which varies in its extension (Fig. 49). This groove increases significantly the contact surface of the tadpole with the substrate and was invariably present in *Thoropa* tadpoles. *Cycloramphus* tadpoles lack this tail grove, and Lutz (1929: 20) stated that these larvae adhere to vertical walls without using their tails, therefore it is used only for locomotion. As far as I know, this character has never been described for any other taxa before and it is a unique synapomorphy of *Thoropa* (Dias et al. in prep.).

Some authors (e.g., Barth 1956) have suggested that the well-developed jaw sheaths could perform some part in hooking the tadpole to the rock. Wassersug and Heyer (1983: 767) rejected this hypothesis, given that it would prevent air breathing, and they speculated that both *Cycloramphus* and *Thoropa* are obligate air breathers. I also found no evidence for mouth usage in the adhesion mechanism; however, I found lungs reduced (character 395.0) and shrunken (character 396.0) in *Thoropa megatympanum* and small and inflated (character 396.1) in *Thoropa miliaris*—it seems that lungs would not play an important role in gas exchange for either. On the other hand, I found branchial filaments present in the branchial baskets of cycloramphid tadpoles but with very reduced spiracle opening, and lacking an inner wall (character 236.0); this could suggest branchial gas exchange, but with low water flux in the branchial chamber. This hypothesis is compatible with the ecological data: cycloramphids live in saxaticulous environments with (sometimes very) restricted water flow. According to Noble (1929: 300), the long tail presented by *Cycloramphus* may perform some important part in respiration, which is consistent with the presence of poorly developed lungs in these tadpoles. Nevertheless, there are information that still need to be included in this hypothesis; Lutz (1929: 20) attested that tadpoles of *Cycloramphus* "cannot stay in the water unless they emerge at least with the anterior part of their body". Studies on the ecophysiology of these tadpoles are needed in order to test these hypotheses.

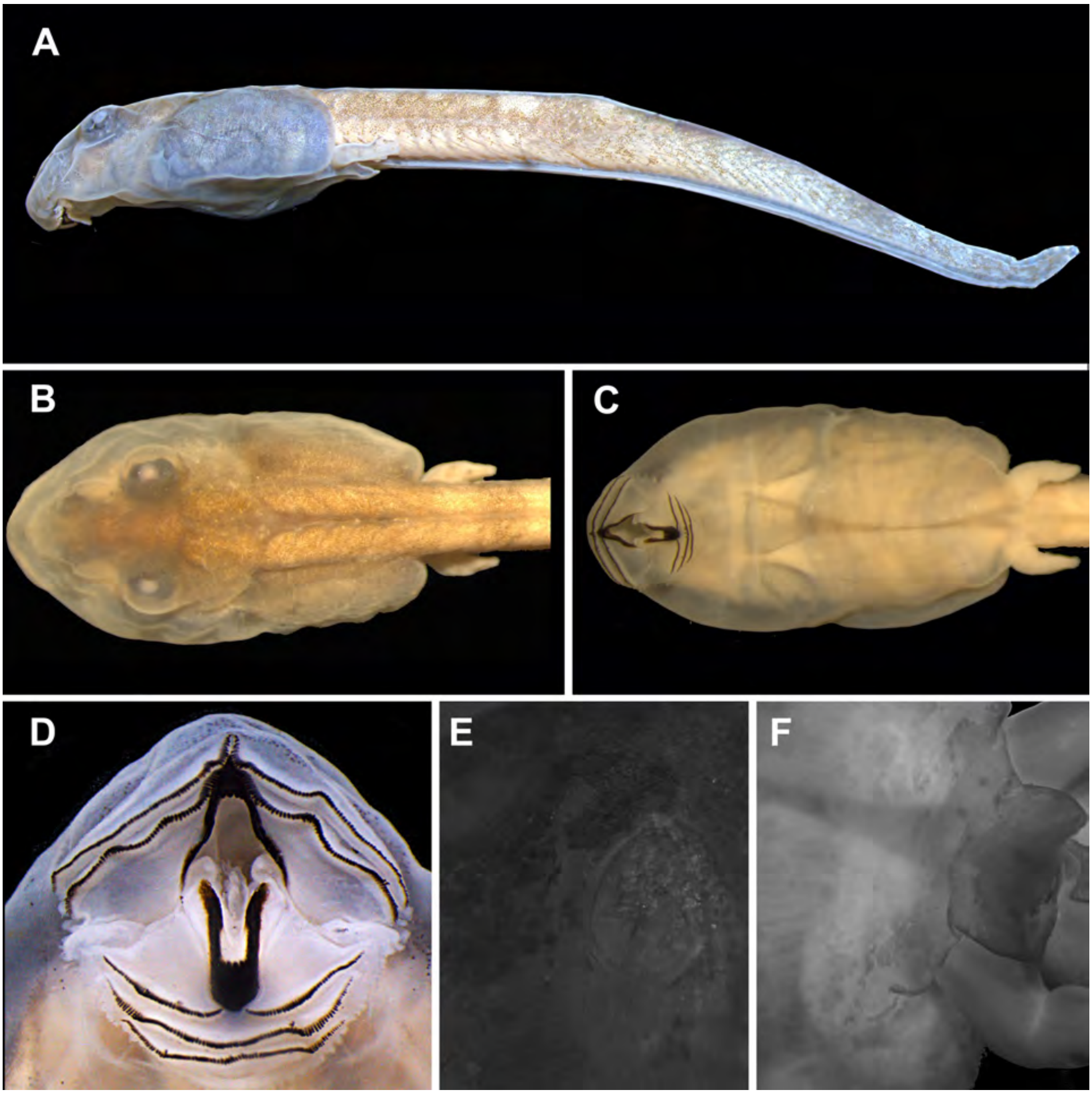

Figure 48. The tadpole of *Thoropa miliaris* in lateral (A), dorsal (B), and ventral (C) views. Detail of the oral dis (D), reduced spiracle, lacking inner wall (E), and vent tube (F).

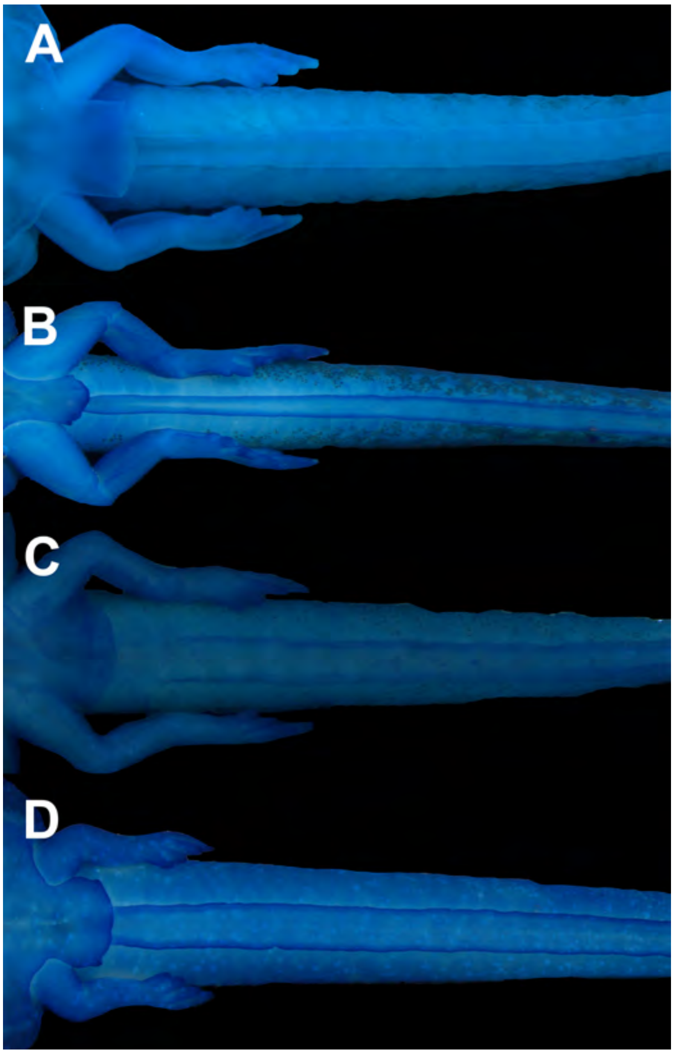

Figure 49. Medial groove formed in the ventral fin of *Thoropa miliaris* (A), *Thoropa megatympanum* (B), *Thoropa saxatilis* (C), and *Thoropa taophora* (D).

Most anurans present a well-marked lateral line system (Lannoo 1987, 1999; Schlosser 2002b) that permit the aquatic tadpoles to perceive mechanical movements in the surrounding water. The functioning of the lateral line is directly related to an aquatic environment. The loss or reduction of the stitches have been reported for some few taxa (e.g., *Osteopilus brunneus*; Lannoo et al. 1987), and Lannooo (1987: 121) suggested that these taxa would be less sensitive to minute water displacement. The semi-terrestrial tadpoles of Cycloramphidae present some contact with water fillets, but they never emerge on any liquid. I found stitches of the lateral line system to be absent in all examined cycloramphid tadpoles (characters 282.0 to 296.0). Given the complete out of water lifestyle of Cycloramphidae larvae, this was not a surprising condition. Further investigation at a more detailed level (SEM, histology) are still necessary in order to determine if the neuromasts are completely missing or just reduced in numbers and not forming stitches. It is worth to know that the absence of stitches was a constant condition in non-aquatic tadpoles herein examined, as in the nidiculous tadpoles of *Allobates* for instance.

Cycloramphid larvae present highly variable cranial muscles (Fig. 50). The most striking difference when compared to typical pond dwellers is the absence of the slips of ceratobranchial II and III of the m. subarcualis rectus I (character 428.0 and 429.0). Moreover, these larvae present a unique insertion for that muscle; in *Thoropa* and *Cycloramphus*, the m. subarcualis rectus I has a single slip that inserts in a median raphe shared with a "Y" (character 430.1). I named this element "Y" due to the absence of a homology hypothesis to stablish its relationships. I listed three possible hypotheses for the identity of that muscular element: 1) Y element is a continuation of the rectus abdominis (rectus abdominis anterior); 2) the Y element is a second myotome of the subarcualis rectus I and the medial raphe represents a closed myosepta; and 3) the Y element represents an unnamed muscle that evolved only in cycloramphid larvae.

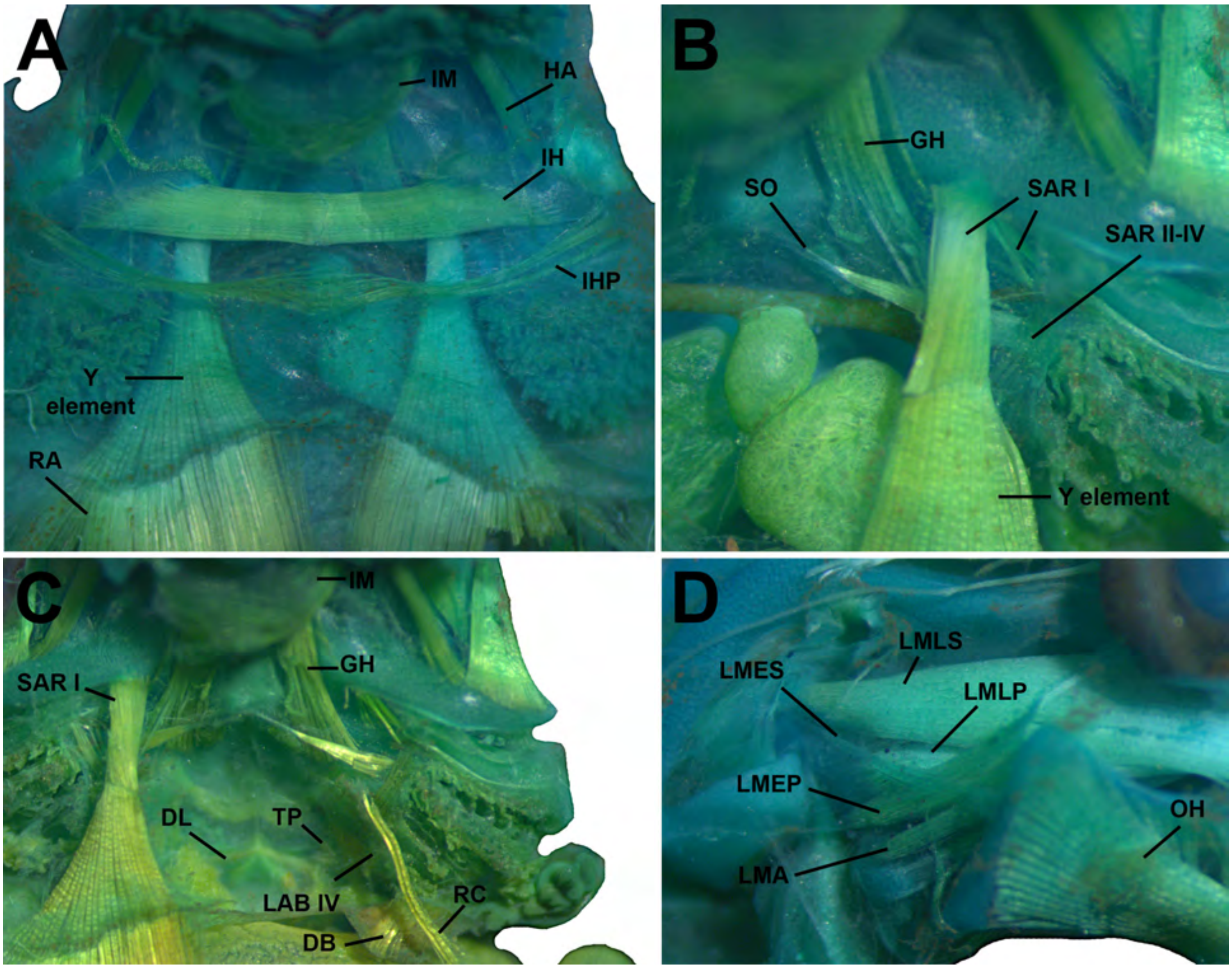

Figure 50. Cranial muscles of *Thoropa miliaris* tadpoles; detail of the branchial basket (A); detail of the SAR-I (B); detail of the RC (C); detail of the levator muscles (D). DL, dilator larynges; GH, geniohyoideus; HA, hyoangularis; IH, interhyoideus; IHP, interhyoideus posterior; IM, intermandibularis; LMEP, levator mandibulae externus profundus; LMES, levator mandibulae externus superficialis; LMLP, levator mandibulae longus profundus; LMLS, levator mandibulae longus superficialis; OH, obritohyoideus; RA, rectus abdominis; SAR-I, subarcualis rectus I; SAR II–IV, subarcualis rectus II–IV; SO, subarcualis obliquus; TP, tympanopharyngeous; Y, "Y" element.

The available evidences make it impossible to test any of these hypothesis; however, although its identity is not known, the function of the "Y" element may be discussed. The origin and insertion of the muscle element suggests that its contraction may act in association with the contraction of the rectus abdominis, rectus cervicis and levator archum branchialium III; effects of the contraction of these muscles may be the shortening of the abdomen regarding the trunk and/or the lowering/elevation of the buccal floor. Either way, those muscles may act in helping the tadpoles to adhere to the rock surface by creating a concavity between the tadpoles` ventral surface and the surrounding areas, creating a vacuum effect. Haas et al. (2014) provided images showing that the tadpoles of *Rhinella rumboli* may compress their bodies against surfaces (Fig. 1C: 185), creating an adhesion pressure—*Rhinella rumboli* is part of the *Rhinella veraguensis* group, which is known by the presence of belly sucker in some representatives. This mechanism could explain the presence of the "Y" element in cycloramphids and also elucidate the peculiar insertion of the m.l.a.b. III in cycloramphids.

In the Anura larvae, the m.l.a.b. originates on the ventrolateral otic capsule and inserts on the distal margin of the ceratobranchial III (Starrett 1973; Haas 2003). In cycloramphids, however, this muscle becomes massive and inserts on the peritoneum (character 269.1), near the insertion of the rectus abdominis, diaphragmatobranchialis, and rectus cervicis. By presenting this peculiar insertion, the contraction of the m.l.a.b. III generates force in the body wall, possibly helping to create a concavity in the branchial basked area; such concavity, together with the presence of the flattened dermal expansions, and the "Y" element, could act in adhering the body to the substrate.

The feeding habits of semi-terrestrial tadpoles are as interesting as the adhesion mechanism and gas exchange, given that filtering is not an option in terrestrial environment. The semi-terrestrial tadpoles of Cycloramphidae have well-developed, fully keratinized (characters 214.3 and 219.3), laterally compressed (characters 216.3 and 219.3), massive (character 221.1) jaw sheaths powered by robust levator mandibulae muscles (character 449.1), suggesting strong jaws that could be employed in a macrophagous diet. The buccopharyngeal cavity presents a general reduction on the number of papillae; *Thoropa* and *Cycloramphus* present a single pair of infralabial papillae (characters 350.1, 351.0, and 352.0), lack prepocked papillae (character 372.0), and present reduced number of supranumerary papillae in the buccal roof and floor. Moreover, secretory pits (characters 379.0 and 384.0) and secretory ridges (character 380.0) are absent in these tadpoles. Wassersug and Heyer (1983) reported mineral grains, algal filaments and a portion of an arthropod exoskeleton in the guts of *Thoropa petropolitana* and attested that the "branchial food trap morphology and the little that is known about the ecology of these larvae would seem to preclude planktonic suspension feeding" (p.768). My results support Wassersug and Heyer`s (1983) claim and, additionally, point to a macrophagy diet in these larvae. The combination of these characters seems to suggest that Cycloramphidae larvae feed only on macro elements found on the rock surface. Further studies of gut content and, preferably, of isotope composition (Altig et al. 2007) may provide further evidences in support of this hypothesis.

This study is the most comprehensive regarding semi-terrestrial larvae characters. Nevertheless, data are restricted to few species of *Cycloramphus*, none of which represents the *Cycloramphus bolitoglossus* and the *Cyloramphus eletherodcatylus* species groups that possess endotrophic, nidiculous tadpoles (Heyer and Crombie 1979; Heyer 1983). Moreover, I could not include the also endotrophic tadpoles of *Zachaenus* (Lutz 1944). Unfortunately, information on the internal anatomy of other semi-terrestrial tadpoles (e.g., *Petroapedes*) does not exist, preventing further comments on the specialized characters of these larvae.

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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APPENDIX I

Described tadpoles of Dendrobatoidea, including internal morphology anatomy.

Taxa	External Morphology	Buccopharyngeal cavity	Chondrocranium	Cranial Muscles	Comments
Adelphobates castaneoticus	Caldwell and Myers 1990				
Adelphobates quinquivittatus	Caldwell and Myers 1990				
Allobates bromelicola	La Marca and Mijares-Urrita 1997				
Allobates brunneus	Lima *et al.* 2009				
Allobates caeruleodactylus	Caldwell *et al.* 2002				
Allobates chalcopis	Kaiser and Altig 1994				
Allobates femoralis	Lescure 1976; Silverstone 1976; Duellman, 1978; Lescure, 1984; Duellman 2005; Hero, 1990; Rodríguez and Duellman 1994 Duellman 2005; Lamotte and Lescure 1977				
Allobates goianus	Bokermann 1975				
Allobates granti	Kok *et al.* 2006b				

Allobates grillisimilis	Simões *et al.* 2013				
Allobates holdi	Simoes *et al*. 2010				
Allobates insperatus	Edwards 1974; Duellman 1978				As *marchesianus*
Allobates kingsburyi	Castillo-Trenn 2004				
Allobates magnussoni	Lima *et al*. 2014				
Allobates mandelorum	La Marca 1993				
Allobates marchesianus	Caldwell *et al.* 2002; Hero 1990; Rodríguez and Duellman 1994				
Allobates mcdiarmid	Reynolds and Foster 1992				
Allobates nidicola	Caldwell and Lima 2003				
Allobates niputidea	Grant *et al.* 2007				
Allobates olfersioides	Verdade and Rodrigues 2007				
Allobates paleovarzensis	Lima *et al*. 2010				
Allobates pittieri	La Marca 2004				
Allobates subfolionidificans	Liema *et al.* 2007				
Allobates sumtuosus	Kok and Ernst 2007; Simões and Lima 2012				

Allobates talamancae	Dunn 1924; Breder 1946; Edwards 1974; Savage 2002				
Allobates tapajos	Lima *et al.* 2015				
Allobates trilineatus	Duellman 2005				
Allobates undulatus	Myers and Donnelly 2001				
Allobates wayuu	Acosta and Coloma 1999				
Ameerega altamazonica	Twomey and Brown 2008a				
Ameerega bilibguis	Duellman 1978 Poelman *et al.* 2010				as *parvulus*
Ameerega bracattus	Cope 1887; Haddad and Martins 1994				
Ameerega flavopicta	Haddad and Martins 1994				
Ameerega hahneli	Lescure 1976; Haddad and Martins 1994; Duellman 2005; Rodríguez and Duellman 1994; Menin *et al*. 2017				
Ameerega macero	Rodríguez and Myers 1993				
Ameerega parvula	Poelman *et al*. 2010; Rodríguez and Duellman 1994				
Ameerega petersi	Silverstone 1976				
Ameerega picta	Lescure, 1976; Silverstone 1976; Haddad and Martins 1994; Duellman 2005; Lamotte and Lescure 1977; Schulze *et al.* 2015				
Ameerega pulchripectra	Rodríguez and Myers 1993				
Ameerega rubriventris	Lotters *et al*. 1997				

Ameerega silverstonei	Silverstone 1976; Myers and Daly 1979				
Ameerega smaragdina	Silverstone 1976				
Ameerega trivittata	Wyman 1859; Silverstone 1976; Rodríguez and Duellman 1994				
Andinobates abditus	Myers and Daly 1976b				
Andinobates altobueyensis	Silverstone 1975				
Andinonobates bombetes	Myers and Daly 1980				
Andinobates claudiae	Jungfer *et al.* 2000???				
Andinobates fulguritus	Silverstone 1975				
Andinobates minutus	Silverstone 1975				
Andinobates opisthomelas	Silverstone 1975				
Andinobates tolimensis	Bernal *et al.* 2007				
Andinobates virolinensis	Carranza and Pinilla 1992				
Anomaloglossus baeobatrachus	Edwards 1974				

Anomaloglossus beebei	Kok *et al.* 2006b				
Anomaloglossus degranvillei	Lescure 1975, 1984				
Anomaloglossus kaiei	Kok *et al.* 2006a				
Anomaloglossus parkerae	Duellman 1997				
Anomaloglossus roraima	Kok *et al.* 2013				
Anomaloglossus stepheni	Juncá *et al*. 1994				
Anomaloglossus tamacuerensis	Myers and Donnelly 1997				
Anomaloglossus tepuyensis	Myers and Donnelly 2008				
Anomaloglossus wothuja	Barrio-Amorós et al. 2004				
Anomalogossus paderioi	Kok 2010				
Aromobates alboguttatus	Edwards 1974; Mijares-Urrutia and La Marca 1997				
Aromobates duranti	Mijares-Urrutia and La Marca 1997				
Aromobates haydeeae	Mijares-Urrutia and La Marca 1997				

Aromobates leopardalis	Mijares-Urrutia 1991				
Aromobates mayorgai	La Marca and Mijares-Urrutia 1988				
Aromobates meridensis	Edwards 1974; Mijares-Urrutia and La Marca 1997				
Aromobates nocturnos	Myers *et al.* 1991				
Aromobates orostoma	Mijares-Urrutia and La Marca 1997				
Aromobates serranus	Mijares-Urrutia and La Marca 1997				
Aromobatis molinari	La Marca 1985				
Colostethus brachihistriatus	Grant and Castro 1998				
Colostethus inguinalis	Savage 1968; Edwards 1974				
Colostethus latinasus	Dunn 1924; Savage 1968; Edwards 1974				
Colostethus panamensis	Savage 1968				
Colostethus pratti	Dunn 1924; Savage 1968				
Colostethus ruthveni	Ruthven and Geig 1915; Kaplan 1997				
Colostethus ucumari	Grant 2007				

Colostethys ramirezi	Rivero and Serna 1995				
Dendrobates auratus	Pope, 1941; Eaton 1941; Dunn, 1941 Breder 1946; Senfft 1936; Savage 1968; Silverstone 1975; Savage 2002				
Dendrobates tinctorius	Hoogmoed 1969; Silverstone 1975; Lescure 1984		Haas 1995		
Dendrobates truncatus	Lynch 2006				
Epipedobates anthonyi	Silverstone 1976		Haas 1995		
Epipedobates boulengeri	Barbour 1905; Silverstone 1976; Anganoy-Criollo and Cepeda-Quilindo 2017		Haas 1995		
Epipedobates darwinwallacei	Dias *et al*. In press				
Epipedobates espinosai	Funkhouser 1965; Silverstone 1976				
Epipedobates machalilla	Edwards 1974; Coloma 1995			as "*decussatus*"	
Epipedobates narinensis	Muses-Cisnero *et al*. 2008; Anganoy-Criollo and Cepeda-Quilindo 2017				
Excidobates captivus	Twomey and Brown 2008b				
Excidobates condor	Almendaríz *et al.* 2012				
Exidobates mysteriosus	Schult 1990				

Hyloxalus anthracinus	Edwards 1974; Coloma 1995				
Hyloxalus awa	Edwards 1974; Coloma 1995			as “*phaleromystaxl*”	
Hyloxalus azureiventris	Lotters *et al*. 2000				
Hyloxalus bocagei	Páez-Vacas *et al.* 2010				
Hyloxalus chlorocraspedopus	Caldwell 2005				
Hyloxalus craspedoceps	Duellman 2004				
Hyloxalus delatorreae	Coloma 1995				
Hyloxalus edwardsi	Lynch 1982b				
Hyloxalus elachyhistus	Edwards 1971; 1974				
Hyloxalus eleutherodactylys	Duellman 2004				
Hyloxalus exasperatus	Edwards 1974; Duellman and Lynch 1988			as “*cruciarius*”	
Hyloxalus fascinigrus	Grant and Castro 1998				
Hyloxalus fuliginosus	Edwards 1974			As “*argus*” and *fuliginosus*	

Hyloxalus idiomelus	Duellman 2004				
Hyloxalus infraguttatus	Coloma 1995				
Hyloxalus insulatus	Duellman 2004				
Hyloxalus italoi	Páez-Vacas *et al*. 2010				
Hyloxalus jacobuspetersi	Edwards 1974				
Hyloxalus leucophaeus	Duellman 2004			as "*orthius*"	
Hyloxalus maculosus	Páez-Vacas *et al.* 2010				
Hyloxalus nexipus	Duellman 2004				
Hyloxalus peruvianus	Melin 1941?				
Hyloxalus pulchellus	Edwards 1974				
Hyloxalus sauli	Edwards 1974; Duellman 1978				
Hyloxalus shuar	Edwards 1974			as "*percnopalmus*"	
Hyloxalus sordidatus	Duellman 2004				
Hyloxalus subpunctatus	Stebbins and Hendrickson 1959; Edwards 1974; Anganoy-Criollo 2013	Wassersug 1980	Haas 1995		
Hyloxalus sylvaticus	Barbour and Noble 1920; Edwards 1974; Duellman and Wild 1993; Duellman 2004				

Hyloxalus toachi	Coloma 1995				
Hyloxalus veertebralis	Edwards 1974; Coloma 1995				
Hyloxalus yasumi	Páez-Vacas *et al.* 2010				
Mannophryne collaris	La Marca 1994				
Mannophryne cordilleriana	La Marca 1994				
Mannophryne herminae	Edwards 1974; La Marca 1994				
Mannophryne neblinae	La Marca 1994				
Mannophryne oblitterata	Dixon and Rivero-Blanco 1985				
Mannophryne olmonae	Edwards 1974; Lehtinen and Hailey 2008				
Mannophryne riveroi	Danoso-Barros 1965 "1964"; Edwards 1974; La Marca 1994				
Mannophryne trinitatis	Boulenger 1895; Kenny 1969; Edwards 1974				as “*praecia*” and *trinitatus*
Mannophryne venezuelensis	Manzanilla *et al.* 2007				
Mannophryne yustizi	La Marca 1989				
Oophaga arborea	Myers *et al.* 1984				
Oophaga granulifera	Hersek *et al.* 1992; Van Wijngaarden and Bolaños 1992; Savage 2002				

Oophaga histrionica	Silverstone 1975				
Oophaga pumilio	Starett 1960; Savage 1968; Silverstone 1975; Savage 2002				
Oophaga speciosa	Jungfer 1985				
Paruwrobates erythromos	Vigle and Miyata 1980				
Paruwrobates whymperi	Edwards 1974	Wassersug and Heyer 1988			
Phyllobates bicolor			Haas 1995	Haas 2001	
Phyllobates lugubris	Savage 1968; Donnely *et al*. 1990; Savage 2002				
Phyllobates terribilis	Myers *et al.* 1978				
Phyllobates vittatus	Savage 1968; Silverstone 1976; Savage 2002				
Ranitomeya amazonica	Brown *et al*. 2011		Krings *et al.* 2017	Krings *et al.* 2017	
Ranitomeya benedicta	Brown *et al*. 2008		Krings *et al.* 2017	Krings *et al.* 2017	
Ranitomeya defleri	Twomey and Brown 2009				
Ranitomeya fantastica	Brown *et al*. 2008				
Ranitomeya flavovittata	Brown *et al*. 2011				
Ranitomeya imitator	Brown *et al*. 2011		Krings *et al.* 2017	Krings *et al.* 2017	

Ranitomeya reticulata	Brown *et al*. 2011		Krings *et al*. 2017	Krings *et al*. 2017	
Ranitomeya sirensis	von May *et al*. 2008				
Ranitomeya summersi	Brown *et al*. 2008				
Ranitomeya tararo	Brown *et al*. 2011				
Ranitomeya ukarii	Brown *et al*. 2011				
Ranitomeya vanzolinii	Brown *et al*. 2011		Krings *et al*. 2017	Krings *et al*. 2017	
Ranitomeya variabilis	Masche *et al*. 2010; Brown *et al*. 2011				
Ranitomeya yavaricola	Perez-Peña *et al*. 2010				
Rheobates palmatus	Dunn 1944; Edwards 1974; Lynch 2006				
Rheobates pseudopalmatus	Rivero and Serna 1995				
Silverstoneia daly	Grant and Myers 2013				
Silverstoneia flotator	Dunn 1924; Íbañez and Smith 1995; Savage 2002				
Silverstoneia minima	Grant and Myers 2013				
Silverstoneia nubicola	Dunn 1924; Savage 1968; Edwards 1974; Ibáñez and Smith 1995; Savage 2002	Wassersug 1980	Haas 1995		

APPENDIX II

Species authorship: terminals and species cited in the text

"Colostethus" sp. ruthveni-like "
"Colostethus" ruthveni Kaplan, 1997"
A. insperatus (Morales, 2002)
Adelphobates castaneoticus (Caldwell and Myers, 1990)
Adelphobates galactonotus (Steindachner, 1864)
Adelphobates quinquevittatus (Steindachner, 1864)
Adenomera Steindarchner 1867
Allobates aff. juanii (Morales, 1994)
Allobates algorei Barrio-Amor—s and Santos, 2009
Allobates amissibilis Kok et al. 2013b
Allobates bacurau Sim›es, 2016
Allobates caeruleodactylus (Lima and Caldwell, 2001)
Allobates chalcopis (Kaiser et al., 1994)
Allobates conspicuus (Morales, 2002)
Allobates crombiei (Morales, 2002)
Allobates femoralis (Boulenger, 1884)
Allobates flaviventris Melo-Sampaio et al., 2013
Allobates fratisenescus (Morales, 2002)
Allobates gasconi (Morales, 2002)
Allobates granti (Kok et al., 2006a)
Allobates grillisimilis Sim›es et al., 2013b
Allobates hodli Sim›es et al., 2010
Allobates humilis (Rivero, 1980)
Allobates juanii (Morales, 1994)
Allobates kingsburyi (Boulenger, 1918)
Allobates magnussoni Lima et al., 2014
Allobates masniger (Morales, 2002)
Allobates nidicola (Caldwell and Lima, 2003)
Allobates niputidea Grant et al., 2007
Allobates olfersioides (Lutz, 1925)
Allobates ornatus (Morales, 2002)
Allobates paleovarzensis Lima et al. 2010
Allobates PEGM1
Allobates PEGM3
Allobates peruvianus (Melin, 1941)
Allobates pittieri (La Marca et al., 2004)
Allobates PortoWalter2
Allobates sp kapawi
Allobates sp. other
Allobates sp. Alto Mazan
Allobates sp. Cando
Allobates sp. Caraj‡s
Allobates sp. Castanho
Allobates sp. Cruzeiro do Sul
Allobates sp. Cuyabeno
Allobates sp. Ecuador
Allobates sp. Iç‡
Allobates sp. Liberdade
Allobates sp. M_ndez
Allobates sp. Manaus 1
Allobates sp. Neblina
Allobates sp. Negro

Allobates sp. RioItuxi
Allobates sp. Saul
Allobates sp. small
Allobates subfolionidificans (Lima et al., 2007)
Allobates sumtuosus (Morales, 2002)
Allobates talamancae (Cope, 1875)
Allobates tapajos Lima et al., 2015
Allobates trilineatus (Boulenger, 1884)
Allobates undulatus (Myers and Donnelly, 2001)
Allobates zaparo (Silverstone, 1976)
Allophrnidae Grandison 1978
Allophryne ruthveni Gaige, 1926
Alsodes neuquensis Cei, 1976
Alsodes vanzolinii (Donoso-Barros, 1974)
Alsodes verrucosus (Philippi, 1902)
Alsodidae Wagler 1830
Altiphrynoides malcolmi Fouquet, Recoder, Teixeira, Cassimiro, Amaro, Camacho, Damasceno, Carnaval, Moritz, and Rodrigues, 2012,
Alytes Boulenger 1899
Amazophrynella Cope 1863
Amazophrynella manaos Rojas et al. 2014
Amazophrynella minuta (Melin, 1941)
Ameerega altamazonica Twomey and Brown, 2008b
Ameerega bassleri (Melin, 1941)
Ameerega berohoka Vaz-Silva and Maciel, 2011
Ameerega bilinguis (Jungfer, 1989)
Ameerega boehmei L_tters et al., 2009
Ameerega braccata (Steindachner, 1864)
Ameerega cainarachi (Schulte, 1989)
Ameerega flavopicta (Lutz, 1925)
Ameerega hahneli (Boulenger, 1884)
Ameerega ignipedis Brown and Twomey, 2009
Ameerega macero (Rodr'guez and Myers, 1993)
Ameerega parvula (Boulenger, 1882b)
Ameerega pepperi Brown and Twomey, 2009
Ameerega petersi (Silverstone, 1976)
Ameerega picta (Bibron in Tschudi, 1838)
Ameerega pongoensis (Schulte, 1999)
Ameerega pulchripecta (Silverstone, 1976)
Ameerega rubriventris Lotters et al.,1997a
Ameerega silverstonei (Myers and Daly, 1979)
Ameerega simulans (Myers et al., 1998)
Ameerega smaragdina (Silverstone, 1976)
Ameerega sp zaparo auctorum
Ameerega sp. PortoWalter1
Ameerega trivittata (Spix, 1824)
Ameerega yoshina Brown and Twomey, 2009
Ameerega yungicola L_tters et al., 2005
Amolops ricketti Smith 1939
Anaxyrus Steindarchner 1864
Anaxyrus boreas (Baird and Girard, 1852)
Andinobates aff. minutus (Shreve, 1935)
Andinobates altobueyensis (Silverstone, 1975a)
Andinobates bombetes (Myers and Daly, 1980)
Andinobates cassidyhornae Am_zquita et al., 2013a
Andinobates claudiae (Jungfer et al., 2000)
Andinobates dorisswansonae (Rueda-Almonacid et al., 2006)
Andinobates fulguritus (Silverstone, 1975)
Andinobates geminisae Batista et al., 2014
Andinobates minutus (Shreve, 1935)

Andinobates opisthomelas (Boulenger, 1899)
Andinobates sp.
Andinobates sp. Choco1
Andinobates sp. Supat‡
Andinobates tolimense (Bernal et al., 2007)
Andinobates victimatus M‡rquez et al., 2017
Andinobates virolinensis (Ruiz-Carranza and Ramírez-Pinilla, 1992)
Anolis pentaprion "Nieden 1911 "1910"
Anomaloglossus aff. degranvillei (Lescure, 1975)
Anomaloglossus apiau Fouquet et al., 2015
Anomaloglossus baeobatrachus (Boistel and Massary, 1999)
Anomaloglossus beebei (Noble, 1923)
Anomaloglossus degranvillei (Lescure, 1975)
Anomaloglossus kaiei (Kok et al., 2006b)
Anomaloglossus megacephalus Kok et al. 2010
Anomaloglossus praderioi (La Marca, 1997)
Anomaloglossus roraima (La Marca, 1997)
Anomaloglossus rufulus (Gorzula, 1990)
Anomaloglossus sp.
Anomaloglossus sp. A
Anomaloglossus sp. Ayanganna
Anomaloglossus sp. B
Anomaloglossus sp. Brownsberg
Anomaloglossus sp. C
Anomaloglossus sp. Tafelberg
Anomaloglossus sp. Thomasing
Anomaloglossus stepheni (Martins, 1989)
Anomaloglossus tamacuarensis (Myers and Donnelly, 1997)
Anomaloglossus tepuyensis (La Marca, 1997)
Anomaloglossus verbeeksnyderorum Barrio-Amor—s et al., 2010a
Anomaloglossus wothuja (Barrio-Amor—s et al., 2004)
Anotheca Mivart 1869
Anotheca spinosa"Nieden 1911 "1910"
Aromobates cannatellai Barrio-Amorós and Santos, 2012
Aromobates ericksonae Barrio-Amorós and Santos, 2012
Aromobates meridensis (Dole and Durant, 1972)
Aromobates molinarii (La Marca, 1985)
Aromobates nocturnus Myers et al., 1991
Aromobates ornatissimus Barrio-Amor—s et al. 2011
Aromobates saltuensis (Rivero, 1980)
Aromobates sp.
Aromobates sp. LosAlcavares
Aromobates sp. Mucuchies
Arthroleptidae Stejneger 1899
Arthroleptides Duméril and Bibron 1841
Ascaphus Ruthven 1916
Ascaphus truei Stejneger 1899
Atelognathus Gray 1825
Atelognathus patagonicus (Gallardo, 1962)
Atelopus Spix 1824
Atelopus carrikeri Fouquette 1961
Atelopus spurrelli Boulenger, 1914
Atelopus zeteki Dunn, 1933
Batrachyla leptopus Bell, 1843
Batrchylidae Spix 1824
Boana Cope 1867
Boana boans Linnaeus 1761
Boana pardalis Tschudi 1838
Boana rufitela Schmidt 1933
Boana semilineata Taylor 1940

Bokermannohyla circundata Temminck and Schlegel 1838
Bombina Gray 1825
Boophis Boulenger 1900
Bromeliohyla bromeliacea Taylor 1951
Bromeliohyla dendroscarta Wied-Neuwied and Prinz 1824
Bufo japonicas Barrio 1980
Bufonidae Silverstone 1975
Bufonidae Cope 1868
Cardioglossa Hoffmann 1878
Centrolenidae Cochran 1938
Centrolenidae Duméril and Bibron 1841
Ceratohryidae Bonaparte 1850
Ceratophrys Tschudi 1838
Ceratophrys cranwelli Werner 1897
Ceratophrys cranwelli Barrio, 1980
Chacophrys pierottii (Vellard, 1948)
Colostethus argyrogaster (Morales and Schulte, 1993)
Colostethus brachistriatus Rivero and Serna, 1986
Colostethus cf. pratti
Colostethus fraterdanieli Silverstone, 1971
Colostethus imbricolus Noble 1924
Colostethus imbricolus Silverstone, 1975b
Colostethus inguinalis Miranda-Ribeiro 1920
Colostethus inguinalis (Cope, 1868)
Colostethus latinasus (Cope, 1863)
Colostethus panamansis (Dunn, 1933)
Colostethus pratti (Boulenger, 1899)
Colostethus ramirezi Rivero and Serna, 2000
Colostethus sp.
Colostethus sp. Gorgona
Colostethus sp. pratti-like
Cophomantinae Fitzinger 1843
Crossodactylodes Cope 1865
Crossodactylus Jiménez de la Espada 1870
Crossodactylus caramaschii Bastos and Pombal, 1995
Crossodactylus schmidti Gallardo, 1961
Cycloramphidae Beireis 1783
Cycloramphus Cope 1886
Cycloramphus acangatan Verdade and Rodrigues, 2003
Cycloramphus bandeirensis Heyer, 1983
Cycloramphus bolitoglossus Boulenger 1889
Cycloramphus boraceiensis Heyer, 1983
Cycloramphus eleutherodactylus Stejneger 1906
Cycloramphus eleutherodactylus (Miranda-Ribeiro, 1920)
Cycloramphus fuliginosus Tschudi, 1838
Cycloramphus organensis Weber et al., 2011
Cycloramphus stejnegeri Günther 1858
Dendrobates auratus (Girard, 1855)
Dendrobates leucomelas Steindachner, 1864
Dendrobates tinctorius (Cuvier, 1797)
Dendrobates truncatus (Cope, 1861)
Dendrobatoidea Otth 1837
Dendrophryniscus leucomystrax Izecksohn, 1968
DendrophyniscusFitzinger 1843
Dendropsophus Daudin 1800
Dendropsophus leucophyllatus Campbell and Smith 1992
Dendropsophus microcephalus Stuart 1954
Dendropsophus nanus "Lütken 1864 ""1863!"
Dendropsophus phlebodesGrandidier 1877
Denrophryniscus brevipollicatus Jiménez de la Espada, 1870

Discoglossidae	Thomas 1966
Discoglossus	Myers 1987
Dryophytes	Noble 1921
Dryophytes femoralis	Barbour 1909
Duellmanohyla	Boulenger 1899
Duellmanohyla schmidtorum	Günther 1881
Duttaphrynus stomaticus	Fitzinger 1843
Dyscophus antongilii	Formas 1989
Ectopoglossus isthminus (Myers et al., 2012)
Ectopoglossus saxatilis sp. nov.
Edalorhina perezi Jim_nez de la Espada, 1870
Eletherodactylus coqui	Ortiz and Ibarra-Vidal 1992
Epipedobates	Veloso, Celis-Diez, Guerrero, Méndez-Torres, Iturra-Constant and Simonetti 2005
Epipedobates anthonyi	"Boulenger 1895 ""1894"""
Epipedobates anthonyi (Noble, 1921)
Epipedobates boulengeri	Wandolleck 1907
Epipedobates boulengeri (Barbour, 1909)
Epipedobates darwinwallacei Cisneros-Heredia and Y‡nez-Mu–oz, 2010
Epipedobates espinosai (Funkhouser, 1956)
Epipedobates machalilla (Coloma, 1995)
Epipedobates tricolor	Cannatella 1986
Epipedobates tricolor (Boulenger, 1899)
Espadarana prosoblepon (Boettger, 1892)
Eupsophus	Bokermann 1962
Eupsophus calcaratus	Fitzinger 1843
Eupsophus calcaratus (GŸnther, 1881)
Eupsophus emiliopugini	Fowler 1913
Eupsophus emiliopugini Formas, 1989
Eupsophus nahuelbutensisBlake 1973
Eupsophus queulensis	Boettger 1881
Eupsophus roseus (Dum_ril and Bibron, 1841)
Excidobates captivus Myers, 1982
Excidobates condor Almend‡riz et al. 2012
Excidobates mysteriosus (Myers, 1982)
Fritziana goeldii	Hewitt 1913
Fritziana ohausi	Barbour, T., and A. Loveridge 1928
Frostius Daudin 1802
Frostius pernambucensis	Barbour and Loveridge 1928
Gastrotheca	Boettger 1893
Gastrotheca riobambae	Laurenti 1768
Geocrinia	Fitzinger 1826
Gephyromantis granulatusGünther 1858
Heleophryne natalensis	Peters 1882
Hophlophryne rogersi	Boulenger 1896
Hoplobatrachus tigrinus	Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada and Vilà, 2009
Hoplophryne	Cope 1863
Hyalinobatrachium fleischimanni	"Savage 1967 ""1966"""
Hyalinobatrachium fleischmanni (Boettger, 1893)
Hyla Laurent 1986
Hylodes	"Peters 1880 ""1879"""
Hylodes amnicola Pombal et al., 2002
Hylodes japi S‡ et al., 2015
Hylodes meridionalis (Mertens, 1927)
Hylodes nasus (Lichtenstein, 1823)
Hylodes ornatus (Bokermann, 1967b)
Hylodes perere Silva and Benmaman, 2008
Hylodes phyllodes Heyer and Cocroft, 1986
Hylodes pipilans Canedo and Pombal, 2007
Hylodes sazimai Haddad and Pombal, 1995
Hylodidae	Günther 1901

Hylorina Gaige 1929
Hyloscirtus Gray 1831
Hyloxalus anthracinus (Edwards, 1971)
Hyloxalus awa (Coloma, 1995)
Hyloxalus azureiventris (Kneller and Henle, 1985)
Hyloxalus bocagei Jim_nez de la Espada, 1870
Hyloxalus cepedai (Morales, 2002)
Hyloxalus chlorocraspedus (Caldwell, 2005)
Hyloxalus delatorreae (Coloma, 1995)
Hyloxalus elachyhistus (Edwards, 1971)
Hyloxalus idiomelus (Duellman, 2004)
Hyloxalus infraguttatus (Boulenger, 1898)
Hyloxalus insulatus (Duellman, 2004)
Hyloxalus italoi P‡ez-Vacas et al., 2010
Hyloxalus jacobuspetersi (Rivero, 1991b)
Hyloxalus lehmanni (Silverstone, 1971)
Hyloxalus leucophaeus (Duellman, 2004)
Hyloxalus maculosus (Rivero, 1991a)
Hyloxalus nexipus (Frost, 1986)
Hyloxalus picachos (Ardila-Robayo et al., 2000)
Hyloxalus pulchellus (Jim_nez de la Espada, 1875)
Hyloxalus sauli (Edwards, 1974)
Hyloxalus shuar (Duellman and Simmons, 1988)
Hyloxalus sordidatus (Duellman, 2004)
Hyloxalus sp AguaAzul
Hyloxalus sp ElCopal
Hyloxalus sp Ibague
Hyloxalus sp Masvalle
Hyloxalus sp MonteOlivo
Hyloxalus sp Moraspungo
Hyloxalus sp SanMiguelDeSalcedo
Hyloxalus subpunctatus (Cope, 1899)
Hyloxalus sylvaticus (Barbour and Noble, 1920)
Hyloxalus toachi (Coloma, 1995)
Hyloxalus vergeli Hellmich, 1940
Hyloxalus vertebralis (Boulenger, 1899)
Hyloxalus yasuni P‡ez-Vacas et al., 2010
Hymenochirus Fitzinger 1861
Hypsiboas boans (Linnaeus, 1758)
Ikakogi Budgett 1899
Incilius Budgett 1899
Incilius periglenes Smith 1925
Indirana Smith 1925
Indirana beddomei Andersson 1903
Insuetophrynus acarpicus Barrio, 1970
Isthmohyla pseudopoma Fitzinger 1826
Isthmohyla zeteki Laurenti 1768
Kaloula pulchra Tschudi 1838
Leipelma Boulenger 1882
Leiuperinae Boulenger 1895a
Leoprodactylus fuscus Bonaparte 1850
Lepidobatrachus Kuhl and Van Hasselt 1822
Lepidobatrachus laevis Stejneger 1926
Lepidobatrachus laevis Budgett, 1899
Leptobrachella Taylor 1920
Leptobrachella mjobergi Gallardo 1961
Leptodactylidae Miranda-Ribeiro 1920
Leptodactylodon Yang 1991
Leptodactylus Dubois, Ohler and Biju 2001
Leptodactylus fuscus (Schneider, 1799)

Leptodactylus pentadactylus Boulenger 1888
Leucostehus fugax (Morales and Schulte, 1993)
Limnomedusa macroglossa (Dum_ril and Bibron, 1841)
Litoria Myers 1942
Macrogenioglottus alipioi Carvalho, 1946
Macrogenioglotus Tschudi 1838
Mannophryne caquetio Mijares-Urrutia and Arends-R., 1999a
Mannophryne collaris (Boulenger, 1912a)
Mannophryne cordilleriana La Marca, 1994a
Mannophryne herminae (Boettger, 1893)
Mannophryne lamarcai Mijares-Urrutia and Arends-R., 1999
Mannophryne larandina (Yœstiz, 1991)
Mannophryne leonardoi Manzanilla et al. 2009
Mannophryne oblitterata (Rivero, 1984)
Mannophryne olmonae (Hardy, 1983)
Mannophryne orellana Barrio-Amor—s et al., 2010d
Mannophryne riveroi (Donoso-Barros, 1965)
Mannophryne sp Cupira
Mannophryne sp ElCastrero
Mannophryne sp Guatopo
Mannophryne trinitatis (Garman, 1888)
Mannophryne urticans Barrio-Amor—s et al. 2010
Mannophryne venezuelensis Manzanilla, Jowers, La Marca, and Garc'a-Par's, 2007
Mannophryne vulcano Barrio-Amor—s et al., 2010
Mannophryne yustizi (La Marca, 1989)
Manophryne sp. Guatopo
Mantella Vogt 1911
Mantidactylus Günther 1858
Megaelosia boticariana Giaretta and Aguiar, 1998
Megaelosia goeldii (Baumann, 1912)
Megaelosia jordanensis (Heyer, 1983)
Megophryidae Straughan 1968
Megophrys Kuhl and Van Hasselt 1822
Megophrys minor "Günther 1869 ""1868"""
Megophrys stejnegeri "Günther 1869 ""1868"""
Melanophryniscus Biju and Bossuyt 2003
Melanophryniscus klappenbachi Prigioni and Langone, 2000
Melanophryniscus moreirae Noble 1926
Melanophryniscus setiba Peloso, Faivovich, Grant, Gasparini, and Haddad, 2012
Melanophryniscus stelzneri (Weyenbergh, 1875)
Meristogenys Kuhl and Van Hasselt 1822
Micrixalidae Boulenger 1896
Micrixalus "Reinhardt and Lütken 1862 ""1861"""
Micrixalus herrei Fitzinger 1843
Microhyla Bauer 1944
Microhyla heymonsi Schmidt 1857
Microhylidae Jungfer, Weygoldt, and Juraske, 1996
Minyobates steyermarki (Rivero, 1971)
Myxophyes balbus Jungfer and Schiesari 1995
Nannophryne Fitzinger 1843
Nannophrys Trueb and Tyler 1974
Nannophrys ceylonensis Boulenger 1900a
Nasikabatrachus Boulenger 1900a
Nectophrynoides Lutz and Carvalho 1958
Nymphargus bejaranoi (Cannatella, 1980)
Occidozyga Boulenger 1896
Occidozyga baluensis "Boulenger 1895 ""1894"""
OdontophrynidaeFitzinger 1843
Odontophrynidae Reichenow 1874
Odontophrynidae "Cruz 1991 ""1990"""

Odontophrynus Bokermann 1966
Odontophrynus Carvalho-e-Silva, da Silva and Carvalho-e-Silva 2009
Odontophrynus achalensis di Tada, Barla, Martori, and Cei, 1984
Odontophrynus americanus (Dum_ril and Bibron, 1841)
Ololygon Lutz 1924
Oophaga arborea (Myers, Daly, and Mart’nez, 1984)
Oophaga granulifera (Taylor, 1958)
Oophaga histrionica (Berthold, 1845)
Oophaga lehmanni (Myers and Daly, 1976a)
Oophaga pumilio Bibron in De la Sagra 1840
Oophaga pumilio (Schmidt, 1857)
Oophaga speciosa (Schmidt, 1857)
Oophaga sylvatica (Funkhouser, 1956)
Oophaga vicentei Günther 1858
Oophaga vicentei (Jungfer et al., 1996)
Osteocephalus oophagous Günther 1862
Osteopilus Parker 1940
Osteopilus brunneus Laurenti 1768
Otophryne Laurenti 1768
Otophryne robusta Wagler 1830
Paratelmatobius Hensel 1867
Paratelmatobius lutzii Taylor 1944
Paruwrobates erythromos (Vigle and Miyata, 1980)
Pelodytes caucasicus Linnaeus 1758
Pelophryne signata Slater 1939
Peltophryne Baird and Girard 1853
Peltophryne peltocephala Linnaeus 1758
Petropedetes Batsch 1796
Phasmahyla Bauer 1986
Phasmahyla cochranae Schulte 1986
Phasmahyla cruzi Myers 1982
Phasmahyla guttata Cope 1862
Philautus silus "Rivero and Serna 2000 ""1995"""
Phyllobates Fitzinger 1826
Phyllobates aurotaenia (Boulenger, 1913)
Phyllobates bicolor Bibron in la Sagra, 1840
Phyllobates lugubris (Schmidt, 1857)
Phyllobates terribilis Myers et al., 1978
Phyllobates vittatus (Cope, 1893)
Phyllomedusidae Spix 1824
Phynobatrachus Spix 1824
Physalaemus gracilis (Boulenger, 1883)
Platyplectrum Carrizo 1992
Pleurodema brachyops (Cope, 1869)
Proceratophrys appendiculata (GŸnther, 1873)
Proceratophrys avelinoi Mercadal de Barrio and Barrio, 1993
Proceratophrys bigibbosa (Peters, 1872)
Proteus Schmidt 1857
Proteus anguinus Duméril and Bibron 1841
Pseudis Duméril and Bibron 1841
Pseudopaludicola falcipes Cope 1865
Pseudopaludicola falcipes Cope 1863
Pseudopaludicola falcipes (Hensel, 1867)
Ptychohyla Cope 1863
Rana Cope 1865a
Rana cascadae Günther 1858a
Rana pretiosa Inger and Haile 1959
Rana temporaria Wiegmann 1834
Ranidae Gallardo 1962
Ranitomeya Tschudi 1838

Ranitomeya amazonica (Schulte, 1999)
Ranitomeya benedicta Brown, Twomey, Pepper, and Sanchez-Rodriguez, 2008
Ranitomeya cf cyanovittata
Ranitomeya cyanovittata P_rez-Pe–a et al., 2010
Ranitomeya defleri Twomey and Brown, 2009
Ranitomeya fantastica (Boulenger, 1884)
Ranitomeya flavovittata (Schulte, 1999)
Ranitomeya imitator Cope 1865a
Ranitomeya imitator (Schulte, 1986)
Ranitomeya reticulata (Boulenger, 1884)
Ranitomeya sirensis (Aichinger, 1991)
Ranitomeya summersi Brown, Twomey, Pepper, and Sanchez-Rodriguez, 2008
Ranitomeya toraro Brown et al., 2011b
Ranitomeya uakarii Brown et al., 2006
Ranitomeya vanzolinii Caramaschi and Sazima 1984
Ranitomeya vanzolinii (Myers, 1982)
Ranitomeya variabilis (Zimmermann and Zimmermann, 1988)
Ranitomeya ventrimaculata (Shreve, 1935)
Ranitomeya yavaricola P_rez-Pe–a et al., 2010
Rhaebo Spix 1824
Rhaebo haematiticus Cope, 1862
Rheobates palmatus (Werner, 1899)
Rheobates pseudopalmatus Wandolleck 1907
Rheobates pseudopalmatus (Rivero and Serna, 2000)
Rhinella Lutz 1925
Rhinella acutirostris Wagler 1827
Rhinella icterica Cope 1866
Rhinella rumbolli Carrizo 1992
Rhinella veraguensis Schmidt 1857
Rhinidermatidae Bonaparte 1850
Rhinoderma Bonaparte 1850
Rhinoderma darwinii Duméril and Bibron 1841
Rupirana Heyer 1999
Rupirana cardosoi Heyer, 1999
Scythrophrys sawayae (Cochran, 1953)
Silverstoneia aff nubicola (Dunn, 1924)
Silverstoneia erasmios Rivero and Serna, 2000
Silverstoneia flotator (Dunn, 1931)
Silverstoneia nubicola (Dunn, 1924)
Silverstoneia punctiventris Grant and Myers 2013
Smilisca Cope 1865
Spea bombifrons Cope 1863
Spea multiplicata Cope 1863
Staurois Cope 1865
Staurois guttatus Günther 1858
Staurois parvus Inger and Haile 1959
Telmatobius Wiegmann 1834
Telmatobius bolivianus Parker, 1940
Theloderma Tschudi 1838
Thoropa Cope 1865
Thoropa megatympanum Caramaschi and Sazima 1984
Thoropa miliaris Spix 1824
Thoropa miliaris (Spix, 1824)
Thoropa petropolitana Wandolleck 1907
Thoropa taophora (Miranda-Ribeiro, 1923)
Vitreorana eurygnatha Guayasamin, Castroviejo-Fisher, Trueb, Ayarzagüena, Rada and Vilà, 2009
Xenopus Wagler 1827
Zachaenus Cope 1866
Zachaenus parvulus (Girard, 1853)

APPENDIX III

Examined material

Adelphobates castaneoticus – **Brazil:** MZUSP 67225.

Adelphobates galactonotus – **Brazil:** Pará: Cachoeira Juruá, Rio Xingu: MZUSP 77116. Caxiuaña, Floresta Nacional de Caxiuanã: TG 3666.

Adelphobates quinquevittatus – **French Guiana:** Mont Sinéry: MNHN 1891.445. Without precise location: MNHN 1981.443, 2008.489, 2008.490.

Allobates alagoanus – **Brazil:** Alagoas: Maceió: Mata do Catolé: MUFAL 10174. Bahia: Igarapuna, Reserva Ecológica Michelin: MZFS 631, 776, 909.

Allobates brunneus – **Brazil:** Mato Grosso: Chapada dos Guimarães: INPA 10029.

Allobates caeruleodactylus – **Brazil:** Amazonas: Castanho: INPA 8037–8041.

Allobates femoralis – **Brazil:** Amazonas: CZPB 398/180, 440/196, 504/219. **Ecuador:** Sycumbíus: Hosteria La Selva: QCAZ 11753. **French Guiana:** Mana: AF 1110. **Brazil:** MZUSP 64321 MZUSP 66330.

Allobates goianus – **Brazil:** MZUSP 80068.

Allobates granti – **French Guiana:** Mitaraka: AF 2768,

Allobates grillisimilis – **Brazil:** Amazonas: norther Madeira-Tapajós interfluve: INPA 30824–28.

Allobates insperatus – **Ecuador:** Santa Cecília: KU 109314.

Allobates juani – **Colombia:** Meta: Villavicencio: Barrio Vanguardia: MAA 159, 262

Allobates kingsburyii – **Ecuador:** Zamora Chinchipe: Panguitza: QCAZ 24642

Allobates marchesianus – **Brazil:** Amazonas: Missão Taracuá: INPA 7943-46. **Colombia:** Vaupés: Taraira: ICN 54959

Allobates masniger – **Brazil:** APL 14294.

Allobates nidicola – **Brazil:** APL 14196

Allobates olfersiodes – **Brazil:** Rio de Janeiro: Floresta da Tijuca: MNRJ 23729.

Allobates paleovarzensis – **Brazil:** Amazonas: Castanho: INPA 20906–97, 20909–16.

Allobates sp.nov. – **Brazil:** Amazonas: Rio Içá: PD(A4).

Allobates subfolinidificans – **Brazil:** Acre: Rio Branco, Parque Zoobotânico: INPA 14817–25.

Allobates sumtuosus – **Brazil:** Amazonas: CZPB 158/60–61.

Allobates talamancae – **Colombia:** Chocó: Quibdo: ICN 460978. ICN 53315 **Panama:** Rio Claro: KU 104235.

Allobates trilineatus – **Colombia:** Amazonas: Letícia: ICN 53116.

Allobates undulatus – **Venezuela:** Amazonas: Cerro Yutagé: AMNH 159143.

Allobates wayuu – **Colombia:** Guajira: Uribá: ICN 433559, 433560.

Ameerega bassleri – **Peru:** San Martín: San Martín: MUSM 22595, 22795. San Juan de Pacayzapa: MUSM 6283.

Ameerega bilinguis – **Ecuador:** Orellana: Parque Nacional Yasuní: QCAZ 32198.

Ameerega flavopicta – **Brasil:** Minas Gerais: Jaboticabus: ZUEC 15166, 15168, 15170, 15174.

Ameerega hahneli – **Colombia:** Amazonas: Leticia: ICN 53105. **Peru:** Panguana: Puerto Inca: MUSM 26937.

Ameerega macero – **Peru:** Madre de Dios: Parque Nacional del Manu, Cocha Cashu Biological Station: AMNH 133207.

Ameerega parvula – **Ecuador:** Napo: Cerca de San Pedro, Río ArajunoQCAZ 32918.

Ameerega petersi – **Peru:** Panguana: Puerto Inca: MUSM 29102. Panguana: Yuyapichis: MUSM 24692.

Ameerega picta – **Bolivia:** Santa Cruz: CFBH 39896.

Ameerega pulchripectra – **Brazil:** Amapá: Serra do Navio: AMNH 137289.

Ameerega silvertoneis – **Peru:** Huánuco: Cordillera Azul, NE Tingo María: AMNH 94795.

Ameerega smaragdina – **Peru:** Pasco: Iscozazin Valley: LACM 64436.

Ameerega trivittata – **Brazil:** Pará: MPEG: 22375, 22377–8, 22412. **Colombia:** Amazonas: Leticia: ICN 53107, 55113. **Peru:** San Martín: San Martín: MUSM 17796.

Andinobates bombetes – **Colombia:** Valle del Cauca: Yotoco: ICN 42287.

Andinobates minutus – **Colombia:** Chocó: Quibdo: ICN 46096. **Panama:** Cerro La Campena: KU 116744.

Andibobates opisthomelas – **Colombia:** Antioquia: Santa Rita: LACM 61067. Caldas: Samaná: ICN 34620. Cauca: Isla de Gorgona: WB 3068.

Andinobates viridis – **Colombia:** Valle del Cauca: Dagua: ICN 32698.

Andinobates virolinensis – **Colombia:** Santander: Charalala: Virolín: ICN 9331, 28409–10, 28412.

Anomaloglossus apiau – **Brazil:** Roraima: Serra do Apiau: Without number.

Anomaloglossus beebei – **Guyana:** Mount Ayaganna, Northeast plateau: ROM 42388. District 8: Kaieteur NP: ROM 42994. IRSNB

Anomaloglossus kaiei PK 1200

Anomaloglossus megacephalus – **Guyana:** Ayaganna, Northeast plateau: ROM 42390.

Anomaloglossus roraima PK 2047

Anomaloglossu sp. – **Guyana:** Mount Wokomung: ROM 43933, 43936.

Anomaloglossus tamacuarensis – **Venezuela:** Amazonas: Sierra Tapirapecó: AMNH 131348.

Anomaloglossus tepuyensis – **Venezuela:** Bolíva: Auyantepui: AMNH 164840.

Aromobates mayorgai – **Venezuela:** Merida: La Azulita: KU 167808.

Aromobates saltuensis – **Colombia:** Cucuta: Tonchala: GAB 126.

Colostethus brachyhistriatus – **Colombia:** Risaralda: Pereira: Bosque Campo Alegre: GGD1084.

Colostethus fraterdanieli – **Colombia:** Antioquia: Betania: ICN 40800, 40801. Urrao: MAA 231. Caldas: Neira: JJS 112. ICN 45928

Colostethus imbricolus – **Colombia:** Chocó: Río Quito: ICN 55314.

Colostethus mertensi – **Colombia:** Cauca: Inderena: ICN 9690.

Colostethus panamansis – **Panama:** Colcé: El Valle: AMNH 69831.

Colostethus pratti – **Panama:** Río Claro: Cerca Río Changena: KU 104232.

Colostethus ramirezi – Colombia:

Colostethus ruthveni – **Colombia:** Magdalena: ICN 19776.

Dendrobates auratus – **Colombia:** Chocó: Capugarná: LEP 098.

Dendrobates tinctorius – **French Guiana:** Nouragues: AF (without number).

Dendrobates truncatus – **Colombia:** Córdoba: Pueblo Nuevo: ICN 48945, 48947. Santander: Sabana de Torres: ICN 54630. Magdalena: Santa Marta: ICN 45735.

Epipedobates anthonyi – **Ecuador**: El Oro: El Progreso: QCAZ 18553, QCAZ 18554, QCAZ 18561. **Ecuador**: Azuay: Santa Isabel: QCAZ 21130.

Epipedobates boulengeri – **Colombia**: Cauca: Isal Gorgona: WB 3054. **Colombia**: Natiño: Tumaco: Llorente: ICN 55653. **Ecuador**: Esmeraldas: Alto Tombo: QCAZ 16960.

Epipedobates espinosai – **Ecuador**: Pichincha: Centro Científico Río Palenque: AMNH 108019.

Epipedobates darwinwallacei – **Ecuador**: Pichincha: El Abrazo del Árbol: MZUTI 2105.

Epipedobates machalilla – **Ecuador**: Manabí: Río Ayampe: QCAZ 10329 (captivity bread), QCAZ 18508–09.

Epipedobates narinensis – **Colombia**: Nariño: Barbacoa: Reserva Natural Biotopo Selva Húmeda: ICN 55646–7, 55649–52, JJM 716.

Excidobates condor – **Ecuador:** Zamora Chichipe: Paquisa, Rio Blanco: EPN 14337.

Hyloxalus anthracinus – **Ecuador:** Morona-Santiago: Páramos de Matanga: QCAZ 2697.

Hyloxalus awa – **Ecuador:** Pichincha: Unión del Toachi: QCAZ 15379.

Hyloxalus bocagei – **Ecuador:** Napo: Rio Reventador: QCAZ 4230. Carretera Quito-Lago Agrio: QCAZ 17769.

Hyloxalus cepedai – **Colombia:** Meta: Villavicencio: ICN 55275.

Hyloxalus craspedoceps – **Peru:** San José de Sisa: El Zapatero: KU 215609.

Hyloxalus delatorre – **Ecuador:** Carchi: Maldonado: QCAZ 2130

Hyloxalus edwardsi – **Colombia:** Cundinamarca: La Calera, Vereda las Moyas: ICN 35814.

Hyloxalus elachyhistus – **Ecuador:** Azuray: La Mercedez: QCAZ 31756 Ecuador, Azuay, La Mercedez. **Peru:** Ayabaca: KU 212487.

Hyloxalus idiomelus – **Peru:** San Martín: Abra Miguel: KU 215607

Hyloxalus infraguttatus – **Ecuador:** Bolívar: Road Bucay-Chillanes, near Río Limón: QCAZ 42304.

Hyloxalus insulatus – **Peru:** Balsas: KU 215600.

Hyloxalus italoi – **Colombia:** Caqueta: Florencia: ICN 23789. Ecuador: Pastaza: Pomona: QCAZ 33220.

Hyloxalus jacobuspetersi – **Ecuador:** Carchi: Carretera Maldonado-Tulcan: QCAZ 18527.

Hyloxalus leucophaeus – **Peru:** Molinopampa: KU 215603.

Hyloxalus maculosus – **Colombia:** Caquetá: Florencia: ICN 23781. Ecuador: Pastaza: Sell: QCAZ 37864.

Hyloxalus mystax – **Ecuador:** Zamora-Chinchipe: Los Encuentros: QCAZ 40068.

Hyloxalus nexipus – **Ecuador:** Morona Santiago: Macas via a Méndez: QCAZ 32899.

Hyloxalus pulchellus – **Colombia:** Cauca: Paletará: ICN 9682. ICN 6980, 12137

Hyloxalus sauli – **Ecuador:** Orellana: Estación Científica Yasuni: QCAZ 14445.

Hyloxalus sordidatus – **Peru:** San José de Sisa: El Zapatero: KU 215611.

Hyloxalus subpunctatus – **Colombia:** Cudinamarca: Bogotá: ICN 45579, 55281, 55283-88; La Calera: ICN 33753. Boyacá: Pajarito: ICN 55279; Sotaquirá: ICN 45567.

Hyloxalus sylvaticus – **Peru:** Caraz: KU 138761.

Hyloxalus toachi – **Ecuador:** Esmeraldas: Durango: QCAZ 17255.

Hyloxalus vertebralis – Ecuador: Azuay: Sigsig: QCAZ 2777.

Hyloxalus whymperi – **Ecuador:** Pichincha: Cerro Tandapi: KU 113312.

Hyloxalus yasuni – **Ecuador:** Orellana: Parque Nacional Yasuní, KM6: QCAZ 45519.

Mannophryne collaris – **Venezuela:** Guárico: KU 167809.

Mannophryne herminae – **Venezuela:** Aragua: Research Station Rancho Grande: KU 139501.

Mannophryne neblinae – **Venezuela:** Aragua: Maracay, Rancho Grande: AMNH 116940.

Mannophryne olmonae – **Trinidad and Tobago:** Tobago Island: Chat-Lotteville: UWIZM 2010.918. Without precise location: CM 4502.

Mannophryne riveiroi – **Venezuela:** Sucre: Cerro Azul: KU 139471.

Mannophryne sp – **Venezuela**: CM 7675, 8971, 9107.

Mannophryne trinitatis – **Trinidad and Tobago:** Trinidad Island: UWIZM 2010.916.

Minyobates steyermaki – **Venezuela:** Amazonas: Cerro Yapacana: AMNH 14972.

Phyllobates aurotaenia – **Colombia:** Chocó: Quibdo: ICN 55662.

Phyllobates lugubris – **Panama:** Almirante: KU 116750.

Phyllobates vittatus – **Costa Rica:** Palmar Norte, Rio Zapote: KU 93934.

Ranitomeya amazonica – **French Guiana:** St Georges: AF 3301.

Ranitomeya imitator – **Peru:** San Martín: Shapaja: KU 215613.

Ranitomeya sirensis – **Peru:** Madre de Dios: Cicra: MUSM 27565.

Ranitomeya variabilis – **Peru:** San Martín: road to Yurimaguas: ZSM008/2010 (captivity breed).

Ranitomeya ventrimaculata – **Colombia:** Amazonas: Leticia: ICN 53026, 53031.

Rheobates palmatus – **Colombia:** Cundinamarca: Albán: ICN 23311. Tibacuy: ICN 55301. Meta: Restrepo: ICN 20693. Santander: Charalalá: ICN 9721. San Vicente de Chucurri: ICN 55303.

Rheobates pseudopalmatus – **Colombia:** MHUA.

Silverstoneia cff. *daly* – **Colombia:** ICN 55313.

Silverstoneia flotator – **Panama:** Río Changena: KU 104227; LACM174570.

Silverstoneia nubicola – **Panama:** Laguna: KU 77604

"*Prostherapis dunni*" – **Venezuela:** El Limón: KU 139468.

Outgroup taxa

Bufonidae

Rhinella marina – **Colombia:** ICN

Hylodidae

Crossodactylus aaenus – **Brazil:** Rio de Janeiro: Guapimirin, Barreira acima do Rio Soberbo: MNRJ 35041, 44595. Duque de Caxias: Taquara, Véu da Noiva: MNRJ 90202.

Crossodactylus cyclospinus – **Brazil:** Minas Gerais: Santa Maria do Salto, Fazendo duas barras: MNRJ 36479.

Crossodactylus gaudichaudii – **Brazil:** Rio de Janeiro: Parque Lage, Floresta da Tijuca: MNRJ 35073, 35087. Horto Botânico: MNRJ 38631. Angra dos Reis: Ilha Grande: MNRJ 80949.

Crossodactylus trachystomus – **Brazil:** Minas Gerais: Ouro Preto, Serra do Bico de Pedra: MNRJ 47935.

Hylodes asper – **Brazil:** Rio de Janeiro: Guapimirin, Barreira acima do Rio Soberbo: MNRJ 35037–38. Paraty, road Paraty-Cunha: MNRJ 45182.

Hylodes babax – **Brazil:** Minas Gerais: Ouro Preto, Floresta Estadual Uaímii: MNRJ 90199.

Hylodes charadranaetes – **Brazil:** Rio de Janeiro: Teresópolis, Parque Nacional da Serra dos Órgãos: MNRJ 45742. Friburgo, Theodoro de Oliveira: MNRJ 67517.

Hylodes fredii – **Brazil:** Rio de Janeiro: Angra dos Reis, Ilha Grande: MNRJ 68308, 90195.

Hylodes heyeri – **Brazil:** Paraná: Morretes: MNRJ 78823. São Paulo: Iguape: MNRJ 89948.

Hylodes lateristrigatus – **Brazil:** Espirito Santo: Santa Tereza, São Lourenço: MNRJ 35056.

Hylodes magalhesi – **Brazil:** Minas Gerais: Camanducaia, Monte Verde: MNRJ 35051.

Hylodes meridionalis – **Brazil:** Santa Catarina: Urubici: MNRJ 87595. Praia Grande: MNRJ 87596.

Hylodes nasus – **Brazil:** Rio de Janeiro: Rio de Janeiro, Floresta da Tijuca: MNRJ 29024, 53443. Horto Botânico: 38362.

Hylodes cf. *ornatus* – **Brazil:** Minas Gerais: Itamonte, Brejo da Lapa: MNRJ 35053.

Hylodes phyllodes – **Brazil:** Rio de janeiro: Angra dos Reis, road to Lídice: MNRJ 35034. São Paulo: Ubatuba, Beach Caçanduquinha: MNRJ 40169.

Hylodes cf. *phyllodes* – **Brazil:** Rio de Janeiro: Rio Claro: MNRJ 87594.

Hylodes pipilans – **Brazil:** Rio de Janeiro: Cachoeiras de Macacu: MNRJ 82402, 82426.

Hylodes uai – **Brazil:** Minas Gerais: Belo Horizonte, Parque das Mangabeiras: MNRJ 35049.

Megaelosia apuana – **Brazil:** Espirito Santo: Domingos Martins, Pedra Azul: MNRJ 26056.

Odontophrynidae

Macrogenioglottus alipioi – **Brazil:** Alagoas: Maceió, Mata do Catolé: MUFAL 9059, 1081. Murici, Fazenda Bananeira: MUFAL 10756.

Leptodactylidae

Leptodactylus fuscus – Brazil: Bahia: Feira de Santana, Serra de São José: MZFS 495.

Pleurodema diplolister – Brazil: Bahia: Feira de Santana: MZFS 326. Elísio Medrado, Serra da Jibóia: MZFS 1324.

Rupirana cardosoi – Brazil: Bahia: Palmeiras: MZFS 519. Caravelas: MZFS: 586.

APPENDIX IV

Genbank accession numbers

Most sequences employed in this study were also used by Grant et al. (2017). Below, I update Grant et al.`s (2017) table with terminals included herein.

Species	**Terminal label**	**MT-CYB**	**H1_ND2**	**MT-CO1**	**RHO**	**H3F3C**	**TYR**	**RAG1**	**SIAH1**	**RNA28S**	**ZEB2**	**POMC**
Amazophrynella manaos	Amazophrynella_manaos_INPA16944		KF433954									
Ameerega trivittata,	Ameerega_trivittata_MJH7483	DQ502543	DQ502111	DQ502821	DQ503224	DQ502334			DQ503086	DQ502985		
Alsodes gargola	Alsodes_gargola_CNP381	JX203955	JX204168									
Alsodes nodosus	Alsodes_nodosus_IZUA3558	JX203960	JX204174		JX204107				JX204241			
Anaxyrus americanus	Anaxyrus_americanus_KU289469	DQ158426					DQ158352				DQ158268	

Anomaloglossus surinamensis	Anomaloglossus_surinamensis_AF3349		KY510159				KY549551	KY549470				KY549512
Anomaloglossus sp north	Anomaloglossus_spnorthFG_AF0953		KY510060				KY549533	KY549450				KY549493
Anomaloglossus sp Bakhuis	Anomaloglossus_spBakhuis_AF3426		KY510165.1				KY549552.1	KY549471				KY549513.1
Anomaloglossus leopardus	Anomaloglossus_leopardus_AF2041		KY510108.1				KY549534.1	KY549452.1				
Anomaloglossus sp Mitaraka	Anomaloglossus_spMitaraka_AF2751		KY510142.1				KY549548.1	KY549467.1				KY549509.1
Anomaloglossus sp Mitaraka2	Anomaloglossus_spMitaraka_AF2732		KY510141.1				KY549547.1	KY549466.1				KY549508.1

Anomaloglossus sp Itoupe 1	Anomaloglossus_spItoupe_PG660		KY510267.1									
Anomaloglossus sp Itoupe 2	Anomaloglossus_spItoupe_PG659		KY510266.1									
Anomaloglossus sp Acari 1	Anomaloglossus_baeobatrachus_acari_MPEG30248		KY510220.1									
Anomaloglossus sp Acari 2			KY510221.1									
Batrachyla taeniata	Batrachyla_taeniata_DBGUCH2943		DQ864550 ; AY578817									
Crossodactylus aeneus	Crossodactylus_aeneus_MTR22741	RM	RM	RM	RM	RM	RM	RM		RM		
Crossodactylus caramaschii	Crossodactylus_caramaschi_CFBHT06917	0	KJ961569	KJ961549	0	0	0	0	0	0	0	0

Crossodactylus gaudichaudii	Crossodactylus_gaudichaudii_MNRJ40552	RM	RM		RM		RM	RM				
Crossodactylus timbuhy	Crossodactylus_timbuhy_UFMGT3379	RM	RM		RM	RM	RM	RM		RM		
Dendrophryniscus brevipolicatus	Dendrophryniscus_brevipollicatus_AF1541		JN867527 ; JN867554									
Dendrophryniscus leucomystax	Dendrophryniscus_brevipollicatus_AF1541		JN867530 ; JN867557									
Frostius pernambucensis	Frostius_erythrophthalmus_MTR22228		MF573828									
Hylorina sylvatica	Hylorina_sylvatica_MACN42530	AY389143	JX204222									
Incilius aucoinae	Incilius_aucoinae_UCR14323	HM563934	HM563819 ; HM563861 ; JN868007	JN867953								

Incilius boucorti	Incilius_bocourti_UTA50920	HM563936	HM563821 ; HM563863 ; JN868008 ; JN868045									
Incilius coccifer	Incilius_coccifer_KU290030	HM563943	DQ158443 ; AY927856 ; JN868015 ; JN868051	JN867963								
Incilius coniferus	Incilius_coniferus_MVZ203775	HM563945	HM563829 ; AY927859 ; JN868001 ; JN868001	JN867965								
Melanophryniscus moreirae	Melanophryniscus_moreirae_CFBHT01521		KU495389.1	KU494596								
Nannophryne variegata	Nannophryne_variegata_IZUA3198		DQ158494 ; DQ158494									
Odontophrynus cultripes	Odontophrynus_cultripes_FSFL875		FJ685688 ; KF214101		KF214203			FJ685708				
Paratelmatobius gaigae	Paratelmatobius_gaigea		EU224397									

	e_CFBH7156											
Peltophryne peltocephala	Peltophryne_peltocephala_Bp019		JF434663	JF434540								
Pleurodema diplolister	Pleurodema_diplolister_MTR3673	JQ937124	JQ937187		JQ937153				JQ937222			
Physalaemus cuvieri	Odontophrynus_cultripes_FSFL875	AY843975	AY843729		AY844717				AY844922			
Proceratophrys cristiceps	Proceratophrys_cristiceps_AF887	FJ685675	FJ685695 ; KF214106		KF214208			FJ685715				
Proceratophrys schichi	Proceratophrys_schirchi_voucher_371	FJ685681	FJ685701 ; KF214112		KF214214			FJ685721				
Rhaebo glaberrimus	Rhaebo_glaberrimus_QCAZ14708		DQ158454									
Rinella marina	Rhinella_marina_MJH3678		DQ283062		DQ283789	DQ284092				DQ283472		

Thoropa megatympanum	Thoropa_megatympanum_MCAM2072		MG799575	MG799626				MG799756				
Thoropa saxatilis	Thoropa_saxatilis_MCP11918		MG799573	MG799619				MG799749				
Vitreorana eurygnatha	Vitreorana_eurygnatha_CFBHT10533b		KU495611	KU494818								
Vitreorana uranoscopa	Vitreorana_uranoscopa_CFBHT12320		KU495613	KU494820								

APPENDIX V

Adult phenotypic characters

All phenomic adult characters and character-states are listed below. For complete character descriptions see Grant et al. (2006, 2017)

0. Dorsal skin texture: (0) smooth; (1) posteriorly granular; (2) strongly granular; (3) speculate. Nonadditive.

1. Palmar skin: (0) taut; (1) loose.

2.. Paired dorsal digital scutes: (0) absent; (1) present.

3. Supernumerary tubercles on hand: (0) absent; (1) present.

4. Distal tubercle on Finger IV: (0) absent; (1) present.

5. Finger IV length: (0) surpassing distal subarticular tubercle of Finger IV; (1) reaching distal 1/2 of subarticular tubercle of Finger IV; (2) not reaching distal subarticular tubercle of Finger IV. Additive.

6. Relative lengths of Fingers II and III: (0) II<<III (1.2 or more times longer); (1) II<III ; (2) II=III; (3) II>III. Additive.

7. Digital discs: (0) absent; (1) present.

8. Finger disc II: (0) unexpanded; (1) weakly expanded; (2) moderately expanded. Additive.

9. Finger disc III: (0) unexpanded; (1) weakly expanded; (2) moderately expanded; (3) greatly expanded. Additive.

10. Finger disc IV: (0) unexpanded; (1) weakly expanded; (2) moderately expanded; (3) greatly expanded. Additive.

11. Finger disc V: (0) unexpanded; (1) weakly expanded; (2) moderately expanded; (3) greatly expanded. Additive.

12. Finger fringe: II preaxial: (0); absent (1) present.

13. Finger fringe: II postaxial: (0) absent; (1) present.

14. Finger fringe: III preaxial: (0) absent; (1) present.

15. Finger fringe: III postaxial: (0) absent; (1) present.

16. Finger fringe: IV preaxial: (0) absent; (1) present.

17. Finger fringe: IV postaxial: (0) absent; (1) present.

18. Finger fringe: V preaxial: (0) absent; (1) present.

19. Finger fringe: V postaxial: (0) absent; (1) present.

20. Metacarpal ridge/fold: (0) absent; (1) present.

21. Finger III swelling in adult males: (0) absent; (1) present.

22. Morphology of swollen third finger in males: (0) pre- and postaxial swelling; (1) weak preaxial swelling; (2) strong preaxial swelling; (3) swelling extending from wrist, mainly preaxial on digit. Nonadditive.

23. Carpal pad: (0) absent; (1) present.

24. Male nuptial excrescenses on Finger II: (0) absent; (1) present.

25. Morphology of male nuptial excrescenses on thumb: (0) large, cornified spines; (1) small, uncornified spines; (2) nonspinous asperities. Additive.

26. Female nuptial excrescences on Finger II: (0) absent; (1) present.

27. Thenar tubercle: (0) absent or small, inconspicuous swelling; (1) large, conspicuous, well defined tubercle.

28. Black arm gland in adult males: (0) absent; (1) present.

29. Tarsal keel: (0) absent; (1) present.

30. Morphology of tarsal keel: (0) straight or weakly curved, extending from inner metatarsal tubercle to center of tarsus; (1) strong, tubercle like (=enlarged, curved) proximally, ext. from metatarsal tubercle; (2) short, tubercle like, not extending from metatarsal tubercle; (3) weak, short dermal thickening, not extending from metatarsal tubercle. Additive.

31. Tarsal fringe: (0) absent; (1) present.

32. Toe disc I: (0) unexpanded; (1) weakly expanded; (2) moderately expanded. Additive.

33. Toe disc II: (0) unexpanded; (1) weakly expanded; (2) moderately expanded. Additive.

34. Toe disc III: (0) unexpanded; (1) weakly expanded; (2) moderately expanded. Additive.

35. Toe disc IV: (0) unexpanded; (1) weakly expanded; (2) moderately expanded; (3) greatly expanded. Additive.

36. Toe disc V: (0) unexpanded; (1) weakly expanded; (2) moderately expanded. Additive.

37. Webbing: Toe I Preaxial: (0) absent; (1) fringe.

38. Webbing: Toe I Postaxial: (0) absent; (1) fringe; (2) 2; (3) 1.5; (4) 1; (5) 0. Additive.

39. Webbing: Toe II Preaxial: (0) absent; (1) 2.5; (2) 2; (3) 1; (4) 0. Additive.

40. Webbing: Toe II Postaxial: (0) absent; (1) 2; (3) 2 (with fringe); (3) 1.5; (4) 1; (5) 0. Additive.

41. Webbing: Toe III Preaxial: (0) absent; (1) fringe; (2) 3.5; (3) 3.5 (with fringe); (4) 3; (5) 2.5; (6) 2; (7) 1.5; (8) 1. Additive.

42. Webbing: Toe III Postaxial: (0) absent; (1) 3; (2) 3 (with fringe); (3) 2.5; (4) 2; (5) 1.5; (6) 1. Additive.

43. Webbing: Toe IV Preaxial: (0) absent; (1) 4; (2) 4 (with fringe); (3) 3.5; (4) 3; (5) 2.5; (6) 2; (7) 1. Additive.

44. Webbing: Toe IV Postaxial: (0) absent; (1) fringe; (2) 4; (3) 3.5; (4) 3; (5) 2.5; (6) 2; (7) 1. Additive.

45. Webbing: Toe V Preaxial: (0) absent; (1) fringe; (2) 2.5; (3) 2; (4) 1.5; (5) 1. Additive.

46. Webbing: Toe V Postaxial: (0) absent; (1) fringe.

47. Metatarsal fold: (0) absent; (1) weak; (2) strong. Additive.

48. Cloacal tubercles: (0) absent; (1) present.

49. Iridescent orange or golden spot at dorsal limb insertions: (0) absent; (1) present.

50. Pale paracloacal mark: (0) absent; (1) present.

51. Thigh dorsal coloration: (0) pale w/ dark spots (forming retic. when spots close together); (1) solid dark (black, brown, blue-green); (2) dark w/ pale spots/bands; (3) solid pale; (4) brown with dark brown bands/blotches; (5) dark with pale longitudinal stripe.

52. Discrete pale proximoventral calf spot: (0) absent; (1) present.

53. Dorsal stripe A occurrence (does not drop to thigh): (0) absent; (1) present.

54. Dorsolateral stripe A length: (0) anterior only (extending from eye to area above arm insertion); (1) complete (extending from eye well past area above arm insertion).

55. Dorsloateral stripe A structure: (0) series of discrete spots; (1) solid.

56. Dorsolateral stripe A ontogeny: (0) present in juveniles only (i.e., lost ontogenetically); (1) present in adults and juveniles.

57. Dorsolateral stripe B (drops to top of thigh, not groin): (0) absent; (1) present.

58. Ventrolateral stripe occurrence: (0) absent; (1) present.

59. Ventrolateral stripe structure: (0) wavy series of elongate spots; (1) straight.

60. Oblique lateral stripe: (0) absent; (1) present.

61. Oblique lateral stripe length: (0) partial; (1) complete.

62. Oblique lateral stripe structure: (0) solid; (1) series of spots; (2) diffuse. Nonadditive.

63. Gular-chest markings: (0) absent; (1) present.

64. Dermal collar: (0) absent; (1) present.

65. Dark lower labial stripe: (0) absent; (1) present.

66. Male throat (vocal sac) color: (0) pale, free or almost free of melanophores; (1) dark due to absence of iridophores; (2) evenly stippled; (3) pale with discrete dark spotting/reticulation/marbling; (4) solid dark; (5) dark with discrete pale spotting/reticulation/marbling; (6) irregular (clumped) stippling or faint, diffuse spotting. Nonadditive.

67. Female throat and chest color: (0) pale, free or almost free of melanophores; (1) irregular (clumped) stippling or faint, diffuse spotting; (2) solid dark; (3) dark with discrete pale spotting/reticulation/marbling; (4) pale with discrete dark spotting/reticulation/marbling; (5) dark with pale medial longitudinal stripe; (6) evenly stippled. Nonadditive.

68. Male abdomen color: (0) pale, free or almost free of melanophores; (1) pale with discrete dark spotting/reticulation/marbling; (2) evenly stippled; (3) dark with discrete pale spotting/reticulation/marbling; (4) irregular (clumped) stippling or faint, diffuse spotting; (5) solid dark. Nonadditive.

69. Female abdomen color: (0) pale, free or almost free of melanophores; (1) pale with discrete dark spotting/reticulation/marbling; (2) solid dark; (3) dark with discrete pale spotting/reticulation/marbling; (4) irregular (clumped) stippling or faint, diffuse spotting; (5) evenly stippled. Nonadditive.

70. Iris coloration: (0) lacking metallic pigmentation and pupil ring; (1) with metallic pigmentation and pupil ring.

71. Large intestine color: (0) unpigmented; (1) pigmented anteriorly; (2) pigmented entirely. Additive.

72. Adult testis color: (0) unpigmented; (1) pigmented medially only; (2) entirely pigmented. Additive.

73. Color of mature ova: (0) unpigmented (white or yellowish); (1) pigmented (animal pole brown).

74. M. semitendinosus insertion: (0) "bufonid type" (ventrad); (1) "ranid type" (dorsad).

75. M. semitendinosus binding tendon: (0) absent; (1) present.

76. M. adductor mandibulae externus superficialis: (0) undivided (s); (1) divided (s+e).

77. M. depressor mandibulae dorsal flap: (0) dorsal flap absent; (1) dorsal flap present.

78. M. depressor mandibulae origin posterior to squamosal: (0) absent; (1) present.

79. M. depressor mandibulae origin on annulus tympanicus: (0) no fibers originating from annulus tympanicus; (1) some fibers originating from annulus tympanicus.

80. Tympanum and m. depressor mandibulae relation: (0) tympanum superficial to m. depressor mandibulae; (1) tympanum covered superficially by m. depressor mandibulae.

81. Vocal sac occurrence: (0) absent; (1) present.

82. Vocal sac structure (sensu Liu, 1935): (0) median, subgular; (1) paired lateral.

83. M. intermandubularis supplementary element occurrence: (0) absent; (1) present.

84. M. intermandibularis supplementary element orientation: (0) anterolateral; (1) anteromedial.

85. Median lingual process (MLP): (0) absent; (1) present.

86. MLP shape: (0) short, bumplike; (1) elongate.

87. MLP tip: (0) blunt; (1) tapering to point.

88. MLP texture: (0) smooth; (1) rugose.

89. MLP orientation when protruded: (0) upright; (1) posteriorly reclined.

90. MLP retractility: (0) nonretractile; (1) retractile.

91. MLP associated pit: (0) absent; (1) present.

92. MLP epithelium: (0) glandular; (1) nonglandular.

93. Advertisement calls: (0) buzz; (1) chirp; (2) trill; (3) retarded trill; (4) retarded chirp. Nonadditive.

94. Male courtship: Stereotyped strut: (0) absent; (1) present.

95. Male courtship: Jumping up and down: (0) absent; (1) present.

96. Female courtship: Crouching: (0) absent; (1) present.

97. Female courtship: Sliding under male: (0) absent; (1) present.

98. Timing of sperm deposition: (0) after oviposition; (1) prior to oviposition.

99. Reproductive amplexus occurrence: (0) absent; (1) present.

100. Reproductive amplexus position: (0) axillary; (1) cephalic.

101. Cloaca-cloaca touching: (0) absent; (1) present.

102. Egg deposition site: (0) aquatic; (1) terrestrial: leaf litter, soil, on or under stones; (2) terrestrial: above ground in vegetation (bromelias etc). Nonadditive.

103. Egg clutch attendance occurrence: (0) absent; (1) present.

104. Egg clutch attendant sex: (0) male; (1) female; (2) both. Nonadditive.

105. Dorsal tadpole transport: (0) absent; (1) present.

106. Sex of nurse frog: (0) male; (1) female; (2) both. Nonadditive.

107. Egg provisioning for larval oophagy: (0) both sexes involved; (1) female only.

108. Adult habitat selection: (0) aquatic riparian (<3 m from water); (1) independent of streams (up to ca. 30 m or more from water).

109. Dial activity: (0) nocturnal; (1) diurnal.

110. Toe trembling: (0) absent; (1) present.

111. Hyalia anterior process: (0) absent; (1) present.

112. Shape of terminal phalanges: (0) T-shaped; (1) knobbed.

113. Epicoracoid fusion in adults: (0) entirely fused (Kaplans E); (1) anteriorly fused, posteriorly free (Kaplan C); (2) fused at anterior extreme, free posteriorly (Kaplan A). Additive.

114. Epicoracoid overlap in adults: (0) no overlap (Kaplans B); (1) partial overlap (Kaplans E); (2) partial overlap (Kaplans C); (3) partial overlap (Kaplans A). Nonadditive.

115. Angle of clavicles: (0) laterad, perpendicular to sagittal plane; (1) directed posteriorly directed anteriorly.

116. Acromion process: (0) cartilaginous, distinct; (1) calcified/ossified fully, continuous with clavicle and scapula

117. Prezonal element (omosternun): (0) absent; (1) present.

118. Prezonal element (omosternum) anterior expansion: (0) not expanded distally, tapering to tip; (1) weakly expanded, to 2.5x style at base of cartilage or equivalent; (2) extensively expanded distally, 3.5x or greater. Additive.

119. Prezonal element (omosternum) shape of anterior terminus: (0) rounded or irregularly shaped; (1) distinctly bifid.

120. Prezonal element (omosternum) shape of posterior terminus: (0) simple; (1) notched, forming two struts continuous with epicoracoid cartilage

121. Prezonal element (omosternum) ossification: (0) entirely cartilaginous; (1) medially ossified (cartilaginous base and tip); (2) basally ossified (cartilaginous tip); (3) entirely ossified. Additive.

122. Suprascapula anterior projection: (0) cartilaginous; (1) heavily calcified.

123. Sternum shape: (0) simple, ovoid, or irregular; (1) medially divided, bifid.

124. Zygomatic ramus of squamosal: (0) elongate, slender, pointed; (1) very long and slender; (2) robust, truncate, and elongate; (3) shorter and less robust but still well defined; (4) well defined, moderate length, abruptly directed ventral; (5) inconspicuous, poorly differentiated; (6) very small, inconspicuous, hook-like; (7) miniscule bump; (8) robust, elongate, in broad contact with the maxilla. Nonadditive.

125. Orientation of alary process of premaxilla: (0) tilted anteriorly; (1) directed dorsally (vertical, not tilted); (2) tilted posteriorly. Additive.

126. Palatines: (0) absent; (1) present.

127. Quadratojugal-maxilla relation: (0) overlapping; (1) separated.

128. Nasal-maxilla relation: (0) separated; (1) in contact.

129. Nasal-sphenethmoid relation: (0) separate; (1) overlapping or fused.

130. Frontoparietal fusion: (0) entirely free (articulating, but not fused); (1) fused posteriorly fused along entire length.

131. Frontoparietal-otoccipital relation: (0) free, articulating but not fused; (1) fused.

132. Exoccipitals: (0) free, separate; (1) fused sagitally.

133. Maxillary teeth: (0) absent; (1) present.

134. Maxillary tooth structure: (0) pedicelate; (1) nonpedicelate.

135. Vomerine teeth: (0) absent; (1) present.

136. Retroarticular process of mandible: (0) absent; (1) present.

137. Expansion of sacral diapophyses: (0) unexpanded; (1) weakly expanded (1.5–2.5X); (2) strongly expanded. Additive.

138. Sacrum and vertebra 8: (0) free; (1) fused.

139. Vertebae 1 and 2: (0) free; (1) fused.

140. Vertebae 2 and 3: (0) free; (1) fused.

141. Ability to sequester liophilic alkaloids: (0) absent; (1) present.

142. Batrachotoxins (BTX): (0) absent; (1) present.

143. Histrionicotoxins (HTX): (0) absent; (1) present.

144. Pumiliotoxins (PTX): (0) absent; (1) present.

145. Allopumiliotoxins: (0) absent; (1) present.

146. Homopumiliotoxins: (0) absent; (1) present.

147. Decahydroquinolines (DHQ): (0) absent; (1) present.

148. 3,5-Disubstituted pyrrolizidines (3,5-P): (0) absent; (1) present.

149. 3,5-Disubstituted indolizidines (3,5-I): (0) absent; (1) present.

150. 5,8-disubstituted indolizidines (5,8-I): (0) absent; (1) present.

151. Dehydro-5,8-Indolizidines (Dehydro-5,8-I): (0) absent; (1) present.

152. 5,6,8-Trisubstituted indolizidines (5,6,8-I): (0) absent; (1) present.

153. 4,6-Disubstituted quinolizidines (4,6-Q): (0) absent; (1) present.

154. 1,4-Disubstituted quinolizidines (1,4-Q): (0) absent; (1) present.

155. Lehmizidines (Lehm): (0) absent; (1) present.

156. Epiquinamide: (0) absent; (1) present.

157. 2,5-Disubstituted pyrrolidines (PYR): (0) absent; (1) present.

158. 2,6-Disubstituted piperidines (Pip): (0) absent; (1) present.

159. Gephyrotoxins (GTX): (0) absent; (1) present.

160. Coccinelline-like tricyclics (Tricyclic): (0) absent; (1) present.

161. Cyclopentylquinolizidines (CPQ): (0) absent; (1) present.

162. Spiropyrrolizidines (SpiroP): (0) absent; (1) present.

163. Indolic alkaloids: (0) absent; (1) present.

164. Epibatidines: (0) absent; (1) present.

165. Noranabasamine: (0) absent; (1) present.

166. N-methyldecahydroquinolines (N-MeDHQ): (0) absent; (1) present.

167. Pumiliotoxin 7-hydroxylase: (0) absent; (1) present.

168. Tetrodotoxin (TTX): (0) absent; (1) present.

169. Chromosome number (2n): (0) 18; (1) 20; (1) 22; (2) 24; (3) 26; (4) 28; (5) 30. Additive.

APPENDIX VI

Complete list of phenotypic synapomorphies

'Thoropa_miliaris_AF1434','180(0-1)', '181(0-1)', '273(1-0)', '276(1-0)'
'Silverstoneia_flotator_KS35','274(1-0)', '285(0-1)', '298(0-1)', '413(1-2)', '433(1-2)', '436(1-2)', '447(0-1)'
'Rhinoderma_darwinii_IZUA3504','197(1-0)', '198(1-0)', '208(1-0)', '210(1-0)', '213(1-0)', '219(1-0)', '234(1-0)', '245(0-1)', '246(1-0)', '248(0-2)', '251(4-1)', '252(0-1)', '261(1-0)', '262(1-0)', '263(1-0)', '277(0-1)', '278(0-1)', '279(0-1)', '280(0-1)', '461(123-0)', '464(0-1)', '465(0-1)', '481(0-1)', '494(1-0)', '505(1-0)', '506(1-0)', '510(3-1)', '513(0-1)', '516(1-0)', '519(2-3)', '549(12-0)', '556(1-2)', '557(1-2)', '560(0-1)'
'Ranitomeya_ventrimaculata_JDL24489','9(2-3)', '215(0-1)', '229(1-0)', '235(0-1)', '271(0-1)', '280(1-0)', '283(0-1)', '303(1-0)'
'Ranitomeya_variabilis_Sucumbios_OMNH34091','149(1-0)', '152(0-1)', '153(0-1)'
'Ranitomeya_vanzolinii_OMNH36035','68(1-3)', '69(1-3)', '151(0-1)', '158(0-1)', '227(1-0)', '236(1-0)', '237(2-0)', '244(0-3)', '252(0-1)', '253(0-2)', '263(1-2)', '273(0-1)', '283(0-1)', '287(0-1)', '288(0-1)', '290(0-1)', '291(0-1)', '296(0-1)', '302(0-1)', '389(1-0)', '420(1-0)'
'Ranitomeya_uakarii_MPEG12394','11(3-2)', '65(0-1)'
'Ranitomeya_summersi_Chipaota_JLB07','9(2-3)', '51(0-5)', '145(1-0)', '150(0-1)', '166(0-1)'
'Ranitomeya_sirensis_JCS','9(2-3)', '29(1-0)', '33(0-2)', '34(1-2)', '212(0-1)', '237(2-3)', '243(0-1)', '267(0-3)', '280(1-0)', '283(0-1)', '287(0-1)', '288(0-1)', '290(0-1)', '291(0-1)', '296(0-1)', '347(1-0)', '357(0-1)', '372(0-1)', '377(1-0)'
'Ranitomeya_reticulata_MJH3754','4(1-0)', '9(2-1)', '10(3-2)', '11(3-2)', '33(0-1)', '36(1-0)', '57(1-0)', '104(0-2)'
'Ranitomeya_imitator_KS13','29(1-0)', '33(0-1)', '146(0-1)', '148(0-1)', '152(0-1)', '153(0-1)', '157(0-1)', '179(1-0)', '180(1-0)', '181(1-0)', '255(1-0)', '263(1-0)', '265(0-1)', '272(0-1)', '279(1-2)', '280(1-0)', '442(1-0)'
'Ranitomeya_flavovittata_Roberts','35(2-1)', '36(2-1)', '53(0-1)'
'Ranitomeya_defleri_JLB08_004','9(2-3)', '352(1-0)', '385(1-0)'
'Ranitomeya_cyanovittata_186','4(0-1)', '9(2-3)'
'Ranitomeya_amazonica_JLB08_019','4(1-0)', '238(0-1)', '240(2-1)', '252(0-1)', '287(0-1)', '293(0-1)'
'Ranitomeya_uakarii_JCS','106(0-2)'
'Phyllobates_vitattus_839','20(0-1)', '34(2-1)', '35(2-1)', '51(2-1)', '58(0-1)', '124(6-3)', '144(1-0)', '148(0-1)', '150(0-1)', '156(0-1)', '160(0-1)', '318(0-1)', '359(0-1)', '365(0-1)', '366(1-0)'
'Phyllobates_lugubris_USNMFS195116','47(1-0)', '115(0-1)', '116(0-1)', '118(2-1)', '129(1-0)', '149(1-0)', '152(0-1)', '158(0-1)', '223(0-1)', '229(0-1)', '319(1-0)', '328(1-0)', '338(1-0)', '339(1-0)', '340(1-0)', '353(0-2)', '358(1-0)', '372(1-0)', '374(1-0)'
'Phyllobates_bicolor_1233','139(0-1)', '150(0-1)', '201(1-0)', '226(0-3)', '248(1-2)', '271(0-1)', '339(1-2)', '341(0-1)', '395(2-1)'
'Paruwrobates_erythromos_QCAZ37750','5(0-1)', '8(1-2)', '9(1-2)', '36(1-2)', '47(1-0)', '51(4-1)', '141(0-1)'
'Oophaga_vicentei_KRL789','33(1-0)', '34(1-0)', '35(1-0)', '71(0-2)', '117(1-0)', '137(1-0)', '143(1-0)', '147(1-0)', '148(1-0)', '149(1-0)', '155(1-0)', '202(1-0)', '320(1-0)', '377(1-0)', '382(1-0)', '397(1-0)', '403(0-1)', '418(0-1)', '420(1-0)', '422(1-0)', '423(1-0)', '426(1-0)', '431(0-1)', '479(12-0)', '500(2-1)', '517(0-1)', '518(2-1)', '528(1-0)', '529(0-1)'
'Oophaga_speciosa_CWM17826','6(0-1)', '10(3-2)', '11(3-2)', '27(0-1)', '36(0-1)', '102(1-2)', '227(1-0)', '237(0-2)', '238(1-0)', '254(3-1)', '255(1-0)', '275(1-0)', '284(0-1)', '289(0-1)', '290(0-1)', '291(0-1)', '337(1-0)'
'Oophaga_pumilio_TNHCFS4814','146(0-1)', '151(0-1)', '160(0-1)', '161(0-1)', '162(0-1)'
'Oophaga_pumilio_OMNH33297','146(0-1)', '151(0-1)', '160(0-1)', '161(0-1)', '162(0-1)'
'Oophaga_lehmanni_CWM19050','36(1-0)', '72(2-1)', '146(0-1)', '147(1-0)', '149(1-0)', '151(0-1)', '153(0-1)'

'Oophaga_granulifera_CWM19044','0(0-2)', '47(0-1)', '69(3-2)', '227(1-0)', '304(2-0)'
'Oophaga_arborea_CWM18636','73(1-0)', '115(0-1)', '143(1-0)', '147(1-0)', '148(1-0)', '154(1-0)', '155(1-0)', '158(1-0)', '202(1-0)', '226(0-3)', '227(1-0)', '342(1-0)', '365(0-1)', '374(12-0)', '499(1-0)'
'Megaelosia_goeldii_MZUSP95879','6(1-3)', '24(1-0)', '36(1-2)', '38(2-3)', '40(2-3)', '42(2-4)', '43(2-3)', '44(1-2)', '45(1-2)', '47(0-2)', '81(1-0)', '83(1-0)', '124(2-8)', '169(4-56)', '170(0-1)', '222(1-0)', '241(1-0)', '263(1-0)', '272(0-1)', '297(0-1)', '299(1-0)', '300(1-0)', '301(0-1)', '406(0-1)', '428(1-2)'
'Mannophryne_yustizi_TNHCFS5604','8(1-0)', '47(1-2)', '55(1-0)', '235(0-1)'
'Mannophryne_venezuelensis_TNHCFS5649','5(0-1)', '40(1-2)', '41(2-3)', '42(1-3)', '43(1-2)'
'Mannophryne_trinitatis_MVZ199828','6(2-1)', '14(1-0)', '16(1-0)', '44(1-0)', '45(1-0)', '46(1-0)'
'Mannophryne_riveroi_MIZA319','8(1-2)', '9(1-2)', '10(1-2)', '11(1-2)', '47(1-0)', '62(1-2)', '66(2-0)', '202(0-1)', '237(2-3)', '251(4-3)', '272(0-1)', '279(0-2)', '282(1-0)', '294(1-0)', '339(23-1)', '341(0-1)', '347(1-0)', '376(0-1)', '386(0-1)', '392(0-1)', '395(2-0)'
'Mannophryne_oblitterata_MIZA336','24(0-1)', '38(34-5)', '40(34-5)', '41(4-6)', '42(34-6)', '43(3-4)', '44(23-4)', '45(3-5)', '47(1-2)', '204(0-1)', '235(0-1)', '239(0-1)', '309(1-0)', '320(1-0)', '396(0-1)', '451(0-1)'
'Mannophryne_lamarcai_MIZA318','47(1-2)'
'Mannophryne_herminae_CWM','58(0-1)', '69(0-4)'
'Mannophryne_cordilleriana_TNHCFS5589','8(1-0)', '9(1-0)', '10(1-0)', '11(1-0)', '32(2-1)', '33(2-1)', '34(2-1)', '35(2-1)', '36(2-1)', '47(1-2)', '68(2-0)'
'Mannophryne_caquetio_MIZA337','38(3-2)', '42(3-2)', '43(3-2)'
'Hyloxalus_subpunctatus_TNHCFS4957','204(0-1)', '260(0-1)'
'Hyloxalus_subpunctatus_MUJ5212','308(0-1)'
'Hyloxalus_shuar_CJ2622','108(1-2)', '235(1-0)', '239(0-1)', '248(0-1)', '256(0-1)', '270(0-1)', '272(0-1)', '275(0-1)', '284(1-0)', '291(1-0)', '292(1-0)', '294(1-0)', '295(1-0)', '324(1-0)', '328(1-0)', '332(0-1)', '340(1-0)', '342(1-0)', '372(1-0)', '378(1-0)'
'Hyloxalus_pulchellus_QCAZ15964','66(2-5)', '212(1-0)', '270(0-1)', '388(1-0)', '396(0-1)', '420(2-1)', '428(1-2)', '429(1-2)'
'Hyloxalus_leucophaeus_KU211880','237(2-1)', '269(1-0)', '272(1-0)', '274(1-0)', '283(0-1)'
'Hyloxalus_lehmanni_MAR2675','33(1-2)', '71(0-1)', '212(1-0)', '214(2-3)', '235(1-0)', '237(3-2)', '255(1-0)', '269(1-0)', '291(1-0)', '292(1-0)', '294(1-0)', '295(1-0)', '296(1-0)'
'Hyloxalus_jacobuspetersi_QCAZ37742','21(0-1)', '69(0-3)', '181(0-1)', '236(1-0)', '273(0-1)', '341(1-0)', '343(1-0)', '353(0-1)', '378(1-0)'
'Hyloxalus_delatorreae_KU220621','47(1-0)', '58(0-1)', '108(1-2)', '170(0-1)', '252(1-0)', '349(0-1)', '368(0-1)', '473(1-0)', '556(2-1)'
'Hyloxalus_craspedoceps_MHNSM22882','6(2-3)', '47(1-0)', '54(1-0)', '62(0-2)', '68(3-0)', '69(3-0)', '233(0-1)', '269(0-1)', '270(0-1)', '289(1-0)', '297(0-1)', '309(1-0)', '311(1-0)', '317(0-1)', '328(1-0)', '332(0-1)', '334(1-0)', '350(1-0)', '361(1-2)', '363(0-1)', '364(0-1)', '372(1-0)'
'Hyloxalus_anthracinus_KU223489','5(0-1)', '6(1-2)', '20(0-1)', '28(0-1)', '30(1-2)', '66(2-4)', '68(3-5)', '212(1-0)', '215(2-0)', '232(0-1)', '271(1-0)', '280(0-1)', '318(0-1)', '328(1-0)', '329(1-0)', '332(1-0)', '335(0-5)', '336(1-2)', '339(12-3)', '340(1-0)', '343(1-2)', '356(0-1)', '358(1-2)', '378(1-2)', '399(2-6)', '401(3-4)', '433(1-2)'
'Excidobates_condor_EPN14337','5(0-1)', '10(2-1)', '27(1-0)', '215(0-1)', '229(1-0)', '261(1-0)', '280(0-1)'
'Excidobates_captivus_QCAZ27442','4(1-0)', '29(1-0)', '35(1-2)', '49(0-1)', '53(0-1)', '246(1-0)', '274(3-0)'
'Epipedobates_espinosai_QCAZ27224','50(0-1)', '61(1-0)', '203(1-2)', '212(0-1)', '214(2-1)', '219(2-1)', '257(1-0)', '283(1-0)', '287(1-0)', '288(1-0)', '289(1-0)', '292(1-0)', '293(1-0)', '296(1-0)', '300(1-0)', '312(1-0)', '319(1-0)', '335(1-0)', '349(0-1)', '356(0-1)', '362(0-1)', '364(0-1)', '371(1-0)'
'Crossodactylus_schmidti_MLPA1414','170(0-1)', '237(2-3)', '244(2-3)', '255(1-0)', '270(0-1)', '274(1-0)'
'Colostethus_ruthveni_like_PAG1210','37(0-1)', '40(1-2)', '41(2-3)', '42(1-2)', '43(0-2)', '44(0-1)', '45(0-1)', '46(0-1)', '47(1-2)'
'Colostethus_panamansis_CH5546','45(01-2)', '72(01-2)', '168(0-1)'
'Colostethus_inguinalis_MUJ3247','10(1-2)', '32(1-2)', '36(1-2)', '39(1-2)', '68(0-5)', '269(0-1)', '361(1-2)', '363(0-1)', '372(1-0)', '386(1-0)', '396(1-0)', '426(1-0)', '427(2-0)', '447(0-1)'
'Atelopus_spurrelli_MHNUC273','37(0-1)', '41(6-7)', '42(5-6)', '44(4-5)', '46(0-1)'
'Aromobates_saltuensis_MUJ3726','33(1-2)', '34(1-2)', '35(1-2)', '41(4-3)', '108(1-2)'

'Aromobates_meridensis_CVULA7399','8(1-0)', '9(1-0)', '10(1-0)', '11(1-0)', '21(0-1)', '37(1-0)', '40(2-1)', '43(2-1)', '46(1-0)', '53(1-0)'
'Aromobates_cannatellai_CVULA8325','30(0-1)', '41(4-56)', '42(3-2)', '69(0-4)'
'Anomaloglossus_verbeeksnyderorum_TNHCFS5631','0(1-0)', '39(2-1)', '45(3-2)', '108(1-2)'
'Anomaloglossus_tepuyensis_VUB3734','8(1-2)', '9(1-2)', '10(1-2)', '11(1-2)', '41(4-5)', '67(0-13)', '68(0-34)', '297(0-1)', '335(0-2)', '336(1-0)', '338(1-0)', '353(0-1)', '362(0-1)', '376(0-1)', '417(0-1)', '418(1-0)', '427(2-1)'
'Anomaloglossus_tamacuarensis_MNRJ38049','21(0-1)', '22(1-0)', '61(0-1)', '212(1-0)', '247(0-2)', '263(1-0)', '289(1-0)', '305(1-2)', '311(1-2)', '325(0-1)', '332(1-0)', '336(1-2)', '349(0-1)', '385(1-0)', '408(1-0)', '467(2-0)', '476(0-1)', '479(1-2)', '495(1-0)', '503(0-1)', '520(0-1)', '547(2-3)', '548(2-3)', '551(0-1)', '553(1-2)'
'Anomaloglossus_Tafelberg_UTAA55758','13(0-1)', '38(2-1)', '40(2-3)', '42(2-3)', '44(1-0)', '45(1-0)', '46(1-0)', '60(1-0)', '67(1-4)'
'Anomaloglossus_degranvillei_Vences','5(12-0)', '33(1-2)', '38(2-3)', '53(0-1)', '69(0-4)', '73(1-0)'
'Anomaloglossus_Brownsberg_UTAA56469','8(1-2)', '9(1-2)', '10(1-2)', '11(1-2)', '20(0-1)', '33(1-2)'
'Andinobates_tolimensis_TG2057','170(0-1)', '212(1-0)', '220(1-0)', '274(3-0)', '280(1-0)'
'Andinobates_opisthomelas_TG1591','66(5-4)', '67(3-2)', '116(1-0)', '158(0-1)', '180(0-1)', '181(0-1)', '304(2-1)', '328(1-0)', '347(0-1)', '390(0-1)'
'Andinobates_geminisae_CH9386','67(3-2)', '68(3-5)', '69(3-2)'
'Andinobates_fulguritus_MHNUC340','51(0-5)', '53(0-1)', '60(0-1)', '220(1-0)', '240(2-1)', '243(0-1)', '251(4-1)', '252(0-1)', '253(1-2)', '263(1-0)', '273(0-1)', '299(0-1)', '339(0-1)', '485(0-1)'
'Andinobates_cassidyhornae_GECOH1523C','10(2-1)', '11(2-1)', '204(1-0)', '220(1-0)', '324(0-1)', '342(1-0)', '350(1-0)', '359(0-1)', '369(0-1)', '377(1-0)', '382(1-0)', '383(1-0)', '385(1-0)', '425(0-1)', '429(1-2)', '447(0-1)', '448(0-1)'
'Andinobates_altobueyensis_MAR1597','184(1-0)', '219(3-2)', '253(1-2)', '363(0-1)', '364(1-0)', '377(1-0)', '385(1-0)', '485(0-1)', '493(0-1)', '500(1-0)', '518(1-2)', '541(0-1)', '552(0-1)', '555(1-0)'
'Ameerega_yungicola_CBF3900','49(0-1)'
'Ameerega_trivittata_TNHCFS4966','212(0-1)', '233(1-0)', '235(0-1)', '287(1-0)', '290(1-0)', '291(1-0)', '294(1-0)', '295(1-0)', '342(1-0)', '369(0-1)', '409(0-2)', '427(1-2)', '433(234-0)', '436(0-1)', '441(1-0)', '447(0-1)'
'Ameerega_trivittata_MPEG12504','296(1-0)', '336(0-2)', '377(1-0)', '408(1-0)', '442(0-1)'
'Ameerega_sp_PortoWalter1_MPEG12482','149(0-1)'
'Ameerega_silverstonei_646','8(0-1)', '9(0-1)', '21(1-0)', '30(1-0)', '60(1-0)', '65(0-1)', '67(4-2)', '68(1-5)', '69(1-02)', '116(1-0)', '129(1-0)', '130(1-0)', '131(1-0)', '132(1-0)', '143(1-0)', '147(1-0)', '160(0-1)', '164(0-1)', '181(1-0)', '182(0-1)', '183(0-1)', '232(0-1)', '235(0-1)', '271(1-0)', '388(1-0)'
'Ameerega_pulchripecta_CWM19053','58(0-1)', '70(1-0)', '71(0-1)', '133(1-0)', '162(0-1)', '170(01-2)', '204(0-1)', '246(1-0)', '251(4-3)', '254(1-3)', '274(1-3)'
'Ameerega_pongoensis_EpongoHC11C','52(1-0)'
'Ameerega_petersi_MJH3715','106(0-2)'
'Ameerega_macero_LR742','145(0-1)', '162(0-1)'
'Ameerega_flavopicta_MZUSP111790','30(2-1)', '40(1-2)', '41(2-3)', '42(2-3)', '204(0-1)', '215(2-0)', '279(01-2)'
'Ameerega_cainarachi_MHNSM22720','144(1-0)', '145(0-1)'
'Ameerega_braccata_MRT5603','274(1-3)'
'Ameerega_boehmei_E81_3','65(0-1)'
'Ameerega_bassleri_MHNSM22600','51(1-2)', '67(4-2)', '69(1-2)'
'Ameerega_altamazonica_iso2','133(1-0)', '219(1-2)', '246(1-0)'
'Amazophrynella_minuta_MJH7095','272(1-0)', '287(0-1)', '288(0-1)', '289(0-1)', '291(0-1)', '292(0-1)', '293(0-1)', '305(1-0)', '422(0-1)', '423(0-1)', '424(0-1)', '527(1-0)'
'Allobates_undulatus_AMNHA159139','23(0-1)', '58(1-0)', '65(0-1)', '122(0-1)', '227(0-1)', '232(0-1)', '252(0-1)', '253(0-1)', '269(0-1)', '286(0-1)', '293(0-1)', '296(0-1)', '297(0-1)', '299(0-1)', '300(0-1)', '319(1-0)', '324(0-1)', '339(1-2)', '348(0-1)', '358(01-2)', '362(0-1)', '364(0-1)', '408(1-0)', '428(1-2)'
'Allobates_sp_Neblina_AMCC106112','0(1-2)', '32(1-2)', '36(1-2)', '47(1-2)', '66(2-0)', '73(1-0)'

'Allobates_pittieri_MIZA339','8(1-0)', '11(1-0)', '23(0-1)', '34(2-1)', '35(2-1)', '68(0-2)', '133(1-0)'
'Allobates_niputidea_MUJ3520','5(1-2)', '32(1-0)', '36(1-0)', '42(1-3)', '47(1-0)', '228(0-1)', '248(0-2)'
'Allobates_nidicola_MPEG13821','249(1-0)', '346(0-1)', '491(1-2)', '518(1-2)'
'Allobates_magnussoni_MPEG11923','5(1-0)', '40(0-1)', '41(0-2)'
'Allobates_humilis_CVULA5690','4(0-1)', '6(3-1)', '9(0-1)', '11(1-2)', '30(1-0)', '32(0-1)', '33(1-2)', '37(0-1)', '50(1-0)'
'Allobates_hodli_AbuE2189','42(1-0)', '43(1-0)', '181(0-1)', '204(0-1)', '235(1-0)'
'Allobates_grillisimilis_APL12747','10(1-2)', '60(1-0)', '66(2-0)'
'Allobates_granti_148AF','11(1-0)', '40(0-1)', '41(0-2)', '47(0-1)', '53(1-0)', '201(1-0)', '239(0-1)', '241(1-0)'
'Allobates_chalcopis_Alca1','4(0-1)', '5(2-1)', '9(0-1)', '10(1-2)', '32(0-1)', '34(2-1)', '35(2-1)', '60(1-0)', '66(2-4)', '68(0-4)', '175(1-0)', '179(0-1)', '180(0-1)', '240(1-2)', '245(0-1)', '261(1-0)', '262(1-0)', '263(1-0)', '264(0-1)', '265(1-0)', '275(1-0)', '560(0-1)'
'Allobates_bacurau_INPAH35406','0(1-2)', '34(2-1)', '35(2-1)', '133(1-0)'
'Allobates_amissibilis_MTD47884','8(1-0)', '11(1-0)', '34(2-1)'
'Allobates_algorei_TNHCFS5551','4(0-1)', '6(3-2)', '42(1-0)', '43(1-0)'
'Adelphobates_quinquevittatus_OMNH36665','34(1-2)', '35(1-2)', '57(0-1)', '58(0-1)', '69(3-1)', '179(0-1)', '180(0-1)', '182(1-0)', '183(1-0)', '184(1-0)', '243(0-1)', '273(0-1)', '274(123-0)', '279(1-0)', '282(1-0)', '284(1-0)', '335(2-1)', '382(1-0)', '388(0-1)'
'Adelphobates_castaneoticus_OMNH34517','144(1-0)', '145(1-0)', '150(1-0)', '152(1-0)', '153(0-1)', '320(1-0)', '336(2-4)', '358(0-2)', '383(1-0)', '426(1-0)', '442(1-0)'
'Insuetophrynus_acarpicus_IZUA_3606','175(1-0)', '182(1-0)', '205(0-1)', '255(1-0)', '271(1-0)', '288(0-1)', '291(0-1)', '296(0-1)', '456(1-0)', '457(0-1)', '466(0-2)', '476(0-1)', '482(1-0)', '500(3-0)', '505(1-2)', '506(1-2)', '509(12-0)', '515(0-1)', '519(2-1)', '520(1-2)', '539(1-0)', '550(1-2)', '557(1-0)'
'Hylorina_sylvatica_MACN42530','184(1-0)', '187(0-1)', '188(0-1)', '227(0-1)', '239(0-1)', '246(1-0)'
'Atelognathus_patagonicus_MACN37905','170(01-2)', '212(0-1)', '240(1-2)', '244(012-3)', '251(4-0)', '252(0-1)', '263(1-0)', '266(0-1)', '271(1-0)', '279(0-2)'
'Alsodes_vanzolinii_IZUA3570','226(0-3)', '264(0-1)', '265(1-0)', '279(1-0)', '286(0-1)'
'Alsodes_nodosus_IZUA3558','243(0-1)', '274(1-0)', '275(0-1)', '279(1-2)', '296(1-0)'
'Alsodes_verrucosus_IZUA3576','202(0-1)', '243(0-1)', '271(1-0)', '294(1-0)', '295(1-0)'
'Alsodes_neuquenses_MACN37942','237(2-3)'
'Limnomedusa_macroglossa_MACN38641','215(01-2)', '237(2-3)', '239(0-1)', '242(2-1)', '244(2-0)', '247(0-2)', '252(0-1)', '255(1-0)', '472(0-1)', '478(01-3)', '489(0-1)', '496(0-1)', '501(0-1)', '512(0-3)', '531(0-1)', '557(0-1)'
'Macrogenioglottus_alipioi_CFBH12929','212(0-1)', '237(2-0)', '251(4-1)', '270(0-1)', '272(0-1)', '284(1-0)', '294(1-0)', '295(1-0)'
'Odontophrynus_cultripes_FSFL875','170(0-1)', '237(2-3)', '242(2-0)', '247(01-2)', '270(0-1)', '272(0-1)'
'Odontophrynus_americanus_JF1946','182(1-0)', '183(1-0)', '184(1-0)', '239(0-1)', '244(012-3)', '251(4-1)', '283(0-1)', '294(1-0)', '295(1-0)'
'Proceratophrys_schirchi_voucher_371','214(2-1)', '219(2-1)', '235(0-1)', '239(0-1)', '253(0-1)', '266(01-2)', '271(1-0)', '293(0-1)'
'Proceratophrys_appendiculata_MNRJ53936','177(0-1)', '203(1-0)', '237(2-0)', '247(01-2)', '255(1-0)', '283(0-1)', '300(0-1)', '304(1-0)'
'Proceratophrys_avelinoi_MACN47401','237(2-3)', '251(4-1)', '266(0-1)', '282(1-0)', '284(1-0)', '294(1-0)', '295(1-0)', '433(1-0)', '451(0-1)'
'Proceratophrys_bigibbosa_DB2313','182(1-0)', '183(1-0)', '184(1-0)', '238(0-1)', '268(1-0)', '287(0-1)', '290(0-1)', '291(0-1)', '296(0-1)', '407(1-0)', '433(1-2)'
'Proceratophrys_cristiceps_AF887','226(0-4)', '237(2-0)', '244(012-3)', '247(01-2)', '256(0-1)', '263(1-0)'
'Vitreorana_eurygnatha_CFBHT10533b','170(0-1)', '238(0-1)', '243(0-1)', '265(0-1)', '306(1-0)', '356(0-1)', '382(1-0)'
'Vitreorana_uranoscopa_CFBHT12320','177(1-0)', '181(0-1)', '217(1-0)', '220(01-3)', '226(0-1)', '228(0-1)', '229(1-2)', '237(3-0)', '240(0-1)', '269(0-1)', '279(0-2)', '280(0-2)', '282(1-0)', '284(1-0)', '287(1-0)', '289(1-0)', '290(1-0)', '291(1-0)', '294(1-0)', '295(1-0)', '307(0-1)', '309(0-1)', '328(0-1)', '329(0-1)', '340(0-1)', '359(1-0)'

'Thoropa_saxatilis_MCP11918','238(0-1)', '265(1-0)', '280(0-1)'

'Thoropa_megatympanum_MCAM2072','272(0-1)'

'Thoropa_taophora_USNM209318','519(2-1)'

'Crossodactylus_timbuhy_UFMGT3379','235(1-0)', '247(0-2)', '266(0-2)', '270(0-1)', '286(0-1)'

'Crossodactylus_caramaschi_CFBHT06917','246(1-0)', '247(0-2)', '251(4-3)', '271(1-0)', '272(0-1)', '286(0-1)'

'Crossodactylus_trachystomus_MNRJ38465','248(0-1)', '251(4-2)', '268(1-0)', '271(1-0)', '275(1-0)', '285(1-0)', '299(1-0)', '300(1-0)'

'Crossodactylus_gaudichaudii_MNRJ40552','239(0-1)', '244(2-3)', '276(0-1)', '283(1-0)', '285(1-0)'

'Crossodactylus_aeneus_MTR22741','170(0-1)', '215(1-0)', '242(2-0)', '246(1-0)', '255(1-0)', '290(1-0)', '296(1-0)'

'Hylodes_lateristrigatus_MNRJ56074','286(0-1)', '302(0-1)', '441(1-0)', '445(0-1)', '452(1-0)'

'Hylodes_cf_charadranaetes_MNRJ59065','191(0-1)', '194(2-1)', '276(0-1)', '298(1-0)'

'Hylodes_uai_MCNAMT85','235(1-0)', '243(0-1)', '253(1-0)', '266(0-1)', '272(0-1)', '273(0-1)', '276(0-1)', '289(1-0)', '293(1-0)', '298(1-0)'

'Hylodes_fredi_CTRU168','244(2-3)', '417(0-1)', '418(1-0)', '436(1-0)', '451(1-0)', '455(1-0)', '459(0-1)', '468(0-2)', '509(1-0)', '523(1-3)', '548(12-0)'

'Hylodes_magalhaesi_MTR10992','238(0-1)', '263(1-0)', '408(0-1)', '409(1-0)', '454(2-1)'

'Hylodes_babax_UFMGT4845','177(0-1)', '194(2-1)', '203(1-2)', '212(0-1)', '232(1-0)', '263(1-0)', '270(1-0)', '271(01-2)'

'Hylodes_asper_CFBH4445','170(0-1)', '187(1-0)', '243(0-1)', '244(2-3)', '263(1-2)', '271(1-0)', '275(1-0)', '286(0-1)', '297(0-1)'

'Hylodes_dactylocinus_AF15','185(0-1)', '191(0-1)', '194(2-0)', '219(3-2)', '221(1-0)', '222(1-0)', '237(2-3)', '244(2-0)', '276(0-1)', '283(1-0)'

'Nannophryne_variegata_IZUA3198','203(1-2)', '234(1-2)', '263(1-2)', '271(1-2)', '280(0-1)', '287(0-1)', '288(0-1)', '296(0-1)'

'Peltophryne_peltocephala_Bp019','274(1-0)', '279(01-2)', '323(1-0)', '336(0-2)', '342(1-0)', '352(0-1)', '358(1-2)', '368(0-1)', '378(1-0)', '428(1-2)', '447(0-1)'

'Incilius_coccifer_KU290030','305(1-0)', '358(1-0)', '374(1-2)', '382(1-0)', '385(0-1)'

'Incilius_aucoinae_UCR14323','247(0-2)', '437(0-1)', '455(1-0)', '462(3-2)', '472(0-1)', '485(0-1)', '509(2-0)', '512(0-2)', '518(1-0)', '529(0-1)', '535(1-0)', '540(1-0)', '546(0-1)'

'Incilius_coniferus_MVZ203775','309(1-0)', '311(2-0)', '320(0-1)', '328(0-1)', '329(0-1)', '330(0-1)', '332(1-0)', '336(0-1)', '337(1-0)', '340(0-1)', '364(0-1)', '368(0-1)', '371(0-1)', '376(1-0)', '386(0-1)'

'Frostius_erythrophthalmus_MTR22228','173(012-3)', '174(012-3)', '198(1-0)', '200(1-0)', '201(1-0)', '216(2-0)', '226(0123-4)', '234(1-0)', '251(2-3)', '260(0-1)', '269(0-1)', '270(0-1)', '279(2-0)', '282(1-0)', '294(1-0)', '306(1-0)', '334(1-0)', '337(1-0)', '345(1-0)', '357(1-0)', '358(1-0)', '373(0-1)', '380(1-0)', '384(1-0)', '387(1-0)', '389(0-1)', '559(0-1)', '560(0-1)'

'Dendrophryniscus_leucomystax_MTR15548','246(1-0)', '253(0-1)', '257(0-1)', '275(0-1)', '282(1-0)', '284(1-0)', '294(1-0)', '295(1-0)'

'Dendrophryniscus_brevipollicatus_AF1541','240(1-2)', '269(0-1)', '283(0-1)', '287(0-1)', '288(0-1)', '292(0-1)', '293(0-1)', '559(0-1)'

'Amazophrynella_manaos_INPA6983','265(0-1)', '311(0-1)', '340(0-1)', '346(0-1)', '347(1-0)', '518(1-2)'

'Anomaloglossus_apiau_MZUSP','246(0-1)', '274(0-3)', '279(1-2)'

'Rheobates_pseudopalmatus_MHUA5162','170(0-1)', '204(0-1)', '227(0-1)', '253(0-1)', '269(0-1)', '274(123-0)', '279(12-0)', '309(1-0)', '315(1-0)', '335(1-5)', '336(01-2)', '339(2-3)', '359(1-0)', '363(0-1)', '375(0-2)', '409(12-0)', '415(1-0)', '426(1-0)', '428(1-2)', '448(0-1)', '512(2-3)'

'Ameerega_trivittata_MJH7483','181(1-0)', '228(1-0)', '237(2-3)', '244(012-3)', '270(0-1)', '283(0-1)', '286(0-1)', '335(12-4)', '339(0-1)', '399(2-6)'

'Node 622','244(23-0)', '253(0-1)', '311(1-0)', '319(1-0)', '335(1-2)', '336(12-0)', '413(1-2)'

'Node 623','252(0-1)', '263(1-2)', '281(0-1)', '432(0-1)'

'Node 624','83(1-0)', '114(1-3)', '129(1-0)', '175(1-0)', '182(1-0)', '183(1-0)', '184(1-0)', '216(0123-4)', '220(1-2)', '228(0-1)', '236(1-0)', '237(2-0)', '248(0-2)', '261(1-0)', '262(1-0)', '264(0-1)', '271(1-0)', '273(0-1)', '274(1-4)', '276(0-1)', '277(0-1)', '278(0-1)', '282(1-0)', '284(1-0)', '294(1-0)', '295(1-0)', '409(1-2)', '429(1-0)', '430(0-1)', '444(1-2)', '445(1-0)', '449(0-1)', '455(1-3)', '460(01-2)', '508(1-0)', '513(0-1)', '516(1-0)', '523(1-0)', '525(1-0)', '549(1-0)', '551(0-1)', '559(0-3)'

'Node 625','113(01-2)', '115(0-2)', '126(0-1)', '135(0-1)', '214(2-3)', '221(0-1)', '434(0-1)'

'Node 626','40(3-01)', '42(3-12)', '43(3-12)', '44(4-01)', '45(4-01)', '68(3-0)', '69(3-0)', '123(0-1)', '137(2-1)', '275(0-1)', '557(1-0)'

'Node 627','465(1-0)', '505(0-1)', '506(0-1)'

'Node 628','237(3-2)', '261(0-1)', '262(0-1)', '264(1-0)', '265(0-1)', '291(1-0)', '303(1-0)', '304(2-1)'

'Node 629','175(0-1)', '248(1-0)', '287(1-0)'

'Node 631','42(3-5)', '43(3-4)', '237(2-0)', '268(1-0)', '319(1-0)', '333(0-1)', '341(0-1)', '345(1-2)', '346(0-1)', '347(1-0)', '348(0-1)', '359(1-0)', '376(0-1)', '460(1-23)', '467(1-0)', '479(1-2)'

'Node 632','14(0-1)', '16(0-1)', '67(0-4)', '68(0-1)', '69(0-1)'

'Node 633','71(0-1)', '173(0-1)', '174(0-1)', '176(0-1)', '195(0-1)', '196(0-1)', '200(1-0)', '201(1-0)', '204(0-1)', '215(2-0)', '224(0-1)', '227(0-1)', '266(0-1)', '273(0-1)', '311(1-0)', '313(0-1)', '319(1-0)', '327(0-1)', '328(1-0)', '336(1-0)', '338(1-2)', '339(1-0)', '357(0-1)', '358(1-0)', '369(0-1)', '419(0-1)', '437(0-1)', '456(1-0)', '459(0-1)', '465(0-1)', '466(1-2)', '476(0-1)', '493(1-2)', '495(1-0)', '498(1-0)', '513(0-1)', '518(12-0)', '528(3-1)', '529(0-1)', '548(2-01)', '556(2-1)'

'Node 634','72(01-2)', '279(01-2)', '332(1-0)', '335(01-2)', '436(0-1)', '448(0-1)', '455(0-1234)', '461(2-1)', '463(0-1)', '535(1-0)', '557(0-1)'

'Node 635','5(0-1)', '6(2-3)', '21(0-1)', '58(0-1)', '61(0-1)', '143(0-1)', '149(1-0)', '283(0-1)'

'Node 636','461(3-2)'

'Node 637','2(0-1)', '3(1-0)', '6(1-2)', '7(0-1)', '29(0-1)', '47(0-1)', '74(0-1)', '75(0-1)', '77(0-1)', '80(0-1)', '84(0-1)', '100(0-1)', '105(0-1)', '110(0-1)', '114(1-0)', '118(1-2)', '121(0-1)', '136(0-1)', '169(4-3)', '204(1-0)', '215(01-2)', '309(0-1)', '318(1-0)', '320(0-1)', '328(0-1)', '340(0-1)', '352(0-1)', '367(1-0)', '414(0-1)', '415(0-1)', '417(1-0)', '418(0-1)', '448(1-0)', '455(1-0)', '466(0-1)', '494(1-0)', '528(0-3)', '556(1-2)'

'Node 638','14(0-1)', '16(0-1)', '199(1-0)', '217(1-0)', '238(1-0)', '263(1-0)', '283(1-0)', '332(0-1)', '335(2-0)', '343(1-0)', '344(1-0)', '378(1-0)', '413(1-2)', '429(1-2)', '433(1-3)', '436(1-0)', '439(0-1)', '448(1-0)'

'Node 639','178(0-1)', '214(2-3)', '414(1-0)'

'Node 640','239(0-1)', '252(0-1)', '263(1-0)', '269(0-1)', '283(1-0)', '288(1-0)', '289(1-0)', '290(1-0)', '291(1-0)', '296(1-0)', '308(0-1)'

'Node 641','5(1-2)'

'Node 642','68(0-125)', '74(1-0)', '219(2-3)', '228(0-1)', '241(1-0)', '243(0-1)', '250(0-1)', '252(0-1)', '266(1-2)', '269(0-1)', '274(1-3)', '276(0-1)', '279(2-0)', '280(0-1)', '285(0-1)', '308(0-1)', '346(0-1)', '347(1-0)', '352(1-0)', '354(0-1)', '374(1-0)', '386(1-0)', '393(0-1)', '409(01-2)', '426(1-0)', '436(1-2)'

'Node 643','201(1-0)', '274(1-0)', '528(0-3)', '547(2-1)', '550(0-1)', '555(1-0)'

'Node 644','41(4-6)', '42(4-6)', '44(3-4)', '45(3-5)', '58(0-1)', '65(0-1)', '66(2-5)', '94(0-1)', '97(0-1)', '124(3-2)', '214(2-1)', '219(2-1)', '223(0-1)', '237(2-3)', '244(0-2)', '255(1-0)', '257(0-1)', '266(0-1)', '298(0-1)', '300(0-1)', '335(0-1)', '364(0-1)', '365(0-1)', '366(1-0)', '386(0-1)', '420(1-2)', '451(0-1)', '478(1-3)', '512(01-2)', '518(1-0)'

'Node 645','6(2-1)', '38(3-4)', '39(1-2)', '40(3-4)', '42(3-4)', '43(23-4)', '44(2-3)', '45(2-3)', '47(1-2)'

'Node 646','14(0-1)', '16(0-1)', '30(2-0)', '37(0-1)', '38(012-3)', '40(01-3)', '42(12-3)', '44(01-2)', '45(01-2)', '46(0-1)', '287(0-1)', '288(0-1)', '290(0-1)', '291(0-1)', '296(0-1)', '299(0-1)', '315(0-1)', '324(0-1)', '339(1-2)', '395(1-2)', '535(1-0)'

'Node 647','329(0-1)', '458(0-1)'

'Node 648','51(0-2)', '66(3-0)', '67(4-0)'

'Node 649','4(1-0)'

'Node 650','36(1-2)', '58(0-1)', '93(0-2)', '170(0-1)', '261(1-0)', '262(1-0)', '274(3-1)'

'Node 651','10(2-3)', '11(2-3)', '36(0-1)', '57(0-1)', '69(3-1)', '179(0-1)', '180(0-1)', '181(0-1)', '322(1-0)'

'Node 652','280(0-1)', '371(1-0)'

'Node 653','385(0-1)'

'Node 654','6(2-01)', '116(0-1)', '130(1-2)', '561(0-1)'

'Node 655','8(1-0)', '30(2-3)', '32(1-0)', '34(2-1)', '35(2-1)', '36(1-0)', '47(1-0)', '51(4-0)', '118(2-01)', '133(1-0)', '203(1-2)', '204(0-1)', '214(2-3)', '215(2-0)', '219(2-3)', '221(0-1)', '226(0-3)', '227(0-1)', '228(0-1)', '229(0-1)', '230(0-1)', '231(0-1)', '264(0-1)', '265(1-0)', '274(1-3)', '303(0-1)', '304(1-2)', '335(0-12)', '339(1-

0)', '358(1-0)', '372(1-0)', '380(1-0)', '388(1-0)', '392(1-2)', '393(0-1)', '410(1-0)', '435(0-1)', '439(0-1)', '440(0-1)', '442(0-1)'

'Node 656','71(0-2)', '72(01-2)', '137(0-1)', '319(1-0)', '463(0-1)'

'Node 657','141(0-1)'

'Node 658','150(1-0)', '395(1-2)', '408(1-0)'

'Node 659','9(2-3)', '58(0-1)'

'Node 660','115(0-1)', '271(1-0)'

'Node 661','242(2-0)'

'Node 662','9(2-3)', '34(1-2)'

'Node 663','57(1-0)'

'Node 664','4(1-0)', '202(0-1)'

'Node 665','33(0-1)', '36(1-2)', '342(1-0)'

'Node 666','65(0-1)', '170(0-1)', '219(3-2)', '361(0-1)', '388(0-1)', '400(1-0)', '436(0-1)'

'Node 667','57(1-0)', '204(1-0)'

'Node 668','4(1-0)', '35(2-1)', '66(3-0)', '67(4-0)', '152(0-1)'

'Node 669','271(1-2)', '286(0-1)', '303(1-0)', '319(0-1)', '339(0-1)', '346(0-1)', '352(1-0)', '361(0-1)', '385(1-0)', '400(1-0)', '417(0-1)', '418(1-0)', '436(0-1)'

'Node 670','2(1-0)', '27(1-0)'

'Node 671','146(0-1)', '219(2-1)', '239(0-1)', '243(0-1)', '308(0-1)', '332(1-0)'

'Node 672','6(2-3)', '51(4-2)', '142(0-1)', '271(1-0)', '274(1-0)', '371(1-0)'

'Node 673','51(2-3)', '66(4-2)', '119(0-1)', '144(1-0)', '147(1-0)', '251(4-2)', '318(0-1)', '319(1-0)', '332(1-0)', '340(1-0)', '417(0-1)', '427(2-1)', '435(0-1)'

'Node 674','32(1-0)', '36(1-0)', '56(1-0)', '103(1-0)', '116(0-1)', '163(0-1)', '179(0-1)', '180(0-1)', '181(0-1)', '204(0-1)', '227(0-1)', '228(0-1)', '229(0-1)', '236(1-0)', '237(23-0)', '240(1-2)', '287(0-1)'

'Node 675','128(0-1)', '165(0-1)', '203(1-2)', '246(1-0)', '255(1-0)', '378(1-0)', '420(1-2)'

'Node 676','5(0-1)', '32(1-2)', '129(1-0)', '131(1-0)', '170(0-1)', '182(1-0)', '235(0-1)', '244(0-3)', '263(1-0)', '266(0-2)', '272(0-1)', '279(01-2)', '280(0-1)', '309(1-0)', '311(1-2)', '312(1-0)', '338(1-0)', '339(1-0)', '348(0-1)', '358(1-0)', '361(0-1)', '363(0-1)', '377(1-0)'

'Node 677','67(0-4)', '69(0-1)'

'Node 678','6(2-1)', '30(2-1)', '396(1-0)', '420(1-2)', '472(0-1)'

'Node 679','11(2-3)', '27(1-0)', '69(3-0)', '235(0-1)', '323(1-0)', '487(0-1)', '506(0-1)'

'Node 680','93(0-1)', '101(0-1)', '106(0-1)', '121(1-0)', '122(0-1)', '138(0-1)', '140(0-1)', '155(0-1)', '158(0-1)', '175(1-0)', '179(0-1)', '180(0-1)', '182(1-0)', '183(1-0)', '184(1-0)', '198(1-0)', '200(1-0)', '201(1-0)', '202(0-1)', '204(1-0)', '220(1-0)', '226(3-0)', '275(0-1)', '561(1-2)'

'Node 681','10(2-3)', '71(2-0)', '148(0-1)', '152(0-1)', '170(0-1)', '261(1-0)', '262(1-0)', '272(0-1)', '305(1-0)', '373(0-1)'

'Node 682','155(1-0)', '158(1-0)'

'Node 683','124(6-4)'

'Node 684','6(0-1)', '8(0-1)', '104(0-1)', '117(1-0)'

'Node 685','36(0-1)', '96(0-1)', '98(1-0)', '102(1-2)', '315(0-1)', '320(1-0)', '364(0-1)', '377(1-0)', '417(0-1)', '510(1-0)', '517(0-1)', '528(1-0)', '529(0-1)'

'Node 686','32(0-1)', '33(1-2)', '34(1-2)'

'Node 687','4(1-0)', '9(1-0)', '65(0-1)', '99(0-1)', '127(0-1)', '147(1-0)', '149(1-0)', '153(0-1)', '237(2-1)', '244(0-3)', '252(0-1)', '267(0-2)', '282(1-0)', '284(1-0)', '311(1-0)', '318(0-1)', '327(0-1)', '336(1-0)', '340(1-0)', '383(1-0)', '395(2-1)', '400(1-0)', '448(0-1)', '456(1-5)', '560(0-1)'

'Node 688','184(1-0)', '335(0-234)', '350(1-0)', '357(0-1)'

'Node 689','309(0-1)', '311(1-0)'

'Node 690','440(0-1)'

'Node 691','237(2-3)', '256(0-1)', '270(0-1)'

'Node 692','2(0-1)', '7(0-1)', '14(0-1)', '16(0-1)', '31(0-1)', '37(0-1)', '46(0-1)', '79(1-0)', '82(0-1)', '187(0-1)', '188(0-1)', '285(0-1)', '299(0-1)', '300(0-1)', '309(0-1)', '319(1-0)', '343(01-2)', '378(01-2)', '417(1-0)', '418(0-1)', '421(0-1)', '451(0-1)'

'Node 693','73(1-0)', '102(1-0)', '287(0-1)', '288(0-1)', '290(0-1)', '291(0-1)', '296(0-1)', '341(0-1)'

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'Node 694','53(0-1)'
'Node 695','53(1-0)'
'Node 696','130(0-1)', '209(1-0)', '269(0-1)', '364(0-1)', '409(1-0)'
'Node 697','214(2-3)', '287(1-0)', '288(1-0)', '289(1-0)', '290(1-0)', '291(1-0)', '296(1-0)', '297(0-1)', '458(1-0)', '510(23-1)', '511(0-1)'
'Node 698','32(1-2)', '64(0-1)', '274(1-0)', '318(0-1)', '362(0-1)', '461(3-2)', '472(0-1)', '505(1-0)', '519(2-1)'
'Node 699','53(0-1)', '209(0-1)', '408(1-0)', '466(1-2)', '479(1-2)', '489(0-1)', '518(1-2)'
'Node 700','40(3-1)', '41(4-2)', '42(3-1)', '43(23-1)', '44(2-1)', '45(2-1)', '309(1-0)', '485(0-1)'
'Node 701','286(0-1)', '341(0-1)', '386(0-1)'
'Node 702','39(1-2)', '45(2-3)', '54(1-0)', '284(1-0)', '295(1-0)', '308(0-1)'
'Node 703','44(23-4)'
'Node 704','39(1-2)', '45(2-3)'
'Node 705','6(2-1)', '58(0-1)', '61(0-1)', '335(0-1)', '361(0-1)', '455(0-2)', '465(01-2)', '499(1-2)', '549(1-0)'
'Node 706','9(1-0)', '10(1-0)', '35(2-1)', '38(23-4)', '47(1-2)', '53(1-0)'
'Node 707','62(1-0)'
'Node 708','10(1-2)', '11(1-2)', '41(4-3)', '47(1-0)', '58(0-1)', '69(0-4)', '408(0-1)'
'Node 709','14(1-0)', '16(1-0)', '32(2-1)', '33(2-1)', '34(2-1)', '35(2-1)', '36(2-1)', '37(1-0)', '38(3-4)', '45(2-3)', '67(0-1)', '69(0-4)', '124(3-2)', '138(0-1)', '237(2-3)', '255(1-0)', '263(1-0)', '295(1-0)', '388(1-0)', '392(0-1)', '409(0-1)', '420(1-2)', '426(1-0)', '436(0-1)'
'Node 710','181(0-1)', '204(0-1)', '212(1-0)', '226(0-1)', '228(0-1)', '270(0-1)', '274(1-2)', '407(1-0)', '410(1-0)', '429(1-2)', '458(0-1)', '510(3-1)', '518(2-1)', '535(1-0)'
'Node 711','66(2-5)', '67(0-3)', '252(0-1)'
'Node 712','14(0-1)', '16(0-1)', '30(1-0)', '37(0-1)', '38(0-4)', '39(0-2)', '40(0-4)', '41(0-5)', '42(01-45)', '43(01-4)', '44(0-3)', '45(0-4)'
'Node 713','32(1-0)', '36(1-0)', '279(01-2)', '489(0-1)'
'Node 714','71(0-1)', '116(0-1)', '118(2-1)', '122(0-1)', '123(1-0)', '230(0-1)', '246(1-0)', '247(0-2)', '280(0-1)', '289(1-0)', '290(1-0)', '291(1-0)', '309(1-0)', '311(1-0)', '319(0-1)', '346(0-1)', '385(1-0)', '399(2-1)', '401(3-2)', '407(1-0)', '433(1-2)', '448(1-0)', '483(0-1)', '510(1-3)', '512(0-1)'
'Node 715','108(1-2)', '299(1-0)', '349(0-1)'
'Node 716','252(0-1)', '341(0-1)', '357(0-1)', '436(0-1)', '461(2-1)', '466(2-1)', '529(1-0)', '549(1-0)'
'Node 717','130(0-1)', '137(0-1)', '235(0-1)', '448(0-1)'
'Node 718','312(1-0)', '319(1-0)', '510(3-1)'
'Node 719','61(0-1)'
'Node 720','0(1-0)', '46(0-1)', '47(1-0)', '67(0-6)'
'Node 721','5(0-1)', '6(2-3)', '30(1-2)', '58(0-1)', '63(1-0)', '67(13-0)', '68(3-0)', '69(3-0)', '72(0-2)', '108(1-2)', '170(1-0)', '214(2-1)', '219(2-1)', '223(0-1)', '235(1-0)', '251(4-3)', '253(0-1)', '257(0-1)', '275(0-1)', '299(1-0)', '311(1-2)', '324(1-0)', '332(0-1)', '336(1-2)', '339(1-2)', '349(0-1)', '368(0-1)', '371(0-1)', '372(1-0)', '418(1-2)', '426(1-0)', '549(1-0)'
'Node 722','33(01-2)', '34(1-2)', '35(1-2)'
'Node 723','283(0-1)', '293(0-1)', '461(2-1)', '529(1-0)', '554(0-1)'
'Node 724','63(0-1)', '396(0-1)'
'Node 725','274(1-0)', '332(1-0)'
'Node 726','60(1-0)', '68(3-0)'
'Node 727','47(1-0)'
'Node 728','65(0-1)', '123(1-0)', '184(1-0)', '215(2-0)', '247(0-12)', '264(0-1)', '271(1-0)', '272(0-1)', '279(2-0)', '283(0-1)', '286(0-1)', '293(0-1)', '297(0-1)', '298(0-1)', '332(1-0)', '336(1-0)', '338(1-0)', '356(0-1)', '358(1-2)', '359(0-1)', '363(0-1)', '426(1-0)'
'Node 729','5(0-1)', '30(1-2)', '170(0-1)', '232(0-1)', '246(1-0)', '252(0-1)', '263(1-0)', '270(0-1)', '274(1-0)', '285(0-1)', '309(1-0)', '349(0-1)'
'Node 730','41(4-6)', '227(0-1)', '232(0-1)', '238(1-0)', '239(0-1)', '243(1-0)', '263(1-0)', '268(1-0)', '270(1-0)', '275(0-1)', '286(1-0)', '287(1-0)', '288(1-0)', '289(1-0)', '290(1-0)', '291(1-0)', '296(1-0)', '297(0-1)', '299(0-1)'
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'Node 731','0(1-0)', '38(3-4)', '40(3-4)', '42(3-4)', '43(3-4)', '44(2-4)', '45(2-5)', '47(2-0)', '68(2-0)', '170(1-0)', '184(0-1)', '204(0-1)', '237(3-2)', '253(1-0)', '255(0-1)', '273(1-0)', '279(2-0)', '280(1-0)'
'Node 732','30(0-1)', '32(0-1)', '34(1-2)', '35(1-2)', '36(0-1)', '38(4-3)', '40(4-3)', '41(5-4)', '42(45-3)', '43(4-3)', '44(3-2)', '45(4-2)', '46(0-1)', '47(1-2)', '119(0-1)', '120(0-1)', '124(6-5)', '129(1-0)', '131(1-0)', '132(1-0)', '170(0-1)', '255(1-0)', '270(0-1)', '280(0-1)'
'Node 733','209(0-1)', '243(0-1)'
'Node 734','6(2-3)', '336(1-2)'
'Node 735','0(1-0)', '67(0-3)'
'Node 736','5(0-1)', '30(1-2)'
'Node 737','4(1-0)', '11(1-2)', '14(0-1)', '16(0-1)', '30(1-0)', '33(1-2)', '34(1-2)', '37(0-1)', '38(0-4)', '39(0-2)', '40(0-4)', '41(01-5)', '42(01-5)', '43(012-3)', '44(0-4)', '45(0-5)', '46(0-1)', '47(1-0)', '58(0-1)', '68(3-2)', '246(1-0)', '247(0-1)', '308(0-1)', '322(1-0)', '339(1-0)', '340(1-0)', '359(0-1)', '361(1-3)', '362(0-1)', '364(0-1)', '365(0-1)', '366(1-0)', '389(0-1)', '399(2-1)', '401(3-2)'
'Node 738','184(0-1)', '204(0-1)', '269(1-0)', '274(1-0)', '297(0-1)', '298(0-1)', '300(0-1)', '319(1-0)', '356(1-0)', '371(1-0)', '409(1-0)', '427(2-1)', '460(0-1)', '467(2-1)', '479(1-2)', '491(1-0)', '497(1-0)', '499(1-2)', '506(1-0)'
'Node 739','232(0-1)', '235(0-1)', '256(0-1)', '382(1-0)', '395(2-0)'
'Node 740','6(1-2)', '8(0-1)', '9(0-1)', '10(0-1)', '11(0-1)', '28(0-1)'
'Node 741','408(0-1)'
'Node 742','255(1-0)', '286(0-1)'
'Node 743','170(0-1)', '223(0-1)', '235(0-1)', '255(1-0)', '274(1-0)', '297(0-1)', '300(0-1)', '388(1-0)', '426(1-0)', '433(1-2)', '506(1-0)'
'Node 744','6(1-3)', '37(1-0)', '38(3-2)', '40(3-1)', '42(2-1)', '43(2-1)', '44(1-0)', '45(1-0)', '46(1-0)', '47(2-0)', '68(3-0)'
'Node 745','6(2-1)', '14(0-1)', '16(0-1)', '20(0-1)', '34(1-0)', '35(1-0)', '37(0-1)', '39(01-2)', '40(012-3)', '41(0123-4)', '44(0-1)', '45(0-1)', '46(0-1)', '47(1-2)', '214(2-3)', '247(0-2)'
'Node 746','8(1-0)', '9(1-0)'
'Node 747','8(1-0)', '9(1-0)', '10(1-0)', '11(1-0)', '68(3-4)', '69(3-4)', '223(0-1)', '227(0-1)', '247(0-2)', '253(0-1)', '269(0-1)', '285(0-1)', '286(0-1)', '311(1-2)', '313(0-1)', '320(1-0)', '348(1-0)', '364(0-1)'
'Node 748','232(0-1)', '252(1-0)', '263(1-0)', '270(0-1)', '271(1-0)', '274(1-0)', '388(1-0)'
'Node 749','235(1-0)', '239(0-1)', '243(1-0)', '244(3-0)', '246(1-0)', '263(0-1)', '274(0-1)', '286(0-1)', '300(1-0)', '311(1-2)', '339(1-2)', '389(0-1)', '408(0-1)', '409(1-0)', '436(0-1)'
'Node 750','305(1-2)', '357(0-1)', '362(0-1)', '371(0-1)', '396(1-0)'
'Node 751','170(1-0)', '204(0-1)', '215(2-0)', '238(1-0)', '253(0-1)', '269(0-1)', '271(1-0)', '275(0-1)', '283(1-0)', '293(1-0)', '311(1-0)', '332(0-1)', '336(1-2)', '348(1-0)', '359(0-1)', '364(0-1)', '376(0-1)', '410(1-0)', '426(1-0)', '427(2-1)'
'Node 752','235(1-0)', '239(0-1)', '292(1-0)', '339(1-2)', '348(1-0)'
'Node 753','30(12-0)', '60(1-0)', '68(3-5)', '69(3-2)', '221(0-1)', '226(0-3)', '227(0-1)', '230(0-1)', '248(0-1)', '251(4-1)', '304(1-2)', '559(0-1)'
'Node 754','0(1-2)', '58(0-1)', '66(2-4)', '70(1-0)', '108(1-2)', '215(2-1)'
'Node 755','251(4-2)', '257(1-0)', '279(2-0)', '329(1-0)', '358(1-0)', '360(1-0)', '364(0-1)', '369(0-1)', '409(1-2)', '429(1-2)', '458(0-1)', '490(0-1)', '491(1-2)', '510(3-1)', '518(2-1)', '535(1-0)'
'Node 756','11(1-2)', '33(1-2)', '34(1-2)', '59(0-1)', '215(1-0)', '279(2-0)'
'Node 757','11(1-2)', '20(0-1)', '36(1-2)', '106(0-2)', '203(1-0)', '209(0-1)', '238(1-0)', '244(3-0)', '300(1-0)', '309(1-0)', '314(0-1)', '335(0-4)', '336(1-0)', '348(1-0)', '458(0-1)', '462(3-1)', '464(0-1)', '467(2-1)', '478(1-0)', '479(1-2)', '491(1-0)', '499(1-0)', '505(1-0)', '520(01-2)', '546(1-0)'
'Node 758','237(3-2)', '256(1-0)'
'Node 759','269(0-1)'
'Node 760','34(1-0)', '35(1-0)'
'Node 761','33(01-2)', '34(1-2)', '69(3-2)', '279(1-2)'
'Node 762','214(3-2)', '221(1-0)', '275(1-0)', '279(0-1)', '455(1-0)', '465(0-1)', '469(1-0)', '519(2-1)', '550(0-1)'
'Node 763','553(1-0)'

'Node 764','237(23-0)', '253(1-0)', '273(0-1)', '308(0-1)', '335(2345-1)', '336(12-0)', '358(1-2)', '359(0-1)', '408(1-0)', '409(2-0)', '497(1-0)'
'Node 765','309(0-1)', '339(1-0)'
'Node 766','40(0-1)', '41(0-2)', '66(2-5)', '67(5-3)', '244(0-23)', '518(12-0)', '535(0-1)', '557(1-0)'
'Node 767','181(0-1)', '253(0-1)', '255(1-0)'
'Node 768','341(0-1)'
'Node 769','34(2-1)', '35(2-1)', '47(1-0)', '67(0-5)', '68(0-3)', '69(0-3)', '141(0-1)', '223(0-1)', '233(0-1)', '299(0-1)', '300(0-1)', '309(1-0)', '396(1-0)', '409(01-2)', '455(1234-5)', '472(0-1)'
'Node 770','8(1-0)', '9(1-0)', '50(0-1)', '65(1-0)', '66(5-0)', '67(3-0)', '68(3-0)', '69(3-0)', '183(1-0)', '184(1-0)', '197(1-0)', '239(0-1)', '252(0-1)', '312(1-0)', '364(0-1)', '436(1-0)'
'Node 771','235(0-1)', '269(0-1)', '297(0-1)', '335(2345-1)', '336(12-0)', '348(0-1)', '395(1-2)'
'Node 772','8(1-0)', '9(1-0)', '10(1-0)', '11(1-0)', '51(4-2)', '233(1-0)', '244(0-2)', '256(0-1)', '298(0-1)', '309(0-1)', '426(1-0)', '428(1-2)', '433(1-2)', '436(1-0)', '448(1-0)'
'Node 773','130(1-0)', '131(1-0)', '184(1-0)', '203(1-2)', '226(0-3)', '227(0-1)', '246(1-0)', '247(0-2)', '251(4-3)', '252(0-3)', '263(1-0)', '271(1-0)', '276(0-1)', '285(0-1)', '389(0-1)', '392(0-1)', '436(1-0)', '466(1-2)', '500(3-2)', '510(3-2)'
'Node 774','130(1-0)', '131(1-0)', '184(1-0)', '232(0-1)', '263(1-0)', '275(1-0)', '285(0-1)', '339(1-2)', '371(1-0)', '392(0-1)', '461(1-0)', '482(1-0)', '549(1-0)', '555(1-0)'
'Node 775','0(1-0)', '104(0-2)', '106(0-2)', '153(0-1)', '162(0-1)', '212(0-1)', '214(2-1)', '297(0-1)', '311(12-0)', '318(0-1)', '319(1-0)', '324(0-1)', '332(0-1)', '339(1-3)', '343(1-2)', '378(1-2)', '517(0-1)'
'Node 776','8(1-0)', '9(1-0)', '14(0-1)', '16(0-1)', '20(0-1)', '39(2-3)', '41(6-7)', '65(0-1)', '88(0-1)'
'Node 777','0(1-0)', '1(0-1)', '30(1-0)', '37(0-1)', '38(0-4)', '39(0-2)', '40(0-4)', '41(0-6)', '42(01-6)', '43(01-6)', '44(0-6)', '45(0-5)', '46(0-1)', '85(0-1)'
'Node 778','32(1-0)', '47(1-2)', '67(4-1)'
'Node 779','20(0-1)', '51(0-2)', '58(0-1)', '144(1-0)', '145(1-0)', '149(1-0)', '175(1-0)', '180(0-1)', '232(0-1)', '235(0-1)', '252(0-1)', '254(1-2)', '274(123-0)', '288(0-1)', '295(0-1)', '312(0-1)', '328(1-0)', '332(0-1)', '335(2-0)', '340(1-0)', '365(1-0)', '366(0-1)', '439(1-0)', '464(0-1)'
'Node 780','47(0-1)', '137(1-0)', '251(4-1)', '318(0-1)', '343(0-1)', '383(1-0)', '427(2-1)'
'Node 781','253(0-1)', '357(0-1)', '395(2-1)', '449(0-1)'
'Node 782','11(2-3)', '169(1-0)', '237(2-3)', '257(0-1)', '280(0-1)', '365(0-1)', '366(1-0)', '461(12-3)'
'Node 783','8(0-1)', '9(2-3)', '20(0-1)', '51(0-1)', '69(3-1)', '159(0-1)', '162(0-1)', '219(3-2)', '238(1-0)', '243(0-1)', '244(0-2)', '247(0-2)', '256(0-1)', '283(0-1)', '287(0-1)', '288(0-1)', '295(0-1)', '400(1-0)', '450(0-1)'
'Node 784','72(2-0)', '273(0-1)'
'Node 785','10(3-2)', '11(3-2)', '93(0-2)', '117(1-0)', '147(1-0)', '149(1-0)', '150(1-0)', '152(1-0)', '153(0-1)', '204(1-0)', '228(1-0)', '235(0-1)', '252(0-1)', '269(0-1)', '274(123-0)'
'Node 786','9(2-3)', '30(3-0)', '33(1-2)', '34(1-2)', '35(1-2)', '36(0-1)', '69(3-1)', '146(0-1)', '151(0-1)', '153(0-1)', '155(0-1)', '158(0-1)', '159(0-1)', '160(0-1)', '162(0-1)', '182(1-0)', '183(1-0)', '184(1-0)', '203(2-1)', '204(1-0)', '219(3-2)', '236(1-0)', '237(3-0)', '244(0-3)', '263(1-2)', '279(1-2)', '320(1-0)', '378(0-1)', '450(0-1)'
'Node 787','265(1-0)', '272(0-1)'
'Node 788','243(0-1)'
'Node 789','176(0-1)', '448(1-0)'
'Node 790','21(1-0)', '35(2-3)', '36(1-2)', '40(0-1)', '41(0-2)', '47(1-0)', '50(0-1)'
'Node 791','72(01-2)'
'Node 792','59(0-1)', '232(0-1)', '297(0-1)', '299(0-1)', '324(0-1)', '329(0-1)', '371(1-0)'
'Node 793','21(0-1)', '30(2-1)', '40(0-1)', '41(0-2)'
'Node 794','5(0-1)', '6(2-3)', '36(1-2)', '38(0-2)', '39(0-1)'
'Node 795','50(0-1)', '53(0-1)'
'Node 796','42(1-0)', '71(0-1)'
'Node 797','61(1-0)', '106(0-1)', '364(0-1)', '408(1-0)'
'Node 798','106(1-0)'
'Node 799','45(01-2)', '72(01-2)', '168(0-1)', '182(1-0)', '183(1-0)', '184(1-0)', '204(0-1)', '214(2-1)', '215(2-0)', '232(1-0)', '257(1-0)', '282(1-0)', '284(1-0)', '287(1-0)', '288(1-0)', '289(1-0)', '290(1-0)', '291(1-0)',

'292(1-0)', '293(1-0)', '294(1-0)', '295(1-0)', '296(1-0)', '299(1-0)', '305(1-0)', '332(1-0)', '335(0-2)', '340(1-0)', '342(1-0)', '353(0-2)', '356(1-0)', '359(1-0)', '369(0-1)', '377(1-0)', '382(1-0)', '448(0-1)'

'Node 800','5(1-0)', '237(2-3)', '255(1-0)', '297(1-0)', '312(1-0)', '329(1-0)'

'Node 801','30(2-0)', '37(0-1)', '38(0-23)', '39(0-1)', '40(0-2)', '41(0-34)', '42(1-3)', '43(1-2)', '44(0-12)', '46(0-1)', '47(1-2)', '108(2-1)', '361(0-1)'

'Node 802','170(0-1)', '238(0-1)', '239(0-1)', '242(2-0)', '246(1-0)', '263(1-0)', '272(0-1)', '273(0-1)', '274(01-3)', '275(1-0)', '279(12-0)', '285(0-1)', '300(0-1)', '319(1-0)', '336(12-0)', '349(0-1)', '371(0-1)', '385(1-0)', '408(0-1)', '409(1-0)'

'Node 803','10(1-2)', '59(1-0)', '67(0-3)', '69(0-13)'

'Node 804','42(1-2)', '43(1-2)', '44(0-1)', '45(0-1)', '46(0-1)'

'Node 805','50(0-1)'

'Node 806','8(1-0)', '9(1-0)', '11(1-0)', '47(1-0)'

'Node 807','204(0-1)', '223(0-1)', '253(0-1)', '263(1-0)', '275(1-0)', '309(1-0)', '315(0-1)', '332(1-0)', '336(1-2)', '342(1-0)', '347(1-0)', '372(1-0)', '400(1-0)', '443(1-0)', '466(1-2)', '470(0-1)', '489(0-1)', '495(1-0)'

'Node 808','304(0-1)'

'Node 809','214(2-1)', '409(01-2)', '461(2-3)', '476(0-1)'

'Node 810','183(1-0)', '184(1-0)', '237(2-3)', '244(2-3)', '246(1-0)', '255(1-0)', '273(0-1)', '298(0-1)', '319(1-0)', '336(1-0)', '339(1-2)', '361(0-1)'

'Node 811','21(1-0)', '59(0-1)'

'Node 812','3(1-0)', '4(1-0)', '24(0-1)', '38(4-5)', '39(12-4)', '40(3-5)', '41(4-6)', '42(3-5)', '43(3-4)', '45(4-5)', '72(2-0)', '73(1-0)', '111(0-1)', '114(2-0)', '168(0-1)'

'Node 813','203(1-0)', '237(3-1)', '336(0-12)', '338(1-0)', '339(1-0)', '342(1-0)'

'Node 814','183(1-0)', '216(0-2)', '219(2-1)', '241(1-0)', '251(34-2)', '279(01-2)', '344(1-0)', '377(1-0)'

'Node 815','319(1-0)'

'Node 816','34(2-1)', '35(2-1)'

'Node 817','38(3-4)', '39(1-3)', '41(4-8)', '42(3-6)', '43(23-7)', '44(2-7)', '45(2-5)', '47(1-2)', '69(03-4)', '108(1-0)', '109(1-0)', '118(2-1)', '119(0-1)', '124(3-2)', '128(0-1)', '187(0-1)', '214(2-3)', '215(2-0)', '226(0-3)', '227(0-1)', '232(0-1)', '263(1-0)', '279(01-2)'

'Node 818','42(3-2)', '66(6-0)'

'Node 819','86(1-0)'

'Node 820','5(0-1)', '43(4-3)'

'Node 821','66(2-6)', '274(1-0)', '287(1-0)', '288(1-0)', '291(1-0)', '315(1-0)', '324(1-0)', '339(2-01)'

'Node 822','85(0-1)', '269(0-1)', '341(0-1)', '392(0-1)', '471(0-1)', '472(0-1)', '485(0-1)', '505(1-0)', '519(2-1)'

'Node 823','232(0-1)', '294(1-0)', '295(1-0)', '296(1-0)'

'Node 824','8(1-0)', '9(1-0)', '32(1-0)', '67(0-1)', '68(0-4)', '171(1-0)', '197(1-0)', '198(1-0)', '199(1-0)', '200(1-0)', '201(1-0)', '213(1-0)', '245(0-1)', '248(0-2)', '250(0-1)', '251(4-3)'

'Node 825','22(1-3)', '246(1-0)', '271(1-0)', '282(1-0)', '284(1-0)', '289(1-0)', '290(1-0)', '294(1-0)', '295(1-0)', '296(1-0)', '299(1-0)'

'Node 826','33(2-1)', '38(34-2)', '39(2-1)', '40(34-2)', '41(4-3)', '42(34-2)', '43(3-2)', '44(23-1)', '45(3-1)', '108(1-2)', '269(1-0)'

'Node 827','227(0-1)', '260(0-1)', '261(1-0)', '262(1-0)'

'Node 828','172(1-0)'

'Node 829','0(1-0)', '6(2-3)', '38(2-0)', '39(1-0)', '40(12-0)', '41(23-0)', '42(2-0)', '43(12-0)', '67(0-34)', '68(0-13)', '69(0-13)', '72(0-2)'

'Node 830','14(1-0)', '16(1-0)', '60(1-0)', '86(1-0)', '87(1-0)'

'Node 831','214(2-3)', '237(2-0)', '244(0-2)', '251(4-1)', '274(01-3)', '280(0-1)', '401(3-4)', '439(0-1)', '440(0-1)'

'Node 832','6(2-1)', '34(2-1)', '35(2-1)', '184(1-0)', '203(1-2)', '212(1-0)', '215(2-1)', '226(0-3)', '230(0-1)', '231(0-1)', '253(0-1)', '272(0-1)', '303(0-1)', '304(1-2)', '388(1-0)', '389(1-0)', '392(1-2)', '393(0-1)', '395(2-0)', '407(1-0)', '559(0-1)'

'Node 833','5(1-0)', '227(0-1)', '228(0-1)', '232(0-1)', '240(1-2)', '340(1-0)', '384(1-0)'

'Node 834','53(0-1)', '71(0-1)'

'Node 835','33(1-2)', '38(2-3)', '40(12-3)', '41(23-4)', '42(2-3)', '87(0-1)'

'Node 836','22(1-3)'
'Node 837','5(1-0)', '8(1-2)', '9(1-2)', '10(1-2)', '11(1-2)', '38(4-5)', '67(0-1)'
'Node 838','8(1-0)', '32(1-0)', '38(2-4)', '40(12-3)', '170(0-1)', '179(0-1)', '180(0-1)', '181(0-1)', '237(2-3)', '239(0-1)', '279(1-2)', '305(1-0)', '318(0-1)', '408(1-0)', '436(0-1)'
'Node 839','9(1-2)', '10(1-2)', '11(1-2)', '21(1-0)', '30(12-0)', '42(2-3)', '71(1-2)', '215(1-0)', '235(0-1)', '237(2-3)', '238(1-0)', '257(0-1)', '273(0-1)', '420(1-2)', '433(1-2)'
'Node 840','10(2-1)', '11(2-1)', '229(1-0)', '235(0-1)', '260(0-1)'
'Node 841','34(1-0)', '35(1-0)', '184(0-1)'
'Node 842','212(0-1)', '339(0-1)', '388(0-1)', '410(0-1)'
'Node 843','0(0-2)'
'Node 844','51(0-1)', '461(12-0)', '465(0-1)', '500(2-3)', '546(1-0)'
'Node 845','149(1-0)', '267(0-1)', '272(0-1)', '335(12-3)', '347(1-0)', '458(0-1)', '464(0-1)', '510(123-0)', '518(2-1)', '526(1-0)', '550(0-1)', '551(0-1)'
'Node 846','4(1-0)', '127(0-1)', '228(1-0)', '235(0-1)', '244(0-2)', '251(4-1)', '304(2-1)', '389(1-0)'
'Node 847','253(0-1)', '271(1-0)', '328(1-0)', '473(1-0)'
'Node 848','34(1-0)', '35(1-0)'
'Node 849','0(2-0)', '34(1-2)', '35(1-2)', '47(0-1)', '51(1-2)', '53(0-1)', '204(1-0)', '231(1-0)', '241(1-0)', '253(0-1)', '290(0-1)', '333(0-1)', '385(1-0)', '386(0-1)', '399(2-1)', '400(1-0)', '449(0-1)'
'Node 850','170(0-1)', '247(0-2)', '280(1-0)', '287(0-1)', '336(012-3)', '547(1-2)', '556(2-1)'
'Node 851','238(1-0)', '244(0-3)', '255(1-0)', '274(3-0)', '288(0-1)', '290(0-1)', '291(0-1)'
'Node 852','10(1-0)', '58(0-1)', '67(4-3)', '68(1-3)', '69(1-3)', '148(0-1)', '159(0-1)', '160(0-1)', '162(0-1)'
'Node 853','30(2-1)', '214(2-1)', '219(2-1)', '289(1-0)', '308(0-1)', '319(1-0)', '328(1-0)', '364(0-1)', '433(1-2)', '448(0-1)'
'Node 854','0(1-2)', '42(1-0)', '43(1-0)', '58(1-0)', '67(0-4)', '68(0-1)', '69(0-1)'
'Node 855','52(1-0)'
'Node 856','33(1-0)', '34(1-0)', '35(1-0)', '148(0-1)', '158(0-1)', '237(2-3)', '238(1-0)', '239(0-1)'
'Node 857','348(0-1)', '512(01-3)', '535(1-0)'
'Node 858','11(0-1)', '116(0-1)', '181(0-1)', '279(01-2)', '339(1-0)'
'Node 859','214(1-2)', '219(1-2)', '246(1-0)', '251(4-3)', '257(0-1)', '272(0-1)', '274(1-0)', '280(0-1)', '289(1-0)', '319(0-1)', '335(12-0)', '363(0-1)', '364(1-0)', '388(1-0)'
'Node 860','182(0-1)', '273(0-1)', '312(1-0)', '358(0-1)'
'Node 861','30(1-2)', '276(0-1)', '305(1-0)'
'Node 862','68(1-3)', '69(1-3)', '287(0-1)', '289(0-1)', '290(0-1)', '296(0-1)'
'Node 863','8(0-1)', '9(0-1)', '145(1-0)', '228(0-1)', '336(1-0)', '340(1-0)'
'Node 864','30(1-0)', '279(2-0)'
'Node 865','30(1-0)', '35(1-2)', '274(1-0)'
'Node 866','237(2-3)', '244(012-3)', '282(1-0)', '284(1-0)'
'Node 867','179(0-1)', '214(1-2)', '274(1-3)'
'Node 868','36(0-1)', '179(0-1)', '266(0-1)', '274(1-3)', '353(0-2)', '427(1-2)', '456(1-0)', '475(0-1)', '499(1-0)', '557(0-1)'
'Node 869','5(1-0)', '33(1-2)', '34(1-2)', '35(1-2)', '106(0-2)', '118(2-1)', '123(1-0)', '124(4-6)', '146(0-1)', '164(0-1)', '201(1-0)', '210(1-0)', '235(0-1)', '242(2-1)', '365(0-1)', '366(1-0)', '401(3-1)'
'Node 870','10(1-0)', '40(0-1)', '41(0-2)', '42(0-2)', '43(0-1)', '65(0-1)'
'Node 871','33(1-0)'
'Node 872','214(1-2)', '219(1-2)', '247(0-2)', '251(2-1)', '261(0-1)', '344(0-1)'
'Node 873','246(1-0)', '253(0-1)', '275(0-1)', '284(1-0)', '323(1-0)'
'Node 874','40(0-1)', '41(0-2)', '68(1-3)', '69(1-3)'
'Node 875','9(1-2)', '10(1-2)', '183(1-0)', '184(1-0)', '212(0-1)', '233(0-1)', '237(2-3)', '274(0-1)'
'Node 876','0(1-2)', '4(0-1)', '50(1-0)', '51(4-15)', '57(0-1)', '60(1-0)', '66(2-4)', '67(0-2)', '69(0-1)'
'Node 877','53(1-0)'
'Node 878','4(1-0)', '243(0-1)', '467(2-1)'
'Node 879','279(01-2)', '409(1-2)', '512(0-1)', '517(0-1)'
'Node 880','22(1-2)', '309(1-0)', '335(0-1)', '336(12-0)', '339(1-0)', '386(0-1)', '448(0-1)'

'Node 881','6(2-3)'

'Node 882','5(0-12)', '21(0-1)', '50(0-1)', '58(0-1)', '62(1-2)', '203(1-2)'

'Node 883','10(1-0)'

'Node 884','388(1-0)'

'Node 885','204(0-1)'

'Node 886','5(1-2)', '47(1-0)', '183(1-0)', '184(1-0)', '216(0-2)', '255(1-0)', '335(1-0)', '336(0-1)', '448(1-0)'

'Node 887','40(0-1)', '41(0-2)', '128(1-0)', '252(0-1)', '274(0-123)', '338(1-0)'

'Node 888','21(0-1)', '47(0-1)', '215(0-2)', '242(2-0)', '274(1-0)', '284(0-1)', '289(0-1)', '294(0-1)', '295(0-1)', '296(0-1)', '427(1-2)', '456(1-0)', '467(1-2)', '556(2-1)'

'Node 889','204(0-1)', '233(0-1)', '235(1-0)', '243(0-1)', '252(0-1)', '269(0-1)', '274(0-1)', '332(1-0)', '335(1-5)', '338(1-0)', '343(1-0)', '344(1-0)', '356(0-1)', '378(1-0)', '384(1-0)', '400(1-0)', '401(3-0)', '415(1-0)'

'Node 890','14(0-1)', '16(0-1)', '50(1-0)', '237(2-3)'

'Node 891','40(0-1)', '41(0-2)', '66(2-4)', '106(0-1)'

'Node 892','13(0-1)', '42(1-2)', '43(1-2)'

'Node 893','21(0-1)'

'Node 894','40(0-1)', '102(1-2)'

'Node 895','21(0-1)', '41(0-2)'

'Node 896','30(2-1)', '58(1-0)'

'Node 897','6(3-2)', '43(1-0)', '47(0-1)', '50(1-0)', '133(1-0)'

'Node 898','8(1-0)', '9(1-0)', '10(1-0)', '11(1-0)', '32(1-0)', '34(2-1)', '35(2-1)', '36(1-0)', '118(2-1)', '122(0-1)', '127(0-1)', '181(0-1)', '184(1-0)', '223(0-1)', '228(0-1)', '239(0-1)', '247(0-2)', '255(1-0)', '257(0-1)', '273(0-1)', '274(1-3)', '276(0-1)', '279(01-2)', '305(1-0)', '308(0-1)', '332(1-0)', '342(1-0)', '344(1-0)', '353(0-1)', '365(0-1)', '366(1-0)', '368(0-1)', '377(1-0)', '378(1-0)', '379(0-1)', '383(1-0)', '409(1-2)'

'Node 899','172(1-0)', '173(0-3)', '213(1-0)', '219(1-0)', '234(1-0)', '245(0-1)', '248(0-2)', '250(0-2)', '251(4-1)', '254(1-0)', '261(1-0)', '262(1-0)', '264(0-1)', '265(1-0)', '282(1-0)', '311(12-0)', '317(0-1)', '318(0-1)', '319(1-0)', '320(1-0)', '332(1-0)', '334(1-0)', '337(1-0)', '342(1-0)', '344(1-0)', '347(1-0)', '371(1-0)', '374(1-2)', '377(1-0)', '380(1-0)', '381(1-0)', '387(1-0)', '388(1-0)', '389(0-1)', '394(1-0)', '395(1-0)', '399(2-1)', '401(3-2)', '407(1-0)', '410(1-0)', '422(0-1)', '423(0-1)', '424(0-1)', '433(12-4)', '437(0-2)', '444(1-0)', '445(1-0)', '447(0-1)', '462(1-0)', '463(0-1)', '466(1-0)', '467(1-0)', '473(1-0)', '475(0-1)', '477(0-1)', '478(1-0)', '479(1-2)', '483(1-0)', '493(1-2)', '500(3-0)', '509(2-1)', '512(1-0)', '513(0-1)', '516(1-0)', '517(1-0)', '520(1-2)', '521(1-0)', '528(3-0)', '529(1-0)', '535(1-0)', '536(1-0)', '537(1-0)', '538(1-0)', '539(1-0)', '543(1-0)', '544(1-0)', '545(1-0)', '546(1-0)', '553(1-3)', '556(2-0)', '559(0-2)', '560(0-1)'

'Node 900','58(1-0)'

'Node 901','448(0-1)'

'Node 902','20(0-1)', '30(3-2)', '47(0-1)', '69(3-2)', '160(0-1)', '308(0-1)', '336(2-0)', '342(1-0)', '347(1-0)'

'Node 903','9(2-3)', '51(0-1)', '72(2-0)', '149(1-0)', '220(1-0)', '244(0-2)', '248(0-1)', '283(0-1)', '286(0-1)', '287(0-1)', '288(0-1)', '292(0-1)', '293(0-1)', '295(0-1)', '296(0-1)', '311(1-0)', '353(01-2)', '371(1-0)', '374(1-0)'

'Node 904','243(0-1)', '271(1-2)'

'Node 905','237(2-3)', '288(1-0)', '289(1-0)', '291(1-0)', '297(0-1)'

'Node 906','187(0-1)', '188(0-1)', '324(0-1)', '328(0-1)', '339(1-2)', '340(0-1)', '359(1-0)', '371(0-1)', '376(0-1)', '458(0-1)', '467(12-0)', '509(1-0)', '520(1-0)', '526(1-0)', '527(1-0)', '549(1-2)', '550(1-2)'

'Node 907','182(1-0)', '183(1-0)', '247(0-1)'

'Node 908','238(0-1)', '280(0-1)', '298(0-1)', '300(0-1)'

'Node 909','177(0-1)', '240(1-0)', '257(0-1)'

'Node 910','235(0-1)', '275(0-1)'

'Node 911','257(0-1)'

'Node 912','187(0-1)', '286(0-1)', '287(0-1)', '288(0-1)', '289(0-1)', '290(0-1)', '291(0-1)', '292(0-1)', '296(0-1)'

'Node 913','203(1-2)', '239(0-1)', '244(012-3)', '263(1-0)', '270(0-1)', '271(1-0)', '274(1-0)'

'Node 914','183(0-1)', '184(0-1)'

'Node 915','287(1-0)', '293(1-0)'

'Node 916','272(0-1)', '445(0-1)'

'Node 917','298(0-1)', '440(1-0)'
'Node 918','466(1-2)', '489(0-1)', '494(1-0)', '505(1-0)', '506(1-0)', '549(1-0)', '556(1-2)'
'Node 919','297(0-1)', '301(0-1)', '454(2-1)'
'Node 920','238(0-1)', '239(1-0)', '269(1-0)'
'Node 921','215(1-0)', '232(1-0)', '235(1-0)', '252(0-1)', '270(1-0)', '279(0-2)', '289(1-0)', '291(1-0)', '293(1-0)', '418(1-2)', '420(1-2)', '426(1-0)', '436(1-0)'
'Node 922','239(1-0)'
'Node 923','185(0-1)', '212(0-1)', '226(0-3)', '230(0-1)', '243(0-1)', '247(0-2)', '248(0-1)', '275(1-0)'
'Node 924','212(0-1)', '253(1-0)'
'Node 925','332(0-1)', '376(0-1)'
'Node 926','184(0-1)', '282(1-0)', '284(1-0)', '294(1-0)', '295(1-0)'
'Node 927','251(2-1)'
'Node 928','350(1-0)', '491(1-0)'
'Node 929','227(0-1)', '257(0-1)', '279(01-2)'
'Node 930','309(0-1)', '332(1-0)', '338(1-0)', '339(0-1)', '388(0-1)', '553(3-2)'
'Node 931','212(0-1)', '217(1-0)', '228(1-0)', '229(1-0)', '237(2-0)', '257(0-1)', '261(1-0)', '262(1-0)', '263(1-2)', '264(0-1)', '265(1-0)', '272(1-0)', '283(0-1)', '285(0-1)', '294(0-1)', '295(0-1)', '296(0-1)', '311(1-2)', '389(1-0)', '442(1-0)', '497(0-1)', '499(2-1)', '506(0-1)', '549(1-2)'
'Node 932','247(01-2)', '257(1-0)', '455(0-5)', '458(1-0)', '467(12-0)', '472(0-1)', '496(0-1)', '510(3-1)', '518(2-0)', '520(0-1)', '529(0-1)', '535(1-0)'