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Phylogenetic Systematics of Hylodidae (Amphibia: Anura)

Sistemática filogenética de Hylodidae (Amphibia: Anura)

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RESUMO

Hylodidae é composta por 46 espécies distribuídas em três gêneros: *Crossodactylus* (14 spp), *Hylodes* (25 spp) e *Megaelosia* (7 spp). Essas rãs-de-corredeiras são diurnas e associadas à ambientes encachoeiradas ao longo da Mata Atlântica. O alto nível de especificacidade à esses habitats observado nesse grupo parece estar relacionado com a morfologia externa extremamente conservada; entretanto, outras fontes de evidências tem provado ser úteis para distinção de espécies. Meu estudo foi designado para revisar o *status* atual da sistemática dos hilodídeos através de uma análise de evidência total que representa o máximo de espécies (e populações) possíveis; confirmar o monofiletismo dos taxa válidos atualmente; avaliar a história evolutiva de alguns caracteres; e reconstruir mudanças biogeográficas na distribuição de Hylodidae. Minha análise de evidência total incluiu dados morfológicos (293 caracteres) e moleculares (quatro genes mitocondriais e cinco genes nucleares) para 34371 terminais de hilodídeos mais 45 terminais de grupo externo, resultando em 713 árvores mais parcimoniosas com 32.405 passos. Eu recuperei Hylodidae e todos os seus gêneros como monofiléticos e reconheci 59 linhagens dentro da família. Três sinapomorfias putativas foram identificadas para Hylodidae baseadas na morfologia do saco vocal (saco vocal externo duplo, saco vocal interno duplo e abertura no *m. interhyoideus* por onde o divertículo passa). Análises da distribuição dos hilodídeos revelaram a origem de Hylodidae na bacia Atlântico Leste com subsequentes especiações alopátricas em bacias subjacentes.

ABSTRACT

Hylodidae is composed of 46 species distributed in three genera: *Crossodactylus* (14 spp), *Hylodes* (25 spp), and *Megaelosia* (7 spp). These torrent-frogs are diurnal and associated with riverine habitats throughout the Atlantic Rain Forest. The high degree of habitat specificity observed in this group seems to be associated with an extremely conservative external morphology; however, other sources of evidence have been proved useful to distinguish species. My study was designed to review the status of the current hylodid systematics, performing a total evidence analysis that represents as many species (and populations) as possible; confirm the monophyly of currently valid nominal taxa; investigate the evolutionary history of some morphological characters; and reconstruct biogeographical changes in the distribution of hylodids. My total evidence analysis included morphological (293 characters) and molecular data (four mitochondrial and five nuclear genes) for up to 371 hylodid terminals plus 45 outgroups, and resulted in 713 most parsimonious trees. I recovered Hylodidae and its compounding genera as monophyletic, and recognized 58 lineages within this family. Three synapomorphies were identified for Hylodidae based on vocal sac morphology (external double vocal sac, internal double vocal sac, and opening of the *m. interhyoideus* through which the diverticulum passes). Analysis of the distribution of hylodids revealed the origin of this frog family in the East Atlantic river basin, with subsequent allopatric speciation in adjacent basins.

INTRODUCTION

Hylodidae Günther, 1858 is composed of 46 frog species allocated in three genera: *Hylodes* Fitzinger, 1826 (25 species), *Crossodactylus* Duméril and Bibron, 1841 (14 species), and *Megaelosia* Miranda-Ribeiro, 1923 (seven species) (Frost 2016; Figure 1). This family is endemic to the Atlantic Rain Forest, distributed from Alagoas, northeastern Brazil, to Rio Grande do Sul and Misiones, in southern Brazil and northern Argentina, respectively (Frost 2016). Diurnal habits are prevalent, but some species can be active during the day and at night (Silva and Benmaman 2008), and *Megaelosia apuana* was reported behaving exclusively at night (Pombal *et al.* 2003). Many species are extremely territorial, exhibiting complex behaviors that go from visual displays such as foot flagging (Haddad and Giaretta 1999; Wogel *et al.* 2004; Narvaes and Rodrigues 2005; Forti and Castanho 2012; Caldart *et al.* 2014, Sá *et al.* 2016) to aggressive movements performed during combat between males (*e.g.*, aggressive kicks; Caldart *et al.* 2014).

Species of this family have riparian habits, being exclusively associated with rivulets. This specialized ecology rendered hylodids their common name, the South American torrent frogs. Silva and Benmaman (2008) took into account the extreme association of Hylodes' species with drainage basins—association expressed through a several adaptations to torrent habitat, such as low frequency call and complex social system including visual communication—and hypothesized that the distribution of the species probably reflects the history and relations rivers and basins where they are found. According to these authors, large rivers should act as barriers, isolating species in small tributaries, whereas smaller rivers act as connectors through which the species can disperse.

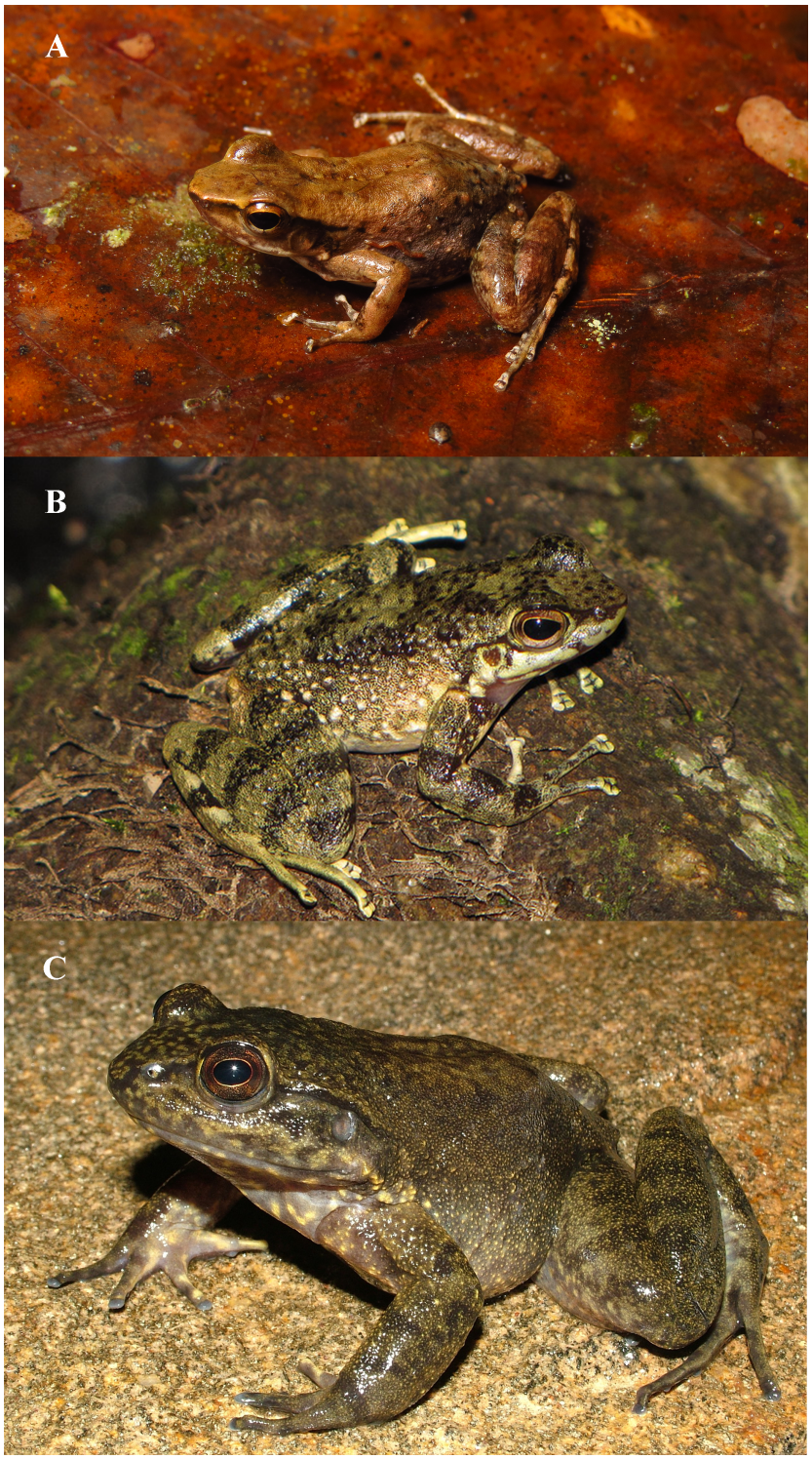

Figure 1. Representatives of Hylodidae: (A) *Crossodactylus timbuhy* (Santa Teresa, ES); (B) *Hylodes asper* (Est. Biol. Boracéia, São Paulo, SP); and (C) *Megaelosia apauna* (Domingos Martins, ES). Photos by M. Texeira Jr. (A, B) and P. Peloso (C).

Many species of Hylodidae are cryptic and exhibit an extremely conservative morphology putatively related to their association with riverine habitats. However, evidence coming from sources other than the external morphology of adult specimens has been proved useful to distinguish species, such as internal morphology (viscera, bones, cartilages, and muscles; *e.g.*, Lynch 1971), tadpoles (pers. obs.), bioacoustics (Canedo 2008), behavior (Caldart *et al.* 2014, Sá *et al.* 2015), and molecules (Fabri 2013). Previous phylogenies included representatives of Hylodidae, but most of them only used one species of each genus. Thus, the relations within the family are still unclear.

Lynch (1971) proposed the first hypothesis of relationships regarding hylodid species, and observed similarities between the subfamily Hylodinae (= Elosiinae) and the family Dendrobatidae. Lynch (1971) pointed out the extreme similarity of their cranial morphology, vertebral columns, T-shape terminal phalanges, dermal glandular pads on top of the digital pads, and the presence of toxic skin secretions, at least in some species; however, the author affirmed that secretions of elosiines had not been chemically analyzed.

Lynch (1971) showed the close relationship between Elosiinae and Dendrobatidae using a phenetic dendrogram. In addition, he supported the genus *Crossodactylus* as "the primitive elosiine", despite considering the loss of the quadradojugal in that genus a derived character. This author also recognized four features of *Crossodactylus* as primitive: the presence of a medial and subgular vocal sac, and the presence of nuptial asperities (cluster of spines), the medial vent on tadpoles, and the ranoid pattern of the thigh musculature.

The first phylogeny including the subfamily Hylodinae was proposed by Haas (2003) mostly based on larval characters. The results found by Haas (2003) supported

those by Lynch (1971), showing the subfamily Hylodinae as sister-group of Dendrobatidae. Nuin and Val (2005) proposed an alternative hypothesis based exclusively on morphological characters of adults. These authors recovered relationships fairly distinct from those proposed by Haas (2003). Nuin and Val's hypothesis showed Hylodinae as sister-group of an unresolved clade containing representatives of Cycloramphidae, Leptodactylidae, and Strabomantidae (*sensu* Frost 2016). The internal relationships of Hylodidae recovered by Nuin and Val (2005) suggested *Crossodactylus* as sister-group of *Hylodes*, and both as sister-group of *Megaelosia*, contradicting Lynch's (1971) hypothesis.

The phylogeny proposed by Frost *et al.* (2006) based mainly on molecular data, suggested Hylodinae as a subfamily of Cycloramphidae. Concerning the internal relationships of Hylodidae, Frost *et al.* (2006) recovered a topology where *Hylodes* and *Megaelosia* are sister groups, and both forming the sister clade of *Crossodactylus*.

The subfamily Hylodinae was elevated to family rank by Grant *et al.* (2006) in their comprehensive study of the superfamily Dendrobatoidae using total evidence. The results recovered by Grant *et al.* (2006) supported those of Lynch (1971) and Hass (2003). Moreover, in Grant *et. al.*'s phylogeny, the clade (Hylodidae + Dendrobatoidae) was recovered as sister group of Bufonidae. The internal relationships among species of Hylodidae recovered in Grant *et al.* (2006) were completely congruent with those of Frost *et al.* (2006).

Pyron and Wiens (2011) proposed the most comprehensive phylogeny of Amphibia based exclusively on molecular data. These authors recovered the clade (Cycloramphidae (Hylodidae + Alsodidae)) and showed that the only sampled species of *Megaelosia* (*M. goeldi*) is actually imbedded in *Hylodes*, reveling the likely paraphyletic condition of this latter genus.

As shown above, several phylogenetic studies that included Hylodidae taxa diverged with respect to the relationships recovered. In addition, no phylogenetic study published until now had the goal of clarifying the internal relationships of Hylodidae. Most analyses included just a few representatives of this family, usually one species of each genus. Indeed, Nuin and Val (2005) were the first to focus on the interspecific relationships hylodids; even though only 13 species were sampled, representing approximately one third of all currently valid nominal species. That said, future investigations of internal relationships in Hylodidae and its position in relation to other families clearly require the inclusion of additional hylodid taxa.

In an unpublished Master's dissertation, Fabri (2013) produced the first taxonomically inclusive phylogeny of *Crossodactylus*, employing exclusively molecular data. This work remains up to date as the most inclusive phylogenetic analysis of Hylodidae. Fabri (2013) recovered *Crossodactylus* as a well-supported group (Goodman–Bremer index = 43), sister of *Megaelosia* + *Hylodes*. *Crossodactylus* was divided into two large clades: Clade A, containing *C. gaudichaudii* complex, *C. aeneus* complex, and a several unidentified terminals from Bahia and Espírito Santo; Clade B, including *C. bokermanni* (= *C. trachystomus*) complex, *C. schmidti* complex, *C. caramaschii* complex, and all unidentified terminals from southern Brazil and from the state of São Paulo. The results found by Fabri offered no support to the species groups proposed by Caramaschi and Sazima (1985), reinforcing Pimenta *et al.*'s (2014) recommendation not to use those phenetic groupings.

Fabri's (2013) phylogeny also included 16 species of *Hylodes* and recovered a clade composed of *H.* cf. *charadranaetes* (*H. nasus* (*H. dactylocinus* (*H. asper*))) as sister of another major clade comprising the other 12 species of the *H. lateristrigatus*

group (*sensu* Heyer 1982) plus *H. glaber*. Heyer's *H. nasus* group was recovered as monophyletic in Fabri's hypothesis. Disregarding the probable misidentification of *H.* cf. *charadranaetes*, all species of *H. lateristrigatus* group were recovered in a unique clade. However, the placement of *H. glaber* (Miranda-Ribeiro 1926) (previously allocated in a monotypic group by Heyer 1982) within the *H. lateristrigatus* group made the monophyly of *H. lateristrigatus* species groups (sensu Heyer 1982) questionable.

Until recently, all phylogenetic studies had only included *Megaelosia goeldii* (Baumann 1912) to represent the genus *Megaelosia*. Fabri (2013) was the first to analyze four species of *Megaelosia*. Surprisingly, her results grouped *M. goedii* as sister-group of *Hylodes*, and all other *Megaelosia* clustered together as sister-group of *M. goeldii* + *Hylodes*. These results clearly render a paraphyletic *Megaelosia*.

TAXONOMY HISTORY

The name Hylodidae was proposed by Günther (1858) for the genera *Crossodactylus* Duméril and Bibron 1841, *Hylodes* Fitzinger 1826, *Phyllobates* Duméril and Bibron 1841, and *Platymantis* Günther 1858. However, Miranda-Ribeiro (1923) proposed the name Elosiidae for the genus *Crossodactylus*, *Hylodes*, and *Megaelosia* Miranda-Ribeiro 1923. Lutz (1930) defined this group as a subfamily of Leptodactylidae Werner 1896 (1838). After that, Savage (1973) changed the name of this subfamily to Hylodinae claiming its taxonomic priority. Finally, Grant *et al.* (2006) elevated this subfamily to family rank, using the name Hylodidae proposed by Günther (1858), comprising the genera *Crossodactylus*, *Hylodes*, and *Megaelosia*.

Crossodactylus

Crossodactylus was proposed by Duméril and Bibron in 1841, who designated *C. gaudichaudii* Duméril and Bibron, 1841 as type species of the genus. I will provide just a brief summary of the most relevant taxonomic acts that affected *Crossodactylus*. For more details, see Pimenta (2008) and Pimenta *et al.* (2014, 2015).

Duméril and Bibron (1841) described *Crossodactylus gaudichaudii* in the same work where they proposed the genus *Crossodactylus*. Bell (1843) described *Limnocharis fuscus* based on a specimen collected by C. Darwin in Rio de Janeiro. Fitzinger (1860) identified some individuals from the expedition 'Fragata Nova' as *Phyllobates fuscigula* Fitzinger 1860 and others as *C. gaudichaudii*; however, Seindachner (1865) concluded that both species are the same taxon. Cope (1866) synonymized *Crossodactylus* to *Phyllobates*, resulting the new combination *Phyllobates gaudichaudii* (Duméril and Bibron 1841). Two years later, Steindachner (1867) named *P. fuscigula*, a junior synonym of *C. gaudichaudii*, ignoring Cope's decision.

The species *Tarsopterus trachystomus* was described by Reinhardt and Lütken (1862 "1861") and this genus was considered very close to *Crossodactylus*. Boulenger (1882) considered *T. trachystomus* a junior synonym of *C. gaudichaudii*; however, the author also considered the genus *Crossodactylus* a junior synonym of *Leptodactylus* Fitzinger 1826, resulting in the new combination *Leptodactylus gaudichaudii*. Finally, Miranda-Ribeiro (1923) revalidated *Crossodactylus* based on pectoral girdle morphology and absence of vomerine teeth (characters that are present in *Leptodactylus*). Lutz (1930) provided a taxonomic review of Elosiinae (including the genus *Basanitia* Miranda-Ribeiro (1923) with reservation (*i.e.*, he already had doubts about the inclusion of *Basanitia* in Elosiinae), now a junior synonym of

Ischnocnema Reinhardt and Lütken 1862), and synonymized *Calamobates boulengeri* De Witte, 1930 with *C. fuscigula* Lutz 1930, posteriorly synonymized with *C. dispar* Lutz 1925 by Cochran (1955).

Caramaschi and Sazima (1985) recognized three species groups in this genus: the *C. gaudichaudii* group, including *C. aeneus* Müller 1924, *C. bokermanni* Caramaschi and Sazima 1985, and *C. gaudichaudii* Duméril and Bibron 1841, characterized by protruding snout and distinct canthus rostralis; the *C. trachystomus* group, including *C. dispar* A. Lutz 1925, *C. grandis* B. Lutz 1951, and *C. trachystomus* (Reinhardt and Lütken 1862), characterized by short, rounded snout, and less evident canthus rostralis; and the monospecific group of *C. schmidti* Gallardo 1961, characterized by very short snout and rounded canthus rostralis. All species described subsequently by Caramaschi and Sazima (1985) and before Pimenta et al. (2014), *i.e.*, *C. dantei* Carcerelli and Caramaschi 1992, *C. lutzorum* Carcerelli and Caramaschi 1992, *C. caramaschii* Bastos and Pombal 1995, and *C. cyclospinus* Nascimento, Cruz, and Feio 2005, were allocated in the *C. gaudichaudii* group; except by *C. bokermanni* Caramaschi and Sazima 1985, whose inclusion in that group was questioned by Pimenta *et al.* (2008).

In a recent paper, Pimenta *et al.* (2014) described two new species, *C. timbuhy* Pimenta, Cruz, and Caramaschi 2014 and *C. werneri* Pimenta, Cruz, and Caramaschi 2014; and resurrected another one, *C. boulengeri* (De Witte 1930). In their discussion, they report several problems with the characters used by Caramaschi and Sazima (1985) to delimit species and groups in *Crossodactylus*. These authors discouraged the use of phenetic groups, but refrained from proposing new taxonomic groupings. Thus, the three species described in their paper, and also *C. franciscanus* Pimenta, Caramaschi, and Cruz 2015, described in the following year, were not included in any

group proposed by Caramaschi and Sazima (1985). Reinforcing their skepticism with respect to the validity of previously defined species groups of *Crossodactylus*, Pimenta *et al.* (2015) synonymized *C. bokermanni* with *C. trachystomus*, two species that belonged to different species group as per Caramaschi and Sazima (1985).

Hylodes

Hylodes was proposed by Fitzinger (1826) for the species *Hylodes gravenhorstii* (Fitzinger 1826), a *nomen nudum*, and *Hyla ranoides* (Spix 1824). Wagler (1830) used the name *Hylodes* replacing *Enydrobius*. Tschudi (1838) described a new species for *Hylodes*, *H. martinicensis*, and the genus *Elosia*, whose type species was *Hyla nasus* (Lichtesnstein 1823), wrongly spelled by Tschudi as *Hyla nasuta*. Fitzinger (1843) assigned *H. martinicensis* as type species of *Hylodes*, though this designation was made by monotypy as *Hyla ranoides*. The author also described *Scinacodes* and assigned *Hyla nasus* as its type species, but Cochran (1955) synonymized this genus with *Elosia*. Although Steindachner (1865) synonymized *Elosia* with *Hylodes*, and Stejneger (1904) proposed that synonymy once again, this synonym became broadly accepted only after the revision made by Meyers (1962). This author observed that the name "*Hylodes*" was proposed twice by the same author for two different genera (Fitzinger 1826, 1843). Peters (1872) synonymized *Hyla ranoides* with *Hyla nasus*. However, the type locality of *H. nasus* and the locality where Spix collected *Hyla ranoides* ("Provincia Bahiae") are contradictory. Nascimento *et al.* (2001) suggested that the locality provided by Spix is wrong. For more details, see Canedo (2008).

Heyer (1982) proposed four species groups in *Hylodes* on the basis of external morphology alone. The *H. glaber* group (named as *H. pulcher* group), including only *H. glaber* (=*H. pulcher*; Miranda-Ribeiro 1926), characterized by distinctive,

moderate sized, slender, ranoid-like species; the *H. mertensi* group, including only *H. mertensi* (Bokermann 1956), characterized by a large and robust species with leathery dorsal skin; the *H. nasus* group, nowadays including *H. nasus* (Lichtenstein 1823), *H. asper* (Müller 1924), *H. cardosoi* Lignau, Canedo, and Pombal 2008, and *H. dactylocinus* Pavan, Narvaes, and Rodrigues 2008, characterized by moderate to large size, robust body with granular dorsal surfaces, and absence of light dorsolateral stripes; and the *H. lateristrigatus* group, currently including *H. lateristrigatus* (Baumann 1912), *H. perplicatus* (Miranda-Ribeiro 1926), *H. meridionalis* (Mertens 1927), *H. magalhaesi* (Bokermann 1964), *H. ornatus* (Bokermann 1967), *H. regius* Gouvêa 1979, *H. babax* Heyer 1982, *H. vanzolini* Heyer 1982, *H. otavioi* Sazima and Bokermann 1983, *H. charadranaetes* Heyer and Cocroft 1986, *H. phyllodes* Heyer and Cocroft 1986, *H. sazimai* Haddad and Pombal 1995, *H. heyeri* Haddad, Pombal, and Bastos 1996, *H. uai* Nascimento, Pombal, and Haddad 2001, *H. amnicola* Pombal, Feio, and Haddad 2002, *H. fredi* Canedo and Pombal 2007, *H. pipilans* Canedo and Pombal 2007, *H. perere* Silva and Benmaman 2008, and *H. japi* Sá, Canedo, Lira, and Haddad 2015, characterized by small to moderate size, body slender, ranoid-like, dorsum smooth, and in most members with light dorsolateral stripes. Heyer's (1982) phenetic groups have not been tested phylogenetically; yet, the groupings proposed in that study have been broadly employed in the taxonomic literature of *Hylodes* until presently (*e.g.*, Sá *et al.* 2015).

Megaelosia

Miranda-Ribeiro (1923) described the genus *Megaelosia* to allocate *Elosia bufonia* Girard 1853, but the specimen described was found to correspond to *Megaelosia goeldii*, previously described by Baumann (1912). Later, *Elosia bufonia*

was considered a synonym of *M. goeldii* (Lutz 1930, Bokermann 1966). Until the early 1970s, *Megaelosia* was considered a monotypic genus (Lynch 1971). The second species was only described in 1985 (*Megaelosia lutzae* Izecksohn and Gouvea 1987). Giaretta *et al.* (1993) described additional species for *Megaelosia* during their taxonomic revision. In that work, the author confirmed the validity of *Megaelosia massarti* (De Witte 1930), questioned (but never changed) by Lutz (1930), Cochran (1955), and Bokermann (1966), and described a new species, *Megaelosia bocainensis* Giaretta, Bokermann, and Haddad 1993. Two more species were described after this revisionary study, *M. boticariana* (Giaretta and Aguiar 1998) and *M. apuana* (Pombal *et al.* 2003).

Currently, this genus is composed of seven species: *M. goeldii* (Baumann 1912), *M. massarti* (De Witte 1930), *M. jordanensis* (Heyer 1983), *M. lutzae* Izecksohn and Gouvêa 1987, *M. bocainensis* Giaretta, Bokermann, and Haddad 1993, *M. boticariana* Giaretta and Aguiar 1998, *M. apuana* Pombal, Prado and Canedo 2003. No species groupings were proposed for *Megaelosia* thus far.

CONCLUSION

- *Thoropa millilaris* and the superfamily Dendrobatoidea (Aromobatidae + Dendrobatidae) were recovered as sister group of Hylodidae.
- Hylodidae and its three compounding genera, *Crossodactylus*, *Hylodes*, and *Megaelosia*, were recovered as monophyletic with high support.
- I detected 59 lineages within Hylodidae. For *Crossodactylus*, I recognized 20 lineages distributed in three major clades (*Crossodactylus* 'MG',

Crossodactylus ‘SP / South’, and *Crossodactylus* ‘SE / NE’). Regarding *Megaelosia*, I defined six lineages. And, for *Hylodes*, I recognized 33 lineages distributed in five major clades (*Hylodes* ‘South’, *Hylodes* ‘Serra do Mar / no spine’, *Hylodes* ‘Serra do Mar / spine’, *Hylodes* ‘MG / ES’, and *Hylodes* ‘Serra da Mantiqueira’).

- The phenetic groups of *Hylodes* and *Crossodactylus* proposed in 1980s were not recovered as monophyletic clades.
- Several characters were revealed as synapomorphic for Hylodidae, such as the condition of the vocal sac and its relation with the *interhyoideus* muscle; presence of anteromedial supplementary element of *m. intermandibularis*; and the presence of supernumerary papillae in the oral disc of tadpoles.
- The origin of Hylodidae was inferred in the East Atlantic basin, and subsequent allopatric speciation in adjacent river basins is hypothesized to have produced the taxonomic diversity currently observed in this group.

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