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# Phylogenetic Systematics of Hylodidae (Amphibia: Anura)

Sistemática filogenética de Hylodidae (Amphibia: Anura)



São Paulo

2017

**Cover:**

Representation of *Hylodes asper* performing foot-flagging movement.

Illustration in watercolor by Paulo Presti (Jan, 2017).

Rachel Montesinos Martins Pereira

# Phylogenetic Systematics of Hylodidae (Amphibia: Anura)

Sistemática filogenética de Hylodidae (Amphibia: Anura)

Tese apresentada ao Instituto de  
Biotecnologia da Universidade de São  
Paulo, para a obtenção de Título de  
Doutor em Ciências Biológicas, na  
Área de Zoologia.

Orientador: Taran Grant

São Paulo

2017

Ficha Catalográfica

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Montesinos, Rachel

Sistemática Filogenética de Hylodidae  
(Amphibia: Anura)

XIII + 284pp.

Tese (Doutorado) - Instituto de Biociências  
da Universidade de São Paulo. Departamento de  
Zoologia.

1. Hylodidae 2. Filogenia 3. Evidência

Total 4. Parcimônia

Universidade de São Paulo. Instituto de  
Biociências. Departamento de Zoologia.

Comissão Julgadora:

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Prof(a). Dr(a).

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Prof(a). Dr(a).

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Prof(a). Dr(a).

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Prof(a). Dr(a).

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Prof. Dr. Taran Grant

Orientador



*Aos meus pais, Nélida e José Carlos.*

## AGRADECIMENTOS

À FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo) pela concessão das bolsas de Doutorado no país (Proc. # 2012/22566-3) e de BEPE (Bolsa de Estágio de Pesquisa no Exterior, Proc. # 2014/04077-0).

Ao meu orientador Taran Grant, por todos as conversar, conselhos e puxões-de-orelha. Taran certamente é um exemplo de profissional e foi uma honra muito grande poder tê-lo como orientador.

À Kevin de Queiroz, meu *sponsor* durante os oito meses que trabalhei no National Museum of Natural History, Smithsonian Institute, Washington, DC, USA. Aproveito aqui para agradecer a todos os profissionais do Smithsonian que me deram apoio durante minha passagem por lá, Roy McDiarmid, Addison Wynn, Kenneth Tighe, Jeremy Jacobs e Daniel Mulcahy do “Division of Amphibians and Reptiles”. Além de Dave Johnson, Bruce Collette e David Santana do “Division of Fishes”.

À Danielle Grant, principal colaboradora deste trabalho, pela inclusão de aproximadamente 150 terminais na presente análise.

À Miguel Trefaut Rodrigues, Célio Haddad, Paulo Garcia, José Pombal Jr. e Luciana Nascimento pela doação de alíquotas de tecidos e empréstimo de espécimes.

À Estevão Jasper Comitti, Emanuel Texeira da Silva e Clodoaldo Lopes de Assis que espontaneamente me ofereceram tecidos de algumas de suas coletas.

Aos funcionários do IB que sempre estavam dispostos a ajudar quando solicitado. Agradecimento especial aos técnicos do Laboratório de Molecular, Sabrina, Manu e Bia; e ao Phillip, técnico do Micro-CT.

Aos meus amigos do Laboratório de Anfíbios, Adriana, André, Boris, Carola, Denis, Gabriel, Isabela, Jhon, Júlia, Maíra, Marco, Mariane, Marvin, Pedro e Rafael.

Sem deixar de mencionar os que atualmente não estão no lab, mas fizeram parte desses 4 anos de convívio, Ana Paula, Carol, Jéssica e Juliana. Mais do que colegas de trabalho, somos todos amigos. Obrigada por todos os momentos, desde discussões sobre assuntos relevantes na ciência até piadas e comentários inúteis que fazia do nosso ambiente de trabalho ao mesmo tempo profissional e divertido.

À diretoria da SBH (Márcio, Rafael, Bianca, Fausto, Vivian e Thaís), a qual faço parte desde 2013 e que me fizeram acreditar na força da Herpetologia e batalhar para que cresça ainda mais.

Aos colegas de departamento pelos diversos momentos de discussão e festejos. Um agradecimento especial a todos aqueles que fizeram parte da comissão organizadora do CVZoo durante os quatro anos que estive envolvida nesse projeto que me enche de orgulho. Também tive a oportunidade de fazer vários amigos nos Departamentos de Fisiologia, Ecologia, Botânica e Genética. Seria impossível listar nomes aqui, mas a todos vocês, meu muito obrigada.

Aos amigos que fiz durante minha estadia em Washington. Muitos eram os brasileiros e a “*brazilian mafia*” foi extremamente valiosa para que eu me sentisse sempre em casa. Não posso deixar de incluir os amigos que fiz no POETS (happy-hour de sexta-feira do Smithsonian), certamente várias dessas pessoas se tornaram amigos que sempre irei querer por perto, mesmo que tão distantes.

A todos os que foram meus *roommates* durante esses quatro anos em SP (Thais, Juan, Marcos, Patrícia, Anne e Alípio). Sem esquecer de citar a Jenny, minha *roommate* durante o período que morei em Washington, DC. Obrigada pela oportunidade de viver o dia-a-dia com vocês, cada um de vocês me trouxe um aprendizado novo.

À minha família de São Paulo, Adri, Mari e Pedro (e nossos pets, Frida e Brigithe), sem deixar de incluir Anne e André que estão sempre presentes. Obrigada por todos os bons momentos vividos em nossa casinha. Não poderia deixar de falar que sem esses cinco queridos esta tese não teria a mesma qualidade. Muito, muito obrigada!

À toda minha família espalhada pelo Sudeste que compreenderam minha ausência e sempre me incentivaram a seguir em frente. Aqui, me sinto na obrigação de fazer um agradecimento a parte para minha tia Nélia, que sempre foi uma referência para mim. Minha tia, no início da década de 50, enfrentou uma sociedade machista saindo de casa aos 18 anos para fazer a faculdade que tanto sonhava. O fato de eu ter saído de casa para fazer o Mestrado e Doutorado sempre a fez dizer que eu a tinha puxado. E é verdade, mas ela me influenciou não só na decisão de sair da zona de conforto para lutar por uma carreira bem sucedida, ela também me ensinou a ser uma mulher empoderada e independente.

Por último, e certamente mais importante, à Nélida e José Carlos, a quem dedico esta tese. Meus pais sempre me apoiaram e me incentivaram em todas as minhas decisões, desde a escolha do curso de Biologia até a saída do país para estágio de pesquisa. Morando em outro estado (e durante oito meses, em outro país), em diversos momentos não pude estar presente quando eles precisaram do meu apoio. Mas, mesmo assim, eles não permitiram que as dificuldades vividas por eles influenciassem minha vida acadêmica. Portanto, por todo apoio (desde financeiro até emocional), eu sou extremamente grata aos dois; e é por isso que esta tese é dedicada a eles. Sem o apoio incondicional dos meus pais, eu não teria chegado onde estou hoje. Amo vocês.

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## 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 *Megaelasia* 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 *Megaelasia 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.

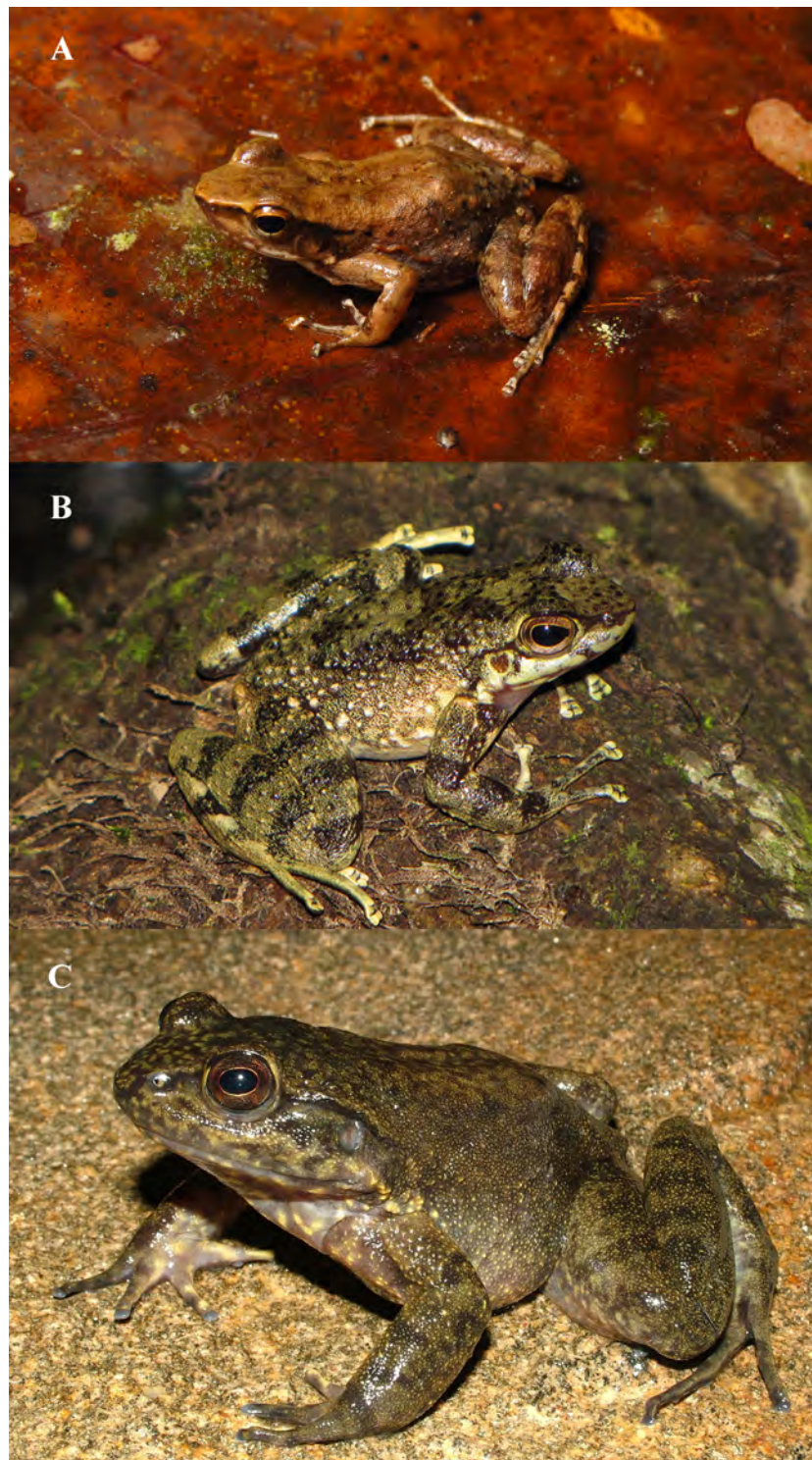


Figure 1. Representatives of Hylodidae: (A) *Crossodactylus timbuihy* (Santa Teresa, ES); (B) *Hylodes asper* (Est. Biol. Boracéia, São Paulo, SP); and (C) *Megaelosia apauna* (Domingos Martins, ES). Photos by M. Texeira Jr. (A, B) and P. Peloso (C).

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 Haas (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*, revealing 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. schmidtii* 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. goeldii* 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*.

## GOALS

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; evaluate the evolutionary history of some characters; and evaluate the evolution of its geographic distribution.

In order to provide the necessary background for a better understanding of the systematics of Hylodidae and its compounding genera, I revise their taxonomic history in the following section.



## 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. cyclopinus* 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. weneri* Pimenta, Cruz, and Caramaschi 2014; and resurrected another one, *C. boulegeri* (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* (Lichtenstein 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. fredii* 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.

## MATERIAL AND METHODS

### TAXON SAMPLING

#### **Ingroup sampling**

This study covers a larger part of the taxonomic diversity of Hylodidae known to date, in addition to putative new species and recently sampled populations. In total, I obtained DNA sequence data for 326 terminals, representing 34 of the 46 valid nominal species currently allocated in Hylodidae (7 *Crossodactylus*, 23 *Hylodes*, and 4 *Megaelosia*; see Appendix 1). Because several species of Hylodidae have not been collected for many decades, approximately one quarter of its known taxonomic diversity could not be sampled for molecular data.

Morphological data (at least external morphology) were generated for most species of Hylodidae (41 species). Nevertheless, I opted for analyzing morphology data exclusively from species for which DNA sequences were produced. Thus, seven species were removed from my analysis (*C. boulengeri*, *C. cyclospinus*, *C. dispar*, *C. grandis*, *C. lutzorum*, *C. weneri*, and *H. vanzolini*). This decision was made to avoid soft polytomies resulting from absence of phylogenetic information (Maddison 1989). The total sample used in this study covered approximately 75% of the currently

known taxonomic diversity of Hylodidae. The geographic distribution of the samples analyzed is shown in **Figure 2**.

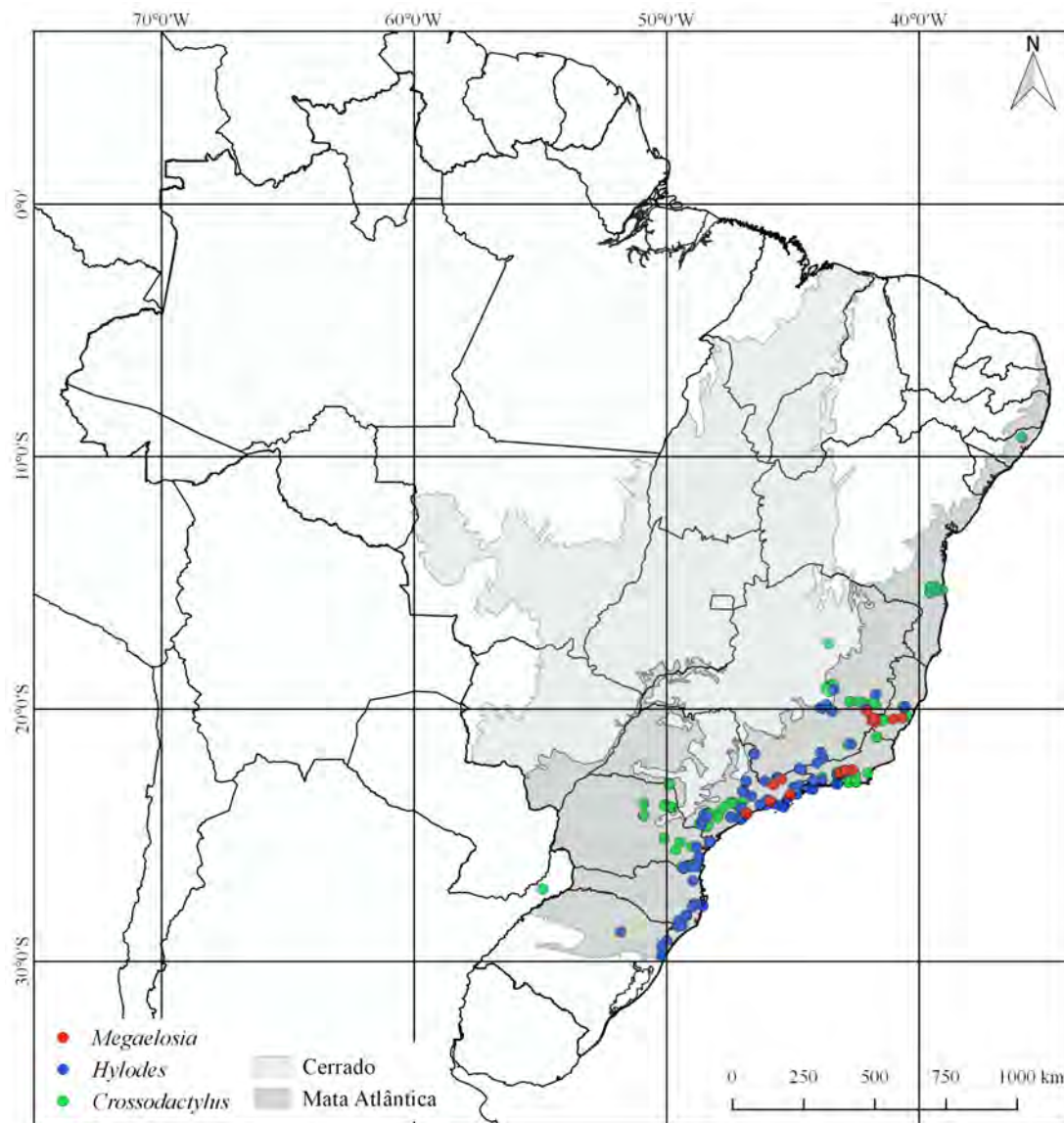


Figure 2. Distribution of Hylodidae samples used in this study.

### **Outgroup sampling**

The selection of outgroup terminals followed two different steps: (1) choice of families to be sampled, and (2) choice of species representing each family. For the former step, I selected all families that were recovered as closely related or sister group of Hylodidae in previous analyses (Haas 2003; Nuin and Val 2005; Frost *et al.*

2006; Grant *et al.* 2006; Pyron and Wiens 2011). Therefore, my matrix include representatives of 18 families: Allophrynidae, Alsodidae, Aromobatidae, Batrachylidae, Brachycephalidae, Bufonidae, Centrolenidae, Ceratophryidae, Craugastoridae, Cycloramphidae, Dendrobatidae, Elutherodactylidae, Hemiphractidae, Hylidae, Leptodactylidae, Odontophrynidae, Rhinodermatidae, and Telmatobidae. The choice of species in each family followed recommendations from Grant *et al.* (2006), as well as the availability of sequences in Genbank. In total, 45 species (terminals) were included as outgroup (Appendix 2). *Hemiphractus helioi*<sup>1</sup> was selected to root the phylogenetic trees generated.

## PHENOTYPIC CHARACTERS SAMPLING

A total of 292 phenotypic characters were codified, representing seven independent systems: external morphology, viscera, muscles, osteology, chromosomes, behavior of adults, and external morphology of tadpoles. Of the 292 characters, 267 were primarily coded by myself; the other 25 were completely or partially taken from the literature and/or collaborators. For bone and cartilage analyses I used three different techniques: clear and double stain (C&S), computed tomography scanning (CT-Scan), and 3D digital x-ray. Specimens were cleared and double-stained following Taylor and Van Dyke's (1985) protocol. To observe muscles, I highlighted them using a diluted lugol solution. See Table 01 for details.

The morphological matrix analyzed was constructed with aid of the software Mesquite v. 3.1.0 (Maddison and Maddison 2014; Appendix 03).

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<sup>1</sup> *Hemiphractus helioi* was included in my analyses as a chimeric terminal. The data analyzed for this species correspond to Genbank molecular sequences generated by Faivovich *et al.* (2005) plus morphological data coded by myself from two specimens (male and female) of *H. johnstoni*. See 'Total evidence analysis' section for details.



Table 01. Characters systems used in this study. For each character system, I specify the number of characters codified (#Ch); the source of information, *i.e.*, if characters were codified by myself (M), collaborators (C), or come from the literature (L); and the main references on which the characters were based. **X** in bold represents the main source of information.

Character system	#Ch	Source			References
		M	C	L	
External morphology	127	<b>X</b>	X		Liu (1935), McDiarmid (1971), Trueb and Duellman (1986), Nuin and Val (2005), Grant <i>et al.</i> (2006), Vieira (2010), Rada (2012)
Viscera	09	<b>X</b>	X		Duellman and Trueb (1986), Grant <i>et al.</i> (2006), Rada (2012), Franco-Belussi <i>et al.</i> 2013, 2016)
Musculature	30	<b>X</b>	X		Noble (1922), Trewavas (1933), Tyler (1971), Lynch (1993), Burton (1998a, 1998b, 2004), Silva (1998), Manzano (2000), Faivovich (2002), Grant <i>et al.</i> (2006), Manzano <i>et al.</i> (2008), Blotto (2013), Vieira (2010), Rada (2012)
Osteology	99	<b>X</b>	X		Trewavas (1933), Lynch (1971), Trueb (1973, 1993), Fabrezi (1992, 1993), Silva 1998, Burton (1998), Grant <i>et al.</i> (2006), Vieira (2010), Rada (2012)
Tadpole	23	<b>X</b>	<b>X</b>	X	P. Dias (pers. comm.), Montesinos <i>et al.</i> (ump. data), tadpole's descriptions
Chromosomes	1			<b>X</b>	Beçak (1968), Bogart (1970), Denaro (1972), Giaretta <i>et al.</i> (1993), Melo <i>et al.</i> (1995), Rosa <i>et al.</i> (2003), Campos (2010), Amaro <i>et al.</i> (2012), Aguiar Jr. <i>et al.</i> (2004)
Behaviour	1			<b>X</b>	Narvaes and Rodrigues (2005), Forti and Castanho (2012), Caldart <i>et al.</i> (2014), and Sá <i>et al.</i> (2016)

## GENOTYPIC CHARACTERS SAMPLING

### Sequences obtained in this study

In order to build a solid hypothesis of relationships that encompasses terminals of both deep and shallow taxonomic ranks, I selected nine genes with a wide range of molecular variability: the mitochondrial genes H-strand transcription unite 1 (H1)—

which includes 12S ribosomal, tRNA<sup>val</sup>, and 16S ribosomal sequence—, cytochrome *b* (*cytb*), and cytochrome oxidase c subunit I (COI); and the nuclear protein coding genes histone H3, rhodopsin (Rhod), tyrosinase (Tyr), recombination activating gene 1 (RAG1), and the nuclear 28S ribosomal gene. All primers used in this study are listed in Table 02.

Table 02. Primers used in this study. Mitochondrial and nuclear primers are listed, respectively, above and below the line that divides the table.

Primer	Direction	Primer sequence (5'-3')	Source
<b>12S rDNA</b>			
MVZ59	Forward	ATAGCACTGAAAAYGCTDAGATG	Graybeal 1997
12S-FH	Reverse	CTTGGCTCGTAGTTCCTGGCG	Palumbi <i>et al.</i> 1991
12S-AL	Forward	AAACTGGGATTAGATACCCCACTAT	Goebel <i>et al.</i> 1999
MVZ50	Reverse	TYTCGGTGTAAGYGARAKGCTT	Graybeal 1997
<b>16S rDNA</b>			
AR	Forward	CGCCTGTTTATCAAAAACAT	Palumbi <i>et al.</i> 1991
BR	Reverse	CCGGTCTGAACTCAGATCACGT	Palumbi <i>et al.</i> 1991
L13	Forward	TTAGAAGAGGCCAAGTCGTAACATGGTA	Feller & Hedges 1998
Titus1	Reverse	GGTGGCTGCTTTTAGGCC	Titus & Larson 1996
L2A	Forward	CCAAACGAGCCTAGTGATAGCTGGTT	Hedges 1994
H10	Reverse	TGATTACGCTACCTTTGCACGGT	Hedges 1994
<b>Cytochrome oxidase c subunit I</b>			
LCO1490	Forward	GGTCAACAAATCATAAAGATATTGG	Folmer <i>et al.</i> 1994
HCO2198	Reverse	TAAACTTCAGGGACCAAAAAATCA	Folmer <i>et al.</i> 1994
An1F	Forward	HAAYCAYAAAGAYATYGG	M. Lira, pers. comm.
An1R	Reverse	CCRAARAATCARAADAARTGTTG	M. Lira, pers. comm.
<b>Cytochrome b</b>			
MVZ15	Forward	GAACTAATGGCCCACACWWTACGNAA	Moritz <i>et al.</i> 1992
Cytb2	Reverse	AAACTGCAGCCCCTCAGAAATGATATTTGTCCTCA	Kocher <i>et al.</i> 1989
<b>Rhodopsin exon 1</b>			
Rhod1A	Forward	ACCATGAACGGAACAGAAGGYCC	Bossuyt & Milinkovitch 2000
Rhod1C	Reverse	CCAAGGGTAGCGAAGAARCCTTC	Bossuyt & Milinkovitch 2000
<b>Tyrosinase exon 1</b>			
TyrC	Forward	GGCAGAGGAWCRTGCCAAGATGT	Bossuyt & Milinkovitch 2000
TyrG	Reverse	TGCTGGCRTCTCTCCARTCCCA	Bossuyt & Milinkovitch 2000
<b>Histone H3</b>			
H3F	Forward	ATGGCTCGTACCAAGCAGACVGC	Colgan <i>et al.</i> 1999
H3R	Reverse	ATATCCTTRGGCATRATRGTGAC	Colgan <i>et al.</i> 1999
<b>Recombination activating gene 1</b>			
RAG1-TG1F	Forward	CCAGCTGGAAATAGGAGAAGTCTA	Grant <i>et al.</i> 2006
RAG1-TG1R	Reverse	CTGAACAGTTTATTACCGACTCG	Grant <i>et al.</i> 2006
<b>28S</b>			
28S-V	Forward	AAGGTAGCCAAATGCCTCATC	Hillis & Dixon 1991
28S-JJ	Reverse	AGTAGGGTAAAACCTAACCT	Hillis & Dixon 1991

## Laboratory protocols

Whole cellular DNA was extracted from ethanol-preserved tissues (liver or thigh muscle) with DNeasy (QIAGEN, Valencia, CA) isolation kit, following the

manufacturer's guidelines. DNA amplification was carried out in 96-well plates for 25µL reaction using Thermo Master Mix (2X) kit (Fermentas) or handle mix (2,5 µL of Buffer, 2 µL of Mg, 1 µL of DNTP, and 0,15 µL of Taq). PCR cycles consisted of an initial denaturing step of 3min at 96°C, followed by 35 cycles of amplification (denaturation for 30s at 96°C, annealing for 30s at 45°–59°C (see table xx for details), and extension for 60s at 60°C or 72°C), with a final extension step set to 60°C or 72°C for 7min. PCR products were cleaned using Agencourt AMPure XP, and then sequenced by a third party (Macrogen Inc.; Seoul, Korea) using fluorescent-dye labeled terminators (ABI Prism Big Dye Terminators v. 1.1 cycle sequencing kits) in an ABI 3730XL (Applied Biosystems, Foster City, CA). All sample were sequenced in both directions to check for potential sequencing errors. Chromatograms obtained from the automated sequencer were read, contigs (sets of overlapping sequences) were assembled, and complete sequences were edited using the sequence editing software Geneious version 9.1.2 (Kearse *et al.* 2012).

All sequences were cross-checked and compared with Genbank sequences using NCBI's (National Center of Biotechnology Information) BLAST (Basic Local Alignment Search Tool) to identify possible sequencing and identification errors, and cross-contamination. All contaminated fragments were excluded prior to analyses.

### **Sequences from Genbank**

I searched the Genbank database (last access in December 14, 2016) for sequences of all named species of Hylodidae plus selected outgroup. Of the total set of sequences recovered, only those corresponding to the exact molecular loci selected for this study were compiled, totaling 326 ingroup terminals of Hylodidae plus 45 terminals of outgroup taxa. All outgroup sequences were gathered from Genbank,

except *Bokermannohyla* sp. DAF11-056 and *Rhinella* sp. DAF11-101. See Appendices 1 and 2 for a full list of sequences analyzed.

I performed preliminary alignments and phylogenetic analyses to identify potential contamination problems and misidentifications of Genbank sequences. As a result, I excluded from my primary molecular dataset all sequences from Nuin (ump. data), Rodrigues *et al.* (2005), Heinicke *et al.* (2009), and Fouquet *et al.* (2013). Also, RAG1 sequences from De Sá *et al.* (2014) and Fouquet *et al.* (2013) were excluded because they correspond to a portion of the RAG1 gene different from that massively sequenced for this study.

### **Complete molecular dataset**

In addition to the sequences generated by myself, I included unpublished sequences of 150 terminals from my collaborator D. Fabri. Summing up Genbank data and freshly produced sequences, my full molecular data set comprised 371 terminals, corresponding to 79 species. Of those, 326 terminals (34 species) correspond to Hylodidae. No chimeric terminals were assembled, meaning that each terminal corresponds to a different voucher, and loci that could not be sequenced for a given terminal were treated as missing. See Appendices 1 and 2 for details.

## **PHYLOGENETIC METHODS**

### **Treatment of phenotypic characters**

Based on the argument of Grant *et al.* (2006), the phenotypic data for each species were duplicated for each conspecific terminal in order to reduce ambiguous

optimizations due to missing entries. Specimens of a same species were considered as a unique terminal. In cases where characters were polymorphic within a species, the terminal was coded as possessing all states possible for those characters.

### **Treatment of genotypic characters**

Gaps were treated as a fifth character-state. Treating them as missing data would result in erroneous interpretation as a transformation from one nucleotide into another, and not as the transformation events they actually reflect, *i.e.*, the insertion or deletion of a nucleotide (indels).

Sequences were aligned using the MAFFT v. 7.222 (Kato et al. 2002) plugin in Geneious v. 9.1.2 (Kearse *et al.* 2012), with E-INS-i strategy (and default parameters). This preliminary alignment was only used to identify highly conserved regions in all sequences and partition the data of each locus into homologous blocks, when necessary (Wheeler *et al.* 2006). All homologous blocks were entered in POY unaligned.

### **Total evidence analyses**

The term “total evidence”, postulated by Kluge (1989), has as main premise the simultaneous utilization of all evidence, using all possible data sources and all terminals at the same taxonomic level (Grant *et al.* 2006), furthering a more robust hypothesis test (Kluge 1997). There is no reason to use these sets of data in different analyses or apply different weighting regimes to them (Wheeler *et al.* 2006). In a total evidence analysis, we should use all kind of independent evidence (*e.g.*, morphological, genetic, behavior, bioacoustics, *etc.*) from several semaphoronts of a species (male and female juvenile and adult; *sensu* Henning 1966). As highlighted

above, I codified morphological, genetic, and behavior characters from male, female, juveniles, and tadpoles.

Molecular and morphological data were concatenated for each terminal, *i.e.*, chimerical terminals were avoided. Exceptions occurred in three outgroup terminals: Hemiphractidae was represented by molecular sequence data of *Hemiphractus helioi* and morphological data of *H. johnsoni*; Bufonidae by molecular sequence data of *Rhynella pygmea* and morphological data of *R. major*; and Cycloramphidae by molecular sequence data of *Cycloramphus boraceiensis* and morphological data of *C. brasiliensis*.

### **Choice of phylogenetic method**

I employed the parsimony criterion (Kluge 2001), a non-parametric and non-probabilistic method. I chose only one criterion, instead of multiple ones. The distinct criteria have different motivations, assumptions, and epistemological justifications (Giribert *et al.* 2002), and it is not possible to compare the results of one method with those produced using others methods.

Historically, the parsimony assumptions started on century XIV, on the principle of Ockham's razor that can be interpreted as stating: "...among competing hypotheses, the one with the fewest assumptions should be selected..." In phylogenetic systematics, parsimony is a historical inference that selects as optimal the hypothesis of cladistic and patristic relationships that maximizes explanatory power by minimizing the number of causal events required to explain the data (Kluge and Grant 2006, Grant and Kluge 2009). Its justification as optimality criterion anchored by the anti-superfluity principle (ASP; Barnes 2000, Baker 2003) and Popperian refutationism (Popper 1959, 1983). According to the ASP, the simplest

hypothesis (*i.e.*, the one that requires the least transformation events) to explain the character-states observed in the terminal taxa is the most refutable one and hence has greater explanatory power. According Kluge and Grant (2006), “...*explanatory power is maximized by minimizing the number of transformation events required to explain the character-states of the terminal taxa as hypotheses of homology...*”

Thereby, simultaneous analysis of all available evidence maximizes explanatory power in that it characterizes a more severe test by maximizing precision, and minimizing incongruence among independent data by minimizing the total number of hypotheses of transformation events (Grant and Kluge 2003, Kluge and Grant 2006). For these reasons, I adopt the total evidence approach (Kluge 1989) that combines all available data and the optimal cladogram is obtained from the full set of characters, instead of partitioning the data and performing distinct analyses.

The choice of POY as the software to run the analyses was also done so as to maximize explanatory power by taking advantage of the analytical framework of dynamic homology (Wheeler 1996). Through dynamic homology, the most parsimonious solution is sought by generating different nucleotide alignment for each topology obtained in order to minimize transformation events in DNA sequences, and thus, minimize the length of most parsimonious tree (Wheeler 2001).

## PHYLOGENETIC ANALYSES

We employed tree-alignment (*e.g.*, Sankoff 1975, Wheeler 1996, Varón and Wheeler 2012, 2013) in POY 5.1.1 (Wheeler *et al.* 2014), which tests hypotheses of nucleotide homology dynamically by optimizing unaligned DNA sequences directly onto alternative topologies (Kluge and Grant 2006, Wheeler *et al.* 2006; Grant and

Kluge 2009) while simultaneously optimizing prealigned transformation series (*e.g.*, morphology) as standard matrices. We assigned equal weights to all classes of transformations.

During the process of assembling the final dataset, we performed dozens of preliminary analyses combining heuristic algorithms into a variety of search strategies. Based on the efficacy of those preliminary runs (data not shown), we analyzed the final dataset using the following three-step search strategy.

Step 1: Using the standard direct optimization algorithm (Wheeler 1996), we ran one 24 h search using 512 CPUs (= 12.288 CPU-hours) using the command “search”, which implements a driven search composed of random addition sequence Wagner builds, Subtree Pruning and Regrafting (SPR), 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. The driven search was composed of 1655 RAS + SWAP, 1866 Tree Fusing, and 644 Parsimony Ratcheting.

Step 2: We swapped the optimal tree from step 1 and calculated its cost using the approximate iterative pass algorithm (Wheeler 2003a) and generated the matrix version of the tree-alignment (*i.e.*, the implied alignment; Wheeler 2003b).

Step 3: To verify the length reported by POY and search for better and/or additional trees given the implied alignment, we performed an aggressive search of the implied alignment matrix in TNT v1.5 (Goloboff *et al.* 2008, Goloboff and Catalano 2016; equal costs for all transformations, gaps treated as fifth state),



stopping when a stable consensus was reached five times (xmult= replications 10 rsc  
css xss ratchet 10 drift 10 fuse 5 consense 5).

Once we identified the most parsimonious trees, we performed several *a posteriori* analyses. First, we used Mesquite (Maddison and Maddison 2014) to examine and plot unambiguously optimized synapomorphies shared across all optimal trees. Second, we estimated support (Grant and Kluge 2008a) for the clades present in the optimal trees using the Goodman-Bremer measure (GB; Goodman *et al.* 1982, Bremer 1988, Grant and Kluge 2008b) in TNT v1.5 (Goloboff *et al.* 2008, Goloboff and Catalano 2016) using the optimal tree-alignment matrix and the parameters specified in the bremer.run macro (for details see Goloboff *et al.* 2008) with inverse-constraint searches limited to 10 min.

All compute-intensive analyses were run on Ace, a high-performance computing cluster 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 256 GB (16 × 16 GB), and two with 512 GB (32 × 16 GB), and QDR 4x InfiniBand (32 GB/s) networking.

## SPECIES IDENTIFICATION

For species identification, the tree topology obtained was considered in advance. Also, the branch lengths and uncorrected pair-wise distance were used. The fragment H1 was used for pairwise comparisons because that locus is widely represented in my dataset (see Appendix 2) and is sufficiently variable. Although genetic distances were used to guide some identification, I did not adopt the barcode philosophy that arbitrarily considers a specific distance to species delimitation.

## SPECIES DISTRIBUTION AND BIOGEOGRAPHIC ANALYSES

For all collection localities for which geographic coordinates were not available, coordinate data were obtained with aid of Google Earth Pro v.7.1.7. Distribution maps were constructed using QUANTUM GIS v.2.16 using altitudinal and hydrographic shape files. I optimized the occurrence data of hylodids in the main Brazilian river basins over my strict consensus tree using the character optimization procedure of Maddison and Maddison (1997) in Mesquite v. 3.1.0 (Maddison and Maddison 2014), in order to reconstruct historical biogeographical changes in their distribution ranges. Additionally, I employed Parsimony Analysis of Endemicity (PAE, Rosen [1988a,b]) to investigate whether (and which of the) major river basins throughout the Atlantic Rain Forest indeed represent distinct areas of endemism. PAE employs presence/absence data to recover relationships based on two assumptions: (1) the absence of a taxon is “primate” and its presence is “derived”, and (2) the hypothetical “ancestral” or “outgroup” area is one in which none of the sample sets of the current taxa exist. Although PAE is based on a cladistic methodology, this is not a cladistic method because it does not take into account the phylogeny of the taxa to construct area cladograms (Rosen 1988a,b).

## RESULTS

### TRANSFORMATION SERIES OF THE PHENOTYPIC CHARACTERS

The morphological evidence observed in this study included 292 characters. The phenotypic characters are described bellow and were split in systems of characters. Thus, the characters systems are:

- (A) External morphology of adults: 127 characters
- (B) Viscera of adults: 09 characters
- (C) Myology of adults: 30 characters
- (D) Osteology of adults: 99 characters
- (E) Chromosomes: 1 character
- (F) External morphology of larvae: 23 characters
- (G) Behavior: 1 character

### PHENOTYPIC CHARACTERS DESCRIPTION

#### **External morphology**

##### 01-03: External vocal sac

Liu (1935) defined three main types of vocal sacs: simple and subgular; double and subgular; and double and lateral. Liu also defined two subdivisions for each type of sac, being external or internal. The external vocal sac is a skin modification forming a sac, and the internal sac is a buccal floor expansion and/or an *interhyoideus* muscle modification (see *miological characters* for more details of internal vocal

sac). The external vocal sac, if present, is a skin modification varying in condition and position. Lutz (1930) already considered these characters as evidence to distinguish species of *Crossodactylus* and *Hylodes*. The author designated *Hylodes*, in Portuguese, as “*machos com duas vesículas vocaes eversiveis*” (in a free translation, males with two eversive vocal vesicles) and *Crossodactylus* as “*machos sem vesículas vocaes eversiveis*” (in a free translation, males without eversive vocal vesicles).

01. External vocal sac: Occurrence

(0) absent

(1) present

Remarks: This character refers to the modification of the gular skin. All species of *Hylodes* in this study have external vocal sac (state 1). The only male of *Megaelasia* observed in this study – *Megaelasia goeldii* – do not have external vocal sac (state 0; reversion  $1 \rightarrow 0$ ); however, data from literature report *M. apuana* and *M. massarti* with visible external vocal sac (state 1). I did not observe a visible vocal sac in any species of *Crossodactylus*. Several species of this genus are described with a single, subgular, median vocal sac; except for *C. caramaschii* (Bastos & Pombal, 1995), *C. cyclopinus* (Nascimento *et al.* 2005), and *C. dispar* (Pimenta *et al.*, 2014). However, I did not observe this condition in the specimens analyzed in this study. Thus, we decided to codify only visible external vocal sacs and the species of *Crossodactylus* were codified with state 0. Exception is made only for *C. schmidtii* because we have records of live specimen that show a visible, paired, and subgular vocal sac (V. Caldart, pers. comm; Fig. 01A).

02. External vocal sac: Condition

(0) singular

(1) paired

Remarks: All species of *Hylodes* and *Megaelosia* that have a vocal sac present the condition of paired vocal sacs (state 1). *Crossodactylus schmidtii* also have a paired structure. All species used as outgroup that have vocal sac present the singular condition (state 0).

03. Paired external vocal sac: Position

(0) subgular

(1) lateral

Remarks: *Crossodactylus* does not have an expanded vocal sac (Ch. 01, state 0); thus, the subgular condition presented in some species of this genus can be observed only during the vocalization. Recently, V. Caldart (pers. com.) observed paired, subgular vocal sac in *C. schmidtii* (state 0; **Figure 3A**). All species of *Hylodes* and *Megaelosia* that possess a double vocal sac, present the lateral condition (state 1; **Figure 3B**). Transformation 0 → 1 is recovered as synapomorphy for *Hylodes* + *Megaelosia*.

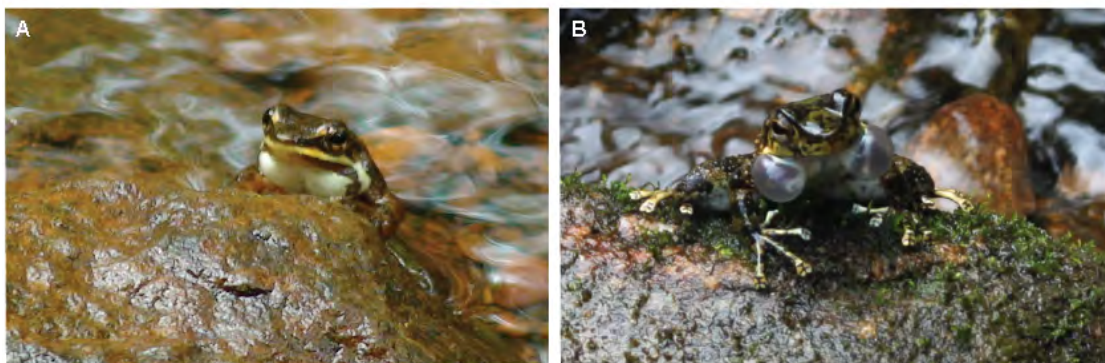


Figure 3. Double external vocal sac: (A) subgular in *C. schmidtii*, (B) lateral in *H. asper*. Photos by Vinícius Caldart and Adriana Jeckel.

#### 04. Tympanic membrane

The tympanic middle ear is composed minimally of a tympanic membrane, middle ear cavity, and middle ear bones. The loss of this structure is widespread among anurans, with at least a few species of several families lacking the entire tympanic middle ear (Jaslow *et al.* 1988). The tympanic membrane is formed by a highly differentiated thin, non-glandular skin (Pereyra *et al.* 2016) that covers the tympanic annulus. Pimenta *et al.* (2015) cited the distinctness of the membrane as a diagnostic character in *Crossodactylus*' species. Besides absence and presence, I codified the distinctness of this structure.

(0) absent

(1) present, not evident

(2) present, evident

Non additive

Remarks: All species of Hylodidae present the tympanic membrane; however, this structure is not clearly observed in any species of *Megaelosia* (**Figure 4A**), in *C. dantei*, and in some species of *Hylodes* (*H. glaber*, *H. japi*, *H. meridionalis*, *H. perplicatus*, *H. regius*, and *H. uai*). In others hylodids, this structure is totally visible (**Figure 4B**). This differentiation is better visualized on **Figure 4**. The absence is only reported for *Ceratophrys cornuta* and one specimen of *Physalaemus cuvieri*. Transformation 1 → 2 is recovered in the clade that contain all *Hylodes*, except *Hylodes* 'South' clade, reversion of this condition (2 → 1) is reported in *C. dantei*, *H. uai*, and *H. ornatus*.

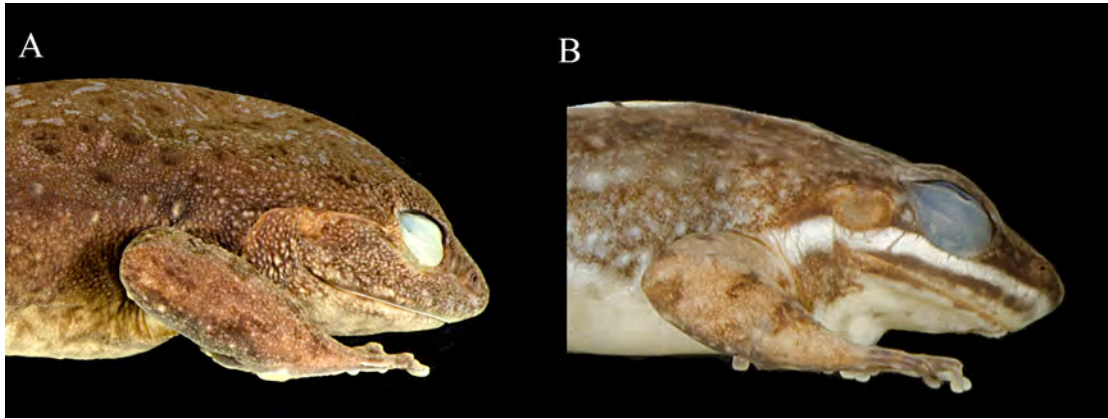


Figure 4. Tympanum: (A) not evident in *M. goeldii* AMNH 103950, (B) evident in *C. schmidtii* AMNH 190684.

#### 05-10: Nuptial excrescences

The most notable secondary sexual character in anurans, besides vocal sacs, is the nuptial excrescence of males (Duellmann and Trueb 1994). They are modified epidermal and dermal tissue typically located in the second digit (*sensu* Shubin and Alberch (1986), Fabrezi and Alberch (1996)) of the hand (Noble 1931). Normally, the epidermis of the excrescence is distinctively thick, heavily keratinized, and dark colored. This structure can vary from hypertrophied glands that form external protrusion of the skin, to pad mostly glandular without a thick epidermis (Fujikura *et al.* 1988, Luna *et al.* 2012). Noble (1931, p. 126) states that these structures “*serve to maintain the grip of the male on a struggling female and consequently would have no use in the latter sex*”. However, the author observes the peculiarity of *Crossodactylus gaudichaudii*, which presents “*conspicuous black spines*” in females; the female’s spines are usually smaller but are frequently more numerous than male’s spines (Noble 1931, Noble’s figures 44a,b). The paradoxical condition in female of *Crossodactylus* was stated by Lutz (1930), which observed a variation in number between three and six. In recent metamorphosed individuals, the number of spines may be fewer (Lutz 1930).

05. Nuptial excrescences, males, finger II: Occurrence

(0) absent

(1) present

Remarks: I did not analyze the excrescences histologically; consequently, in some species I was not able to assume the presence of the nuptial pad. Males of all species of *Megaelosia* and most species of *Hylodes* have the nuptial excrescences codified as absent (state 0). The nuptial excrescences are present (state 1; **Figure 5**) in all males of *Crossodactylus* and in three species of *Hylodes* (*H. fredei*, *H. pipilans*, and *H. phyllodes*). Transformation 0 → 1 is recovered as synapomorphy of ‘Hylodes Serra do Mar / spine’ clade.

06. Nuptial excrescences, males, finger II: Condition

(0) asperity

(1) spines

Remarks: All Hylodidae that possess nuptial excrescences presents spines (state 1, **Figure 5**). Asperity (state 0) is reported in the representative of *Rhinella*.

07. Spine, male, finger II: Keratinization

(0) non-keratinized

(1) keratinized

Remarks: Species of the clade composed by *H. fredei*, *H. phyllodes* and *H. pipilans* possess small and non-keratinized spines (state 0; **Figure 5A**). Males of all species of *Crossodactylus* present keratinized spines (state 1; **Figure 5B**), bigger in



relation to spines present in *Hylodes*, except *C. dantei* that has unpigmented spines (transformation 1 → 0). Species from outgroup do not present keratinization.

08. Spine, male, finger II: Quantity

(0) one

(1) two

(2) three

(3) four

(4) five

(5) more than five

Additive

Remarks: Among species of *Crossodactylus*, I noted a variation on amount of spines, but the most common state was state 2 (three spines; **Figure 5B**); however, in most species this number showed an interspecific variation. The three species of *Hylodes* that have spines (*H. fredii*, *H. phyllodes*, and *H. pipilans*) present several small spines (state 5, more than five; **Figure 5A**).

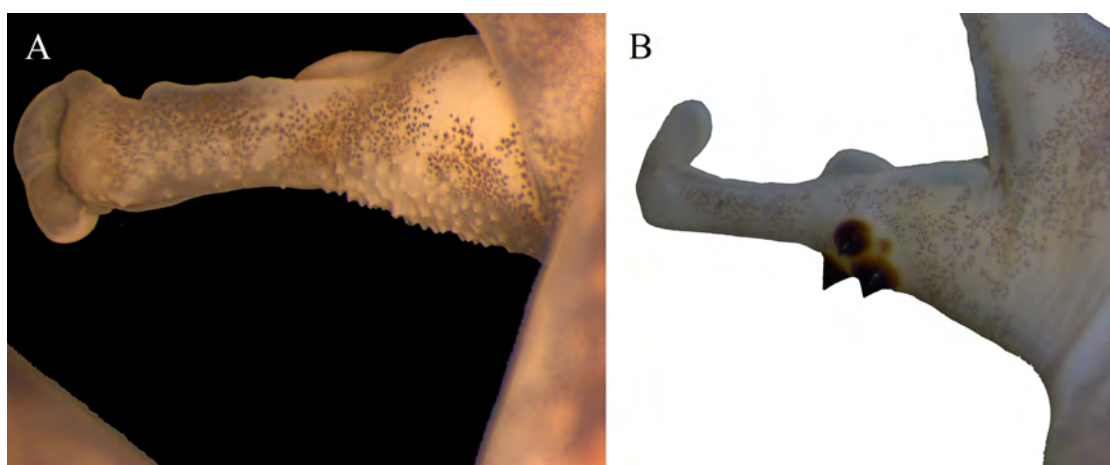


Figure 5. Nuptials excrescences with spines: (A) non-keratinized, with more than five spines in *H. fredii* MNRJ 38983, (B) keratinized, with three spines in *C. grandis* USNM 164108.

09. Nuptial excrescences, females, finger II: Occurrence

(0) absent

(1) present, spine

Remarks: Females of *Megaelosia* e *Hylodes* do not have nuptial excrescences (state 0), however females of *C. bokermanni*, *C. caramaschii*, *C. grandis*, *C. schmidti*, *C. timbuhy*, *C. trachystomus*, and *C. wernerii* present nuptial excrescence (state 1). I did not observe asperity in females; thus, the condition 1—“present”—means “presence of spines”. No females from outgroup are reported with spines. Noble (1931) reported the peculiarity of the presence of spines in female of *Crossodactylus*, and this condition is rare within Anura.

10. Spine, females, finger II: Keratinization

(0) non-keratinized

(1) keratinized

Remarks: Females from the species *C. aeneus*, *C. caramaschii*, and *C. gaudichaudii* present keratinized spines (state 1). In addition, only *C. dantei* and *C. timbuhy* present non-keratinized spines (state 0). Ambiguities are reported for *C. schmidti* and *C. trachystomus*.

11-42: Finger fringe on hand

Lutz (1930) refers to the finger fringe as “*orlas membranaceas*” (in English, membranaceous borders) in the three genera of Elosiinae. The finger fringe is a group of characters defined by Grant *et al.* (2006). However, these authors only codified their presence in each side (pre and postaxial) of each finger. In this study, I also

defined the absence and presence in each side of fingers, as well as the level of development of each fringe. According to our observations, all fringes rise on anterior portion of the finger and grow through the finger base (posterior portion). As in Dendrobatoidea codified by Grant *et al.* (2006), species of Hylodidae have finger fringes, and these fringes vary independently in each side of each finger in relation to the presence and level of development. Variation was also found between males and females. In this study, the characters have been defined for presence, level of extension (distal-proximal), and level of expansion for each side of each finger; all conditions were distinguished by sex. The development of the fringe is gradual and starts on the tip of the finger. For this reason, I considered the character of development level as additive. In this study, I adopted the finger nomenclature proposed by Shubin and Alberch (1986) and Fabrezi and Alberch (1996) that assume the finger I lost, counting from II to V. In accordance with the nomenclature used by Grant *et al.* (2006), the medial margin of the finger was defined as preaxial, and the lateral margin was defined as postaxial. **Figure 6A** illustrates these characters.

11. Preaxial fringe, finger II, males: Extension

(0) absent

(1) do not reach subarticular tubercle

(2) reach subarticular tubercle

(3) surpass subarticular tubercle

(4) along all finger

Additive

Remarks: Preaxial fringe not reaching the subarticular tubercle is the predominant condition in Hylodidae (state 1; 10 species). The transformation 0 → 1 is

reported as synapomorphy for Hylodidae. The conditions “absent” (state 0; 6 species) and “reach subarticular tubercle” (state 2, 6 species) are also observed in the family. Only in *H. regius* the fringe surpasses subarticular tubercle (state 3). No specimen present preaxial fringe along all finger (state 4). Synapomorphies regarding the character are: transformation 0 → 1 in Hylodidae, transformation 1 → 2 in the clade (*C. aff. caramaschii* SP (*Crossodactylus* sp. PR East, *C. caramaschii*), and two independent transformations 2 → 0 in *H. fredii* and *H. magalhaesi*.

12. Preaxial fringe, finger II, males: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Most males that have preaxial fringe on finger II present only an expansion of the skin (state 0; 11 species). Transformations 0 → 1 and 0 → 2 are reported as synapomorphy for *H. perere* and *H. japi*, respectively.

13. Preaxial fringe, finger II, females: Extension

(0) absent

(1) do not reach subarticular tubercle

(2) reach subarticular tubercle

(3) surpass subarticular tubercle

(4) along all finger

Additive

Remarks: Different from males, absence of preaxial fringe (state 0; 8 species) and fringe reaching subarticular tubercle (state 2; 8 species) are the predominant conditions among females of Hyloidae. The condition most predominant in males is only found in females of four species (state 1). No species is reported with fringe along all finger. Transformation 1 → 2 is reported as synapomorphy for *H. ornatus*.

14. Preaxial fringe, finger II, females: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: No female is reported with developed preaxial fringe on finger II. Fringe formed by an expansion of skin is predominant (state 0; 10 species), followed by five species that presented undeveloped fringe on preaxial finger II (state 1). Transformation 0 → 1 is reported in two independent clades, *H. japi* and *M. goeldii*.

15. Postaxial fringe, finger II, males: Extension

(0) absent

(1) do not reach subarticular tubercle

(2) reach subarticular tubercle

(3) surpass subarticular tubercle

(4) along all finger

Additive

Remarks: Postaxial fringe reaching subarticular tubercle is the predominant condition in Hyloidae (state 2; 18 species), followed by the condition ‘do not reach

subarticular tubercle' (state 1; 5 species). Synapomorphies are reported regarding this character: transformation 0 → 1 in Hylodidae, transformation 1 → 2 in the clade (*C. aff. caramaschii* SP (*Crossodactylus* sp. PR East, *C. caramaschii*) and *C. dantei*, and transformation 2 → 4 in *H. aff. asper* SP.

16. Postaxial fringe, finger II, males: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: The three conditions occur at almost the same proportion in Hylodidae. The conditions 'expansion of skin' (state 0) and 'form fringe' (state 1) are the predominant states with seven species each; however, six species present a developed fringe (state 2). Transformation 0&1 → 2 are reported in *H. japi*, and 1 → 2 in *H. magalhaesi*.

17. Postaxial fringe, finger II, females: Extension

(0) absent

(1) do not reach subarticular tubercle

(2) reach subarticular tubercle

(3) surpass subarticular tubercle

(4) along all finger

Additive

Remarks: Most species of Hylodidae present postaxial fringe that reach subarticular tubercle (state 2; 13 species). Absence (state 0) is reported only in three

species of *Crossodactylus*. Fringe not reaching subarticular tubercle (state 1) is reported only in *C. gaudichaudii*, and fringe surpassing the subarticular tubercle (state 3) is reported in *M. apuna* and *M. massarti*. No species is reported with fringe along all finger. Synapomorphies regarding this character are: transformation 1 → 2 in *Hylodes* + *Megaelosia*, transformation 2 → 1 in *H. fredii*, transformation 2 → 3 in the clade that contains all *Megaelosia*, except *M. goeldii*.

18. Postaxial fringe, finger II, females: Expansion

- (0) skin expansion
- (1) fringe
- (2) developed fringe

Additive

Remarks: Expansion of skin is prevalent in females of *Hylodes* (state 0; 13 species). Seven species present undeveloped fringe (state 1), however no females present developed fringe (state 2). Transformation 0 → 1 is synapomorphy for the clade *Hylodes* ‘Serra do Mar / no spine’, with a reversion 1 → 0 in *H. aff. asper* SP. Transformation 0 → 1 is also synapomorphy for *H. japi* and *M. goeldii*.

19. Preaxial fringe, finger III, males: Extension

- (0) absent
- (1) do not reach subarticular tubercle
- (2) reach subarticular tubercle
- (3) surpass subarticular tubercle
- (4) along all finger

Additive

Remarks: Preaxial fringe on finger III is presented in all males of Hylodidae. The predominant condition is fringe along all finger (state 4; 14 species), followed by ‘fringe reaching subarticular tubercle’ (state 2; 8 species) and fringe surpassing subarticular tubercle only found in *Hylodes* species (state 3; 4 species). Fringe not reaching subarticular tubercle (state 1) is only found in *C. timbuhy*. Transformation 0 → 4 is recovered as synapomorphy of Hylodidae. Reversion of the state 4 is observed in many clades within *Hylodes*. Reversion 4 → 2 & 3 is reported in *Hylodes* ‘Serra do Mar / no spine’ clade, returning to the condition 4 (3 → 4) only in *H. asper*. Reversion 4 → 3 is found in *Hylodes* ‘MG / ES’ clade and *H. regius* + *H. magalhaesi*, with another reversion (3 → 2) in *H. magalhaesi*. Reversion 4 → 2 is found independently in *H. fredii* and *H. perere*.

20. Preaxial fringe, finger III, males: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Most species of Hylodidae have males with fringe. Developed (state 2) and undeveloped (state 1) fringe occur in eight and 10 species, respectively. Expansion of skin (state 0) is found in six species. Transformation 0 → 2 is recovered as synapomorphy for *H. japi*, *H. magalhaesi*, and *H. perere*. Transformation 1 → 0 is recovered in *H. ornatus*.

21. Preaxial fringe, finger III, females: Extension

(0) absent



- (1) do not reach subarticular tubercle
- (2) reach subarticular tubercle
- (3) surpass subarticular tubercle
- (4) along all finger

Additive

Remarks: All females of Hylodidae present preaxial fringe on finger III. The condition ‘do not reach subarticular tubercle’ is only found in 2 species of *Hylodes*. The most prevalent condition is fringe reaching subarticular tubercle (state 2; 7 species), followed by fringe surpassing subarticular tubercle (state 3; 6 species), and fringe along all finger (state 4; 5 species). Synapomorphies of this character are: transformation 3 → 4 in the clade contain *Megaelosia*, except *M. goeldii*, transformation 2 → 1 in *H. ornatus*, transformation 2&3 → 1 in *H. fredii*, transformation 3&4 → 2 in *C. dantei*.

## 22. Preaxial fringe, finger III, females: Expansion

- (0) skin expansion
- (1) fringe
- (2) developed fringe

Additive

Remarks: Developed fringe (state 2) is not reported in females of *Hylodes*. Undeveloped fringe (state 1) is found in 13 species and just a expansion of skin (state 0) is found in 12 species. Transformation 0 → 1 is observed in *C. dantei*. Reversion 1 → 0 is observed in the clades *H. pipilans* + *H. fredii* and (*H. ornatus* (*H. regius*, *H. magalhaesi*)).

23. Postaxial fringe, finger III, males: Extension

(0) absent

(1) do not reach subarticular tubercle

(2) reach subarticular tubercle

(3) surpass subarticular tubercle

(4) along all finger

Additive

Remarks: Absence of postaxial fringe on finger II in males (state 0) is reported only in two species of *Crossodactylus* and no species present fringe along all finger (state 4). Fringe reaching the subarticular tubercle is the predominant condition in Hyloidae (state 2; 16 species), followed by the conditions ‘do not reach subarticular tubercle’ (state 1; 8 species) and ‘surpass subarticular tubercle’ (state 3; 2 species). This character is recovered as synapomorphy for Hyloidae (0 → 1). Transformation 1 → 3 is reported in *C. dantei*, and transformation 2 → 1 is reported in *H. magalhaesi* and *H. perere*.

24. Postaxial fringe, finger III, males: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Developed fringe (state 2) is reported in eight species, all of them of the genus *Hylodes*. Also eight species is reported with undeveloped fringe (state 1) and ‘expansion of skin’ (state 0) is found in five species. Transformation 1 → 0 is

reported in *Crossodactylus* ‘MG’ clade, *C. schmidti*, and *H. ornatus*; transformation 1 → 2 is reported in *H. japi*, *H. magalhaesi*, and *H. perere*.

25. Postaxial fringe, finger III, females: Extension

(0) absent

(1) do not reach subarticular tubercle

(2) reach subarticular tubercle

(3) surpass subarticular tubercle

(4) along all finger

Additive

Remarks: When present, fringe of females of Hylodidae never surpasses subarticular tubercle (*i.e.*, states 3 and 4 was not reported). Absence of fringe is reported in two species of *Crossodactylus*. Fringe reaching subarticular tubercle is the predominant condition in females (state 2; 10 species), followed by ‘do not reach subarticular tubercle’ condition (state 1; 6 species). The only synapomorphy regarding this character is the transformation 2 → 1 in the clade that contain all major clades of *Hylodes*, except *Hylodes* ‘South’ clade.

26. Postaxial fringe, finger III, females: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Developed postaxial fringe on finger III (state 2) is only found in *H. cardosoi*. Undeveloped fringe is reported in 11 species of *Hylodes* and *Megaelosia*.

Expansion of skin is found in nine species; all species of *Crossodactylus* that I was able to codify this character (3 species) presented this condition. Transformation 1 → 0 is reported in *H. pipilans* + *H. fredii* and the clade (*H. ornatus* (*H. regius*, *H. magalhaesi*)).

27. Preaxial fringe, finger IV, males: Extension

(0) absent

(1) on distal and medial phalanges, almost reach distal subarticular tubercle

(2) on distal and medial phalanges, reach distal subarticular tubercle

(3) on distal and medial phalanges, surpass distal subarticular tubercle

(4) on all phalanges, almost reach proximal subarticular tubercle

(5) on all phalanges, reach proximal subarticular tubercle

(6) on all phalanges, surpass proximal subarticular tubercle;

(7) on all phalanges, along all finger.

Additive

Remarks: All males of Hylodidae present fringe on finger IV. The most predominant conditions are ‘reach proximal subarticular tubercle’ (state 5; 15 species) and ‘almost reach proximal subarticular tubercle’ (state 4; 12 species). Transformation 0 → 4&5 is recovered as synapomorphy for Hylodidae.

28. Preaxial fringe, finger IV, males: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Developed fringe (state 2) is found in 15 species of *Hylodes*. Expansion of skin (state 0) is reported in three species of *Crossodactylus*. Undeveloped fringe is found in six species (one *Crossodactylus* and five *Hylodes*). Transformation 2 → 1 is recovered in the clade that contain all *Hylodes* clades, except *Hylodes* ‘South’ clade, with the reversion 2 → 1 in *H. ornatus* and *H. amnicola*.

29. Preaxial fringe, finger IV, females: Extension

(0) absent

(1) on distal and medial phalanges, almost reach distal subarticular tubercle

(2) on distal and medial phalanges, reach distal subarticular tubercle

(3) on distal and medial phalanges, surpass distal subarticular tubercle

(4) on all phalanges, almost reach proximal subarticular tubercle

(5) on all phalanges, reach proximal subarticular tubercle

(6) on all phalanges, surpass proximal subarticular tubercle;

(7) on all phalanges, along all finger.

Additive

Remarks: Only three states are observed for this character (states 4, 5, and 6). Fringe reaching proximal subarticular tubercle is the predominant condition (state 5; 11 species), followed by fringe reaching proximal subarticular tubercle (state 4; 5 species) and fringe surpassing subarticular tubercle (state 6; 3 species). Transformation 5 → 6 is recovered in the clade contain all *Megaelosia*, except *M. goeldii* and transformation 5 → 4 is recovered in *C. dantei*.

30. Preaxial fringe, finger IV, females: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Developed preaxial fringe on finger IV (state 2) is not reported in females of Hylodidae. Undeveloped fringe is the predominant condition (state 1; 14 species), followed by expansion of skin (state 0; 11 species). Transformation 1 → 0 is recovered in the clades *H. pipilans* + *H. fredii* and (*H. ornatus* (*H. regius*, *H. magalhaesi*)). Transformation 0 → 1 is recovered in *C. dantei*.

31. Postaxial fringe, finger IV, males: Extension

(0) absent

(1) on distal and medial phalanges, almost reaching distal subarticular tubercle

(2) on distal and medial phalanges, reach distal subarticular tubercle

(3) on distal and medial phalanges, surpass distal subarticular tubercle

(4) on all phalanges, almost reaching proximal subarticular tubercle

(5) on all phalanges, reach proximal subarticular tubercle

(6) on all phalanges, surpass proximal subarticular tubercle;

(7) on all phalanges, along all finger.

Additive

Remarks: All species of Hylodidae present fringe, the conditions observed is states 1, 2, 4, and 5. Fringe almost reaching proximal subarticular tubercle is the predominant condition in Hylodidae (state 4; 15 species); followed by ‘almost reach distal subarticular tubercle’ (state 1; 4 *Crossodactylus*’ species), and ‘reach distal subarticular tubercle’ and ‘reach proximal subarticular tubercle’ (states 2 with 2 *Crossodactylus*’ species and state 5 with 2 *Hylodes*’ species, respectively).

Transformation 0 → 1&2 is recovered as synapomorphy for Hylodidae.

Transformation 1&2 → 4 is found in *C. caramaschii* and 4 → 5 in *H. fredii*.

32. Postaxial fringe, finger IV, males: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Most males of Hylodidae present developed postaxial fringe (state 2; 15 species). Six species present undeveloped fringe (state 1) and 3 species of *Crossodactylus* present expansion of skin (state 0). Transformation 1 → 2 is reported for the clade that comprises all Hylodes, except Hylodes ‘South’ clade, with reversion 2 → 1 in *H. ornatus* and *H. amnicola*.

33. Postaxial fringe, finger IV, females: Extension

(0) absent

(1) on distal and medial phalanges, almost reaching distal subarticular tubercle

(2) on distal and medial phalanges, reach distal subarticular tubercle

(3) on distal and medial phalanges, surpass distal subarticular tubercle

(4) on all phalanges, almost reaching proximal subarticular tubercle

(5) on all phalanges, reach proximal subarticular tubercle

(6) on all phalanges, surpass proximal subarticular tubercle;

(7) on all phalanges, along all finger.

Additive

Remarks: Absence of postaxial finger on finger IV in females (state 0) is reported in two species of *Crossodactylus*. Fringe almost reaching proximal subarticular tubercle is the predominant condition (state 4; 12 species), followed by fringe reaching distal subarticular tubercle (state 2; 3 species) and almost reaching distal subarticular tubercle (state 1; 2 species). No female present fringe that extends more than proximal subarticular tubercle. Transformation 1&2 → 4 is recovered as synapomorphy of *Hylodes* + *Megaelosia*. Transformation 1 → 0 is recovered in *C. dantei* and *H. fredii*.

34. Postaxial fringe, finger IV, females: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: No female present developed postaxial fringe on finger IV (state 2). Undeveloped fringe is reported in most species of Hylodidae (state 1; 14 species); however any species of *Crossodactylus* present this condition. Expansion of skin is found in all genera (state 0; 8 species). The only transformation for the character (1 → 0) is reported in the clade (*H. ornatus* (*H. regius*, *H. magalhaesi*)).

35. Preaxial fringe, finger V, males: Extension

(0) absent

(1) on distal and medial phalanges, almost reaching distal subarticular tubercle

(2) on distal and medial phalanges, reach distal subarticular tubercle

(3) on distal and medial phalanges, surpass distal subarticular tubercle



- (4) on all phalanges, almost reaching proximal subarticular tubercle
- (5) on all phalanges, reach proximal subarticular tubercle
- (6) on all phalanges, surpass proximal subarticular tubercle;
- (7) on all phalanges, along all finger.

Additive

Remarks: Preaxial fringe of all *Hylodes* species almost reaches or reaches proximal subarticular tubercle (state 4 with 10 species and state 5 with 7 species, respectively). Most males of *Crossodactylus* present fringe reaching the distal subarticular tubercle (state 2, 4 species). Fringe almost reaching (state 1) and surpassing distal tubercle (state 3) is observed in only one species. Transformation 0 → 1 is recovered as synapomorphy for Hylodidae. Transformation 4 → 5 is found independently in the clade *H. meridionalis* + *H. aff. meridionalis* SC, *H. amnicola*, and *H. aff. asper* SP.

36. Preaxial fringe, finger V, males: Expansion

- (0) skin expansion
- (1) fringe
- (2) developed fringe

Additive

Remarks: Most males of *Hylodes*, but any *Crossodactylus*, present developed fringe (state 2; 15 species). Undeveloped fringe (state 1) is found in six *Hylodes* and one *Crossodactylus*. Expansion of skin (state 0) is reported in only two *Crossodactylus*. Transformation 2 → 1 is recovered in *H. amnicola* and *H. ornatus*.

37. Preaxial fringe, finger V, females: Extension

- (0) absent
- (1) on distal and medial phalanges, almost reaching distal subarticular tubercle
- (2) on distal and medial phalanges, reach distal subarticular tubercle
- (3) on distal and medial phalanges, surpass distal subarticular tubercle
- (4) on all phalanges, almost reaching proximal subarticular tubercle
- (5) on all phalanges, reach proximal subarticular tubercle
- (6) on all phalanges, surpass proximal subarticular tubercle;
- (7) on all phalanges, along all finger.

Additive

Remarks: Most females of Hyloidae present preaxial fringe on finger V reaching distal subarticular tubercle (state 2; 6 species), followed by fringe almost reaching proximal subarticular tubercle (state 4; 4 species), fringe reaching proximal subarticular tubercle (state 5; 3 species) and almost reaching distal subarticular tubercle (state 1; 3 species). Fringe surpassing distal subarticular tubercle is only found in *C. timbuhy* (state 3). Fringe is not observed in *C. trachystomus* (state 0). Transformation 1 → 2&3&4 is recovered as synapomorphy for *Hyloides* + *Megaelosia*. Transformation 2&3&4 → 5 is reported in *H. ornatus* and clade *H. meridionalis* + *H. aff. meridionalis* SC.

38. Preaxial fringe, finger V, females: Expansion

- (0) skin expansion
- (1) fringe
- (2) developed fringe

Additive

Remarks: No developed preaxial fringe is found in females of Hylodidae (state 2). Most females are reported with undeveloped fringe (state 1; 15 species), followed by expansion of skin (state 0; 10 species). Transformation  $0 \rightarrow 1$  is recovered in *C. dantei*, and transformation  $1 \rightarrow 0$  is recovered in *H. pipilans* + *H. fredii* and in the clade that comprises *H. ornatus*, *H. regius*, and *H. magalhaesi*.

39. Postaxial fringe, finger V, males: Extension

(0) absent

(1) on distal and medial phalanges, almost reaching distal subarticular tubercle

(2) on distal and medial phalanges, reach distal subarticular tubercle

(3) on distal and medial phalanges, surpass distal subarticular tubercle

(4) on all phalanges, almost reaching proximal subarticular tubercle

(5) on all phalanges, reach proximal subarticular tubercle

(6) on all phalanges, surpass proximal subarticular tubercle;

(7) on all phalanges, along all finger.

Additive

Remarks: All males of Hylodidae present postaxial fringe on finger V. Species with fringe almost reaching distal subarticular tubercle (state 1) and present in all finger (state 7) is not reported. Fringe almost reaching and reaching proximal subarticular tubercle are predominant (state 4 with 10 species and state 5 with 9 species, respectively). Transformation  $0 \rightarrow 3\&4$  is recovered as synapomorphy of Hylodidae, with reversion ( $3\&4 \rightarrow 2$ ) in *C. caramaschii*. Transformation  $3 \rightarrow 6$  is recovered in *C. dantei*.

40. Postaxial fringe, finger V, males: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Developed fringe is reported only in *Hylodes* (state 2; 15 species) and expansion of skin is reported only in *Crossodactylus* (state 0; 4 species). Seven species are reported with undeveloped fringe (state 1). Transformation 2 → 1 is found in *H. ornatus* and *H. amnicola*.

41. Postaxial fringe, finger V, females: Extension

(0) absent

(1) on distal and medial phalanges, almost reaching distal subarticular tubercle

(2) on distal and medial phalanges, reach distal subarticular tubercle

(3) on distal and medial phalanges, surpass distal subarticular tubercle

(4) on all phalanges, almost reaching proximal subarticular tubercle

(5) on all phalanges, reach proximal subarticular tubercle

(6) on all phalanges, surpass proximal subarticular tubercle;

(7) on all phalanges, along all finger.

Additive

Remarks: All females of Hylodidae present postaxial fringe on finger V, exception is only found in *C. trachystomus* (state 0). Fringe almost reaching distal subarticular tubercle (state 1) and present in all finger (state 7) is not reported. Fringe almost reaching proximal subarticular tubercle is predominant (state 4; 7 species), followed by fringe reaching proximal subarticular tubercle (state 5; 6 species) and reaching distal subarticular tubercle (state 2; 5 species). Transformations 4 → 3 and 4

→ 2 are recovered in *H. ornatus* and *H. fredei*, respectively. Transformation 2&3&4  
 → 5 is recovered in *C. gaudichaudii* Região dos Lagos and *C. gaudichaudii* Floresta da Tijuca.

42. Postaxial fringe, finger V, females: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Females do not present developed postaxial fringe on finger V (state 2). All species *Hylodes*, most species of *Megaelosia* and two *Crossodactylus* present undeveloped fringe (state 1; 27 species). Expansion of skin is found in eight species (state 0). Transformation 0 → 1 is recovered in *C. dantei*, and transformation 1 → 0 is found in *H. pipilans* + *H. fredei* and (*H. ornatus* (*H. regius*, *H. magalhaesi*)).

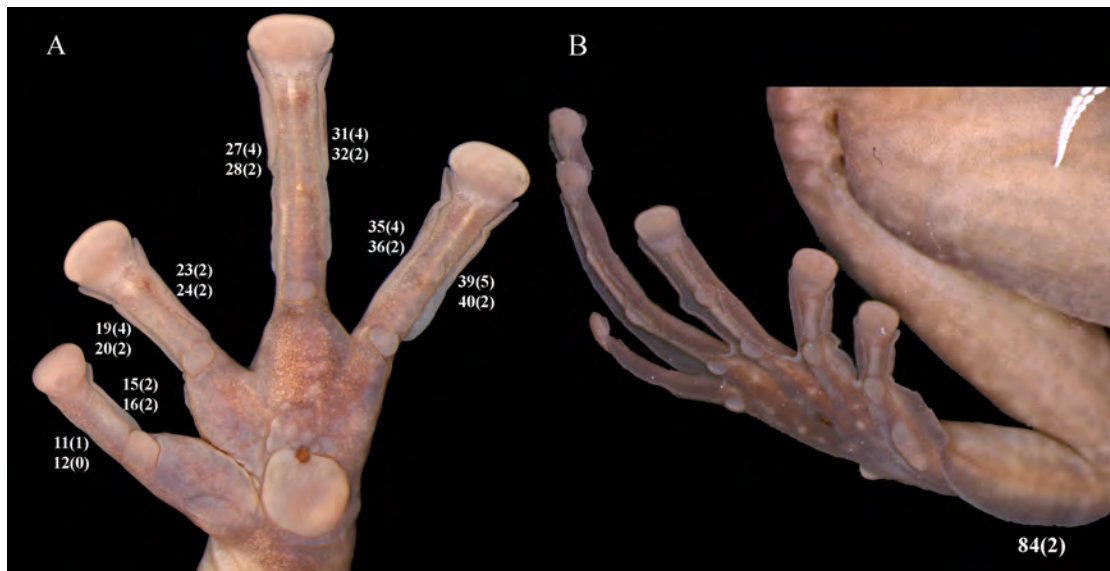


Figure 6. *H. asper* (RJ) MZUSP 112641: (A) Extension and expansion of finger fringes; (B) presence and expansion of toe membrane and tarsal fold.

43. Paired dorsal digits scutes

Lutz (1930) characterized Elosiinae by the “*fórmula especial dos discos terminaes que na face superior mostram uns sulcus separando dous lobules lateraes*”. Noble (1931) noted the occurrence of this pair of dermal scutes in each digit tip in Elosiinae and Dendrobatidae. Griffiths (1959) said that the scutes are “*really glandulo-muscular organs and probably function to facilitate adhesion to foliage etc.*”. However, Grant *et al.* (2006) claimed that no evidence has been presented in support of Griffiths’ thesis and their functional significance remains unknown.

(0) absent or inconspicuous

(1) present

Remarks: In this study, I observed paired dermal scutes in almost all species of Hylodidae, with exception of some species of *Crossodactylus* (*C. carmaschii*, *C. dantei*, *C. schimdti*, and *C. trachystomus*) that have inconspicuous (and, sometimes, absent) dermal scutes (**Figure 7A**). All species of *Hylodes* and *Megaelosia* present evident scutes (**Figure 7B**). Regarding the outgroup species, only the representatives of Dendrobatoidea (*R. palmatus* and *A. trivitatta*) present the paired scutes. Transformation 0 → 1 is recovered as synapomorphy of (*Thoropa milliaris* (Dendrobatoidea, Hylodidae). The similarity of this character in Hylodidae and Dendrobatoidea made Noble (1931) states that “*Dendrobatidae have clearly arisen from the bufonid Crossodactylus or a form closely allied to it*”.

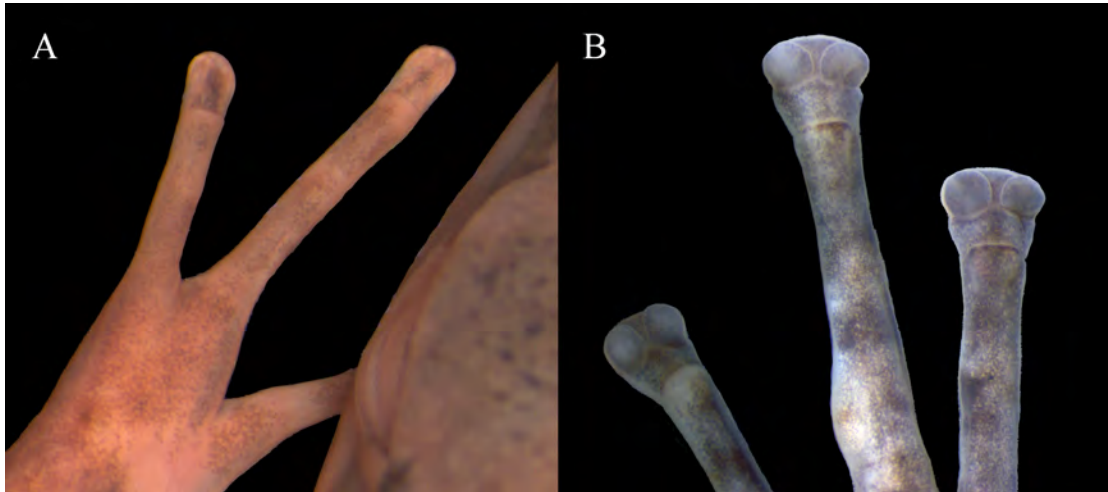


Figure 7. Paired dorsal digits scutes: (A) inconspicuous in *C. trachystomus* MNRJ 5356, (B) present in *H. perplicatus* USNM 245935.

#### 44-83: Dermic expansions on foot fingers

Grant *et al.* (2006) named this character as toe webbing. This character is used since Noble (1923). Lutz (1930) highlighted that the name *Crossodactylus* was given due to this condition on their toe. Pimenta *et al.* (2015) states the dimorphism sexual regarding fringes on toes.

All species of Hylodidae have a dermic expansion on foot fingers. These characters vary independently between species, sex, and fingers. These characters were defined by presence/absence, and differentiated by sex and each side of each finger. Preaxial and postaxial sides follow the same nomenclature of hand fingers.

**Figure 6B** illustrates these characters.

44. Preaxial fringe, toe I, male: Occurrence

(0) absent

(1) present

Remarks: Present in all males of Hylodidae (state 1). Transformation 0 → 1 is reported for the clade that comprise the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

45. Preaxial fringe, toe I, male: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Most males of Hylodidae have developed preaxial fringe on toe I (state 2). No species present expansion of skin (state 0). Transformation 2 → 1 is reported in the clade that contain *H. nasus*, *Hylodes* sp. Jucituba SP, *H. asper*, and *H. aff. asper* SP; the clade that contains *H. phyllodes*, *H. aff. phyllodes* Itanhaém SP, *H. aff. phyllodes* Rio Claro RJ, *H. aff. phyllodes* Paranapiaca SP, *H. aff. phyllodes* Bocaina SP/RJ, *H. aff. phyllodes* Ubatuba SP; *H. meridionalis*; and *H. ornatus*.

46. Preaxial fringe, toe I, female: Occurrence

(0) absent

(1) present

Remarks: All female of Hylodidae present preaxial fringe on toe II. As found in males, transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

47. Preaxial fringe, toe I, female: Expansion



(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Most female of *Hylodes* and *Crossodactylus* have undeveloped preaxial fringe on toe I (state 1). Developed fringe is reported in all species of *Megaelosia*, transformation 1 → 2. Transformation 0 → 1 is reported in *H. pipilans* and *H. fredei*, and *H. ornatus*.

48. Postaxial fringe, toe I, male: Occurrence

(0) absent

(1) present

Remarks: All male of Hylodidae present postaxial fringe on toe I. Transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

49. Postaxial fringe, toe I, male: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Most male of Hylodidae have developed postaxial fringe on toe I. Transformation 2 → 1 is reported in *H. ornatus*; the clade that contains *H. nasus*, *Hylodes* sp. Juquitiba SP, *H. asper*, and *H. aff. asper* SP; the clade *H. meridionalis* and

*H. aff. meridionalis* SC; and the clade that contains *H. phyllodes*, *H. aff. phyllodes* Itanhaém SP, *H. aff. phyllodes* Rio Claro RJ, *H. aff. phyllodes* Paranapiacá SP, *H. aff. phyllodes* Bocaina SP/RJ, *H. aff. phyllodes* Ubatuba SP.

50. Postaxial fringe, toe I, female: Occurrence

(0) absent

(1) present

Remarks: All females of Hylodidae have postaxial fringe on toe I. Transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

51. Postaxial fringe, toe I, female: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Most females of *Hylodes* and *Crossodactylus* possess developed postaxial fringe on toe I (state 1), three species of *Hylodes* possess only expansion of skin (state 0). Developed fringe is reported in *Megaelosia*, transformation 1 → 2. Transformation 1 → 0 is reported in *H. ornatus* and the clade *H. pipilans* + *H. pipilans*.

52. Preaxial fringe, toe II, male: Occurrence

(0) absent

(1) present

Remarks: All Hylodidae present preaxial fringe on toe II (state 1). Transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

53. Preaxial fringe, toe II, male: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Transformation 0 → 2, developed fringe, is reported as synapomorphy for Hylodidae. Four reversions 2 → 1 occur independently in *Hylodes*: *H. regius*; the clade that comprises *H. nasus*, *Hylodes* sp. Jucituba, *H. asper*, and *H. aff. asper*; the clade *H. meridionalis* + *H. aff. meridionalis* SC; and the clade with *H. phyllodes* and all *H. aff. phyllodes*, from Itanhaém, Rio Claro, Paranapiacaba, Bocaina, and Ubatuba.

54. Preaxial fringe, toe II, female: Occurrence

(0) absent

(1) present

Remarks: All hylodids' females present preaxial fringe on fringe II (state 1). Transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

55. Preaxial fringe, toe II, female: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Female of all *Crossodactylus* and most *Hylodes* present undeveloped fringe (state 1), transformation 1 → 0 occur in *H. ornatus* and *H. pipilans* + *H. fredii*. Transformation 1 → 2, developed fringe, is found in *Megaelosia*.

56. Postaxial fringe, toe II, male: Occurrence

(0) absent

(1) present

Remarks: Males of all hylodids present postaxial fringe on toe II (state 1). Transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

57. Postaxial fringe, toe II, male: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Males of most hylodids present developed postaxial fringe on toe II (state 2). Transformations 2 → 1, undeveloped fringe, occur four times: *H. regius*; the

clade that comprises *H. nasus*, *Hylodes* sp. Juquitiba, *H. asper*, and *H. aff. asper*; *H. meridionalis* + *H. aff. meridionalis*; and the clade with *H. phyllodes* and all *H. aff. phyllodes*, from Itanhaém, Rio Claro, Paranapiacaba, Bocaina, and Ubatuba.

58. Postaxial fringe, toe II, female: Occurrence

(0) absent

(1) present

Remarks: Transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae. Females of all hylodids present postaxial fringe on toe II (state 1).

59. Postaxial fringe, toe II, female: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Females of all *Crossodactylus* and most *Hylodes* present undeveloped postaxial fringe on toe II (state 1) and transformation 1 → 0 occurred in *H. ornatus* and *H. pipilans* + *H. fredii*. Transformation 1 → 2, developed fringe, is found in all *Megaelosia*.

60. Preaxial fringe, toe III, male: Occurrence

(0) absent

(1) present

Remarks: Males of all hylodids present preaxial fringe on toe III (state 1). Transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

61. Preaxial fringe, toe III, male: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Male of all *Crossodactylus* and most *Hylodes* present developed preaxial fringe on toe III (state 2). Transformations 2 → 1, undeveloped fringe, occur four times: *H. regius*; the clade that comprises *H. nasus*, *Hylodes* sp. Juquitiba, *H. asper*, and *H. aff. asper*; *H. meridionalis* + *H. aff. meridionalis*; and the clade with *H. phyllodes* and all *H. aff. phyllodes*, from Itanhaém, Rio Claro, Paranapiacaba, Bocaina, and Ubatuba.

62. Preaxial fringe, toe III, female: Occurrence

(0) absent

(1) present

Remarks: Females of all hylodids present preaxial fringe on toe III (state 1). Transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

63. Preaxial fringe, toe III, female: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Females of all *Crossodactylus* and most *Hylodes* present undeveloped preaxial fringe on toe III (state 1) and reversion  $1 \rightarrow 0$ , expansion of skin, occur in *H. ornatus* and *H. pipilans* + *H. fredii*. Transformation  $1 \rightarrow 2$ , developed fringe, is found in *Megaelosia*.

64. Postaxial fringe, toe III, male: Occurrence

(0) absent

(1) present

Remarks: Males of all Hylodidae present postaxial fringe on toe III (state 1). Transformation  $0 \rightarrow 1$  is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

65. Postaxial fringe, toe III, male: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Males of all *Crossodactylus* and most *Hylodes* present developed postaxial fringe on toe III (state 2). Transformations  $2 \rightarrow 1$ , undeveloped fringe, occur

four times: *H. regius*; the clade that comprises *H. nasus*, *Hylodes* sp. Juquitiba, *H. asper*, and *H. aff. asper*; *H. meridionalis* + *H. aff. meridionalis*; and the clade with *H. phyllodes* and all *H. aff. phyllodes*, from Itanhaém, Rio Claro, Paranapiacaba, Bocaina, and Ubatuba.

66. Postaxial fringe, toe III, female: Occurrence

(0) absent

(1) present

Remarks: Females of all hylodids present postaxial fringe on toe III (state 1).

Transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

67. Postaxial fringe, toe III, female: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Females of all *Crossodactylus* and most *Hylodes* present undeveloped postaxial fringe on toe III (state 1) and reversion 1 → 0, expansion of skin, occur in *H. ornatus* and *H. pipilans* + *H. fredii*. Transformation 1 → 2, developed fringe, is found in *Megaelosia*.

68. Preaxial fringe, toe IV, male: Occurrence

(0) absent



(1) present

Remarks: Males of all hylodids present preaxial fringe on toe IV (state 1). Transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

69. Preaxial fringe, toe IV, male: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Males of most hylodids present developed preaxial fringe on toe IV (state 2). Transformations 2 → 1 occurs four times: *H. regius*; the clade that comprises *H. nasus*, *Hylodes* sp. Jucituba, *H. asper*, and *H. aff. asper*; *H. meridionalis* + *H. aff. meridionalis*; and the clade with *H. phyllodes* and all *H. aff. phyllodes*, from Itanhaém, Rio Claro, Paranapiacaba, Bocaina, and Ubatuba.

70. Preaxial fringe, toe IV, female: Occurrence

(0) absent

(1) present

Remarks: Females of Hylodidae present preaxial fringe on toe IV (state 1). Transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

71. Preaxial fringe, toe IV, female: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Females of *Crossodactylus* and most *Hylodes* present undeveloped preaxial fringe on toe IV (state 1), transformation  $1 \rightarrow 0$ , expansion of skin, occur in *H. ornatus* and *H. pipilans* + *H. fredii*. Transformation  $1 \rightarrow 2$ , developed fringe, is found in *Megaelosia*.

72. Postaxial fringe, toe IV, male: Occurrence

(0) absent

(1) present

Remarks: All males of Hylodidae present postaxial fringe on toe IV (state 1). Transformation  $0 \rightarrow 1$  is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

73. Postaxial fringe, toe IV, male: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Males of most Hylodidae present developed postaxial fringe on toe IV (state 2). Transformations  $2 \rightarrow 1$ , undeveloped fringe, occur four times: *H. regius*;

the clade that comprises *H. nasus*, *Hylodes* sp. Jucituba, *H. asper*, and *H. aff. asper*; *H. meridionalis* + *H. aff. meridionalis*; and the clade with *H. phyllodes* and all *H. aff. phyllodes*, from Itanhaém, Rio Claro, Paranapiacaba, Bocaina, and Ubatuba.

74. Postaxial fringe, toe IV, female: Occurrence

(0) absent

(1) present

Remarks: Females of all hylodids present postaxial fringe on toe IV (state 1).

Transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

75. Postaxial fringe, toe IV, female: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Females of *Crossodactylus* and most *Hylodes* present undeveloped postaxial fringe on toe IV (state 1), with reversion for expansion of skin (1 → 0) in *H. ornatus* and *H. pipilans* + *H. fredii*. Transformation 1 → 2, developed fringe, is found in *Megaelosia*.

76. Preaxial fringe, toe V, male: Occurrence

(0) absent

(1) present

Remarks: Male of all hylodids present preaxial fringe on toe V (state 1). Transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

77. Preaxial fringe, toe V, male: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Males of *Crossodactylus* and most *Hylodes* present developed preaxial fringe on toe V (state 2). Transformations 2 → 1, undeveloped fringe, occur four times: *H. regius*; the clade that comprises *H. nasus*, *Hylodes* sp. Juquitiba, *H. asper*, and *H. aff. asper*; *H. meridionalis* + *H. aff. meridionalis*; and the clade with *H. phyllodes* and all *H. aff. phyllodes*, from Itanhaém, Rio Claro, Paranapiacaba, Bocaina, and Ubatuba.

78. Preaxial fringe, toe V, female: Occurrence

(0) absent

(1) present

Remarks: All females of Hylodidae present preaxial fringe on toe V (state 1). Transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

79. Preaxial fringe, toe V, female: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Females of *Crossodactylus* and most *Hylodes* present undeveloped fringe on toe V (state 1), with reversion for expansion of skin,  $1 \rightarrow 0$ , in *H. ornatus* and *H. pipilans* + *H. fredii*. Transformation  $1 \rightarrow 2$ , developed fringe, is found in *Megaelosia*.

80. Postaxial fringe, toe V, male: Occurrence

(0) absent

(1) present

Remarks: Males of all Hylodidae present postaxial fringe on toe V (state 1). Transformation  $0 \rightarrow 1$  is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

81. Postaxial fringe, toe V, male: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Developed postaxial fringe on toe V is present in all males of *Crossodactylus* and most *Hylodes*. Reversion  $2 \rightarrow 1$ , undeveloped fringe, occur four

times: *H. regius*; the clade that comprises *H. nasus*, *Hylodes* sp. Juquitiba, *H. asper*, and *H. aff. asper*; *H. meridionalis* + *H. aff. meridionalis*; and the clade with *H. phyllodes* and all *H. aff. phyllodes*, from Itanhaém, Rio Claro, Paranapiacaba, Bocaina, and Ubatuba.

82. Postaxial fringe, toe V, female: Occurrence

(0) absent

(1) present

Remarks: Females of all Hylodidae present postaxial fringe on toe V (state 1).

Transformation 0 → 1 is reported for the clade that comprises the families included in this study, except Hemiphractidae, Brachycephaloidea, Odontophrynidae, and Leptodactylidae.

83. Postaxial fringe, toe V, female: Expansion

(0) skin expansion

(1) fringe

(2) developed fringe

Additive

Remarks: Females of *Crossodactylus* and most *Hylodes* present undeveloped postaxial fringe on toe V (state 1), with reversion for expansion of skin, 1 → 0, in *H. ornatus* and *H. pipilans* + *H. fredii*. Transformation 1 → 2, developed fringe, is found in *Megaelosia*.

84-85: Tarsal fringe

These characters followed Grant *et al.* (2006), who defined the tarsal fringe as “a conspicuous dermal flap that runs along the entire length of the preaxial edge of the tarsus”. When present, the tarsal fringe is normally more developed in males than females.

84. Tarsal fringe in males

(0) absent

(1) present, weak

(2) present, well developed

Additive

Remarks: All hylodids' males present tarsal fringe, most of them present a well-developed fringe (state 2; **Figure 6B**). A weak fringe is just found in some younger individuals (state 1). For that reason, this character is considered additive. Most outgroup species do not present a tarsal fringe (state 0), except for *Cycloramphus brasiliensis* and *Rheobates palmatus*. Transformation  $0 \rightarrow 2$  is recovered as synapomorphy of Hylodidae, and  $2 \rightarrow 1$  in *H. meridionalis*.

85. Tarsal fringe in females

(0) absent

(1) present, weak

(2) present, well developed

Additive

Remarks: All females of Hylodidae also present tarsal fringe, however the frequency of weak developed fringe is higher than in males. All females of *Megaelusia* have a well-developed tarsal fringe. Females of the outgroup do not have

this structure. Transformation  $0 \rightarrow 1$  is recovered as synapomorphy of (*Thoropa milliaris* (Dendrobatoidea, Hylodidae)). Transformation  $1 \rightarrow 2$  is recovered in *Megaelosia* and *H. cardosoi*.

#### 86. Metatarsal fold

Grant *et al.* (2006) defined the metatarsal fold as “*a dermal thickening running from the postaxial edge of the base of toe V (often coextensive with the fringe, if present) along the outer edge of the sole toward the outer metatarsal tubercle*”.

(0) absent

(1) present, weak

(2) present, well developed

Additive

Remarks: *Crossodactylus* and *Hylodes* species do not present metatarsal fold (state 0). Only representatives of *Megaelosia* present this character. However, within this genus, the fold is weak (*e.g.*, *M. boticariana*; state 1) or well developed (*e.g.*, *M. goeldii*; state 2). Transformation  $0 \rightarrow 1$  is reported as synapomorphy of *Megaelosia*, with reversion  $1 \rightarrow 0$  in *M. massarti*. Transformation  $1 \rightarrow 2$  is found in *M. goeldii*.

#### 87-101: Skin texture

Noble (1931) defined an Amphibian as “*cold-blooded vertebrates having a smooth or rough skin rich in glands which keep it moist*”. Grant *et. al.* (2006) states that “*even ‘smooth’ skin may appear shagreen or faintly granular under high magnification*”. I considered as texture: granules, spicules, tubercles, and folds.

#### 87-89: Dorsal skin texture



Grant *et al.* (2006) codified the dorsal skin texture as a single character with four states (absent, posteriorly granular, strongly granular, and speculate). Here, I am not sure about the homology of granule and spicule on the skin, for this reason I decided to separate the kind of texture (granular and speculate) in two different characters. Additionally, I also codified the distribution of the granules as a distinct character.

87. Granules, dorsal skin: Occurrence

(0) absent;

(1) present

Remarks: All species of Hylodidae present granules on dorsal skin. Some specimens are codified as absent, but most of them are old and poorly preserved animals. Thus, the condition absent (state 0) might be an artifact of preservation. Transformation  $1 \rightarrow 0$  is reported in *C. dantei* and the clade that contains representatives of the families Bufonidae, Hylidae, Alsodidae, Rhinodermatidae, and the subfamily of Leiuperinae (*P. cuvieri*).

88. Granules, dorsal skin: Distribution

(0) posteriorly and laterally

(1) all dorsum

Remarks: Most species of Hylodidae present the granule on posteriorly and laterally part of dorsum. The species that present granules in all dorsum are *H. asper* (RJ), *H. asper* (SP), and *H. dactylocinus*. Ambiguity is found in *H. cardosoi*.

89. Spicules, dorsal skin: Occurrence

(0) absent

(1) present

Remarks: No species of Hylodidae present spicules. This condition is found just in the bufonid *Rhinella major*.

#### 90-99: Tubercles

##### 90. Thenar tubercle

The thenar tubercle located at the base of the thumb is oval (Lynch and Duellman 1997). Here, I followed Grant *et al.*'s decision, which joined the conditions absent and inconspicuous at the same character. Grant *et al.* (2006) based their codification on Caldwell and Myers (1990) that noted some variation in *Adelphobates quinquevittatus*. In some specimens it is altogether undetectable, whereas in others possible vestiges of it were detected as possibly represented by slight epidermal thickening. Thus, Grant *et al.* (2006) states that the dermal features can be lost as an artifact of preservation combining the apparent completed absence and inconspicuous epidermal thickening.

(0) absent or inconspicuous

(1) present

Remarks: All species observed present a thenar tubercle (state 1). Only few specimens present an inconspicuous tubercle, however it can be an artifact of preservation.

91. Cloacal tubercles

Also named as “cloacal ornamentation”, these structures are granules, normally white, localized ventrally and laterally to the cloacal opening.

(0) absent

(1) present

Remarks: This structure is extremely variable within the species of Hyloidae. Tubercles are observed in all specimens of *H. fredii*, *H. meridionalis*, *H. regius*, *H. sazimai*, *H. uai*, *M. apuana*, *M. boticariana*, and *M. massarti*. Other than that, the species that do not present this structure are *C. dantei*, *H. amnicola*, *H. charadranaetes*, *H. dactylocinus*, *H. heyeri*, *H. japi*, *H. lateristrigatus*, *H. nasus*, *H. phyllodes*, *H. pipilans*, and *M. goeldii*. For the other species, this character is codified with ambiguity. Ambiguity is also found in *Leptodactylus fuscus*, *Cycloramphus brasiliensis*, *Rhinella major*, and *Vitreorana eurignatha*. The other species from outgroup the tubercles are not observed (state 0). Transformation 0 → 1 is reported in *H. meridionalis*, *H. fredii*, and the clade that contains all *Megaelasia*, except *M. goeldii*.

92-94: Supralabial tubercles

Cochran (1955 “1954”) reports this structure as “a row of small spines, sometimes black-tipped, around the outer edge of the upper lip. [...] Most frequently these spines are not black, being the same as the lips in color; in these cases they are hard to see, as they are almost microscopic in size”. Cochran also highlights some differences in this character between males and females saying, “in the females the lip is either smooth or has a row of small spicules. In some males the spicules are equally poorly developed”. Here, I decided to codify male and female separately. Heyer *et al.*

(1990) reported “a row of small brown-tipped tubercles on the edge of the upper lip” in some large males of *C. dispar*. Canedo (2008) reports that *Hylodes* differs from *Megaelasia* by presenting males with small tubercles on the posterior margin of the lips. Pimenta *et al.* (2014) report that the presence, degree of development, and color of the upper lip spines varied greatly within species of *Crossodactylus*.

92. Supralabial tubercles, male: Occurrence

(0) absent

(1) present

Remarks: Males of all species of Hylodidae present supralabial tubercles (**Figure 10A**), exception is found only in *H. glaber* and *M. apuana*. Regarding outgroup species, these tubercles are only found in *Rhinella major*.

93. Supralabial tubercles, male: Pigmentation

(0) not pigmented

(1) pigmented

Remarks: The pigmentation of these tubercles is not common. I just found pigmented tubercles in some specimens of *Crossodactylus* (**Figure 10A**) and *Rhinella major*.

94. Supralabial tubercles, female: Occurrence

(0) absent

(1) present, unpigmented

Remarks: Females of *C. aeneus*, *C. schmidtii*, *C. trachystomus*, *H. asper* SP, *H. cardosoi*, and *H. japi* presents supralabial tubercles. No female are observed with

pigmented tubercles; thus, for this character, the presence condition means “presence of unpigmented tubercles”. Female from outgroup do not present supralabial tubercles. Transformation  $0 \rightarrow 1$  was reported in *H. aff. asper* SP and *H. japi*.

95. Dorsolateral light tubercles

Canedo (2008) reported three kinds of tubercles on dorsolateral region external to the fold: few, big, light, and evident tubercles; regular size, and variable amount, some of those light; and absent or inconspicuous tubercles. Here, I decided to limit the codification in present and absent because the amount and size of tubercles seems subjective.

(0) absent

(1) present

Remarks: Dorsolateral tubercles are found in all specimens of *C. gaudichaudii*, *H. cardosoi*, *H. dactylocinus*, and *Megaelosia goeldii* observed in the study (state 1). In many other species of Hylodidae, this character is observed in few specimens, and is codified with ambiguity. Within outgroup species, the absence of these tubercles is reported in *Cycloramphus brasiliensis* and *Ceratophrys cornuta* (state 0). Transformation  $0 \rightarrow 1$  occurs six times independently: in the clade that contains the families Ceratophryidae, Batrachylidae and Cycloramphidae; in the clade with the representatives of *Hylodes* ‘Serra do Mar / no spine’ clade, except *H. charadranaetes*; *H. meridionalis*; *H. fredii*; *H. regius*; and *M. goeldii*.

96-97: Supernumerary tubercles

Lynch and Duellman (1997) reported supernumerary tubercles (called accessory tubercles by Savage [1987]) on the fleshy part of the palm. According to them, these

usually are low and difficult to see clearly, but it can be prominent and conical (*e.g.*, *Barycholos pulcher*). Grant *et al.* (2006) reported that some dendrobatids exhibit a tiny tubercle-like thickening on the outer edge (not the fleshy part) of the palm, but the authors do not consider this to be homologous with the supernumerary tubercles of other taxa.

96. Supernumerary tubercles, hand

(0) absent

(1) present

Remarks: These tubercles are observed in all specimens of *C. gaudichaudii*, *H. cardosoi*, *H. dactylocinus*, and the four species of *Megaelosia* (state 1). However, ambiguity is reported in several other species of Hylodidae. Regarding the outgroup species, the tubercles are not observed in *Amereega trivitatta*, *Rheobates palmatus*, *Ceratophrys cornuta*, and *Allophryne ruthveni* (state 0). Transformation 1 → 0 is reported in *A. ruthveni* and *Hylodes*.

97. Supernumerary tubercles, foot

Region: Feet (sole)

(0) absent

(1) present

Remarks: Supernumerary tubercles are not found in any species of Hylodidae (state 0). These tubercles are only observed on the outgroup species *Hemiphractus johnsoni*, *Physalaemus cuvieri*, *Pristimantis fenestratus*, and *Rhinella major* (state 1). Ambiguity is reported for *Leptodactylus fuscus* and *Vitreorana eurygnatha*.

Transformation 0 → 1 is reported in the clade that contains Bufonidae and the Leiuperinae (*P. cuvieri*).

98-99: Postrictal tubercles

Tubercles located above the tympanum and posterior the buccal opening. Pimenta *et al.* (2014, 2015) report that all species of *Crossodactylus* examined in their study presented “*an elongated swelling between the tympanum and the shoulder*”. Here, when present, my codification followed Pimenta *et al.* (2014, 2015), which divided this character in two states: single large tubercle, and a line of small tubercles.

98. Postrictal tubercles: Occurrence

(0) absent

(1) present

Remarks: My results agree with those from Pimenta *et al.* (2014), *i.e.*, all species of *Crossodactylus* observed here present postrictal tubercles. Also, most species of *Hylodes* present this character (state 1). Transformation 1 → 0 is found in *H. magalhaesi* and in the clade that contains *H. phyllodes* and the five lineages of *H. aff. phyllodes* (Itanhém, Rio Claro, Paranapiacaba, Bocaina, and Ubatuba).

99. Postrictal tubercles: Condition

(0) single, large

(1) more than one, aligned, small

Remarks: All species of *Crossodactylus* and several species of *Hylodes* present a single large postrictal tubercle (state 0). A line of small tubercles is found in *H. heyeri*, *H. lateristrigatus*, *H. meridionalis*, and *H. nasus* (state 1).

## 100-101: Fold

### 100. Dorsolateral fold

(0) absent or inconspicuous

(1) present

Remarks: I opted to join the conditions absent and inconspicuous in state 0 because the “weak fold” seemed just an artifact of preservation. Absent or inconspicuous dorsolateral fold is observed in all species of *Crossodactylus*, most species of *Megaelosia* and some species of *Hylodes*. A conspicuous dorsolateral fold is observed in several species of *Hylodes* and *M. goeldii* (state 1). Regarding the outgroup species, *Hemiphractus johnsoni*, *Vitreorana eurygnatha*, *Allophryne ruthveni*, and *Ceratophrys cornuta* present dorsolateral fold.

### 101. Supratympanic fold

(0) absent

(1) present, weak

(2) present, conspicuous

Additive

Remarks: All Hylodidae have a supratympanic fold (states 1 or 2). This character presents a great variation within the family and, also, within most species. The absence of a supratympanic fold is observed in only one specimen of *C. aeneus* and *H. babax*, but it seems to be an artifact of preservation. Transformation 1 → 2 is reported four times independently in all parts of the tree: in the clade with



representatives of Ceratophryidae, Batrachylidae, and Cycloramphidae; *C. dantei*; *H. regius*; and *M. goeldii*.

#### 102-127: Coloration

##### 102-103: White lateral stripe

This stripe extends from the tip of the snout, crosses the maxillary region to reach the anterior region of the arm. When present, this stripe can vary in pattern of coloration.

##### 102. White lateral stripe: Occurrence

(0) absent

(1) present

Remarks: The presence of this stripe is observed in all species of *Crossodactylus* and *Hylodes* (state 1; **Figure 8**). However, species of *Megaelosia* do not have this condition (state 0). This stripe is also found in *Leptodactylus fuscus*, *Rheobates palmatus*, *Amereega trivitatta*, and *Dendropsophus minutus*. Transformation 1 → 0 occurred in *Megaelosia*; in the clade with Bufonidae and Leiuperinae; and in the clade with representatives of Ceratophryidae, Batrachylidae, and Cycloramphidae

##### 103. White lateral stripe: Color pattern

(0) uniform in all extension

(1) stripe filled by white spots

Remarks: The uniform condition of the lateral stripe is observed in most species of *Crossodactylus* and *Hylodes* (state 0; **Figure 8A**). In some species this stripe is irregular and is normally filled by white spots (state 1; **Figure 8B**). The species that the state 1 was observed are *C. aeneus*, *C. dantei*, *C. timbuhy*, *H. heyeri*, *H. nasus*, *H. ornatus*, and *H. otavioi*. Transformation 0 → 1 occurs in *H. ornatus* and *H. otavioi*.

#### 104. Canthal dark stripe

The canthal dark stripe is immediately above the white lateral stripe, starting on the tip of snout to reach the eye.

(0) absent

(1) present

Remarks: The canthal dark stripe is present in all species of *Crossodactylus* and *Hylodes* (state 1; **Figure 8**); however it is absent in few specimens of *C. gaudichaudii*, *C. schmidti*, *C. trachystomus*, *H. asper* (RJ), *H. asper* (SP), *H. cardosoi*, *H. charadranaetes*, *H. lateristrigatus*, and most specimens of *H. glaber*. Regarding the outgroup species, this stripe was observed in *Leptodactylus fuscus*, *Dendropsophus minutus*, *Rhinella major*, *Ceratophrys cornuta*, and *Rheobates palmatus*. This stripe was not observed in any species of *Megaelasia* (state 0; transformation 1 → 0).

#### 105. Canthal white line

The canthal white line is very thin and, when present, is above the canthal dark stripe.

(0) absent

(1) present

Remarks: Interspecific variation is observed in several species of *Crossodactylus* and *Hylodes* (**Figure 8**). In outgroup species, it is only present in *Physalaemus cuvieri* and *Amereega trivitatta*. Transformation 1 → 0 is reported in *H. regius* and *P. cuvieri*.

#### 106-107: Dorsolateral stripe

The dorsolateral stripe normally extends from the eyes toward the posterior body, and does not cross the flank.

#### 106. Dorsolateral stripe: Occurrence

(0) absent

(1) present

Remarks: Great variation is observed within Hylodidae. This character varies within the three genera, and interspecifically. In outgroup species, the dorsolateral stripe is observed in *Amereega trivitatta*, *Dendropsophus minutus*, and *Allophryne ruthveni*, and it is ambiguous in *Leptodactylus fuscus* and *Physalaemus cuvieri*. The other outgroup species do not presented this stripe. Transformation 0 → 1 is reported in *A. ruthveni*.

#### 107. Dorsolateral stripe: Extension

(0) partial

(1) complete

Remarks: When present, the dorsolateral stripe can be partial or complete. The partial condition is more frequent within Hylodidae (state 0). Only the species *H. lateristrigatus*, *H. meridionalis*, *H. sazimai*, and *H. uai* present the complete condition

(state 1). *Leptodactylus fuscus* presents an incomplete dorsolateral stripe, while *Physalaemus cuvieri*, *Amereega trivitatta*, and *Allophryne ruthveni* present a complete stripe. Transformation 0 → 1 is recovered as synapomorphy of *Hylodes* ‘MG/ES’ + *Hylodes* ‘Serra da Mantiqueira’ clades, and of *H. meridionalis*.

#### 108. Ventrolateral stripe

The ventrolateral stripe crosses the ventral edge of the flank between the belly and the flank.

(0) absent

(1) present

Remarks: The ventrolateral stripe is observed only in *H. amnicola* and *H. fredii*.

All other species observed here do not present this structure; however, ambiguity is found in some species within Hylodidae and outgroup. Transformation 0 → 1 is recovered in *H. fredii*.

#### 109-110: Obliquolateral stripe

The obliquolateral stripe extends from the groin and crosses diagonally toward the eyes. Edward (1974) described the partial stripe that extends from the groin not reaching the eyes, and complete stripe that reaches the eyes in dendrobatids.

#### 109. Obliquolateral stripe: Occurrence

(0) absent

(1) present

Remarks: The obliquolateral stripe is observed in many species of Hylodidae (state 1; **Figure 8**). However, the presence of this structure can vary within each

species. The species that present this structure without ambiguity are *H. fredii*, *H. japi*, *H. otavioi*, *H. perere*, *H. pipilans*, and *H. regius* (transformation 0 → 1). None of the species of *Megaelosia* present this stripe (state 0).

110. Obliquolateral stripe: Extension

(0) partial

(1) complete

Remarks: The complete stripe is found in *H. babax*, *H. heyeri*, *H. lateristrigatus*, *H. otavioi* (state 1; **Figure 8A**). The species *C. gaudichaudii*, *H. japi*, *H. ornatus*, and *H. perplicatus* present both conditions. All species from the outgroup species that have an obliquolateral stripe present the partial condition (state 0; **Figure 8B, C**). Transformation 0 → 1 is recovered in *Hylodes* ‘MG/ES’ clade.

111-112: Vertebral stripe

This stripe starts between the eyes and crosses the dorsal region toward the end of urostylum. When present, the stripe can be complete or partial. The partial condition usually seems a dashed line.

111. Vertebral stripe: Occurrence

(0) absent

(1) present

Remarks: This stripe (**Figure 8D**) is more common in *Crossodactylus* species, however it have a great interspecific variation. Only *C. dantei* presents the vertebral stripe, and ambiguity is found in *C. caramaschii*, *C. gaudichaudii*, *C. timbuhy*, and *C. trachystomus*. Within *Hylodes*, ambiguity is observed in *H. lateristrigatus* and *H.*

*ornatus*. Species of *Megaelosia* do not present this structure. Regarding the outgroup species, *Ceratophrys cornuta* and *Allophryne ruthveni* have the vertebral stripe, and ambiguity is registered in *Hemiphractus johnsoni* and *Physalaemus cuvieri*. Transformation 0 → 1 is recovered in *A. ruthveni*.

112. Vertebral stripe: Extension

(0) partial

(1) complete

Remarks: The partial condition (**Figure 8D**) is predominant in hylodids (state 0). Only *C. trachystomus* presents the complete vertebral stripe (state 1). *Physalaemus cuvieri*, *Ceratophrys cornuta*, and *Allophryne ruthveni* also present the complete condition.

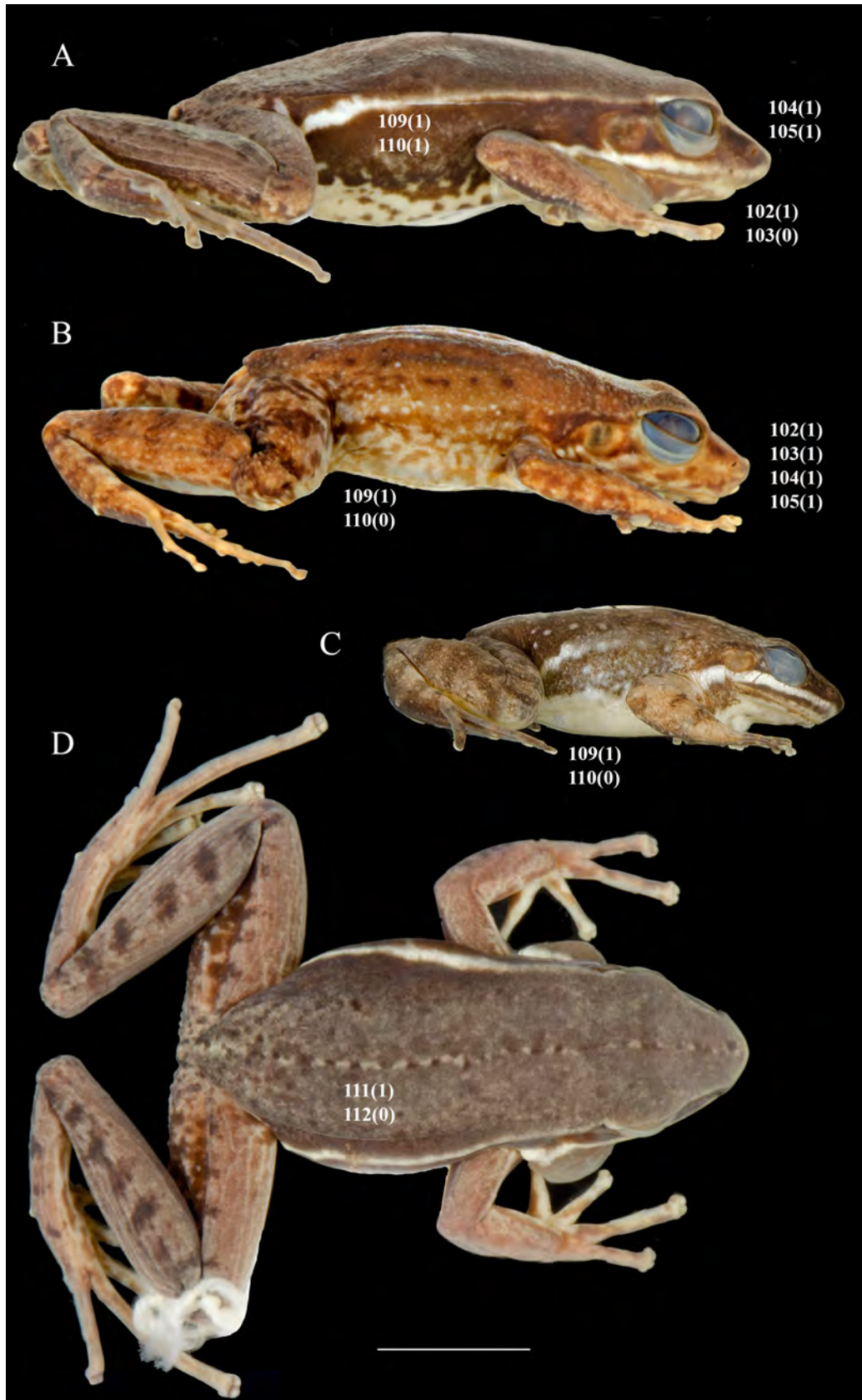


Figure 8. Stripes: (A) *H. glaber* AMNH 103901, (B) *H. nasus* AMNH 72455, (C) *C. schmidtii* AMNH 190684, (D) *H. glaber* AMNH 103896. Animals are in proportional size (scale bar = 1cm).

113. Pale cloacal mark:

A white region around the cloaca is common in Hylodidae. The mark is usually located dorsally and laterally around the cloaca.

(0) absent

(1) present

Remarks: This character varies within the species of Hylodidae. The pale cloacal mark is observed in all specimens of *H. fredii*, *H. magalhaesi*, *H. nasus*, *H. ornatus*, *H. pipilans*, *H. regius*, and *H. sazimai* (state 1). No species of *Megaelosia* presents this mark (state 0). Regarding the outgroup species, this mark is found in *Leptodactylus fuscus*, *Hemiphractus johnsoni*, *Physalaemus cuvieri*, and *Allophryne ruthveni*. Transformation 0 → 1 is recovered in *P. cuvieri*.

114-117: Color pattern on dorsal thigh

Several species present transversal stripes on dorsal thigh. These stripes can be solid or poorly defined, and can vary in number. Here, I codified the occurrence, condition and quantity of these stripes. The presence of spots on dorsal thigh rather than stripes is uncommon but present in Hylodidae.

114. Transversal stripes, dorsal thigh: Occurrence

(0) absent

(1) present

Remarks: The presence of transversal stripe is common in Hylodidae, at least, in some specimens of each species (state 1). Absence of these stripes is observed in all specimens of *C. dantei*, *H. dactylocinus*, *H. meridionalis*, *H. otavioi*, *H. regius*, *M. boticariana*, and *M. massarti* (state 0). Regarding the outgroup species, the stripes are



found in *Leptodactylus fuscus*, *Hemiphractus johnsoni*, *Physalaemus cuvieri*, and *Ceratophrys cornuta*. The presence of this character is recovered as synapomorphy of Hylodidae (transformation 0 → 1) and for *P. cuvieri*. Reversions occur six times independently: *H. otavioi*; *H. regius*; *C. dantei*; *H. meridionalis*; *H. dactylocinus*; the clade that comprises *M. massarti*, *Megaelosia* sp. Serra do Mar N SP, and *M. boticariana*.

115. Transversal stripes, dorsal thigh: Condition

(0) complete stripes

(1) dotted or poorly defined stripes

Remarks: When present, the transversal stripes are usually complete and well-define; however, ambiguities are found in several species. Transformation 0 → 1 are reported in the clade that comprises *Hylodes* ‘Serra do Mar / spine’, ‘MG / ES’, and ‘Serra da Mantiqueira’ clades.

116. Perpendicular stripes, dorsal thigh: Quantity

(0) one

(1) two

(2) three

(3) four

(4) five

(5) six

Non additive

Remarks: The amount of stripes varies within the species. Four stripes is the condition most found in Hyloidae. The transformation 4 → 3 is recovered in *Hylodes*.

117. Spots, dorsal thigh

(0) absent

(1) present

Remarks: Spots are observed in *C. dantei*, *C. trachystomus*, *H. cardosoi*, *H. glaber*, *H. magalhaesi*, *H. meridionalis*, and *H. phyllodes*; but only *C. dantei* and *H. meridionalis* without ambiguity (state 1). In most case, these spots are small pigmentations covering the dorsal surface of thigh. In *H. glaber*, I could observe bigger, rounded, and well-defined spots. Transformation 0 → 1 is recovered in *C. dantei* and *H. meridionalis*.

#### 118-120: Dorsal skin

In preserved animals, iridophores and melanophores are found on the dorsal skin. When present, this pigmentation can be spots, irregular botches, or stripes. This character does not evaluate the background coloration of the skin, but only the pigmentation pattern above it. This decision was made because many individuals observed in this study were collected many decades ago, and most of them lost their original coloration.

118. Iridophores on dorsal skin:

(0) absent

(1) present

Remarks: Within Hylodidae, the genus *Hylodes* has more species with iridophores on dorsal skin. Transformation 0 → 1 is recovered as synapomorphy for *Hylodes*, with reversion 1 → 0 in *H. japi*.

119. Melanophores on dorsal skin:

(0) absent

(1) present

Remarks: Melanophores are present in almost all species of Hylodidae, with exception in *H. perplicatus*, *H. regius*, *M. goeldii*, and *M. massarti*. Transformation 0 → 1 confirms this character as synapomorphy for Hylodidae, with reversion 1 → 0 in *H. regius*, *M. massarti*, and *M. goeldii*.

120. Pigmentation pattern on dorsal skin

(0) spots

(1) irregular blotches

(3) longitudinal stripes

Non additive

Remarks: The pattern most observed in Hylodidae is irregular blotches. Transformation 1 → 0 is reported for *H. dactylocinus*.

#### 121-122: Ventral skin

For the same reason discussed in dorsal skin coloration, the background color of the ventral skin was not evaluated here. I observed the occurrence of iridophores and melanophores on ventral skin.

121. Iridophores on ventral skin

(0) absent

(1) present

Remarks: Iridophores on ventral skin are not found in *Crossodactylus*, except for few specimens of *C. trachystomus*. In *Hylodes*, this pigmentation is found in *H. amnicola*, *H. babax*, *H. heyeri*, *H. japi*, *H. regius*. Also, *M. apuana* and *M. boticariana* present iridophores. Ambiguity is found in five species of *Hylodes*. Regarding the outgroup species, iridophores are observed in specimens of *Hemiphractus johnsoni* and *Amerrega trivitatta*, and one specimen of *Physalaemus cuvieri*, *Pristimantis fenestratus*, and *Cycloramphus brasiliensis*.

122. Melanophores on ventral skin

(0) absent

(1) present

Remarks: Melanophores is found, at least, some species of almost all species of Hylodidae. This pigmentation is absent only in *H. cardosoi*, *H. dactylocinus*, *M. apuana*, and *M. boticariana*. Melanophores on belly is reported as synapomorphy for Hylodidae (0 → 1), with reversion 1 → 0 in *H. cardosoi* + *H. dactylocinus*.

123-125: Gular skin

As in dorsal and ventral skin, the background color of the gular skin is not evaluated. I observed the occurrence of iridophores and melanophores on gular skin. Also, I evaluated the occurrence and condition of a longitudinal dark stripe located posteromedially of the gular region.

123. Iridophores on gular skin

(0) absent

(1) present

Remarks: Every species that present iridophores on ventral skin, also present on the gular. Only *M. massarti* present iridophores exclusively on gular skin. Transformation 0 → 1 is reported in *Allophryne ruthveni*, *Physalaemus cuvieri*, in the clade with all *Megaelosia*, except *M. goeldii*.

124. Melanophores on gular skin

(0) absent

(1) present

Remarks: The same pattern of iridophores occurs concerning melanophores. Every species that have melanophores on the belly, present it on the gular. The exceptions are *H. cardosoi* and *H. dactylocinus* that present pigmentation only on the gular region, and *M. massarti* that present melanophores only on the belly. Melanophores on gular skin is reported as synapomorphy of Hylodidae (0 → 1), with reversion 1 → 0 in the clade with all *Megaelosia*, except *M. goeldii*.

125. Posteromedial longitudinal dark stripe, gular

(0) absent

(1) present, weak

(2) present, conspicuous

Additive

Remarks: A posteromedial dark stripe was observed in almost all species of Hylodes, varying between a weak or a conspicuous stripe. This pattern of coloration

was not found in *H. asper* (RJ), *H. magalhaesi*, *H. meridionalis*, *H. uai*, *M. apuana*, *M. boticariana*, and *M. massarti*. Among outgroup species, the absence of this stripe was predominant. This stripe is recovered as synapomorphy of Hylodidae (0 → 1), with reversion in *H. meridionalis* (1 → 0), in the clade with all *Megaelosia*, except *M. goeldii* (1 → 0), and *H. magalhaesii* (1&2 → 0). Transformation 1 → 2 is reported in *H. perere*.

126. Posterodorsal dark outline, tympanum

In many species, I observed an outline around all posterior and dorsal regions of the tympanum. This outline could be a weak and difficult to be observed or evident.

(0) absent

(1) present, weak

(2) present, conspicuous

Additive

Remarks: The posterodorsal dark outline is observed in at least some specimens of *Crossodactylus*, and in most species of *Hylodes*. Other than that, no species of *Megaelosia* present this pigmentation. Almost all species of *Crossodactylus* presented ambiguity between the two states (state 1 and 2). In *Hylodes*, the conspicuous outline is more frequent than the weak one. This character is reported as synapomorphy (0 → 1) for the clade that comprises *Hylodes*, except *Hylodes* ‘South’ clade, with reversion in *H. amnicola* (1&2 → 0), *H. dactylocinus* (1 → 0), and *H. fredii* (1 → 0). Transformation 1 → 2 is recovered in the clade that comprises *H. phyllodes* and the five lineages *H. aff. phyllodes*.

127. Paracloacal dark stripes

A pair of dark stripes can be visible in some specimens of Hylodidae. Grant *et al.* (2006) codified a pale paracloacal mark in dendrobatids, but I am convinced it is not homologous with the ones found in hylodids. The pale paracloacal mark reported by Grant *et al.* (2006) “*is along the posterior surface of the thigh... originates adjacent to the vent at the base of the thigh*”. The paracloacal dark stripes reported in this study are restricted to the adjacent vent region, not reaching the thigh. This character was recovered as synapomorphy of *Hylodes* (0 → 1), with reversion 1 → 0 in *H. fredei*.

(0) absent

(1) present, weak

(2) present, conspicuous

Additive

Remarks: Paracloacal dark stripes are found in almost all species of *Crossodactylus* and *Hylodes*; only *C. dantei* and *H. fredei* do not present this pigmentation. *Megaelosia* also does not present it. The absence of this pigmentation is predominant between the outgroup species.

## **Viscera**

Amphibians have pigmented cells in their internal organs. These cells can be melanocytes, when are originated from ectodermal neural crest (Franco-Belussi *et al.* 2013), or melanomacrophages, originated from hematopoietic stem cells (Colombo *et al.* 2011, Franco-Belussi *et al.* 2016). The interpretation of the visceral pigmentation followed the protocol proposed by Franco-Belussi *et al.* 2009, which delimited four conditions based on the differences in the intensity of pigmentation. The categories

proposed by the authors vary from absence of pigmentation (category 0) to entirely pigmented (category 3), with the categories 1 and 2 representing a gradual increase in the intensity of pigmentation. Here, I considered the categories 1 and 2 as a single state. This decision was made to avoid subjectivity in my codifications. Thus, when necessary, the pigmentation was divided in three conditions (*sensu* Franco-Belussi *et al.* [2009]): unpigmented (“category 0”), partially pigmented (“categories 1 and 2”), and completely pigmented (“category 3”). The only exception was the spleen, a hematopoietic organ that has a complex degree of color variation. For photos illustrating these characters see **Figure 9**.

#### 128. Adult testis: Pigmentation

Canedo (2008) considered the testicle of *Megaelosia* as unpigmented, whereas *Crossodactylus* has a pigmented testicle. Grant *et al.* (2006) observed that the testis pigmentation increases ontogenetically and considered this character as additive. Franco-Belussi *et al.* (2009) observed the testis pigmentation in some Leptodactylidae species from the genera *Leptodactylus*, *Physalaemus*, and *Pseudopaludicola*, and their results showed that, especially on Leiuperinae subfamily (*Physalaemus* and *Pseudopaludicola*), there is an intraspecific variation in this character. However, no intraspecific variation was observed among the species of *Dendropsophus* studied in Franco-Belussi *et al.* (2011).

(0) unpigmented

(1) partially pigmented

(2) completely pigmented

Additive



Remarks: This character was coded only from adults. Here, we follow the Grant *et al.*'s (2006) codification that also considered it as additive. Completely pigmentation was found in all species of *Crossodactylus* (**Figure 9C**); however, *C. trachystomus* have a partially pigmented testis (**Figure 9B**). Within *Hylodes*, *H. asper*, *H. asper* (SP), *H. charadranaetes*, *H. glaber*, and *H. lateristrigatus* does not present coloration on the testis. Regarding the outgroup, only *Physalaemus cuvieri* presents testis' pigmentation (state 1). Unfortunately, I had access of only one female specimen of *M. goeldii*. Thus, the male internal morphology of *Megaelosia* was not included in this study. Partially pigmented testis was recovered as synapomorphy of Hylodidae and *P. cuvieri* (0 → 1); while within Hylodidae, in *Hylodes* 'Serra do Mar / no spine' clade, a reversion occurred (1 → 0).

129. Adult testis: Size

This character was observed only in adult males, through the comparison between the testis and the kidney.

(0) small, approx. 1/3 of the kidney

(1) medium, approx. 1/2 of the kidney

(2) big, > 2/3 of the kidney

Additive

Remarks: The small condition (**Figure 9A**) was observed only in *H. lateristrigatus*; the other species having medium or big testis. Transformation 1&2 → 0 is recovered in *Physalaemus cuvieri*.

130. Mature oocytes: Pigmentation

Duellman and Trueb (1994) postulated “eggs deposited in sites exposed to sunlight gave melanin deposits over the animal hemisphere, whereas most eggs deposited in places not exposed to sunlight lack the pigment. [...] The occurrence of melanin in eggs exposed to sunlight suggests that the melanin may function to protect the embryo from ultraviolet radiation or to increase the temperature of the egg through greater heat absorption”. However, Grant *et al.* (2006) partially refused their hypothesis given that many species of dendrobatids with “pigmented eggs lay clutches that are not exposed to sunlight”.

(0) unpigmented, white or cream

(1) completely pigmented, brown or black

Remarks: Most species of Hylodidae have unpigmented oocytes (state 0; **Figure 9D**). The pigmentation is observed only in *C. caramaschii*, *H. asper* (SP), and some specimens of *H. nasus*.

### 131. Lung: Pigmentation

The lung pigmentation is defined as small dark punctuations on its translucent wall. When present, these punctuations never cover the entire lung.

(0) unpigmented

(1) partially pigmented

Remarks: Dark pigmentation (**Figure 9G**) was found in 14 species distributed in all Hylodidae genera, and in six species of the outgroup. Transformation 1 → 0, unpigmented lung (**Figure 9C**), is reported in *Crossodactylus* ‘SE / NE’ clade, with transformation 0 → 1 occurring in *C. dantei*.

### 132. Liver: Pigmentation

- (0) unpigmented
- (1) partially pigmented
- (2) completely pigmented

Additive

Remarks: Liver pigmentation was observed in all species of Hylodidae. The variation observed within the family is on the level of pigmentation, which can be partially (**Figure 9E, F**) or completely (**Figure 9D**) pigmented. Regarding the outgroup, only *Physalaemus cuvieri* and *Vitreorana eurygnatha* have unpigmented livers. Transformation 1 → 2 is recovered as a synapomorphy of *Hylodes*. Transformation 1 → 0 is reported in *Physalaemus cuvieri*.

133. Liver: Size of lobes

The liver has three lobes; however, for this character the size of the left and right lobes was compared.

- (0) Approximately equal
- (1) different

(2) Remarks: Most species observed here have different sizes on the left and right lobes (**Figure 9F**). Species that present approximately equal sizes (**Figure 9E**) are *C. caramaschii*, *H. charadranates*, *H. meridionalis*, and *M. goeldii*. Ambiguity was found in *C. gaudichaudii*, *H. asper* (RJ), *H. cardosoi*, *H. glaber*, and *H. phyllodes*. Transformation 1 → 0 is reported in the clade that comprises *C. caramaschii*, *C. aff. caramaschii*, and *Crossodactylus* sp. 'PR East', and the clade *H. meridionalis* and *H. aff. meridionalis* SC.

134. Liver: Relation between lobes

When the size between the left and right lobes was different, I codified each lobe in relation to the other.

(0) left lobe larger

(1) right lobe larger

Remarks: Within Hylodidae, the left lobe is predominately larger than the right one (**Figure 9F**). Only in *C. dantei* the right lobe is larger, and in *H. cardosoi* this character was ambiguous. This pattern is also observed within the outgroup species, excepting *Vitreorana eurygnatha*, which right lobe is larger than the left one. Transformation 0 → 1 was recovered in *C. dantei*.

#### 135. Atrium: Pigmentation

In some species I observed that the atrial region of the heart is darker than the ventricular region. This pigmentation could be visible in the entire atrial region or in part of it.

(0) unpigmented, white or cream

(1) partially pigmented

(2) Completely pigmented

Additive

Remarks: Pigmentation was observed in species of all genera of Hylodidae (**Figure 9H**). A complete pigmentation was observed in, at least, some specimens of *C. aeneus*, *C. schmidtii*, *C. trachystomus*, *H. asper* (RJ), *H. asper* (SP), *H. cardosoi*, *H. perplicatus*, and *M. goeldii*. Transformation 1 → 2 is reported for *Allophryne ruthveni*.

136. Spleen: Pigmentation

The spleen had a great variation on the color pattern, from completely unpigmented to totally dark.

(0) unpigmented

(1) with few dark spots

(2) marbled or completely dark

Non additive

Remarks: Unpigmented spleen was observed only in some specimens of *C. aeneus*, *C. gaudichaudii*, and *C. trachystomus*. All species of *Hylodes* and *Megaelosia* observed here showed some level of pigmentation, which range from few dark spots (**Figure 9G**) to marbled or completely dark (**Figure 9A**). Other than that, most outgroup species presented unpigmented spleen; pigmentation is observed only in *Vitreorana eurygnatha* (state 1), *Allophryne ruthveni* (state 2), and *Cycloramphus brasiliensis* (states 1 and 2).

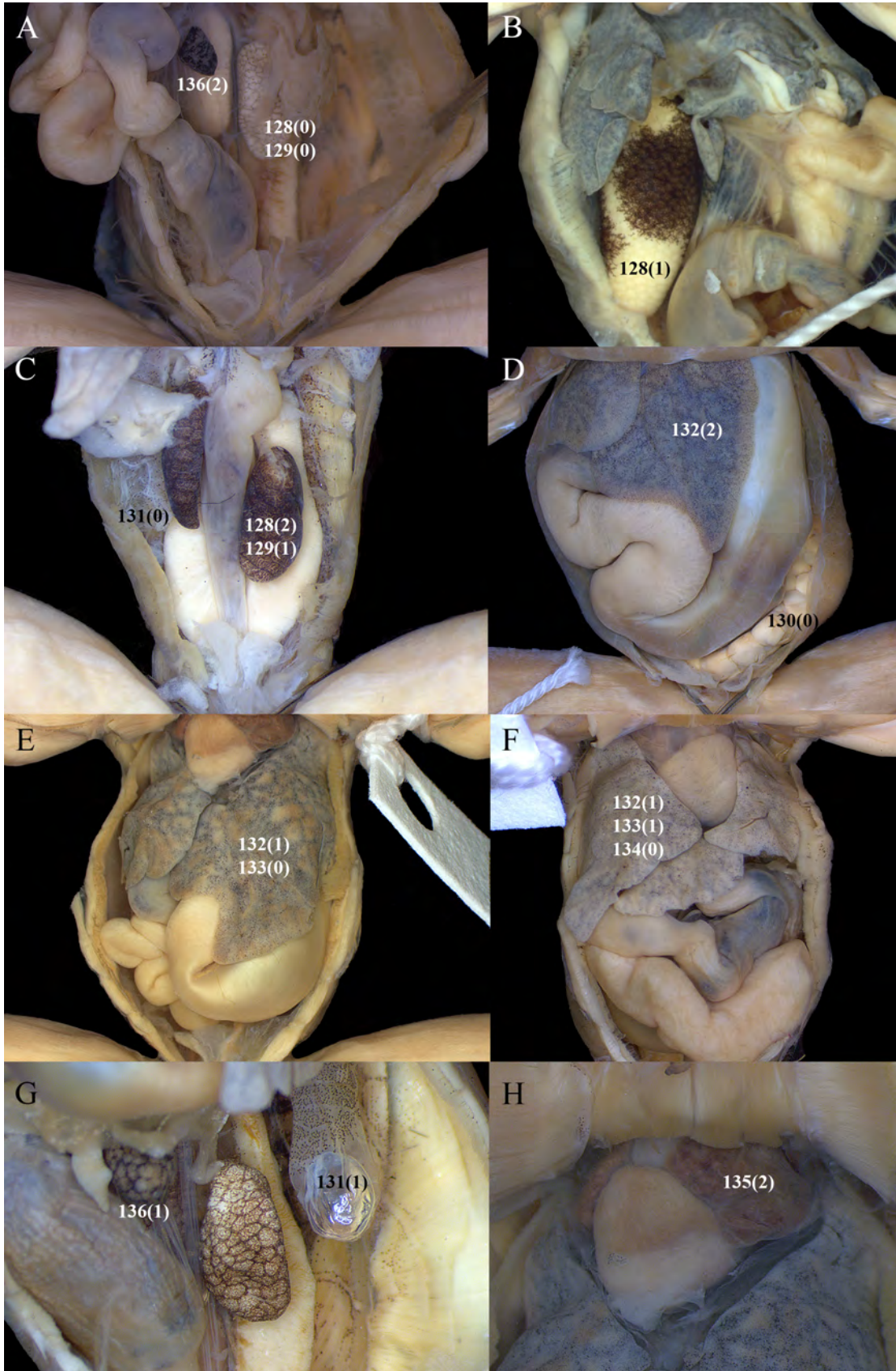


Figure 9. Series of transformation of characters of viscera: (A), (E), and (H) *H. asper* RJ MZUSP 112639, (B) *H. perplicatus* MTR 26735, (C) *C. dantei* MNRJ 39446, (D) *H. uai* MZUSP 23861, (F) and (G) *H. magalhaesi* MZUSP 112662.

## Musculature

### 137-150: Mandibular musculature and associated internal vocal sac

The basic configuration of the mandibular musculature in anurans consists of the *mm. submentalis*, *intermandibularis* and *interhyoideus* (Trewasas 1933, Tyler 1971, Duellman and Trueb 1994). The *m. submentalis* is small with transversal fibers and it is the most anterior muscle (Tyler 1971). The *m. intermandibularis* is usually the largest muscle, composed of more or less transverse fibers that insert on a medial aponeurosis or raphe; the most important variation of these muscle is the differentiation of supplementary elements, which lie ventral to the medial insertion (Tyler 1971). The *m. interhyoideus* is located posteriorly. Its variation of size and structure is associated with the variation in the vocal sac structure (Tyler 1971, Duellman and Trueb 1994). Here, I observed variation regarding the association of the *mm. submentalis* and *intermandibularis*, the medial insertion of *mm. intermandibularis* and *interhyoideus*, the supplementary elements condition, and the variation of the *m. interhyoideus*. Also, I codified the internal vocal sac associated with these muscles. The **Figure 10** illustrates some of these variations.

#### 137. *M. intermandibularis* vs. *m. submentalis*: Position

(0) *m. intermandibularis* overlaps *m. submentalis*

(1) anterior margin of *m. intermandibularis* medially adjacent to the posterior edge of *m. submentalis*

(2) *m. intermandibularis* does not overlap *m. submentalis*, wide gap between the muscles

Additive

Remarks: Overlapping of the *m. submentalis* is predominant within *Hylodes* (state 0), whereas most species of *Crossodactylus* presented *m. intermandibularis* medially adjacent to the posterior edge of *m. submentalis* (1). However, transformation 0 → 1 occurred in *H. asper* + *H. aff. asper* SP. Gap between these muscles was observed only in *Hemiphractylus jonhsoni* and *Ceratophrys cornuta*.

138. *M. intermandibularis* vs. *m. submentalis*: Degree of overlap

(0) *m. intermandibularis* overlaps all posterior edge of *m. submentalis*

(1) *m. intermandibularis* overlaps only the posterolateral region of *m. submentalis*

(2) *m. intermandibularis* overlaps only medially the posterior edge of *m. submentalis*

Non additive

Remarks: This character was codified only for those individuals that presented the *m. intermandibularis* overlapping the *m. submentalis* (Ch. 137, state 0). All *Crossodactylus* and the single species of *Megaelosia* observed (*M. goeldii*) present the overlap only on the posterolateral region (state 0). Within *Hylodes*, the superposition is present in all (state 0) or only medially (state 1) the posterior edge. Transformation 1 → 0&2 occurs in *Hylodes*. The outgroup species present the conditions 1 or 2, with five species each. Transformation 2 → 1 is a synapomorphy of (*Thoropa milliaris* (Dendrobatoidea, Hylodidae)), and autopomorphy for *Allophryne ruthveni* and *Physalaemus cuvieri*.

139. *M. intermandibularis*, medial portion:

(0) raphe



(1) aponeurosis

Remarks: Both conditions are widely distributed within Hylodidae and the outgroup species. Transformation 1 → 0 is reported in *C. dantei* and *Hylodes* 'South' clade.

140. *M. intermandibularis*, apical supplementary element: Occurrence

(0) absent

(1) present

Remarks: All Hylodidae presents the apical supplementary element (state 1), except *Megaelosia goeldii* (state 0). On outgroup, this structure is observed in *Amereega trivitatta*, *Rheobates palmatus*, and *Physalaemus cuvieri*. Thus, transformation 0 → 1 is recovered as synapomorphy for (*Thoropa miliaris* (Dendrobatoidea, Hylodidae)) and an autopomorphy for *P. cuvieri*.

141. *M. intermandibularis*, apical supplementary element: Type

(0) anterolateral

(1) anteromedial

Remarks: All Hylodidae presents the anterolateral condition (state 0) and it is here recovered as synapomorphy for the family (1 → 0). The anteromedial element (state 1) is observed only in *Physalaemus cuvieri*, *Pristimantis fenestratus*, and *Rheobates palmatus*.

142. *M. intermandibularis*, apical supplementary element: Condition

(0) incomplete

(1) complete

Remarks: The apical supplementary element can be incomplete (state 0, *i.e.*, the principal fibers of the *m. intermandibularis* are dorsally partially visible) or complete (state 1, *i.e.*, the principal fibers of the *m. intermandibularis* are totally covered). Within Hylodidae, the incomplete condition was observed in *C. aneus*, *H. amnicola*, *H. cardosoi*, *H. charadranaetes*, *H. magalhaesi*, and *H. phyllodes*; whereas the complete element was found in *C. dantei*, *C. schmidti*, *C. trachystomus*, *H. asper* (RJ), *H. asper* (SP), *H. heyeri*, *H. sazimai*, and *H. uai*.

143. *M. interhyoideus*: Fibers

(0) continuous

(1) medial interruption

Remarks: The medial interruption of the fibers of the *m. interhyoideus* (state 1) is observed in several species of Hylodidae and in the outgroup. Transformation 1 → 0 is recovered in *H. ornatus* and in the clade with *C. caramaschii*, *C. aff. caramaschii*, and *Crossodactylus* sp. Paraná East.

144. *M. interhyoideus*, medial portion: Type of interruption

(0) raphe

(1) aponeurosis

Remarks: When present, the interruption can be a raphe or an aponeurosis. The aponeurosis is predominant in Hylodidae, whereas only *Vitreorana eurygnatha* presents this condition within the outgroup species. In Hylodidae, a raphe is observed in *C. schmidti*, *H. charadranaetes*, *H. glaber*, *H. heyeri*, *H. magalhaesi*, *H. perplicatus*, and *H. phyllodes*. Transformation 0 → 1 occurs in the *Hylodes* ‘MG / ES’ clade.

145. *M. interhyoideus*: Condition

(0) not differentiated in a sac; strained muscle

(1) differentiated in a sac; flaccid muscle

Remarks: All Hylodidae and most outgroup species presented the *m. interhyoideus* not differentiated in a sac (state 0). Transformation 0 → 1 is reported in the clade with representatives of Batrachylidae, Ceratophryidae, and Cycloramphidae.

146. *M. interhyoideus*, anterior edge: Development

(0) undeveloped, approx. 1/5 of the length of the jaw, anteriorly it reaches the level of the anterior edge of tympanic ring

(1) developed, approx. 1/3 of the length of the jaw, reaches the level of the posterior edge of eye

(2) highly developed, approx. 1/2 of the length of the jaw, reaches approx. the level of half of the eye

Additive

Remarks: All Hylodidae presents undeveloped *m. interhyoideus* (state 0). Transformation 0 → 1 is found in *Physalaemus cuvieri*.

147. *M. interhyoideus*, posterior edge: Shape

(0) simple

(1) bilobed

Remarks: Bilobed *m. interhyoideus* is found in only six species of Hylodidae (*C. dantei*, *H. amnicola*, *H. heyeri*, *H. meridionalis*, *H. phyllodes*, and *H. uai*). Transformation 0 → 1 is recovered in *C. dantei*.

148. *M. interhyoideus*, posterior edge: Development:

(0) does not or slightly exceeds the upper jaw

(1) exceeds the upper jaw, reaches about 1/3 and 1/2 of the level of the *m.*

*deltoideus*

(2) exceeds the upper jaw, reaches the level of the posterior portion of *m.*

*deltoideus*

(3) reaches the *m. pectoralis esternalis*

Additive

Remarks: Most Hylodidae presents the *m. interhyoideus* that do not or slightly exceeds the upper jaw (state 0). Two species possess this muscle reaching 1/3 or 1/2 of the *m. deltoideus* (state 1; *H. charadranaetes* and *H. uai*). The conditions 2 and 3 are only reported within outgroup species. Transformation 0 → 2 is found in the clade with representatives of Batrachylidae, Ceratophryidae, and Cycloramphidae.

149. *M. interhyoideus*: Relationship with internal vocal sac

(0) *m. interhyoideus* envelopes internal vocal sac

(1) *m. interhyoideus* divided such that vocal sac passes between muscle fibers

Remarks: All males of Hylodidae, that were dissected in the present study, have an opening on the *m. interhyoideus* by which the vocal sac passes through (state 1). This condition is here considered a putative synapomorphy for this family. For more details, see 'Discussion'.

150. Internal vocal sac, male: Disconnection

The vocal sac mucosa in frogs originates bilaterally and, in most species, fuse in the midline during early stages of post-metamorphic life (Inger and Greenberg 1956, Tyler 1975). However, both invaginations of the buccal cavity can remain disconnected in adults, resulting in ‘internally bilateral’ vocal sacs (McAlister 1959).

(0) disconnection absent (one sac)

(1) disconnection present (two sacs)

Remarks: All species of Hylodidae here dissected have their vocal sacs internally disconnected, resulting in two or double vocal sacs. As the anterior character, this structure is also considered a putative synapomorphy for the family. For more details, see ‘Discussion’.

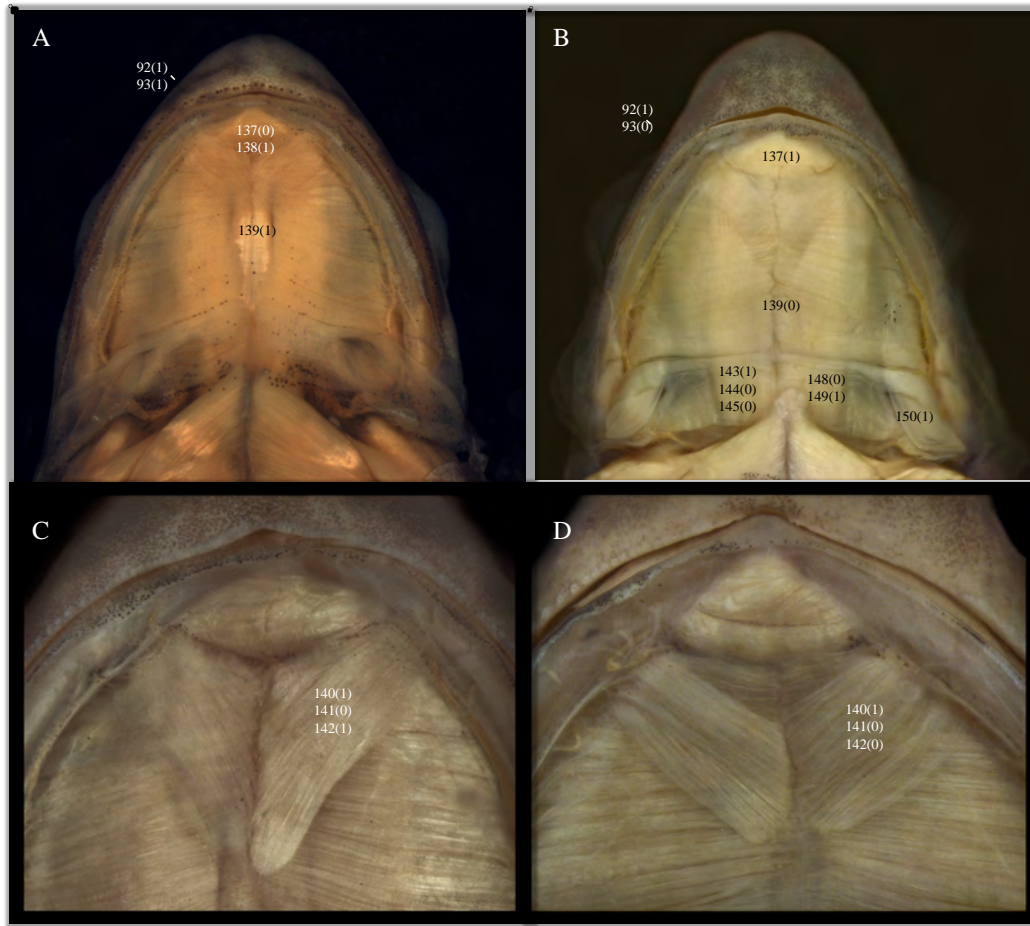


Figure 10. Superficial gular musculature: (A) *C. schmidtii* JF1976; (B) *H. magalhaesi* MZUSP112662; (C) *H. asper* MZUSP112639; (D) *H. cardosoi* MZUSP 112578. Photos by A. Elias-Costa.

151 – 155: *Musculus depressor mandibulae*

This is the muscle that opens the mouth and has variable origins (Manzano *et al.* 2003). There are many discussions on the literature about the utility of this character for phylogenies. Many authors consider this muscle useful to delimit anuran groups (Burton 1983a, b; Myers & Ford 1986; Ford 1989; Savage 1987; Ford & Cannatella 1993; Manzano *et al.* 2003), while others disagree with their opinion (Lynch 1993; Hoyos 1999). I follow the formulae describing three origin points for the *m. depressor mandibulae*: *annulus tympanicus*, otic ramus of squamosal, and dorsal fascia overlaying scapula (Starrett 1968, Savage 1987).

151. *M. depressor mandibulae, pars scapularis*: Occurrence

(0) absent

(1) present

Remarks: All Hylodidae and most species of outgroup present the *pars scapularis* of the *m. depressor mandibulae* (state 1; **Figure 11**). From outgroup, only *Dendropsophus minutus*, *Rhinella major*, *Vitreorana eurygnatha*, and *Allophryne ruthveni* do not have this structure. Transformation 1 → 0 occurred in Centrolenidae + Allophrynidae.

152. *M. depressor mandibulae, pars tympanica*: Occurrence

(0) absent

(1) present

Remarks: All species of *Hylodes* present the *pars tympanica* (state 1). Absence of this structure (state 0) is observed in *C. aeneus*, *C. caramaschii*, *C. dantei*, *C. schmidti*, and *M. goeldii*, besides *Hemiphractus jonhsoni* and *Allophryne ruthveni* from outgroup.

153. *M. depressor mandibulae, pars tympanica*: Size

(0) small (until half of tympanum size)

(1) big (more than half of tympanum size)

Remarks: When present, the *pars tympanica* is normally small in Hylodidae (state 0). Only *H. amnicola*, *H. heyeri*, *H. magalhaesi*, *H. sazimai*, and *H. uai* present this structure reaching more than half of the tympanum size (state 1). On outgroup, both conditions are variable, occurring in six species each.

154. *M. depressor mandibulae, pars squamosalis*, flap: Occurrence

(0) absent

(1) present

Remarks: I considered the flap of the *pars squamosalis* present (state 1; **Figure 11**) when the muscle surpasses dorsally the otic ramus of squamosal. This structure is here reported for some species of *Hylodes* and for most outgroup species. Transformation 0 → 1 is reported in *H. meridionalis* + *H. aff. meridionalis* SC.

155. *M. dorsalis scapulae*: Relation with *m. cucullaris*

The *m. cucullaris* is the major muscle attaching the skull to the pectoral girdle (Duellman and Trueb 1994). This muscle runs behind the *m. dorsalis scapulae*, and it can be totally hidden by the latter muscle.

(0) *m. cucullaris* completely hidden

(1) *m. cucullaris* partially exposed (>1/2 visible)

(2) *m. cucullaris* exposed (> 2/3 visible)

Additive

Remarks: Only some species of *Hylodes* present the *m. cucullaris* partially exposed (state 1). Transformation 1 → 0 is found in (*H. ornatus* (*H. regius*, *H. magalhaesi*), *Crossodactylus* (**Figure 11**) and *M. goeldii* have the muscle completely hidden by the *m. depressor mandibulae*. A more visible *m. cucullaris* is reported only in *Rhinella major*, *Ceratophrys cornuta*, and *Allophryne ruthveni*. Transformation 0&1 → 2 is reported for *A. ruthveni*.

156. *M. levator mandibulae posterior*: Position



This muscle originates on the dorsal surface of the prootic and runs anteroventrally to the mandible. On its way, the muscle assumes a S-shape behind the *m. levator mandibulae externus*.

(0) completely hidden

(1) partially exposed (>1/2 visible)

(2) totally exposed (> 2/3 visible)

Additive

Remarks: A partially exposed *m. levator mandibulae posterior* (state 1; **Figure 11**) is predominant within Hyloidae. A hidden muscle (state 0) is only observed in some species of *Crossodactylus*, *M. goeldii*, and some outgroup species. A totally exposed muscle (state 2) is observed only for *Amereega trivitatta*.

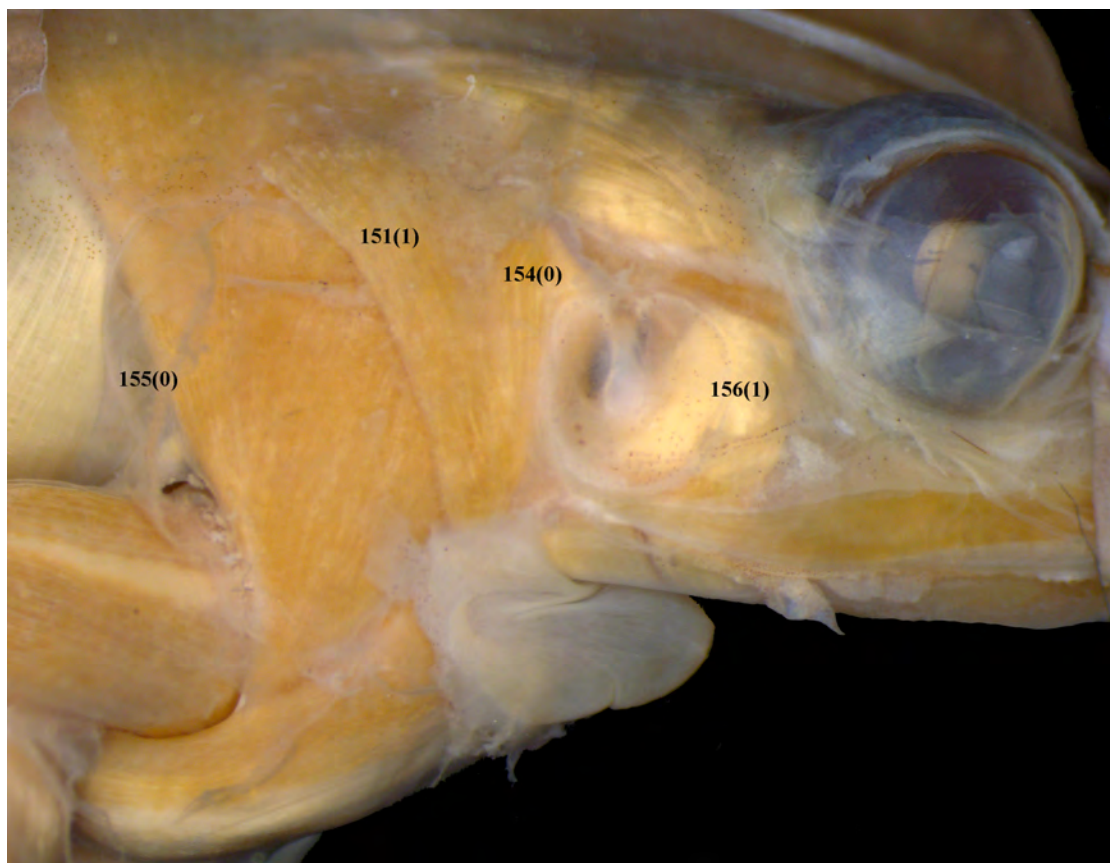


Figure 11. Suspensorium muscles in *C. grandis* MNRJ 48337.

157-158: *Musculus pectoralis*

The *m. pectoralis* presents two distinct portions: (1) portion *abdominalis*, a big muscle that is located on the ventral surface of the body; it inserts on the humerus and its origin is usually on the dorsal surface of the *m. rectus abdominalis*, but in many taxa it can originate near or on the pelvis through a short tendon, as found in *Scinax* by Silva (1998); (2) portion *axillaris*, with origin on the *m. pectoralis abdominalis* and insertion on the humerus medially (Silva 1998). Here, I codified the tendon on the origin and insertion of the *m. pectoralis portio abdominalis*.

157. *M. pectoralis portio abdominalis*: Tendon on the origin

(0) tendon not evident

(1) tendon evident

Remarks: An evident tendon is predominant within Hylodidae. Transformation 1 → 0 is reported in the clade *Hylodes* ‘Serra do Mar / no spine’, except for *H. charadranaetes*.

158. *M. pectoralis portio abdominalis*: Insertion

(0) deep, hidden by *m. episternohumeralis*

(1) superficial

Remarks: All Hylodidae presented a deep insertion of the *m. pectoralis portio abdominalis* (state 0; **Figure 12A**). A superficial insertion is observed in *Hemiphractus johnsoni*, *Dendropsophus minutus*, *Rhinella major*, *Vitreorana eurygnatha*, and *Allophryne ruthveni*.

159. *M. episternohumeralis*: Insertion

The *m. episternohumeralis* is a cylindrical muscle that originates on the epicoracoid and inserts on the humerus (Manzano 2000). The author observed that the *m. flexor carpi radialis superficialis* (MFCRS) hides the insertion of the *m. episternohumeralis* in some specimens.

(0) deep, not visible, below the MFCRS

(1) superficial, visible, anterior to the MFCRS

Remarks: All species of Hylodidae dissected here presents a deep insertion of the *m. episternohumeralis* (state 0; **Figure 12A**). Only *Hemiphractus johnsoni*, *Dendropsophus minutus*, and *Rheobates palmatus* presents a superficial insertion (state 1).

#### 160. *M. flexor carpi radialis superficialis*: Size

The MFCRS is a superficial muscle located on the radial side of the antebrachium, it originates on the distal half of the humerus and inserts on the medial side of the radiale, and by a tendon on the element Y (Manzano *et al.* 2008). Here, I compare the width of this muscle related to the width of the *m. episternohumeralis*.

(0) narrower than *m. episternohumeralis*

(1) same width of *m. episternohumeralis*

(2) wider than *m. episternohumeralis*

Not additive

Remarks: *M. flexor carpi radialis superficialis* narrower than the *m. episternohumeralis* (state 0) is the predominant condition within Hylodidae and outgroup species. Muscles with approx. the same width (state 1; **Figure 12A**) is observed in *C. timbuhy*, *C. trachystomus*, *H. charadranaetes*, *H. heyeri*, *Physalaemus cuvieri*, and *Allophryne ruthveni*; and MFCRS wider than the *m. episternohumeralis*

(state 2) is observed only in *H. magalhaesi*, *H. meridionalis*, *Rhinella major*, and *Ceratophrys ornata*.

161-163: *M. extensor digitorum comunis longus*

This muscle originates in the distal margin of the humerus, runs all radio-ulna and reaches the dorsum of the hand, where it divides until three branches that inserts on metacarpal III, IV, and V (Faivovich 2002). The author also observed a division on the tip of the branch IV. In this study, I also observed this division, but in branch V. Here, I follow the nomenclature used by Rada (2012), which described the branches III, IV, and V as preaxial, medial, and postaxial, respectively.

161. *M. extensor digitorum comunis longus*, preaxial branch: Occurrence

(0) absent

(1) present

Remarks: All species of Hylodidae and most species of the outgroup present the *m. extensor digitorum comunis longus* with two branches (state 0; preaxial branch absent; **Figure 12B**). Three branches are only reported in *Hemiphractus johnsoni*, *Pristimantis fenestratus*, *Dendropsophus minutus*, *Rheobates palmatus*, and *Allophryne ruthveni*. Transformation 0 → 1 is found in *A. ruthveni*.

162. *M. extensor digitorum comunis longus*, medial branch: Insertion

(0) single insertion point

(1) two insertion points

Remarks: Most species of Hylodidae and all outgroup species present a single insertion point for the medial branch of the *m. extensor digitorum comunis longus*

(state 0; **Figure 12B**). Two insertions are observed only in *C. aeneus*, *C. schmidti*, and *H. heyeri*.

163. *M. extensor digitorum comunis longus*, postaxial branch: Insertion

(0) single insertion point

(1) two insertion points

Remarks: Most Hylodidae species present a single insertion of the postaxial branch of the *m. extensor digitorum comunis longus* (state 0). Transformation 0 → 1, two insertion points (**Figure 12B**) is reported in *C. dantei* and all *Hylodes*, except *Hylodes* ‘South’ clade. Regarding the outgroup, only *Rheobates palmatus* presents two insertion points (state 1).

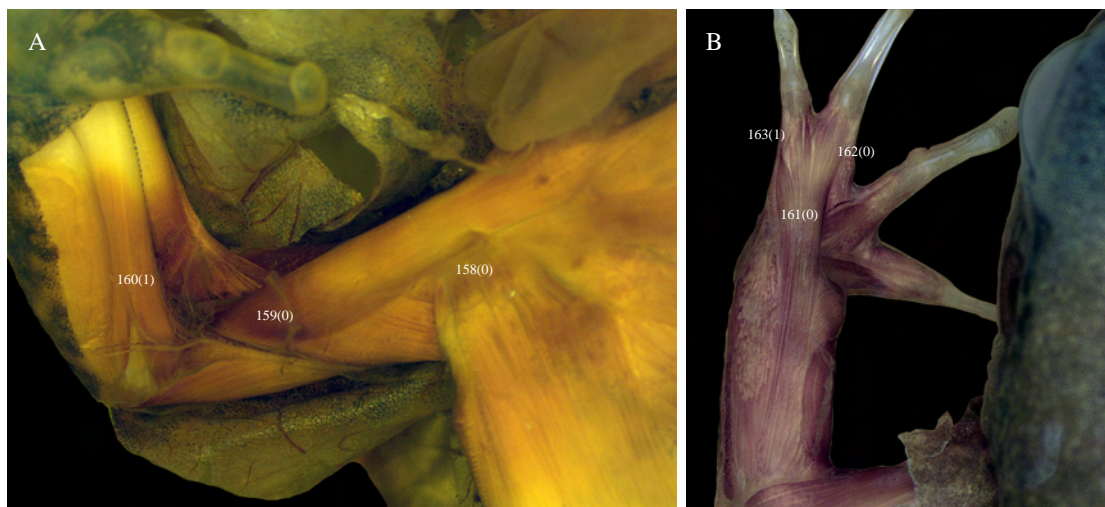


Figure 12. Limb and hand muscles: (A) *C. aeneus* MNRJ39369; (B) *C. trachystomus* UFMG5355

164. *Caput profundus III*: Occurrence

The *caput profundus* arises by a narrow tendon from the distal margin of the Distal Carpals 5-4-3, and tapers to terminate in the *tendo superficialis*, that inserts above the flexor surface of the ultimate phalanx of the third finger (Burton 1998). The

author reported the absence of this character in *Hylodes*, *Megaelosia*, and *Zachaenus* among the Leptodactylid species. According to Burton (1998a), “evidence to support a clade consisting of *Hylodes* and *Megaelosia* but not *Crossodactylus* may be provided by the absence of the *caput profundum*. That this loss has also occurred in *Zachaenus*, representing a different subfamily [of Leptodactylidae], may indicate that it has occurred more than once in the family”.

(0) absent

(1) present

Remarks: All species of *Crossodactylus* dissected here have *caput profundus* III (state 1; **Figure 13A, C**). Transformation 1 → 0 is reported as synapomorphy of all *Hylodes*, except *Hylodes* ‘South’ clade, with reversion (0 → 1) in the clade that comprises *H. ornatus*, *H. regius*, and *H. magalhaesi*. On outgroup, this structure is observed only in *Hemiphractus johnsoni*, *Ceratophrys ornata*, and *Allophryne ruthveni*.

165. *M. lumbricalis longus* IV medial, hand: Branches

According to Manzano *et al.* (2008), the *lumbricalis longus* IV (**Figure 13A**) is a complex muscle with two sets of short branches, two medial and two external branches. The medial branches originate on the superficial tendon IV at the level of the proximal half of metacarpal IV, by means of two short tendons parallel to the superficial tendon. Both branches extend in parallel along the distal half of the metacarpus and distally join the distal extremity of metacarpal IV. When the medial and external branches are not fused, Blotto (2013) observed a division in two branches (one more distally than other), both with common insertion medially at the superficial tendon IV.

(0) unique

(1) split in two branches

Remarks: *M. lumbricalis longus IV medial* splits in two branches with a common insertion medially to the superficialis IV tendon (state 1) in *C. caramaschii*, *C. timbuhy*, *H. asper* (RJ), *H. glaber*, *H. lateristrigatus*, *H. nasus*, and *H. ornatus*. According to Blotto (2013), the split in two branches of the *M. lumbricalis longus IV* medial to the hand is a synapomorphy for Hylodidae. However, the author only analyzed *H. phyllodes* and *C. schmidtii*, and states that an increase of the taxa sampling is extremely necessary to confirm this hypothesis. In the present study, I was not able to codify *C. schmidtii* and the single specimen of *H. phyllodes* that I was able to observe did not present the split tendon (state 0). Additionally, other species than *H. phyllodes* were also codified with an single tendon. My results suggest that the synapomorphy for Hylodidae proposed for this character is questionable.

166. *M. lumbricalis brevis V medial*, toe V: Number of elements

Burton (2004) described the *m. lumbricalis brevis V* (**Figure 13D**) as a medial muscle that divides into two slips, and a lateral muscle. The medial muscle arises from a common tendon with the lateral *m. lumbricalis brevis digiti IV* that divides into a medial slip, with a long tendon of origin and short tendon of insertion, and a lateral slip with a broad fibrous base and a long, flat, narrow tendon of insertion onto the lateroventral side of the metatarsophalangeal joint. Blotto (2013) observed variation regarding the morphology, insertions and origins in both elements. Here, I codified the same character proposed by Blotto (2013) that only quantify the number of elements to avoid homology mistakes.

(0) two

(1) one

Remarks: All species of Hylodidae present one element of the *m. lumbracalis levis V medial* (state 1), with exception of *H. charadranaetes* (state 0). My results corroborated the hypothesis of Blotto (2013). According to this author, the presence of a single element is a plesiomorphic condition in Hylodidae. However, the representative of Dendrobatoidea included in his analysis (*Mannophryne herminae*) possesses two elements. Other families included as outgroup in the present work were analyzed by Blotto (2013), that also observed a single element in *Cycloramphus boraceiensis*, *Thoropa taophora*, *Rhinoderma darwinii*, *Proceratophrys avelinoi*, and *Batrachyla leptopus*.

167. *M. flexor digitorum brevis superficialis*, foot: Sesamoid on insertion tendon

(0) absent

(1) present

Remarks: All species of Hylodidae present a sesamoid on the insertion tendon of the *m. flexor digitorum brevis superficialis*. This result agrees with Blotto (2013) that stated the presence of a sesamoid on the insertion tendon of *flexor digitorum communis longus* as synapomorphy for Hylodidae.



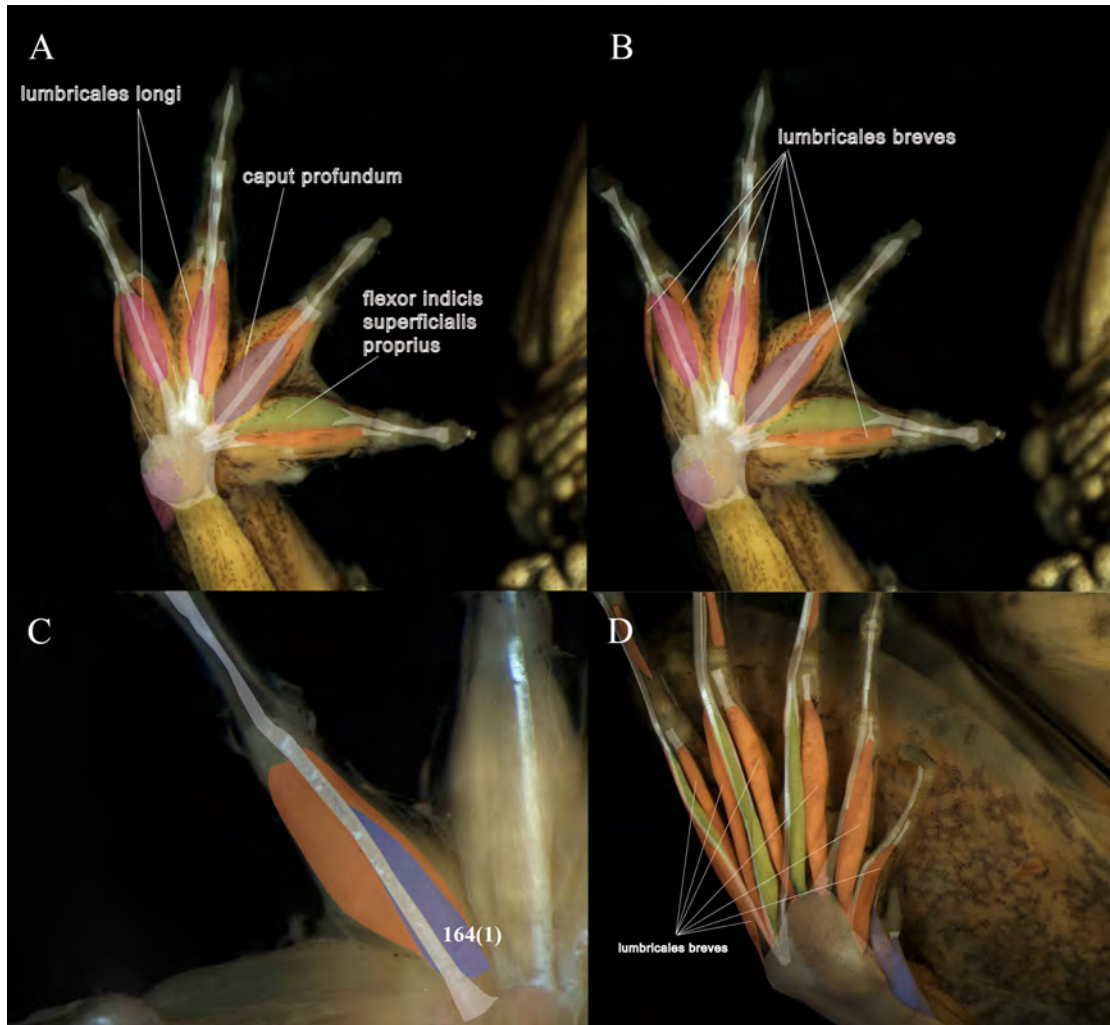


Figure 13. Hand and foot muscles: (A, B, and D) Schemes showing the position of some muscles on the bufonid *Nannophryne variegata* (not included in this study); (C) *C. schmidtii* showing the presence of *caput profundus* III. Photos and schemes made and provided by B. Blotto.

## Osteology

### 168-210: Skull

#### 168-170: Sphenethmoid

Endochondral bone, invariably present, involving the anterior end of the brain

(Trueb, 1973). Visible in dorsal view between the nasals and frontoparietal, and between vomers and parasphenoid, in ventral view. Ontogenetically, all sphenethmoid have a paired stage before fused in a unique bone (Trueb, 1973).

168. Sphenethmoid (dorsal view)

- (0) paired, not fused
- (1) single, anteriorly fused
- (2) single, completely fused

Additive

Remarks: Most Hylodidae and outgroup species present a single and completely fused sphenethmoid (state 2; **Figure 14B**). Only *H. pipilans* and some individuals of *H. nasus* and *H. phyllodes* presented single but not totally fused sphenethmoid (state 1). Paired sphenethmoid is observed only in *Pristimantis fenestratus*, *Cycloramphus brasiliensis*, and one individual of *Hemiphractus johnsoni* and *Rhinella major*.

169. Relation between sphenethmoid extension and nasals (dorsal view):

- (0) sphenethmoid reaches posterior region of nasals
- (1) sphenethmoid reaches the medial region of nasals
- (2) sphenethmoid reaches the anterior region of nasals
- (3) sphenethmoid exceeds nasals anteriorly (**Figure 14B**)

Additive

Remarks: I observe all conditions both in Hylodidae and in outgroup species; intraspecific variation occurs in several species. Transformation 2 → 1 is recovered in *Allophryne ruthveni* and *H. ornatus*, and transformation 2 → 3 is found in *Physalaemus cuvieri*.

170. Posterior edge of sphenethmoid (ventral view)

(0) U- or V-shape

(1) W-shape or undulate

(2) inverted V-shape

(3) straight or slightly concave

Non additive

Remarks: The shape of the posterior edge of the sphenethmoid is also variable inter and intraspecifically. However, the W-shape or undulate edge is the most predominant condition observed (**Figure 14C**).

171. Separation between nasals

The nasal has dermic origin, it is paired and recovers the olfactory region of the skull. The main function of nasals is providing protection for the cartilaginous structures of the anterior and lateral nasal capsules until the ossified part of the sphenethmoid. Each nasal is formed from an ossification center, and these bones are extremely variable in form and size (Trueb, 1973). Lynch (1971) reported that large nasals are present in members with medial contact between them, and small nasals are usually correlated with medial separation. Lynch (1971) reported that the nasals are slightly to moderately separate in *Megaelosia*, and widely separated in *Crossodactylus* and *Hylodes*.

(0) little separated,  $\frac{1}{3}$  the frontoparietal width

(1) well separated,  $\frac{1}{2}$  the frontoparietal width

Remarks: My result disagrees with Lynch (1971). The predominant condition in Hylodidae is nasals little separated from each other (state 0). Some species of *Hylodes* present well-separated nasals (state 1; **Figure 14B**).

#### 172-175: Exoccipitals

Paired bone that consists of the most posterior region of the *neurocranium*, including the surroundings of the *foramen magnum* and occipital condyles (Trueb, 1970).

#### 172. Exoccipitals on dorsal view

(0) fused

(1) free, separated

Remarks: The predominant condition in *Hylodes* and *Crossodactylus* is fused exoccipitals on dorsal view (state 0, **Figure 14A**). *Megaelosia goeldii* presents free separated exoccipitals (state 1). From outgroup, *Physalaemus cuvieri*, *Dendropsophus minutus*, and *Ceratophrys ornata* present the state 1.

#### 173. Exoccipitals on ventral view

(0) fused

(1) free, separated

Remarks: The predominant condition in Hylodidae is fused exoccipitals on ventral view (state 0; **Figure 14C**). Transformation 0 → 1 is reported in *C. dantei*, *Hylodes* “MG / ES” clade, and in the clade that comprises the families Rhinodermatidae, Alsodidae, Hylidae, Bufonidae, and the subfamily Leiuperinae.

174. Occipital condyles

(0) slightly expanded posteriorly

(1) expanded posteriorly

Remarks: Posteriorly expanded occipital condyles (**Figure 14C**) are recovered as a synapomorphy for *Hylodes* (0 → 1).

175. Separation between occipital condyles

(0) slightly separated, less than 75% of frontoparietal width

(1) widely separate, more than 75% of frontoparietal width (**Figure 14C**)

Remarks: Both conditions are widely spread within Hylodidae and in the outgroup species. Transformation 1 → 0 is found in *Physalaemus cuvieri*.

176-177: Frontoparietal

Bone with dermic origin, normally paired; that anteriorly overlaps the posterior portion of the sphenethmoid, and posteriorly recovers the prootic and exoccipitals (Trueb, 1973).

176. Frontoparietal

(0) paired, not fused

(1) fused posteriorly

(2) totally fused

Additive

Remarks: The predominant condition in Hylodidae is frontoparietals fused posteriorly with each other (state 1; **Figure 14A**). *Megaelosia goeldii* and some outgroup species present a totally fused frontoparietal (state 2).

177. Frontoparietal fontanelle

(0) absent

(1) present

Remarks: Absence of fontanelle is widely distributed in all species analyzed in the present study (state 0; **Figure 14A**). Within Hylodidae, I observe fontanelle (state 1) only in *H. magalhaesi*, and in few individuals of *C. aeneus*, *H. perplicatus*, and *H. uai*.

178-179: Quadradojugal

The maxillary arch is composed of three intramembranous bones: quadradojugal, maxilla, and premaxilla. The quadradojugal is a small dermic bone located in the posterolateral region of the skull. It belongs to the maxillary arc, and acts as an articulation point between skull and maxilla. It is highly variable in occurrence, being frequently lost or reduced in small size or reduced ossified species (Trueb, 1973). Lynch (1971) stated that the quadradojugal have been lost in six leptodactylid genera: *Batrachyla*, *Crossodactylus*, *Hylorina*, *Notaden*, *Pleurodema*, and *Pseudopaludicola*.

178. Quadradojugal: Occurrence

(0) absent

(1) present

Remarks: All species included in the present analysis presents quadradojugal (state 1; **Figure 14E**), except *C. aeneus* and *Allophryne ruthveni* (state 0). Transformation 1 → 0 is found in *A. ruthveni*.

179. Quadradojugal: Condition

(0) incomplete, does not reach maxilla

(1) complete, reaches maxilla

Remarks: When present, all *Crossodactylus* present an incomplete quadradojugal (state 0). This result contradicts those reported by Lynch (1971) in which *Crossodactylus* does not have quadradojugal. The other species present a complete quadradojugal (state 1; **Figure 14E**), except for *H. charadranaetes*.

180-182: Premaxilla

It is another bone that compounds the maxillary arch. It is a dermic and paired bone, on the anterior border of the skull (Trueb 1973). In no case are these bones fused (Lynch 1971). It supports the alary processes that are dorsally projected, and the *pars dentalis* and *pars fascialis* (Trueb 1973). Lynch (1971) observed the notable lateral vector on the alary process in representatives of Hylodidae. Additionally, the author reported *Hylodes* and *Crossodactylus* with shallow palatal shelves and long palatal processes.

180. Premaxilla, alary process: Orientation

(0) anterodorsolaterally

(1) posterodorsolaterally

(2) posterodorsally

Non additive

Remarks: All Hylodidae have an anterodorsolateral alary process of premaxilla (state 0; **Figure 14B**). The states 1 and 2 are found only on the outgroup. Orientation

anterodorsolaterally of the alary process of premaxilla is recovered as a synapomorphy of (*Thoropa milliaris* (Dendrobatoidea, Hylodidae)).

181. Premaxilla: Contact between alary process and *pars dentalis*

(0) narrow, until  $\frac{1}{3}$  of *pars dentalis* width

(1) wide, more than  $\frac{1}{3}$  of *pars dentalis* width

Remarks: A narrow contact region is predominant in *Crossodactylus* and *Megaelosia* (state 0). Transformation 0  $\rightarrow$  1 is reported in all clades of *Hylodes* (**Figure 14D**), except in the *Hylodes* 'South' clade; with a reversion 1  $\rightarrow$  0 in *H. aff. asper* SP.

182. Premaxilla, alary process: Anterior edge

(0) simple

(1) bifid

Remarks: Most Hylodidae present bifid anterior edge of premaxilla (state 1; **Figure 14B**). The simple condition (state 0) is found in *C. caramaschii*, *C. dantei*, and few individuals of *C. gaudichaudii*, *C. trachystomus*, and *H. phyllodes*.

#### 183-186: Maxilla

The maxilla is the largest component of the maxillary arch (Trueb 1973). It is a dermal bone that contains the *pars facialis*, *pars palatina*, and *pars dentalis*. The *pars facialis* usually has a preorbital process and less frequently a postorbital process (Trueb 1973).

183. Maxilla, *pars facialis*: Postorbital process



(0) absent

(1) present

Remarks: The absence of postorbital process on pars facialis of maxilla (state 0; **Figure 14E**) is predominant in Hylodidae. Only *M. goeldii*, *H. charadranaetes*, and *H. aff. asper* SP have this process (state 1). Transformation 0 → 1 is reported in *H. aff. asper* SP.

184. Maxilla, *pars facialis*: Preorbital process

(0) absent

(1) present

Remarks: Contrary to the postorbital process, most species of Hylodidae present the preorbital process on the pars facialis of maxilla (state 1; **Figure 14E**). Absence is reported only in few individuals of *C. caramaschii*, *C. gaudichaudii*, *C. trachystomus*, and *H. glaber*. All species from the outgroup present this process, except *Cycloramphus brasiliensis*.

185. Maxilla: Contact with premaxilla in ventral view

(0) absent

(1) present

Remarks: Most species of Hylodidae do not have contact between maxilla and premaxilla (state 0; **Figure 14D**), except *H. amnicola* and some individuals of *H. meridionalis*, *H. perplicatus*, *H. phyllodes*, and *H. uai*.

186. Maxilla: Overlap above premaxilla in lateral view

(0) absent

(1) present

Remarks: The overlap of maxilla above premaxilla is predominant within Hylodidae (state 1; **Figure 14E**). Transformations 1  $\rightarrow$  0 occurs in the clade containing Batrachylidae, Ceratophryidae, and Cycloramphidae, and in the clade with *C. caramaschii*, *C. aff. caramaschii*, and *Crossodactylus* sp. Paraná East.

#### 187-189: Vomers

They are dermic, paired, and laminar bone, located in the palatal region (ventral) between premaxillas and palatines (Trueb, 1973). Normally the vomers have four processes: one anterior, two posterolateral (pre and post coanal) and one posteromedial (or dentigerus, that bears the vomerine teeth, when present). Trueb (1973) reports a great variation related to the vomer size, development of the processes, and presence and pattern of the vomerine teeth. The dentigerus process is located in the posteromedial region, between the choanas. When present, this process may or may not bear a row of teeth in its extension. Their reduction or loss is a derived condition; however, reduction does not necessarily mean that the vomerine teeth are lost (Lynch 1971). According to the author, teeth were lost in *Crossodactylus*.

#### 187. Vomers (ventral view)

(0) small

(1) big

Remarks: All *Crossodactylus* and *M. goeldii* have small vomers (state 0). Big vomers (**Figure 14D**) are recovered as synapomorphy for *Hylodes* (0  $\rightarrow$  1); with reversion in *H. ornatus*.

188. Distance between vomers

(0) little distance between each other, less than parasphenoid width

(1) wide distance between each other, same or more than parasphenoid width

Remarks: Most species of *Crossodactylus* have a wide distance between vomers (state 1; except *C. schmidti*), while all *Hylodes* (**Figure 14D**), *M. goeldii*, and most species of the outgroup have vomers little separated (state 0; except *Rheobates palmatus*).

189. Vomerine teeth: Occurrence

(0) absent

(1) present

Remarks: Within Hylodidae, *Crossodactylus* does not present vomerine teeth (state 0), whereas *Hylodes* and *Megaelosia* possess (state 1; **Figure 14D**). The absence of vomerine teeth (1 → 0) is recovered as synapomorphy for all clades of this analysis, except for the families Hemiphractidae, Brachycephaloidea, Leptodactylinae, and Odontophrynidae. Reversion for state 1 is recovered in the clade *Hylodes* + *Megaelosia* (0 → 1).

#### 190-197: Parasphenoid

Dermic bone, located in the ventral palatal region, that forms a bridge that connects the posterior region of sphenethmoid (coming close to the palatines) and the prootic. Second to Trueb (1973), this is a triradiated bone (normally having an inverted T-shape), composed by the cultriform process and two alary processes. However, the parasphenoid also has a small posteromedial process. The main

variations are related to the size and shape of the cultriform process, the presence and orientation of the alary processes (Trueb, 1973), and the presence and shape of the posteromedial process.

190. Anterior edge of cultriform process of parasphenoid

(0) rounded

(1) pointed (triangular)

(2) M-shape

No additive

Remarks: This character has great intra and interspecific variations.

191. Projections on the anterior edge of cultriform process of parasphenoid

(0) absent

(1) projections little differentiated

(2) projections well differentiated (**Figure 14D**)

No additive

Remarks: All conditions are observed within Hylodidae.

192. Relation between palatines and anterior edge of cultriform process of parasphenoid

(0) does not reach the palatines (**Figure 14C**)

(1) reaches the palatines

Remarks: Both conditions are reported for species of *Crossodactylus* and *Hylodes*. In *M. goeldii* the cultriform process of parasphenoid does not reach the palatines (state 0).

193. Alary processes of the parasphenoid

(0) do not exceed prootic foramen

(1) slightly exceed prootic foramen

(2) widely exceed prootic foramen

Additive

Remarks: Most species of Hylodidae and the outgroup have alary processes of parasphenoid that widely exceed the prootic foramen (state 2; **Figure 14C**). Transformation 2 → 1 is found in Centrolenidae + Allophrynidae.

194. Alary processes of parasphenoid: Orientation

(0) lateral

(1) posterolateral

Remarks: The laterally oriented processes are predominant in *Crossodactylus*, whereas most species of *Hylodes* and *M. goeldii* have posterolaterally oriented processes (state 1; **Figure 14C**). Transformation 0 → 1 is found in *C. dantei*, and 1 → 0 in *H. ornatus*.

195. Alary processes of parasphenoid: Width

(0) narrow

(1) wide

Remarks: Narrow alary processes of parasphenoid (state 0; **Figure 14C**) are predominant within Hylodidae. Transformation 0 → 1 was found in *H. ornatus*.

196. Posteromedial process of parasphenoid

(0) does not exceed half the distance between the posterior edge of alary processes and foramen *magnum* (**Figure 14C**)

(1) reaches half the distance between the posterior border of alary processes and foramen *magnum*

(2) reaches foramen *magnum*

Additive

Remarks: Most species of *Crossodactylus* have a posteromedial process of parasphenoid that reaches half of the distance between the posterior border of the alary process and the foramen *magnum* (state 1). The posteromedial process reaches the foramen *magnum* (state 2) only in *H. heyeri* and *Ceratophrys cornuta*. A short process (state 0) is reported in *M. goeldii*; and both states 0 and 1 are observed among *Hylodes*. Transformation 0 → 1 is report in *H. aff. asper* SP.

197. Posteromedial process of parasphenoid: Shape

(0) rounded

(1) inverted V-shape

(2) W-shape

(3) straight

Not additive

Remarks: Rounded posteromedial process of parasphenoid is predominant in Hylodidae (state 0; **Figure 14C**). Transformation 0 → 2 is found in *H. ornatus* and *C. dantei*.

198-203: Squamosal

It is a dermic and paired bone located in the posterolateral border of the skull (Trueb, 1973). It shows a trirradiated shape, composed by: (1) zygomatic *ramus* (anterodorsal), normally with a free extremity that may or may not reach the maxilla (Grant *et al.* 2006); (2) optic *ramus* (posterodorsal), that articulate with the lateral border of the parotic crest; and (3) ventral *ramus*, that articulate with the quadradojugal.

198. Zygomatic *ramus* of squamosal: Shape

- (0) absent or inconspicuous
- (1) small
- (2) elongate (does not reach maxilla)
- (3) very elongate (reaches the maxilla)

Additive

Remarks: All *Crossodactylus* and *Hylodes* and most outgroup species have elongate zygomatic *ramus* of squamosal that does not reach the maxilla (state 2; **Figure 14F**). A zygomatic *ramus* that reaches the maxilla is observed only in *M. goeldii* (state 3).

199. Anterior edge of zygomatic *ramus* of squamosal: Shape

- (0) rounded
- (1) square
- (2) pointed

Not additive

Remarks: Most Hylodidae have square anterior edge of the zygomatic ramus of squamosal (state 1; **Figure 14F**). Transformation 1 → 2 is reported in all clades

included here, except for Hemiphractidae, Brachycephaloidea, Leptodactylinae, Odontophrynidae, Allophrynidae, and Centrolenidae. Transformation 1  $\rightarrow$  0 is reported in *H. aff. asper* SP.

200. Zygomatic *ramus* of squamosal: Orientation

(0) anterior

(1) anteroventral

Remarks: Most species of Hylodidae have the zygomatic *ramus* anteroventrally oriented (state 0; **Figure 14F**). Transformation 0  $\rightarrow$  1 is reported for the clade *C. caramaschii*, *C. aff. caramaschii*, and *Crossodactylus* sp. Paraná East, and *Hylodes* ‘South’ clade, except *H. meridionalis* + *H. aff. meridionalis* SC.

201. Relation between optic and zygomatic *rami* of squamosal: Length

(0) optic *ramus* shorter than zygomatic *ramus*

(1) optic and zygomatic *ramus* with approx. the same length

(2) optic *ramus* longer than zygomatic *ramus*

Non additive

Remarks: *Hylodes* and *Crossodactylus* have the optic and zygomatic *rami* with approx. the same length (state 1; **Figure 14F**), or optic *ramus* longer than the zygomatic *ramus* (state 2), whereas *M. goeldii* possesses optic *ramus* shorter than the zygomatic *ramus* (state 0). On outgroup, most species have the state 2.

202. Relation between the optic and zygomatic *ramus* of squamosal: Width

(0) optic *ramus* narrower than zygomatic *ramus*

(1) optic and zygomatic *ramus* with approx. the same width (**Figure 14F**)



(2) optic *ramus* wider than zygomatic *ramus*

Non additive

Remarks: The predominant condition in *Crossodactylus* is optic *ramus* wider than the zygomatic *ramus* (state 2). Most *Hylodes* and *M. goeldii* have the inverse condition of that observed in *Crossodactylus*, optic *ramus* narrower than the zygomatic *ramus* (state 0). Transformation 2 → 0 is recovered as a synapomorphy of *Hylodes* + *Megaelosia*.

203. Optic *ramus* of squamosal: Orientation

(0) posterior

(1) posterodorsal

Remarks: Optic *ramus* of squamosal with posterodorsal orientation (state 1; **Figure 14F**) is observed in most species included in the present analysis.

204-207: Pterigoid

Dermic and paired bone located in the posterolateral border of the skull (Trueb, 1973). It shows a tri-radiated shape, composed by anterior, medial, and posterior *rami*. The anterior *ramus* is always longer than the medial and posterolateral *rami* and is either in ligamentous or sutural contact with the maxilla (Lynch 1971).

204. Anterior *ramus* of pterygoid, projection (after contact with upper jaw):

Occurrence

(0) absent

(1) present

Remarks: All species included in this study have the projection of the anterior ramus of pterygoid (state 1; **Figure 14C**), at least in some specimens. Transformation 1 → 0 was recovered in *H. aff. asper* SP.

205. Relation between anterior *ramus* of pterygoid and toothed region of upper jaw

(0) does not reach the level of the toothed region

(1) reaches the level of the toothed region

Remarks: In most species of Hylodidae the contact of the anterior ramus of pterygoid with the upper jaw matches with the point that the toothed region starts (state 1). This coincidence is less common in the outgroup.

206. Relation between length of medial and posterior *rami* of pterygoid

(0) medial *ramus* shorter than the posterior *ramus*

(1) medial and posterior *rami* with approx. the same length

(2) medial *ramus* longer than the posterior *ramus*

Non additive

Remarks: Same length of the medial and posterior *rami* is recovered as a synapomorphy of *Hylodes* (0 → 1; **Figure 14C**). Transformation 1 → 2 occurs in *H. ornatus*. Within outgroup, most species have the medial *ramus* shorter than the posterior (state 0).

207. Relation between width of medial and posterior *rami* of pterygoid

(0) medial *ramus* narrower than the posterior *ramus*

(1) medial and posterior *ramus* with approx. the same width

(2) medial *ramus* wider than the posterior *ramus*

Non additive

Remarks: Medial *ramus* wider than the posterior *ramus* (state 2) is a predominant state in *Crossodactylus* and *Hylodes*, whereas *M. goeldii* has the medial *ramus* narrower than the posterior *ramus* (state 0). Same width (state 1; **Figure 14C**) is only reported in some *Hylodes* species and in few outgroups.

#### 208-210: Tympanic Middle Ear

The tympanic middle ear is composed minimally of a tympanic membrane, tympanic annulus, and columella. The columella is divided into three portions: (1) *pars externa plectri* or extracolumella, (2) *pars media plectri* (“stapes” *sensu* Trueb, 1993, columella *sensu* Cannatella, 1985, Hall and Larsen, 1998; pseudo-columella *sensu* Gaudin, 1969), and (3) *pars interna plectri* (see Pereyra *et al.* 2016). As postulated by Pereyra *et al.* (2016), the presence of the tympanic annulus implies the presence of a columella; however, the absence of this structure does not imply the absence of collumela. Here, I codified the presence of the tympanic annulus and the condition of the *pars externa plectri* (orientation and width).

#### 208. Tympanic *annulus*: Occurrence

(0) absent

(1) present

Remarks: All species observed in the present study have tympanic *annulus* (**Figure 14F**). This characters was not informative.

#### 209. *Pars externa plectri*: Orientation

(0) dorsal

(1) posterodorsal

Remarks: Most species of Hylodidae have the *pars externa plectra* posterodorsally oriented (state 1). Dorsal orientation (state 0; **Figure 14F**) is observed only in *C. dantei*, *H. magalhaesi*, *H. perplicatus*, and *H. phyllodes*.

210. *Pars externa plectri* width:

(0) approx. same width in both extremities (**Figure 14F**)

(1) thin dorsally and wide ventrally

Remarks: Almost all Hylodidae have the *pars externa plectri* thin dorsally and wide ventrally (state 1). Transformation 1 → 0 is found in *C. gaudichaudii* Região dos Lagos and *C. gaudichaudii* Floresta da Tijuca.

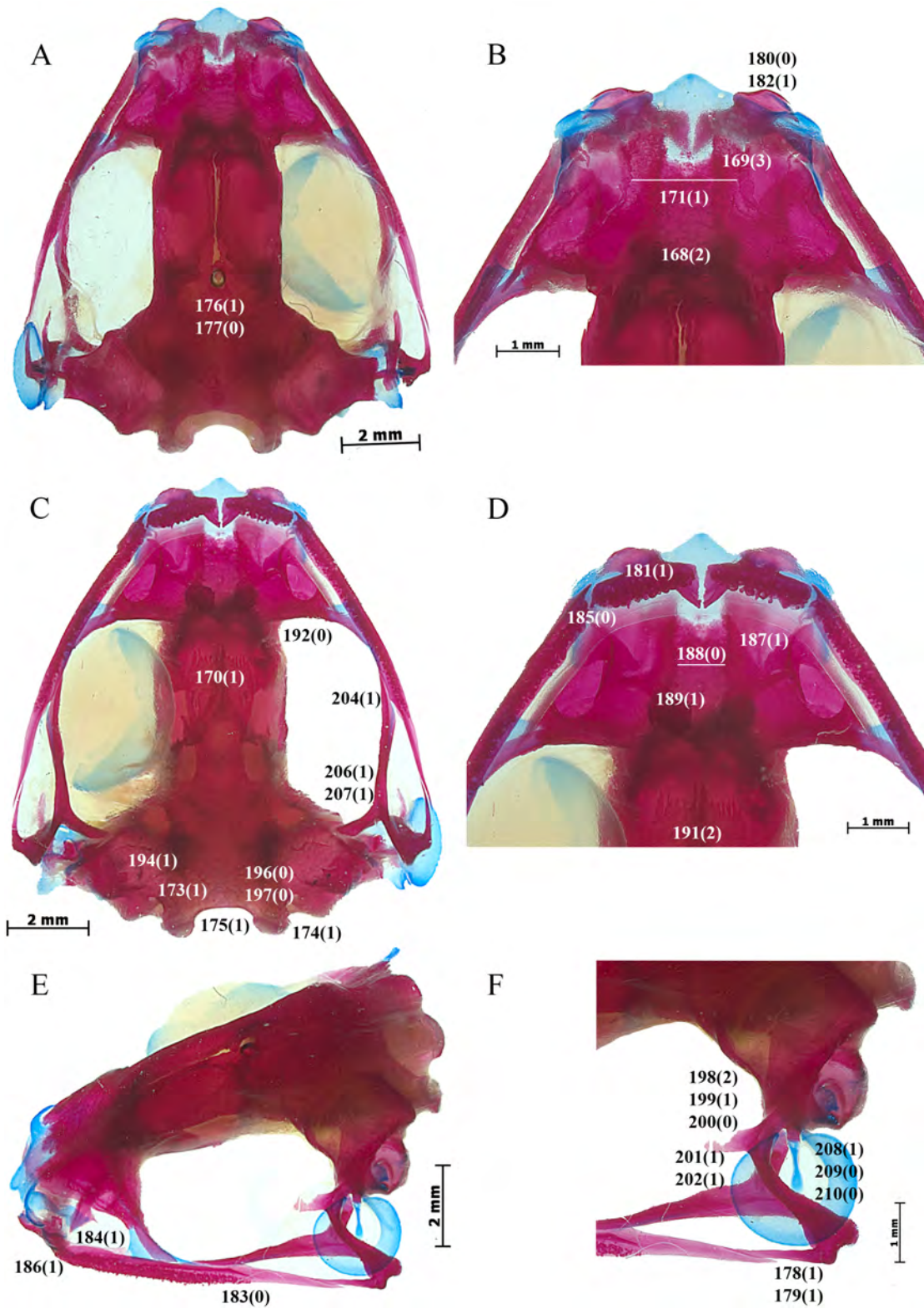


Figure 14. Cranial characteres: *H. charadranates* USNM245900.

**211-219: Hyolaryngeous apparatus**

Structure composed of two units: the hyoid and laryngeal apparatus. They are located ventral to the mandibular arch.

**211-216: Hyoid apparatus**

There is great variation in the hyoid apparatus, specially concerned with the presence or absence of the hyoid processes (Trueb 1973). The hyoid apparatus is composed by the hyoid plate; the hiale, that are dorsally connected with the optic capsule; and three paired processes (anterolateral, posterolateral, and posteromedial). Trueb (1973) states that the hiale “*provides a useful taxonomic character at specific and generic level*”. The author also described a degree of variation in the posterolateral and posteromedial processes. Trewavas (1933) observed a great variation regarding the occurrence, developed, shape and orientation of the different parts of the hyoid apparatus of anurans. **Figure 15** illustrates the characters of this system.

211. Hiale, anterior process of hyoid apparatus

(0) absent

(1) present

Remarks: Most species of Hylodidae have hiale. Transformation 1 → 0 occurred in *H. fredii*.

212. Cartilaginous edge of posteromedial process of hyoid apparatus

(0) short, rounded

(1) elongate

Remarks: All Hylodidae have a short and round cartilaginous edge on the posteromedial processes of the hyoid apparatus. Transformation 0 → 1 occurred in *H. fredei*.

213. Distance between the anterior edges of posteromedial process of hyoid apparatus

(0) wide distance

(1) small distance

(2) connected

Additive

Remarks: Most *Hylodes* have connected posteromedial processes (state 2). Transformation 2 → 1 occurs in *H. fredei*. *Crossodactylus* normally have separated processes (states 0 or 1). Transformation 1 → 0 is found in the clade that comprises *C. caramaschii*, *C. aff. caramachii*, and *Crossodactylus* sp. Paraná East.

214. Hyoid plate

(0) cartilaginous

(1) with little calcification, concentrated in some areas

(2) strongly calcified

Additive

Remarks: The hyoid plate of Hylodidae is usually cartilaginous (state 0) or little calcified (state 1). Hyoid plate strongly calcified is only found in *H. pipilans*. Transformation 0 → 1 is found in *H. asper*.

215. Depth of hyoglossal sinus

(0) does not exceed anterolateral processes

(1) anterior, between anterolateral and posterolateral processes

(2) medial, between anterolateral and posterolateral processes

Additive

Remarks: The most predominant conditions found in Hylodidae are states 1 and 2. Transformation 1 → 2 occurs in *H. asper* + *H. aff. asper* SP. Hyoglossal sinus not exceeding anterolateral process (state 0) is only found in some specimens of *H. nasus*.

216. Depth of posterior edge of hyoid plate

(0) straight

(1) slightly invaginated

(2) strongly invaginated

Additive

Remarks: Strongly invaginated posterior edge of the hyoid plate (state 2) is observed in most hylodids. Transformation 2 → 0 is found in the clade that comprises *C. caramaschii*, *C. aff. caramachii*, and *Crossodactylus* sp. Paraná East.

#### 217-219: Laryngeal apparatus

The laryngeal apparatus is composed of the cricoid cartilage, a rounded structure, and the arytenoid cartilage, a paired structure. There are three processes in the cricoid apparatus, one cardiac process (dorsomedial), one esophageal process (ventromedial), and a pair of bronchial processes (on each side of the cricoid ring). Trueb (1993) affirms that there is variation in the presence and development of the apical and basal cartilages of the arytenoid cartilage.



217. Esophageal process of cricoid cartilage: Shape

(0) simple

(1) triple

Remarks: A simple esophageal process occurs in most hylodid (state 0). Transformation 0 → 1 occurs in the clade with *C. caramaschii*, *C. aff. caramachii*, and *Crossodactylus* sp. Paraná East.

218. Bronchial processes of cricoid cartilage

(0) simple

(1) double

(2) triple

Not additive

Remarks: Most *Crossodactylus* have simple bronchial processes (state 0); whereas *Hylodes* has both, simple or double, processes (states 0 and 1). Transformation 1 → 0 is reported in *Hylodes* ‘Serra do Mar / no spine’ clade, except in *H. charadranaetes*. Triple process (state 2) is observed only in some specimens of *H. meridionalis*.

219. Anterior region of esophageal process of cricoid cartilage

(0) V-shape

(1) U-shape

(2) W-shape

Not additive

Remarks: *Crossodactylus* has a V-shaped anterior region of the esophageal process (state 0); whereas most species of *Hylodes* has the U-shape condition (state

1). Transformation 0 → 1 is reported in *Hylodes* 'Serra do Mar / no spine' clade; with reversion 1 → 0 in *H. aff. asper* SP.

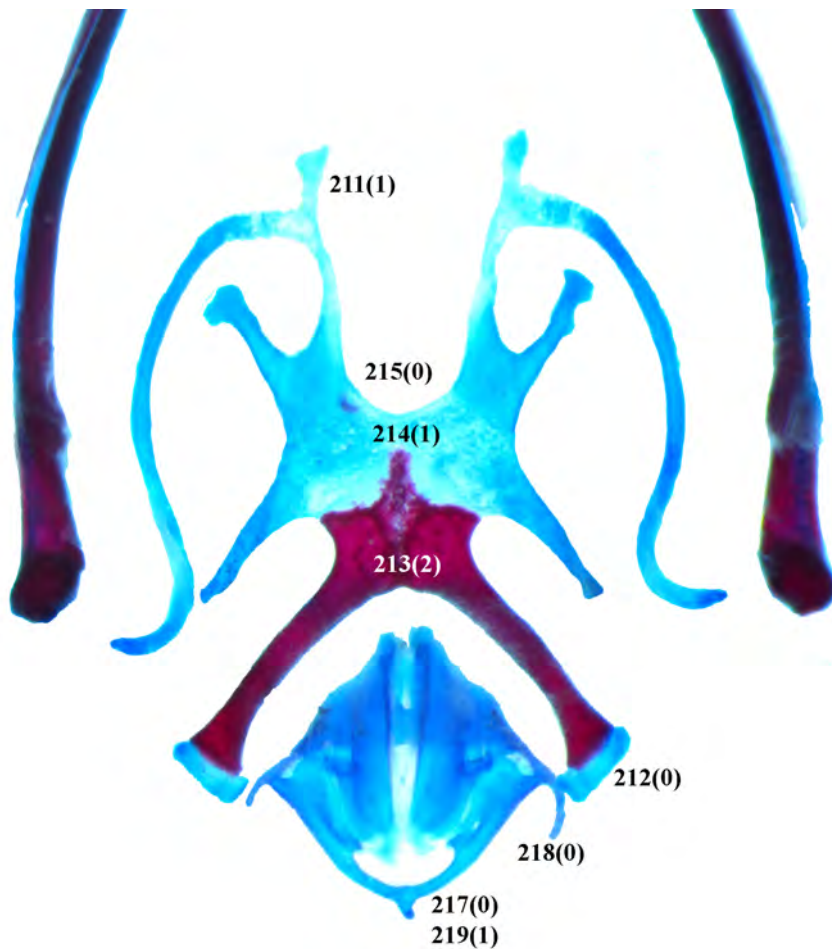


Figure 15. *Hyolaringeous apparatus*: *H. amnicola* MZUSP141747.

### **220-245: Column**

The number of presacral vertebrae in Anura varies between nine and five (Trueb 1973). All Hylodidae have eight presacral vertebrae, and one sacral vertebra. The great variation is related to the orientation, degree of inclination, and expansion of the lateral edge of each vertebrae. **Figure 16C** illustrates some characters codified in this study.

220. Orientation of transverse process of presacral vertebra II

(0) anterolaterally

(1) laterally

(2) posterolaterally

Non additive

Remarks: All *Crossodactylus* and *Hylodes* have the transverse process of presacral vertebra II anterolaterally oriented, whereas *M. goeldii* is laterally oriented

221. Inclination of transverse process of presacral vertebra II

(0) slightly inclined

(1) strongly inclined

Remarks: Most hylodids have a strongly inclined transverse process.

Transformation 1 → 0 is reported for *H. fredii*.

222. Lateral edge of transverse process of presacral vertebra II

(0) not expanded

(1) slightly expanded

(2) expanded

Additive

Remarks: Lateral edge slightly expanded (state 1) was observed in all *Crossodactylus*, and most *Hylodes* species. Transformation 1 → 2 occurred in *H. aff. asper* SP.

223. Orientation of transverse process of presacral vertebra III

(0) anterolaterally

(1) laterally

(2) posterolaterally

No additive

Remarks: Transverse process of presacral vertebra III anterolaterally oriented was predominant within *Crossodactylus* and *Hylodes*. Posterolateral orientation (state 2) is reported for *M. goeldii*.

224. Inclination of transverse process of presacral vertebra III

(0) slightly inclined

(1) strongly inclined

Remarks: Slightly inclined transverse process was predominant in *Hylodes* (state 0). Transformation 0 → 1 occurred in *H. aff. asper* SP, and in the clade comprising *H. phyllodes*, *H. aff. phyllodes* Itanhaém, *H. aff. phyllodes* Rio Claro, *H. aff. phyllodes* Paranapiacaba, *H. aff. phyllodes* Bocaina, and *H. aff. phyllodes* Ubatuba. Within *Crossodactylus*, slightly inclined transverse process (state 0) was observed in *C. aeneus* and *C. trachystomus*; whereas *C. dantei*, *C. gaudichaudii*, and *C. schmidtii* presented strongly inclined processes (state 1).

225. Lateral edge of transverse process of presacral vertebra III

(0) not expanded

(1) slightly expanded

(2) expanded

Additive

Remarks: Expanded transverse process (state 2) is predominant in Hylodidae, followed of slightly expanded condition (state 1). Not expanded transverse process (state 0) is reported only in few individuals of *C. aeneus*, *H. pipilans*, and *H. uai*.

226. Orientation of transverse process of presacral vertebra IV

(0) anterolaterally

(1) laterally

(2) posterolaterally

Non additive

Remarks: Most species of Hylodidae have a transverse process posterolaterally oriented (state 2). Transformation 2 → 1 is reported for *H. aff. asper* SP and the clade that comprise *H. glaber*, *H. japi*, *H. sazimai*, *H. amnicola*, and *H. perere*.

227. Inclination of transverse process of presacral vertebra IV

(0) slightly inclined

(1) strongly inclined

Remarks: All *Crossodactylus*, and most *Hylodes* have slightly inclined transverse process (state 0). Strongly inclined process (state 1) was observed in *M. goeldii*.

228. Lateral edge of transverse process of presacral vertebra IV

(0) not expanded

(1) slightly expanded

(2) expanded

Additive

Remarks: Most *Crossodactylus* have slightly expanded transverse process (state 1); while expanded process was observed in most *Hylodes* (state 2).

229. Orientation of transverse process of presacral vertebra V

(0) anterolaterally

(1) laterally

(2) posterolaterally

Non additive

Remarks: All hylodids have posterolaterally orientation of transverse process (state 2). Lateral orientation (state 1) is observed only in a few specimens of *C. gaudichaudii*.

230. Inclination of transverse process of presacral vertebra V

(0) slightly inclined

(1) strongly inclined

Remarks: Most *Crossodactylus* have slightly inclined transverse process (state 0); while most *Hylodes* and *M. goeldii* have strongly inclined process (state 1).

231. Lateral edge of transverse process of presacral vertebra V

(0) not expanded

(1) slightly expanded

(2) expanded

Additive

Remarks: All hylodids have transverse process of presacral vertebra V not expanded (state 0), the single exception was few specimens of *H. fredii* with slightly expanded process (state 1).

232. Orientation of transverse process of presacral vertebra VI

(0) anterolaterally

(1) laterally

(2) posterolaterally

Non additive

Remarks: *M. goeldii* and most *Crossodactylus* have transverse process of vertebra VI laterally oriented (state 1). The states 1 and 2 were the most common within *Hylodes*. Transformation 1 → 2 occurred in the clade with *H. glaber*, *H. japi*, *H. sazimai*, *H. amnicola*, and *H. perere*; and in *Hylodes* ‘Serra do Mar / no spine’ clade, except for *H. charadranaetes*, with reversion 2 → 1 in *H. aff. asper* SP.

233. Inclination of transverse process of presacral vertebra VI

(0) slightly inclined

(1) strongly inclined

Remarks: Transverse process of vertebra VI is slightly inclined (state 0) in all Hylodidae, with exception of few specimens of *H. meridionalis*, *H. nasus*, and *H. pipilans* (state 1).

234. Lateral edge of transverse process of presacral vertebra VI

(0) not expanded

(1) slightly expanded

(2) expanded

Additive

Remarks: All hylodids have transverse process of vertebra VI not expanded (state 0). Few individuals of *H. fredei* have slightly expanded process (state 1).

235. Orientation of transverse process of presacral vertebra VII

(0) anterolaterally

(1) laterally

(2) posterolaterally

Non additive

Remarks: Transverse process of vertebra VII anterolaterally oriented is observed in all *Crossodactylus*, *M. goeldii*, and some *Hylodes*. Process with lateral orientation is reported for *H. asper* (RJ), *H. cardosoi*, *H. heyeri*, *H. meridionalis*, *H. nasus*, *H. perplicatus*, and *H. pipilans*.

236. Inclination of transverse process of presacral vertebra VII

(0) slightly inclined

(1) strongly inclined

Remarks: Most hylodid have transverse process of vertebra VII slightly inclined (state 0). Only *C. trachystomus* and *H. uai* have strong inclination (state 1).

237. Lateral edge of transverse process of presacral vertebra VII

(0) not expanded

(1) slightly expanded

(2) expanded



Additive

Remarks: All species of Hylodidae have a transverse process on vertebra VII not expanded.

238. Orientation of transverse process of presacral vertebra VIII

(0) anterolaterally

(1) laterally

(2) posterolaterally

Non additive

Remarks: Most hylodids have transverse process on vertebra VIII anterolaterally oriented (state 0). Lateral orientation is observed only in *H. cardosoi* and *M. goeldii*.

239. Inclination of transverse process of presacral vertebra VIII

(0) slightly inclined

(1) strongly inclined

Remarks: Most species of Hylodidae have transverse process on vertebra VIII strongly inclined (state 1); however, *H. asper* (RJ), *H. heyeri*, *H. nasus*, *H. perere*, and one specimen of *C. dantei* and *H. meridionalis* have the slightly inclined condition (state 0).

240. Lateral edge of transverse process of presacral vertebra VIII

(0) not expanded

(1) slightly expanded

(2) expanded

Additive

Remarks: All hylodids have transverse process on vertebra VIII not expanded (state 0).

241. Orientation of sacral diapophyses

(0) anterolaterally

(1) laterally

(2) posterolaterally

Non additive

Remarks: All hylodids have sacral diapophyses posterolaterally oriented (state 2).

242. Inclination of sacral diapophyses

(0) slightly inclined

(1) strongly inclined

Remarks: Most species of Hylodidae have slightly inclined sacral diapophyses; however, several species presented an ambiguous condition for this character. strongly inclined Sacral diapophysis was found in *M. goeldii*, *H. amnicola*, *H. aff. asper* SP, and *H. heyeri*. Transformation 0 → 1 occurred in *H. aff. asper* SP.

243. Expansion of sacral diapophyses

(0) not expanded

(1) slightly expanded (1,5 to 3,5x the base width)

(2) expanded (more than 3,5x the base width)

Additive

Remarks: All hylodids have slightly expanded sacral diapophyses (state 1); however, some species of *C. aeneus* and *C. gaudichaudii* present not expanded sacral diapophyses (state 1).

244. Anteromedial projection of sacral diapophysis

(0) absent

(1) present

Remarks: Anteromedial projection was not reported for Hylodidae (state 0).

245. Urostyle transverse processes

(0) absent

(1) present

Remarks: Transverse process on urostyle was not reported for Hylodidae (state 0).

**246-255: Pelvic girdle and posterior appendages**

In modern anurans, the pelvic girdle is primarily composed of ilium and ischium, and the pubis is reduced to an inconspicuous structure (Trueb 1973). The ilia are paired structures that articulate with the ventral surface of the sacral diapophyses anteriorly, and articulate with each other posteromedially. The ischia are paired and vary in shape within Anura. The pubis is usually present as a ventral cartilaginous element between the ischium and ilium (Trueb 1973).

The posterior appendages are composed of femur, tibia and fibula. The hind foot is composed of five digits with normally 2-3-3-4-3 phalanges, prehallux, the tibiale and fibiale, which are elongated and fused in both extremities, and tarsal and

metatarsal elements (Trueb 1973). **Figure 16B** illustrates some of the characters codified in this study.

246. Femoral crest

(0) absent

(1) present

Remarks: Most species of Hylodidae have femoral crest (state 1).

Transformation 1 → 0 occurred in *H. aff. asper* SP.

247. Ventral angle of acetabulum

(0) acute angle

(1) slightly acute angle

(2) right angle

(3) slightly obtuse angle

Non additive

Remarks: Most Hylodidae have acetabulum with acute angle (state 0). Slightly acute angle (state 1) is reported for *C. caramaschii*; some specimens of *C. aeneus* and *C. dantei* present right angle (state 2). Slightly obtuse angle (state 3) is observed in *C. schmidti* and *H. aff. asper* SP. Transformation 0 → 3 is reported for *H. aff. asper* SP.

248. Dorsal protuberance of acetabulum

(0) absent

(1) present

Remarks: Most hylodid have dorsal protuberance on acetabulum (state 1), excepting *C. schmidti* and *H. aff. asper* SP (state 0). Transformation 1 → 0 is reported for *H. aff. asper* SP.

249. Tibiale and fibulare fusion

(0) fused on distal and proximal extremities

(1) totally fused

Remarks: All hylodids have the tibiale and fibulare fused on distal and proximal extremities (state 0).

250. Number of tarsal elements

(0) two (T1; T2+T3)

(1) three (T1; T2; T3)

Remarks: All hylodids have two tarsal elements (state 0).

251. Number of basal elements of prehallux

(0) one

(1) two

Remarks: All *Crossodactylus*, and several *Hylodes* have two basal elements on prehallux (state 1). One element (state 0) is reported for *H. amnicola*, *H. asper* RJ, *H. cardosoi*, *H. charadranaetes*, *H. heyeri*, *H. magalhaesi*, *H. sazimai*, and few specimens of *H. uai*.

252. Number of distal elements of prehallux

(0) one

(1) two

(2) three

(3) four

Additive

Remarks: Most *Crossodactylus* have two distal elements (state 1), excepting *C. schmidti*, with three elements (state 2). Within *Hylodes*, most species have three elements (state 2); however, two and four elements (states 1 and 3, respectively) were also found. Four elements occur in *H. aff. asper* SP, *H. nasus*, and some specimens of *H. meridionalis* and *H. pipilans*; whereas two elements is observed in *H. magalhaesi* and in few specimens of *H. phyllodes*.

253. Basal contact between metatarsal IV and V

(0) free, metatarsal IV and V are separated

(1) in contact

Remarks: Most species of Hylodidae have metatarsals IV and V in contact (state 1). Transformation 1 → 0 occurred in *H. aff. asper* SP and *H. meridionalis* + *H. aff. meridionalis* SC.

254. Distal edge of terminal phalange

(0) pointed or rounded

(1) bifurcate, Y- or T-shaped

Remarks: All Hylodidae have Y- or T- shaped terminal phalange, and it was recovered as a synapomorphy for the clades (*Thoropa milliaris* (Dendrobatoidea, Hylodidae)), and Centrolenidae + Allophrynidae.

255. Subarticular sesamoid on fingers

(0) absent

(1) present

Remarks: All species have subarticular sesamoid (state 1), except *H. nasus* (state 0).

### **256-267: Scapular girdle**

The scapular girdle is composed of: (1) procoracoid, that forms the anterior part of epicoracoid; (2) epicoracoid, the principal cartilaginous body of pectoral arch, posterior to the level of the clavicles; (3) omosternum, a prezonal associated element, lying anterior to the procoracoid and clavicles; (4) sternum, a flat cartilaginous element, divided in mesosternum and xiphisternum; (5) clavicle, a paired and dermal bones associated with the procoracoid; (6) scapula, an endochondral element that usually articulates with the clavicle and coracoid medially, and with cleithrum and suprascapula laterally; (7) coracoid, endochondral bone that form the medial border of the glenoid fossa laterally and adjoins the epicoracoid cartilages medially; (8) suprascapula, a dorsolateral extension of the scapula; and (9) cleithrum, that lies mainly on the ventral surface of the suprascapula, a distally bifurcated bone in most anurans (Trueb 1973). **Figure 16A** illustrates the characters codified in this study.

256. Omosternum size

(0) undeveloped, not exceeding the coracoid width

(1) developed, exceeding the coracoid width

Remarks: Most Hylodidae have developed omosternum (state 1). Transformation 1 → 0 (undeveloped omosternum) is recovered in the clade *Hylodes* 'MG / ES' + *Hylodes* 'Serra da Mantiqueira'.

257. Anterior edge of omosternum

(0) rounded

(1) pointed

(2) pentagonal

Non additive

Remarks: Rounded anterior edge of omosternum (state 0) is predominant in Hylodidae. The pointed shape (state 1) was observed only in *H. heyeri*, and pentagonal shape (state 2) was observed in *H. magalhaesi* and *H. nasus*.

258. Posterior edge of omosternum

(0) straight

(1) U- or V-shaped

(2) W-shaped

Non additive

Remarks: Most Hylodidae have straight (state 0) or W-shaped (state 2) posterior edge of omosternum. Transformation 2 → 0 was reported in *H. asper* + *H. aff. asper* SP. U- or V-shaped (state 1) was observed only in *H. pipilans*.

259. Omosternum mineralization

(0) cartilaginous

(1) calcified



Remarks: Most hylodids have calcified omosternum (state 1). Transformation 1 → 0 is reported for the clade with *C. caramaschii*, *C. aff. caramaschii*, and *Crossodactylus* sp. Paraná East.

260. Epicoracoid fusion

(0) anterior fusion, posterior edge free

(1) anterior and posterior fusion

Remarks: Anterior and posterior fusion of epicoracoid (state 1) is predominant in Hylodidae. Free posterior edge (state 0) was only observed in *H. nasus* and *H. pipilans*.

261. Epicoracoid overlap

(0) overlap, does not exceeding complementary cartilage

(1) overlap, exceeding complementary cartilage

(2) overlap, exceeding complementary cartilage, with a space between the cartilages

Additive

Remarks: All conditions were observed in *Crossodactylus*. The Overlap of epicoracoid, does not exceeding complementary cartilage (state 0) is predominant within *Hylodes*. Transformation 0 → 1 is reported for the clade that comprises *H. phyllodes*, *H. aff. phyllodes* Itanhaém, *H. aff. phyllodes* Rio Claro, *H. aff. phyllodes* Paranapiacaba, *H. aff. phyllodes* Bocaina, and *H. aff. phyllodes* Ubatuba.

262. Epicoracoid mineralization

(0) cartilaginous

(1) calcified

Remarks: Most Hylodidae have calcified epicoracoid. Transformation 1 → 0 occurred in the clade with *C. caramaschii*, *C. aff. caramaschii*, and *Crossodactylus* sp. Paraná East.

263. Sternum mineralization

(0) cartilaginous

(1) calcified

(2) osseous

Non additive

Remarks: Calcified sternum (state 1) is predominant in Hylodidae. The Exception is the cartilaginous sternum (state 0) in *C. caramaschii*, *C. trachystomus*, *H. aff. asper* SP, and *H. pipilans*, and osseous sternum (state 2) in *H. heyeri* and *H. perplicatus*.

264. Sternum posterior foramen

(0) absent

(1) present

Remarks: Most hylodids do not have foramen on sternum (state 0). Transformation 0 → 1 was recovered in the clade with *H. nasus*, *Hylodes* sp. Jucituba, *H. asper*, and *H. aff. asper* SP.

265. Expansion of posterior edge of sternum

(0) not expanded

(1) expanded

Remarks: An expanded posterior edge of sternum (state 1) is predominant in Hylodidae. Transformation 1 → 0 occurred in the clade *Hylodes* 'MG / ES' + *Hylodes* 'Serra da Mantiqueira'.

266. Coracoid orientation

(0) almost horizontal, or until approx. 30 degrees

(1) approx. 45 degrees

Remarks: Most *Crossodactylus* have coracoid with approx. 45 degrees (state 1). Transformation 1 → 0 occurred in the clade with *C. caramaschii*, *C. aff. caramaschii*, and *Crossodactylus* sp. Paraná East. Within *Hylodes*, almost horizontal or until approx. 30 degrees (state 0) is predominant, excepting *H. amnicola* and *H. heyeri*.

267. Anterior edge of scapula

(0) concave

(1) not concave

Remarks: Most *Crossodactylus* have concave anterior edge of scapula (state 0), except for *C. aeneus*. No concave edge of scapula (state 1) is frequent in *Hylodes*. Transformation 1 → 0 occurred in *Hylodes* 'Serra da Mantiqueira' and in the clade with *H. nasus*, *Hylodes* sp. Jucituba, *H. asper*, and *H. aff. asper* SP.

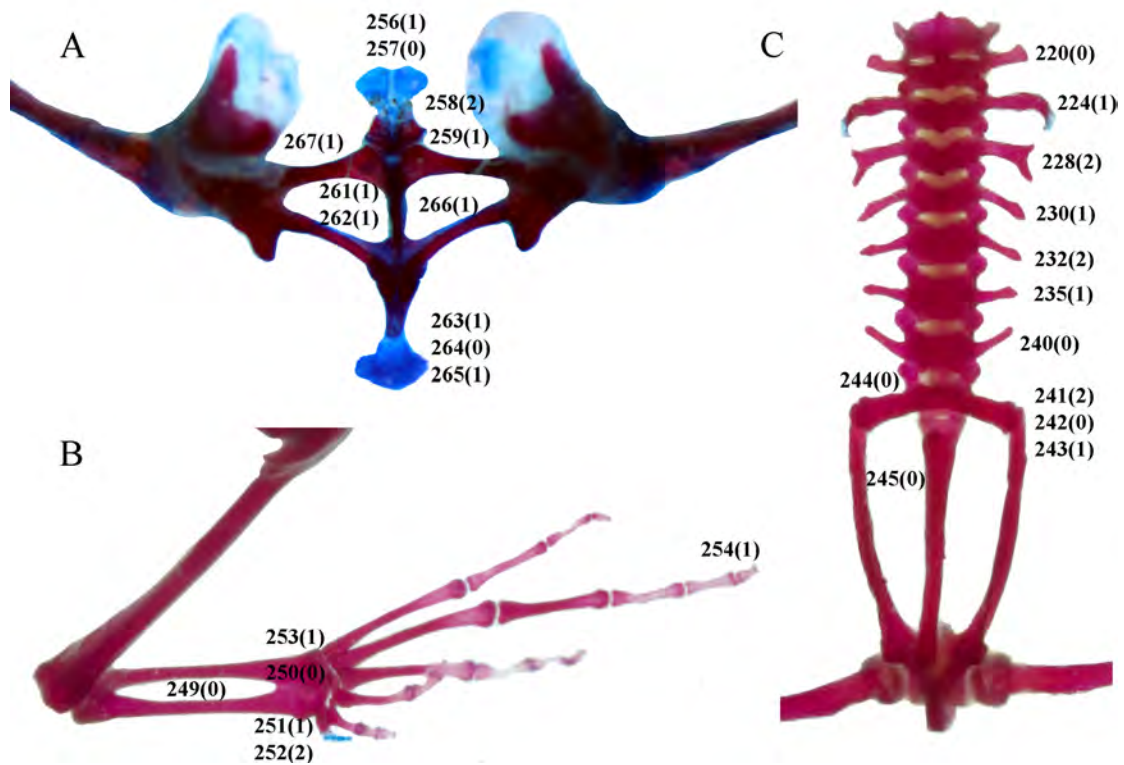


Figure 16. Postcranium: (A) scapular girdle in *C. aeneus* MNRJ39369; (B) foot in *H. charadranaetes* USNM245900; and (C) column in *H. phyllodes* USNM243492.

### Chromosomes

The basic karyotype in anurans seems to be 26 bi-chromosomes; however, diverse lineages of anurans show a reduction from the basic 26 chromosomes, and in some groups of frogs, this basic number is increased (Duellman and Trueb, 1994). Chromosomes analyses in hylodids revealed that *Crossodactylus* is the most karyotypically conserved genus in terms of chromosome number ( $2N = 26$ ), whereas *Megaelosia* is the most diversified genus, with a range of  $2N = 28$  to  $2N = 32$  (e.g., Bogart 1970, Melo *et al.* 1995, Aguiar Jr. *et al.* 2004). The chromosome morphology is well conserved, with greatest variations in the pairs 7-10 (Aguiar Jr. *et al.* 2004). A morphological comparison of each chromosome pair was avoided due to the

difficulties to establish homology between the pairs; thus, I decided to codify only the number of chromosomes.

268. Number of chromosomes

(0)  $2N = 20$

(1)  $2N = 22$

(2)  $2N = 24$

(3)  $2N = 26$

(4)  $2N = 28$

(5)  $2N = 30$

(6)  $2N = 32$

(7)  $2N = 34$

Non additive

Remarks: All *Crossodactylus* and *Hylodes* have  $2N = 26$  (state 3), except for *H. nasus* ( $2N = 24$ ; state 2). *Megaelosia massarti* and *M. jordanensis* is reported with  $2N = 28$  (state 4) and  $2N = 30$ , respectively. A huge variation was found within outgroup species, ranging from  $2N = 20$  in *Leptodactylus fuscus* (state 1) to  $2N = 34$  in *Pristimantis fenestratus* (state 7). The species recovered as sister group of Hylodidae, *Amereega trivitatta* and *Rheobates palmatus*, had the same chromosome number of the predominant Hylodidae's condition ( $2N = 26$ ).

## Tadpoles

Amphibian larvae are potentially informative for systematics and evolutionary studies as individuals in mature stages (Orton 1952, 1953; Lannoo 1987; Haas 2003; Candiote 2007; Candiote and Altig 2010).

### 269. Snout shape

- (0) rounded
- (1) straight (**Figure 18A**)

Remarks: All Hyloidae have round snout shape (state 0), except *H. dactylocinus* (state 1).

### 270 – 274: Nostril

#### 270. Nostril shape

- (0) rounded (**Figure 17C, D**)
- (1) elliptic (**Figure 17A, B**)

Remarks: Rounded nostril is predominant in Hyloidae (state 0).

Transformation 0 → 1 occurred in *Hylodes* 'South' clade.

#### 271. Nostril ornamentation

- (0) Absent (**Figure 17A, B**)
- (1) present (**Figure 17C, D**)

Remarks: Most Hyloidae does not have ornamentation on nostril (state 0).

Absence of ornamentation in the nostril was recovered as a synapomorphy for *Hylodes* (1 → 0).

272. Nostril ornamentation: Type

- (0) crenate (**Figure 17C**)
- (1) leaf-shaped (**Figure 17D**)

Remarks: Few species have ornamentation. Leaf-shaped ornamentation (state 1) is observed only in *H. asper* RJ; whereas crenate nostril (state 0) is observed in *H. fredii*, *H. heyeri*, *H. magalhaesi*, and *H. ornatus*.

273. Nostril pigmentation:

- (0) absent
- (1) present (**Figure 17A, B**)

Remarks: Pigmentation (state 1) is reported for several *Hylodes* species. Transformation 1 → 0 was recovered in *Hylodes* ‘Serra do Mar / spine’ clade, *H. asper*, *H. lateristrigatus* + *H. babax*, and *H. amnicola*.

274. Nostril pigmentation: Type

- (0) limit with an incomplete pigmentation (**Figure 17B**)
- (1) limit with a complete pigmentation (**Figure 17A**)

Remarks: Most species have incomplete pigmentation (state 0) on the nostril. Transformation 0 → 1 occurred in *H. otavioi* and *H. meridionalis* + *H. aff. meridionalis* SC.

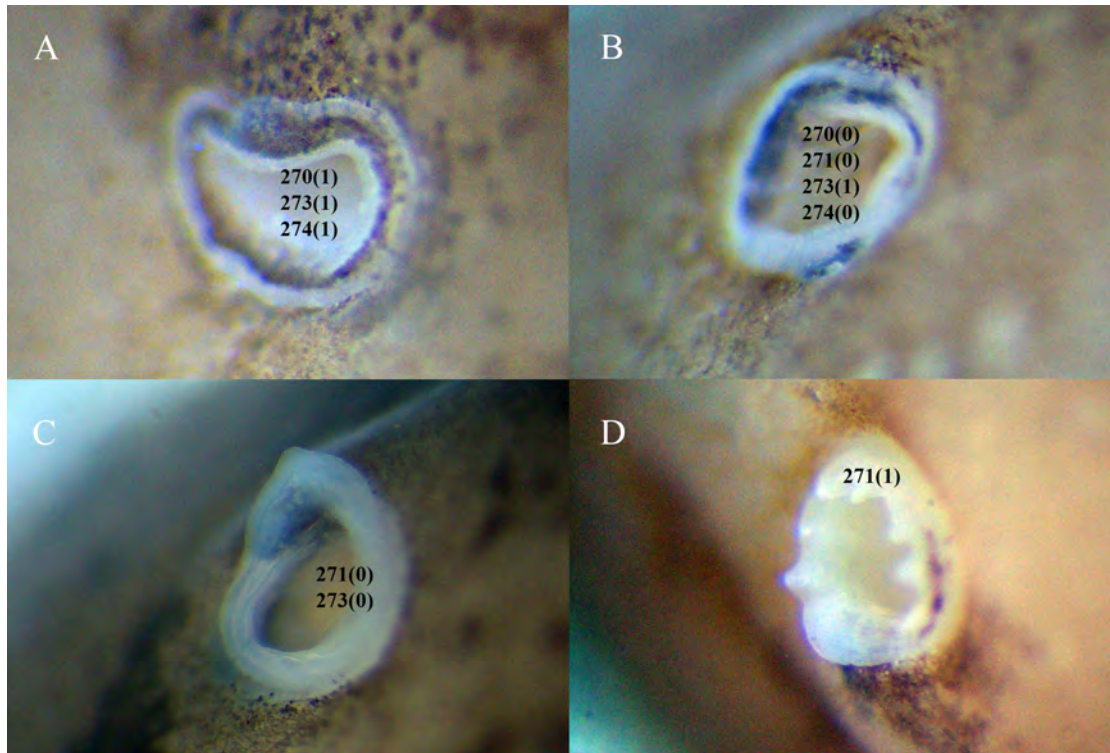


Figure 17. Nostril: (A) *H. meridionalis* CFBH12135, (B) *H. aff. asper* (SP) CFBH9013, (C) *H. asper* (RJ) RU7271, (D) *H. magalhaesi* CFBH25076.

275. Ventral depression prior to the medial convoluted clockwise-spiraled intestine

Species of the genus *Hylodes* are exclusively associated with mountain streams of the Atlantic Forest, and easily diagnosed due to the presence of a ventral depression anterior to the convoluted intestine (Haddad and Pombal 1995).

(0) absent

(1) present (**Figure 18D**)

Remarks: All *Hylodes* species have ventral depression prior to the medial convoluted intestine (state 1). This result agrees with Haddad *et al.* (1996) that stated this condition as common in all *Hylodes*.



276-277: Spiracle

276. Spiracle position

- (0) on the right side of the body
- (1) ventrally
- (2) on the left side of the body (**Figure 18**)

Non additive

Remarks: All Hylodidae present spiracle on the left side of the body (state 2).

277. Spiracle coloration

- (0) whitish
- (1) with a white border (**Figure 18B**)

Remarks: Most hylodids have spiracle with a white border (state 1).

Transformation 1 → 0 occurred in *H. otavioi*, *H. asper* + *H. aff. asper* SP, and the clade that comprise *H. phyllodes*, *H. aff. phyllodes* Itanhaém, *H. aff. phyllodes* Rio Claro, *H. aff. phyllodes* Paranapiacaba, *H. aff. phyllodes* Bocaina, and *H. aff. phyllodes* Ubatuba.

278. Cloacal tube position

- (0) ventral
- (1) on the right side of the body (**Figure 18D**)

Remarks: State 1 is present in all hylodids. Cloacal tube position on the right side of the body is recovered as a synapomorphy (0 → 1) for (*Thoropa milliaris* (Dendrobatoidea, Hylodidae)).



Figure 18. Tadpoles: (A) *H. dactylocinus* MZUSP129281, (B) *H. amnicola* MNRJ 24862, (C) *H. fredii* RU7464, (D) *H. perere* RU2463.

279-285: Lateral line system

Lannoo (1987) and Fabrezi *et al.* (2009) considered seven main lines on each side of the body (**Figure 19**). The anterior lateral line system has four pairs of lines on the larval head: supraorbital line, from the upper labium between nostrils to the

posterior part of the eyes (a posterior supraorbital line is present near the posterior portion of the supraorbital line); infraorbital line, from the lateral margin of the oral disc to the posterior part and below the eyes (a posterior infraorbital lines is present near the posterior portion of the infraorbital line); angular line, from below the eyes extending ventrally and joining in the ventral region; and oral line, from the lateral margin of the oral disc descending to the ventral region (divided in anterior and longitudinal). The posterior lateral line system has three pairs of lines on the larval trunk: dorsal line, arising lateral to the keel of dorsal fin and extending along the base of dorsal fin; medial lines, from behind and below the eye along the caudal musculature; and ventral lines, bordering the abdominal cavity and converging near the vent tube. The left ventral line rounds the spiracle. In this study, I codified the absence and presence of all these lateral lines.

The lateral line system of Hylodidae was poorly detailed or inappropriately described in it tadpole's descriptions. In the original description of the larva of *H. nasus*, Lutz (1930) pointed out the presence of sinuous lines running longitudinally, formed by white points, distant between themselves in large tadpoles, and representing sensory organs. Although Lutz (1930) had mentioned the presence of lateral lines in the description of the first larva of *Hylodes* documented in the literature, many authors did not mention the presence of these structures when describing new larvae even recently. **Figure 19** illustrates the lateral lines system.

279. Supraorbital line

(0) absent

(1) present

Remarks: Supraorbital line is present (state 1) in all species included in the present analysis.

280. Infraorbital line

(0) absent

(1) present

Remarks: Infraorbital line is present (state 1) in all species included in the present analysis, except in *Leptodactylus fuscus* (state 0).

281. Angular line

(0) absent

(1) present

Remarks: Angular line is observed (state 1) in all species included in the present analysis, except in *C. aeneus* (state 0).

282. Oral line

(0) absent

(1) present

Remarks: Oral line is present (state 1) in most species of *Hylodes* (except in *H. sazimai*) and all *Megaelosia*. Absence (state 0) is reported for *Crossodactylus*, excepting *C. schmiti* (state 1).

283. Dorsal line

(0) absent

(1) present

Remarks: Dorsal line is present (state 1) in all species included in the present analysis, except in *Leptodactylus fuscus* (state 0).

284. Medial line

(0) absent

(1) present

Remarks: Medial line is present (state 1) in all species included in the present analysis, except in *Leptodactylus fuscus* (state 0).

285. Ventral line

(0) absent

(1) present

Remarks: Ventral line is found in all hylodids (state 1), except *C. aeneus*. No outgroup species was reported with this character (state 0). Thus, the presence of ventral line is reported as a synapomorphy for Hylodidae (0 → 1).

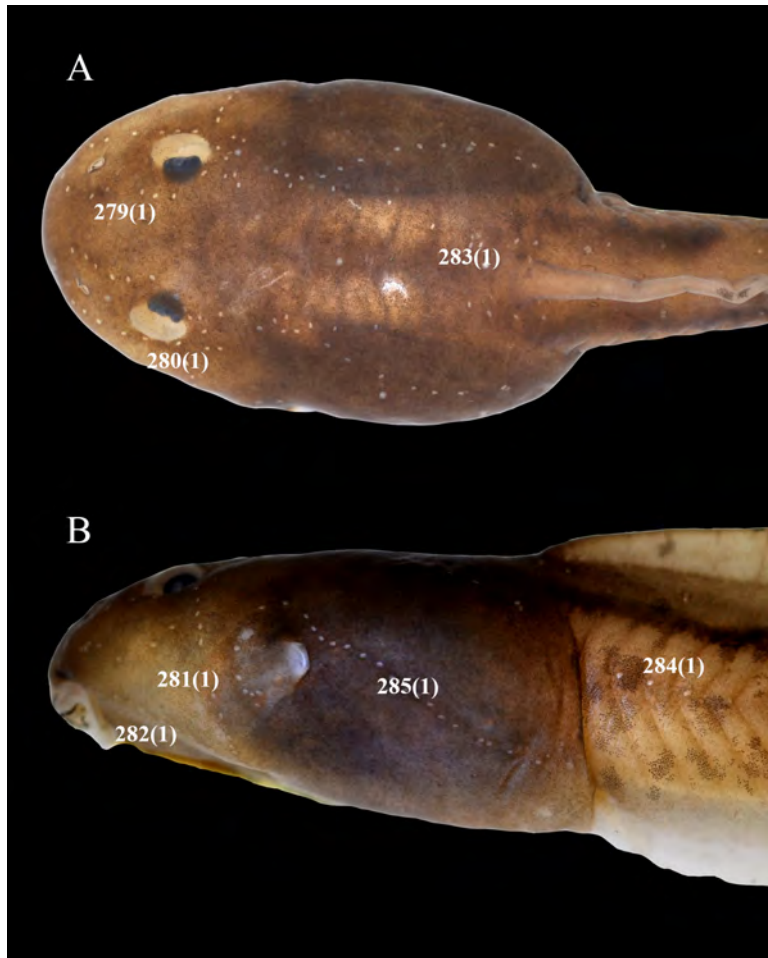


Figure 19. Lateral line system: *H. perere* RU2463.

286. Dorsal fin: Origin

- (0) originates before to the final portion of the body (**Figure 18B**)
- (1) originates immediately to the final portion of the body (**Figure 18A**)
- (2) originates after the final portion of the body (**Figure 18C**)

Non additive

Remarks: Most hylodids and outgroup species have dorsal fin originating immediately to the final portion of the body (state 1). Transformation 1 → 0 is reported for *H. amnicola* and transformation 1 → 2 occurred in *H. meridionalis* + *H. aff. meridionalis* SC.

287 – 291: Oral disc

287. Lateral emargination of the oral disc:

- (0) absent
- (1) present (**Figure 20**)

Remarks: Lateral emargination on the oral disc is reported for all hylodids (state 1). Absence of emargination is observed only in *Leptodactylus fuscus* and *Vitreorana eurygnatha*.

288. Central emargination of the oral disc:

- (0) absent (**Figure 20A**)
- (1) present (**Figure 20B**)

Remarks: Only *Crossodactylus* have central emargination on the oral disc (state 1), and it can be a putative synapomorphy for this genus.

289. Number of anterior teeth lines:

- (0) one
- (1) two (**Figure 20**)
- (2) three

Additive

Remarks: All hylodids have two lines of anterior teeth (state 1).

290. Number of posterior teeth lines:

- (0) one
- (1) two
- (2) three (**Figure 20**)

Additive

Remarks: Three lines of posterior teeth are reported for all Hylodidae (state 2).

291. Supernumerary papillae:

(0) absent

(1) present (**Figure 20**)

Remarks: All Hylodidae have supernumerary papillae (state 1), and this character was not observed on the outgroup, except in *Vitreorana eurygnatha*; thus, this feature is recovered as a synapomorphy for Hylodidae (0 → 1).

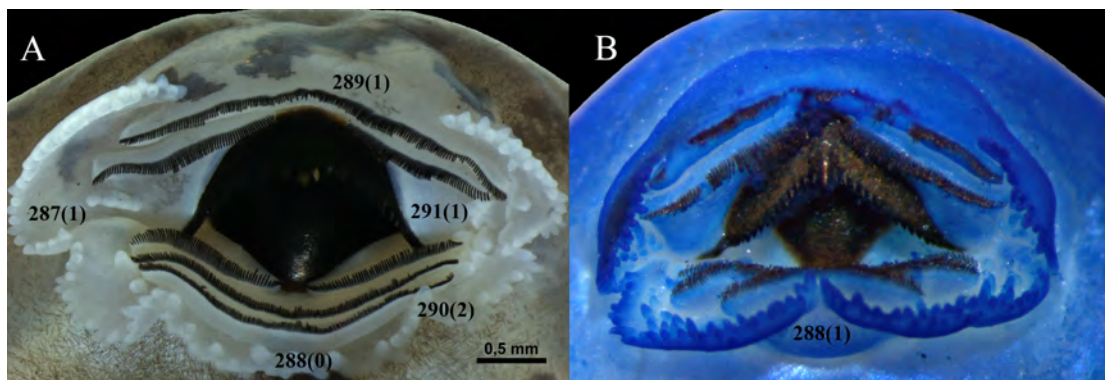


Figure 20. Oral disc: (A) *H. babax* UFV222; (B) *C. gaudichaudii* MNRJ38361 (photo by Pedro Dias)

## Behavior

292. Foot flagging

(0) absent

(1) present



Remarks: Foot-flagging is observed only in some species of *Hylodes* (state 1). No *Crossodactylus* and *Megaelosia* were reported displaying this visual signal (state 0).

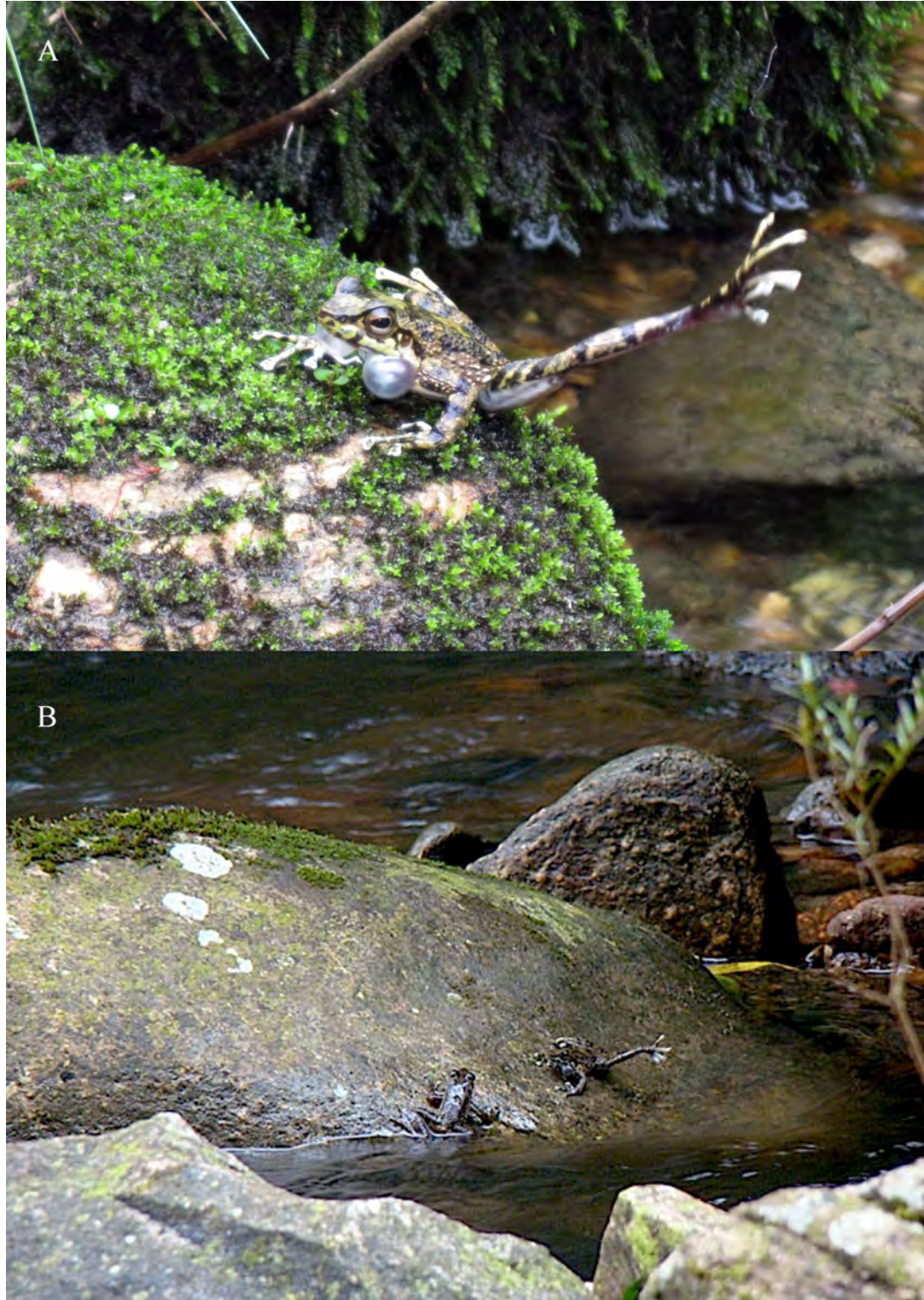


Figure 21. Visual signal, foot-flagging. *Hylodes asper*, Estação Biológica da Boracéia, São Paulo.

## GENERAL PHYLOGENETIC RESULTS

I obtained 713 most parsimonious trees with 32,405 steps. This final result was achieved with the following steps: (1) direct optimization parsimony analysis resulted in one most parsimonious tree with 32,459 steps; (2) a new cycle of branch swapping over this most parsimonious tree resulted in a shorter three with 32,405 steps; (3) an aggressive TNT analysis failed to recover shorter trees, but retrieved 713 equally parsimonious trees with the same cost of the best tree recovered using POY. I summarized the hierarchical relationships of all 713 trees using strict consensus. This strict consensus tree was then used to families' relationships (**Figure 22**), relationship among hylodid genera (**Figure 23**), and relationship among hylodids species (**Figure 25 to Figure 42**).

## OUTGROUP RELATIONSHIPS AND HYLODIDAE MONOPHYLY

The outgroup relationships recovered in the present analysis have several differences in relation to the phylogenetic hypothesis proposed by Pyron and Wiens (2011). Three monophyletic families in Pyron and Wiens' study were recovered as paraphyletic in this study: Cycloramphidae, Hemiphractidae, and Leptodactylidae. Representatives of Cycloramphidae were recovered in two different clades: (1) *Cycloramphus boraceiensis* and *Zachaenus parvulus*, sister group of Batrachylidae; (2) *Thoropa milliaris* as sister group of Dendrobatoidae and Hylodidae. My results corroborate those of Frost et al. (2006), which placed *Thoropa* in its own family, Thoropidae.

Hemiphractidae was represented in my analysis by a Hemiphractinae species of the genus *Hemiphractus* and a Cryptobatrachinae species of the genus *Flectonotus*. The paraphyly of this family was expected because *Hemiphractus helioi* was selected to root the tree. Representatives of Brachycephaloidea (*i.e.*, Eleutherodactylidae, Brachycephalidae, and Craugastoridae) composed the sister clade of all remaining species, including *Flectonotus*. Frost *et al.* (2006) concluded that "Hemiphractinae" as previously defined was composed of three phylogenetically distantly related taxa. Those authors recognized the families Amphignathodontidae (*Flectonotus* and *Gastrotheca*), Cryptobatrachidae (*Cryptobatrachus* and *Stefania*), and Hemiphractidae (*Hemiphractus*). My results agree with Frost *et al.* (2006); however, the inclusion of more taxa (especially from their Cryptobatrachidae) is necessary to corroborate the separation of "Hemiphractinae" in three distinct monophyletic families.

The subfamilies of Leptodactylidae (Leptodactylinae and Leiuperidae) were recovered in distinct positions in my phylogeny. Leiuperinae was recovered as sister group of Bufonidae, whereas Leptodactylinae was placed as sister group of Odontophrynidae. My results corroborate Grant *et al.*'s (2006) hypothesis, supporting Leiuperidae apart from Leptodactylidae.

The other families (*i.e.*, Eleutherodactylidae, Brachycephalidae, Craugastoridae, Odontophrynidae, Allophrynidae, Centrolenidae, Ceratophryidae, Batrachylidae, Telmatobidae, Bufonidae, Hylidae, Alsodidae, Rhinodermatidae, Aromabatidae, and Dendrobatidae) were recovered monophyletic. In my analysis, Odontophrynidae was recovered as sister group of Cycloramphidae (*Zachaenus* and *Cycloramphus*), and Hylidae as sister group of Alsodidae. The monophyletic clade (Allophrynidae + Centrolenidae) was recovered as sister group of Batrachylidae in this study, and the

clade (Batrachylidae (Allophrynidae, Centrolenidae)) as sister group of (Telmatobidae + Ceratophrydae). The clade composed of Batrachylidae, Allophrynidae, Telmatobidae, and Ceratophrydae was recovered as sister group of ((Rhinodermatidae (Leiuperinae, Bufonidae) (*Thoropa milliaris* (Dendrobatidae, Hylodidae))).

Brachycephaloidea (*i.e.*, Craugastoridae, Eleutherodactylidae, and Brachycephalidae) was found to be the sister taxon of all other families included in the present study, except the root (*Hemiphractus helioi*). The other Hemiphractidae, *Flectonotus* sp., was recovered as sister group of all remaining families (*i.e.*, all families included here except Hemiphractidae [*H. helioi*], Craugastoridae, Eleutherodactylidae, and Brachycephalidae). Odontophrynidae is recovered as sister group of the two genera of Leptodactylinae (*Leptodactylus* and *Paratelmatobius*); these clade is the sister group of all remain families. Telmatobidae is the sister group of all remaining clades (*i.e.*, Leptodactylidae [*Physalaemus cuvieri*], Bufonidae, Hylidae, Alsodidae, Rhinodermatidae, Cycloramphidae [*Thoropa milliaris*], Aromobatidae, and Dendrobatidae). The monophyletic clade (Allophrynidae + Centrolenidae) was recovered as sister group of Cycloramphidae (*Zachaenus* and *Cycloramphus*) and Ceratophryidae. The clade (Rhinodermatidae + Alsodidae) was recovered as sister group of Hylidae, and this group as sister of (Leiuperinae + Bufonidae). This later clade, composed of Rhinodermatidae, Alsodidae, Hylidae, Leiuperinae, and Bufonidae, was finally recovered as sister group of the clade (*Thoropa milliaris* (Dendrobatoidea, Hylodidae)).

My result clearly differ from those of Pyron and Wiens (2011) that recovered the following relationships: Brachycephaloidea was sister group of all other families included in the present study; Hemiphractidae was placed as sister group of all families, except those composing Brachycephaloidea, and Hylidae as sister group of

all families, except Brachycephaloidea and Hemiphractidae. Dendrobatoidea (*sensu* Grant *et al.* 2006) was recovered as sister group of Bufonidae, and this clade as sister group of ((Allophrynidae + Centrolenidae) Leptodactylidae). Ceratophryidae was recovered as sister group of a clade composed of (Odontophrynidae ((Telmatobidae (Batrachylidae, Rhinodermatidae)) (Cycloramphidae (Alsodidae, Hylodidae)))). Thus, Hylodidae was recovered as sister group of Alsodidae in Pyron and Wiens (2011).

Contrary to Pyron and Wiens (2011), my analysis retrieved Hylodidae as sister group of (*Thoropa miliaris* (Dendrobatidae, Aromobatidae)) with the following unambiguous phenotypic transformations: presence of paired dorsal digits scutes (Ch. 43: 0 → 1), weak tarsal fringe in females (Ch. 85: 0 → 1), *m. intermandibularis* overlaps the posterolateral region of *m. submentalis* (Ch. 138: 2 → 1), presence of apical supplementary element on *m. intermandibularis* (Ch. 140: 0 → 1), anterodorsolaterally orientation of the alary process of premaxilla (2 → 0), Y- or T-shape of digital edge of terminal phalange (Ch. 254: 0 → 1), and dextral opening of the cloacal tube (Ch. 278: 0 → 1).

The monophyly of Hylodidae has been recovered in several phylogenetic studies (Haas 2003, Nuin and Val 2005, Frost *et al.* 2006, Grant *et al.* 2006, Pyron and Wiens 2011). Here, the monophyly of this family was strongly supported (GB = 82; **Figure 22**); unambiguous phenotypic transformations include preaxial fringe on finger II in males does not reach subarticular tubercle (Ch. 11: 0 → 1), postaxial fringe on finger II in males does not reach subarticular tubercle (Ch. 15: 0 → 1), preaxial fringe on finger III in males present along all fringe (Ch. 19: 0 → 4), postaxial fringe on finger III in males does not reach subarticular tubercle (Ch. 23: 0 → 1), preaxial fringe on finger IV in males almost reach or reach subarticular tubercle (Ch. 27: 0 → 4&5), postaxial fringe on finger IV in males almost reach or reach distal

subarticular tubercle (Ch. 31: 0 → 1&2), preaxial fringe on finger V in males almost reach distal subarticular tubercle (Ch. 35: 0 → 1), postaxial fringe on finger V in males surpass distal subarticular tubercle or almost reach proximal subarticular tubercle (Ch. 39: 0 → 3&4), developed preaxial fringe on toe II in males (Ch. 53: 0 → 2), well developed tarsal fringe in males (Ch. 84: 0 → 2), transversal stripes on dorsal thigh (Ch. 114: 0 → 1), melanophores on dorsal skin (Ch. 119: 0 → 1), melanophores on ventral skin (Ch. 122: 0 → 1), melanophores on gular skin (Ch. 124: 0 → 1), weak posteromedial dark stripe on gular skin (Ch. 125: 0 → 1), partially pigmented testis (Ch. 128: 0 → 1), anteromedial apical supplementary element on *m. intermandibularis* (Ch. 141: 1 → 0), ventral lateral line on tadpole present (Ch. 285: 0 → 1), and presence of supernumerary papillae on oral disc on tadpole (Ch. 291: 0 → 1).

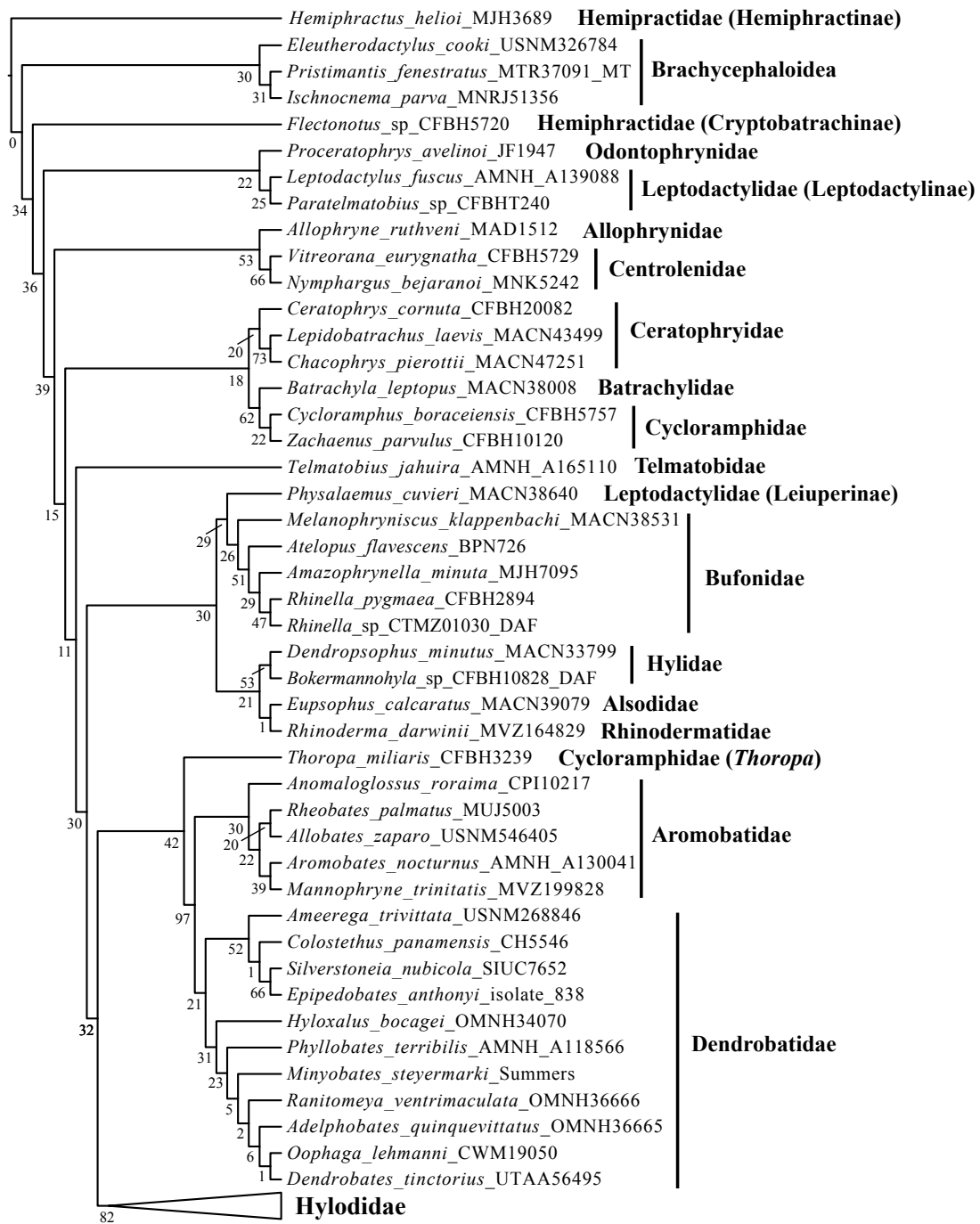


Figure 22. Strict consensus of 713 most parsimonious trees (32,405 steps), showing outgroup relationships, and monophyly and placement of Hylodidae. Numbers under branches correspond to Goodman-Bremer support values.

## RELATIONSHIPS WITHIN HYLODIDAE

All three genera of Hylodidae were recovered as monophyletic. Goodman-Bremer support for the genera were GB = 45 for *Crossodactylus*, GB = 33 for *Megaelosia*, and GB = 65 for *Hylodes*. My phylogenetic results corroborate intergeneric relationship previously hypothesized by Grant *et al.* (2006) and others, being *Crossodactylus* the sister group of *Megaelosia* + *Hylodes* (GB = 33). This later clade was supported by GB = 33. I identified hylodid lineages that represent putative species-level taxa and these lineages, clustered in major clades, were preliminarily named based on their topological arrangement and geographical distribution. See **Figure 23** for relationship among and within hylodid genera, and **Figure 24** for a representation of the major clades in Hylodidae.

My analysis failed to detect any unambiguous phenotypic transformation for *Crossodactylus*. This likely reflects the absence of morphological data for *Crossodactylus* sp. Serra do Teimoso, placed at the base of the genus. This species was not examined morphologically and all its phenotypic characters were scored as “?”. The absence of unambiguous synapomorphies must reflect character optimization limitations, not true homoplasy affecting this section of the tree.

Unambiguous phenotypic transformations supporting the clade *Megaelosia* + *Hylodes* are: paired lateral external vocal sac (Ch. 03: 0 → 1), postaxial fringe on finger II in females reach subarticular tubercle (Ch. 17: 1 → 2), postaxial fringe on finger IV in females almost reach proximal subarticular tubercle (Ch. 33: 1&2 → 4), preaxial fringe on finger V in females reach or surpass distal subarticular tubercle or almost reach proximal subarticular tubercle (Ch. 37: 1 → 2&3&4), presence of



vomerine teeth (Ch. 189: 0 → 1), and optic *ramus* of squamosal narrower than zygomatic *ramus* (Ch. 2 → 0).

Unambiguous phenotypic transformations supporting *Megaelosia*'s monophyly are: developed preaxial fringe on toe I in females (Ch. 47: 1 → 2), developed postaxial fringe toe I in females (Ch. 51: 1 → 2), developed preaxial fringe on toe II in females (Ch. 55: 1 → 2), developed postaxial fringe on toe II in females (Ch. 59: 1 → 2), developed preaxial fringe on toe III in females (Ch. 63: 1 → 2), developed postaxial fringe on toe III in females (Ch. 67: 1 → 2), developed preaxial fringe on toe IV in females (Ch. 71: 1 → 2), developed postaxial fringe on toe IV in females (Ch. 75: 1 → 2), developed preaxial fringe on toe V in females (Ch. 79: 1 → 2), developed postaxial fringe on toe V in females (Ch. 83: 1 → 2), developed tarsal fringe in females (Ch. 85: 1 → 2), developed metatarsal fold (Ch. 86: 1 → 2), loss of white lateral stripe (Ch. 102: 1 → 0), and loss of cantal dark stripe (Ch. 104: 1 → 0).

Finally, unambiguous phenotypic transformations supporting *Hylodes*'s monophyly are: loss of supernumerary tubercles on hand (Ch. 96: 1 → 0), four perpendicular stripes on dorsal thigh (Ch. 116: 4 → 3), iridophores on dorsal skin (Ch. 118: 0 → 1), paracloacal dark stripes (Ch. 127: 0 → 1), liver completely pigmented (Ch. 132: 1 → 2), *m. intermandibularis* overlaps all posterior edge or only medially the posterior edge of *m. submentalis* (Ch. 138: 1 → 0&2), occipital condyles expanded posteriorly (Ch. 174: 0 → 1), big vomers (Ch. 187: 0 → 1), medial and posterior *rami* of pterygoid with approx. de same length (Ch. 206: 0 → 1), nostril without ornamentation (Ch. 271: 1 → 0).



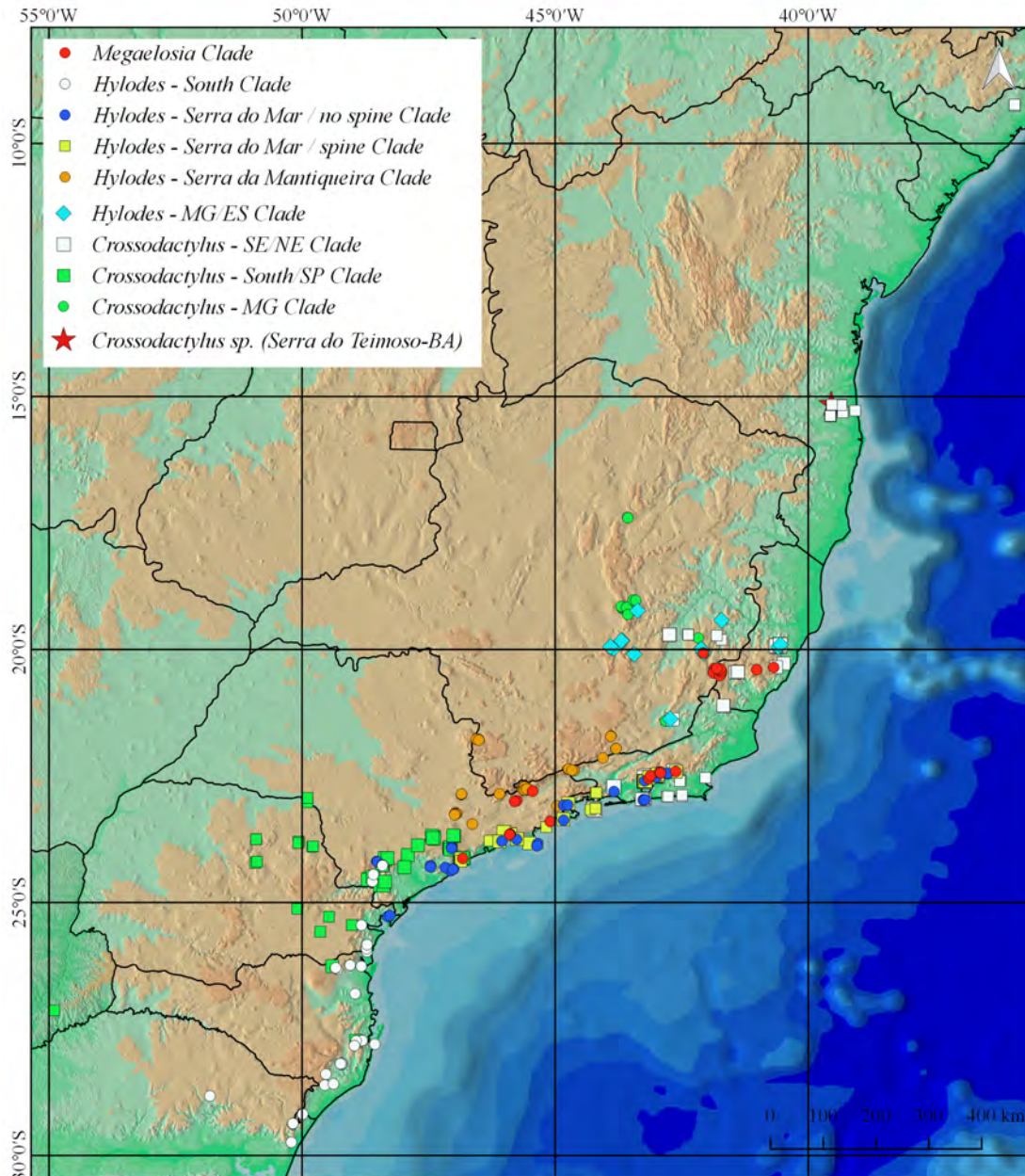


Figure 24. Distribution of the main clades of Hylodidae.

### **Relationships within *Crossodactylus***

Seven species of *Crossodactylus* were included in the present analysis plus several unidentified terminals. I was able to recognize at least 20 lineages in this genus: *Crossodactylus* sp. “Serra do Teimoso BA”, *Crossodactylus* sp. “MG 1”, *Crossodactylus* sp. “MG 2”, *C. trachystomus* 1, *C. trachystomus* 2, *Crossodactylus*

sp. “SC”, *C. schmidti*, *Crossodactylus* sp. “PR West”, *Crossodactylus* sp. “PR East”, *C. caramaschii*, *C. aff. caramaschii* “SP”, *C. gaudichaudii* 1 “Região dos Lagos RJ”, *C. gaudichaudii* 2 “Floresta da Tijuca”, *C. aeneus*, *Crossodactylus* sp. “ES”, *Crossodactylus* sp. “BA”, *C. dantei*, *Crossodactylus* sp. “MG 3”, *Crossodactylus* sp. “MG 4”, and *C. timbuhy*. The single specimen from Serra do Teimoso, Bahia, was recovered as sister group of all species of *Crossodactylus* (see **Figure 23**), and was not included in the major clades defined below.

The 19 remaining lineages were grouped in three major clades: “MG”, “South/SP”, and “SE/NE”. *Crossodactylus* “MG” clade (GB = 1; **Figure 25** and **Figure 26**) is distributed in the East Atlantic basin and on the intersection of this basin and São Francisco basin. It is composed of (1) *Crossodactylus* sp. “MG 1” (GB = 33) with two unidentified specimens from Itamarati de Minas and Caratinga, which form the sister group of (*Crossodactylus* sp. “MG 2” (*C. trachystomus* 1, *C. trachystomus* 2)); (2) *Crossodactylus* sp. “MG 2” (GB = 4) with two unidentified specimens from Olho D’água, which form the sister group of *C. trachystomus* 1 + *C. trachystomus* 2; (3) *C. trachystomus* 1 (GB = 7), composed of five specimens from Serra do Caraça, and two individuals from Conceição do Mato Dentro, which form the sister group of *C. trachystomus* 2; (4) *C. trachystomus* 2 (GB = 4), composed of seven specimens from Serra do Cipó, and one individual from Conceição do Mato Dentro. No unambiguous phenotypic transformations were recovered for this clade.



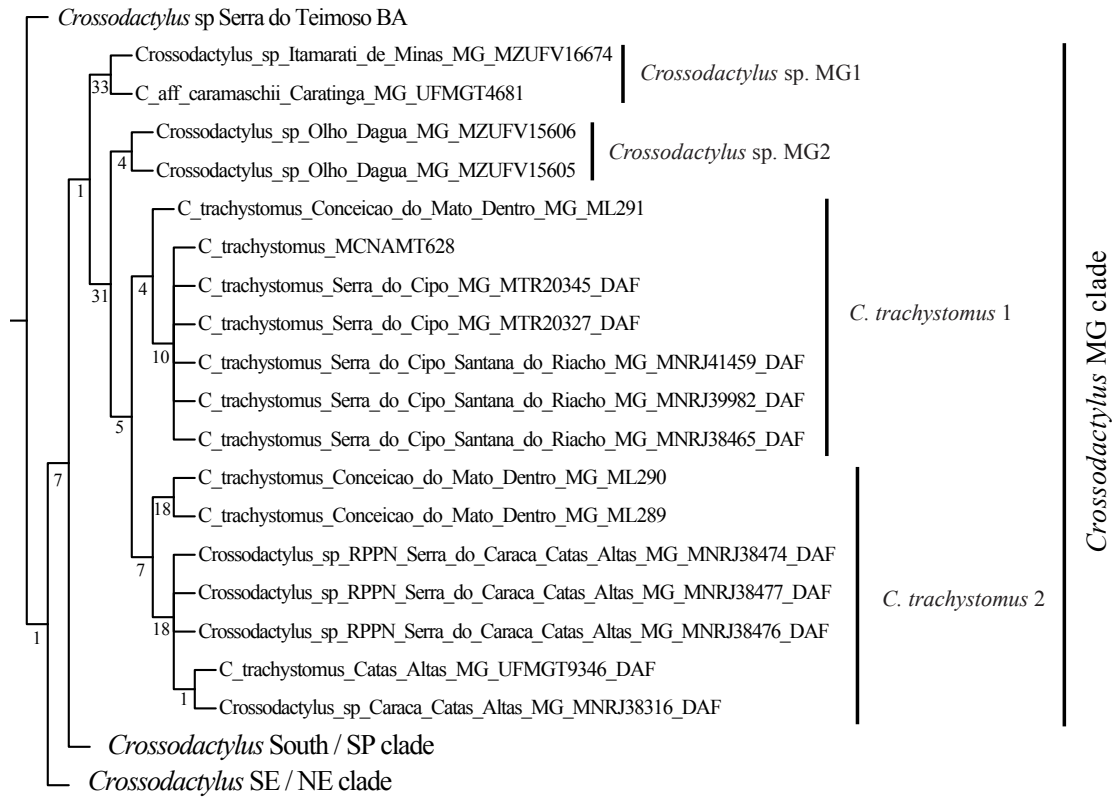


Figure 25. Strict consensus of 713 most parsimonious trees (32,405 steps) showing the relationship within the *Crossodactylus* MG clade. Numbers under branches correspond to Goodman-Bremer support values.

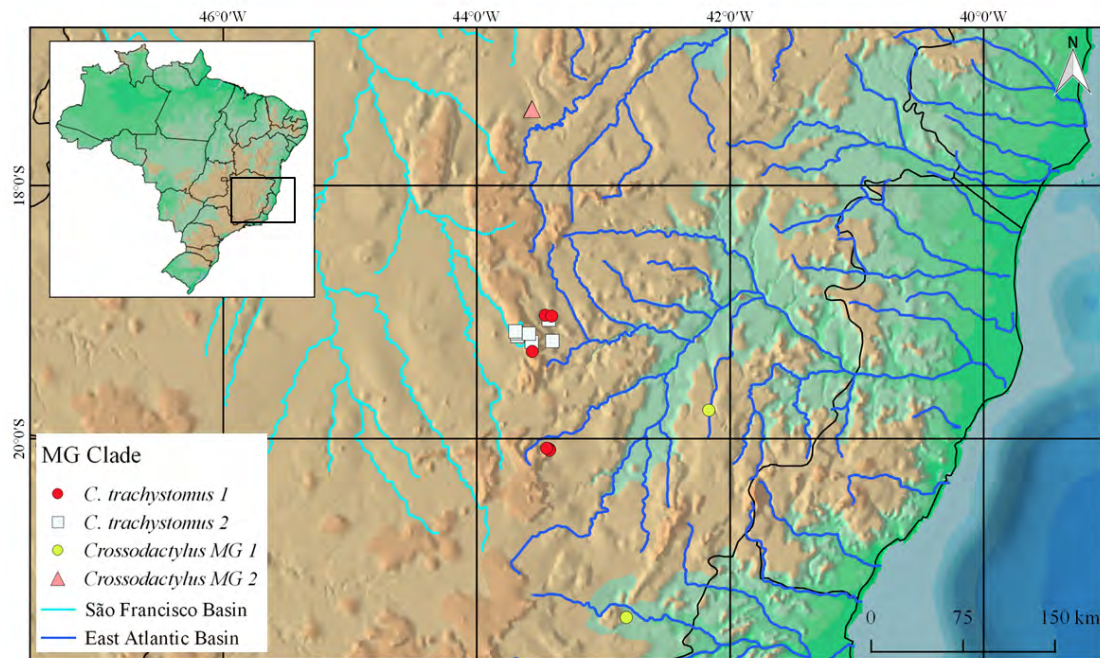


Figure 26. Distribution of *Crossodactylus* 'MG' clade.

The clade “South/SP” (GB = 1; **Figure 27** and **Figure 28**) is distributed in the Paraná River and Southeast Atlantic basins. Composed of: (1) *Crossodactylus* sp. “SC” (GB = 1), with two individuals from São Bento do Sul and Águas Mornas, Southeast Atlantic basin, sister group of ((*C. schmidti*, *Crossodactylus* sp. “PR1”) (*Crossodactylus* sp. “PR2” (*C. caramaschii*, *C. aff. caramaschii* “SP”))); (2) *C. schmidti* composed of only one representative from Misiones, Argentina, sister group of *Crossodactylus* sp. “PR1”; (3) *Crossodactylus* sp. “PR 1 - West” (GB = 10) composed of 10 specimens from Ortigueira, Apucarantina, Wenceslau Bras, and Pinhalão, West PR, and Ourinhos, SP, distributed only in the Paraná River basin; (4) *Crossodactylus* sp. “PR 2 - East” (GB = 32) with four specimens from Piraquara, Balsa Nova, and Ponta Grossa, on the intersection of both basins (Paraná River and Southeast Atlantic), sister group of *C. caramaschii* + *C. aff. caramaschii* “SP”; (5) *C. caramaschii* (GB = 20) composed of 13 terminals from PR and South SP, also occurring in Paraná River and Southeast Atlantic basins, sister group of *C. aff. caramaschii* “SP”; and (6) *C. aff. caramaschii* “SP” (GB = 2) composed of 18 specimens from São Paulo, distributed in in Paraná River and Southeast Atlantic basins. No unambiguous phenotypic transformations were recovered for this clade.

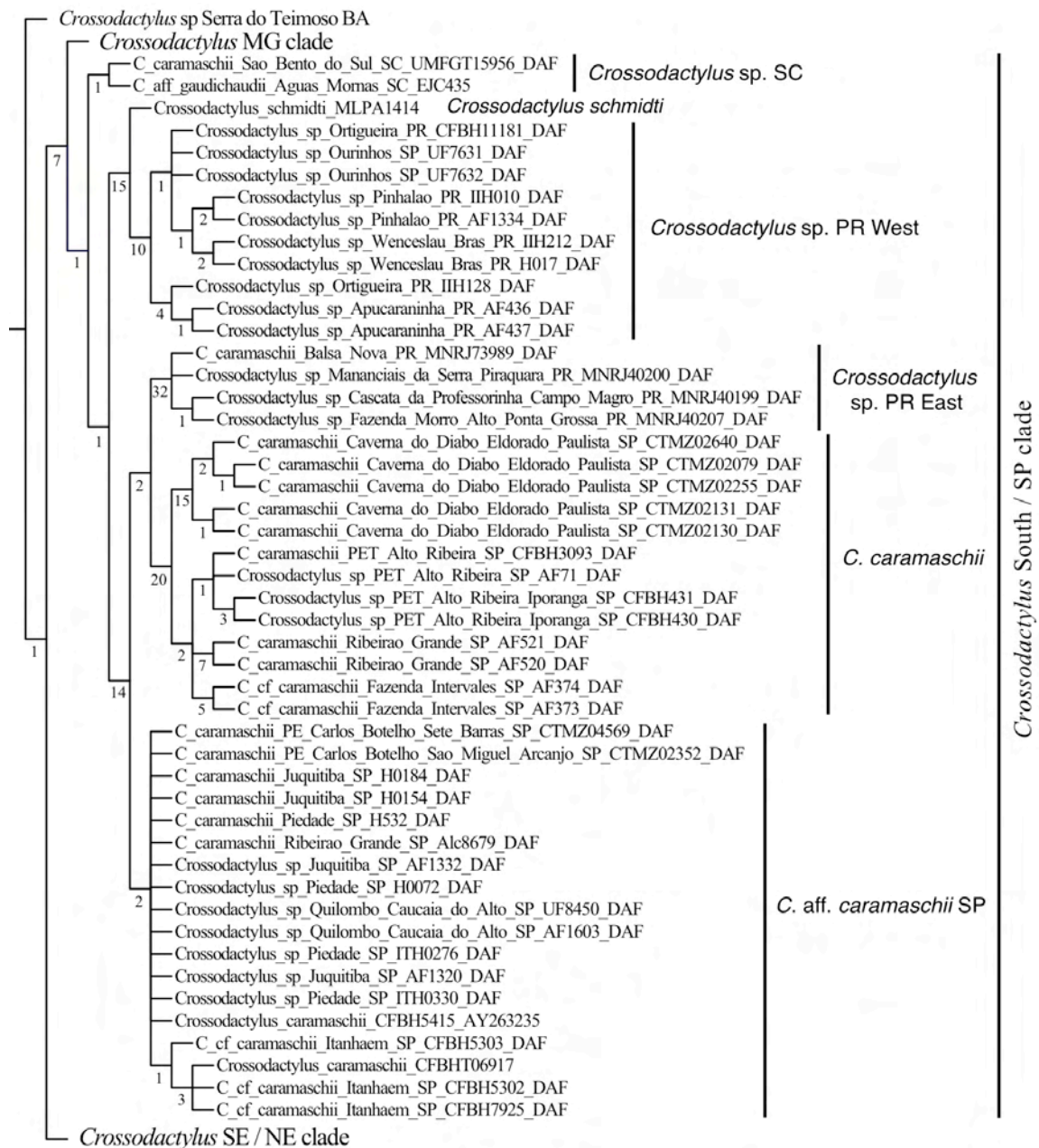


Figure 27. Strict consensus of 713 most parsimonious trees (32,405 steps), showing the relationship within *Crossodactylus* South / SP clade. Numbers under branches correspond to Goodman-Bremer support values.

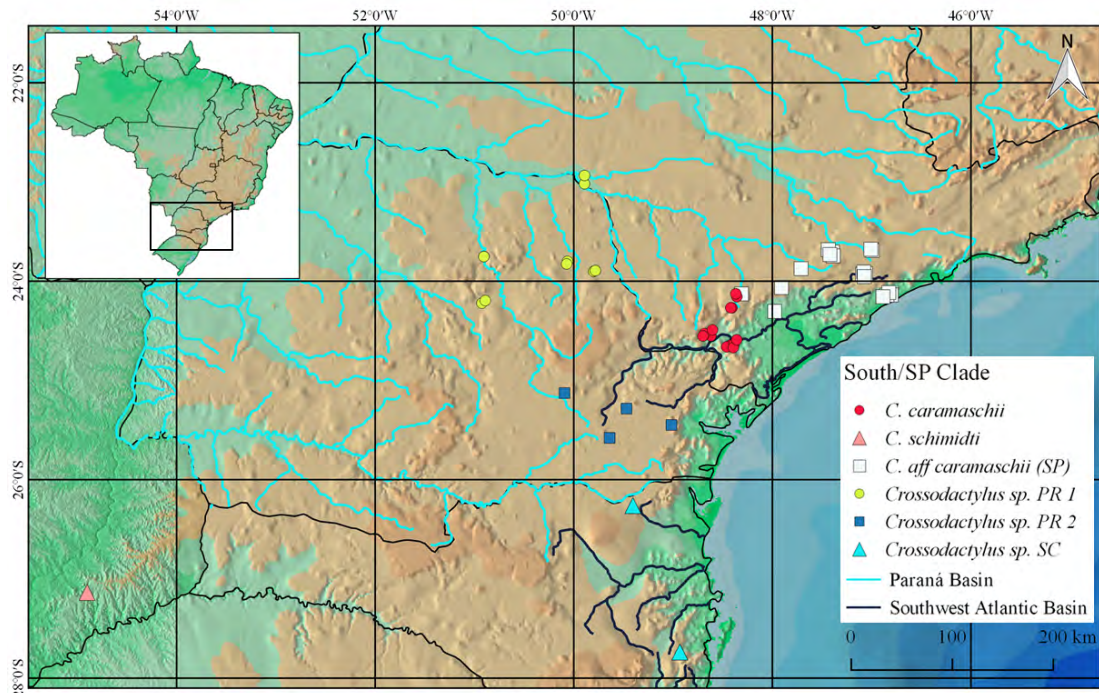


Figure 28. Distribution of *Crossodactylus* ‘South / SP’ clade.

The clade *Crossodactylus* MG + *Crossodactylus* South/SP is supported by the following unambiguous phenotypic transformations: postaxial fringe on finger II in males are only an expansion of skin (Ch. 16: 1 → 0), postaxial fringe on finger III in males are only expansion of skin (Ch. 24: 1 → 0), absent or inconspicuous paired dorsal digits scutes (Ch. 43: 1 → 0).

The clade “SE/NE” (GB = 1; **Figure 29** and **Figure 30**) is predominantly distributed in the East Atlantic basin (except only for *C. dantei*), known from Rio de Janeiro, Espírito Santo, Minas Gerais, Bahia, and Alagoas. This clade comprises the following lineages: (1) *C. gaudichaudii* 1 “Região dos Lagos RJ” (GB = 36), composed of seven terminals from Região dos Lagos and Cachoeira de Macacu, Rio de Janeiro, sister group of all remaining clades; (2) *C. gaudichaudii* 2 “Floresta da Tijuca” (GB = 21), composed of four terminals, all of them from Floresta da Tijuca, Rio de Janeiro, sister group of *C. aeneus*; (3) *C. aeneus* (GB = 7), composed of 17



terminals, all of them from Rio de Janeiro; (4) *Crossodactylus* sp. “ES” (GB = 1), with nine unidentified specimens distributed from Grande Vitória to south of Espírito Santo, sister group of all remaining clades; (5) *Crossodactylus* sp. “BA” (GB = 22), with 12 species from south of Bahia, sister group of all remaining clades; (6) *C. dantei* (GB = 1), represented by a single species that occurs in the North-Northeast Atlantic basin, composed of two terminals (topotypes) that form the sister group of (*Crossodactylus* sp. “MG 3” (*Crossodactylus* sp. “MG 4”, and *C. timbuhy*)); (7) *Crossodactylus* sp. “MG 3” (GB = 3), composed of four species from Cataguases and Marliéria, MG, sister group of *Crossodactylus* sp. “MG 4” + *C. timbuhy*); (8) *Crossodactylus* sp. “MG 4” (GB = 3), composed of six species from Caratinga, Bom Jesus do Galho, and Ipanema, MG; and (9) *C. timbuhy* (GB = 3), composed of eight terminals, all of them from the municipality Santa Teresa, Espírito Santo. The loss of pigmentation on lungs (Ch. 131: 1 → 0) is the only unambiguous phenotypic transformation supporting the clade “SE/NE” clade.

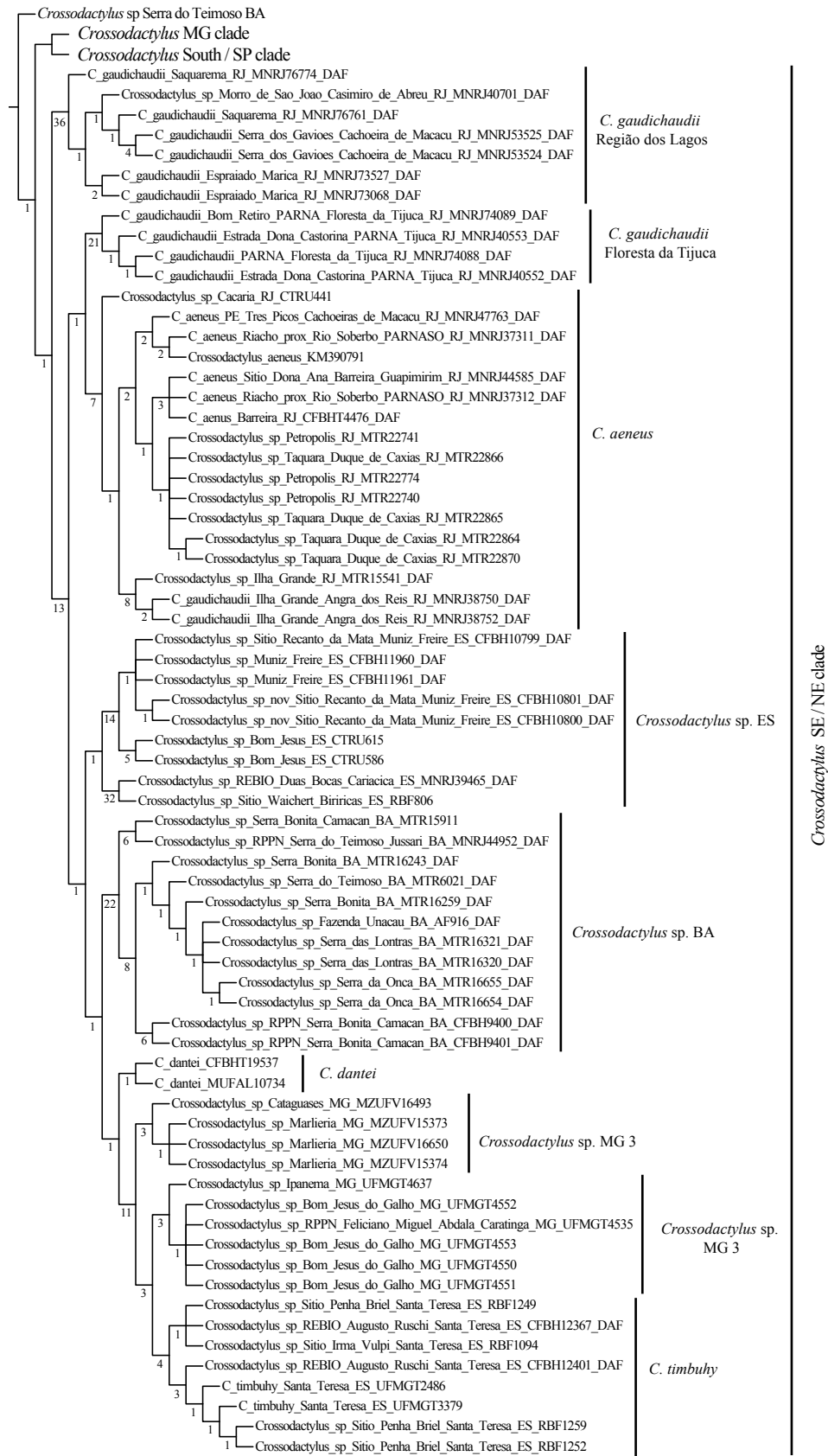


Figure 29. Strict consensus of 713 most parsimonious trees (32,405 steps), showing the relationship within *Crossodactylus* SE / NE clade. Numbers under branches correspond to Goodman-Bremer support values.

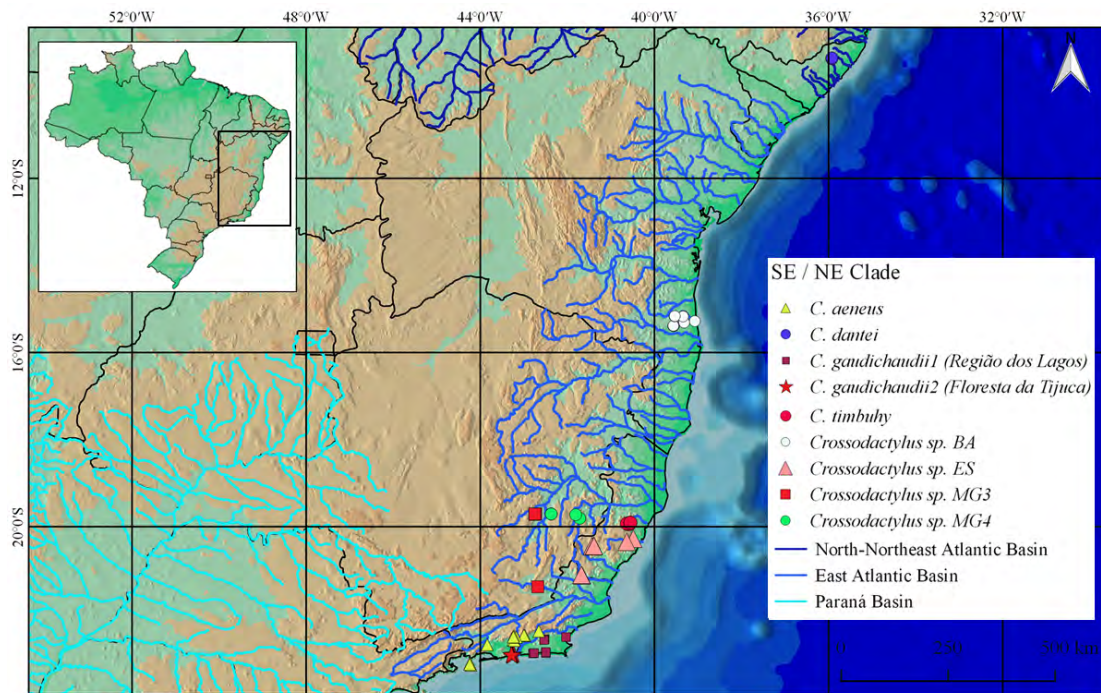


Figure 30. Distribution of *Crossodactylus* ‘SE / NE’ clade.

### Relationship within *Megaelasia*

My analysis included five of the seven valid species currently assigned to *Megaelasia*; however, the topological structure recovered indicates the existence of six distinct lineages: *M. goeldii*, *M. massarti*, *Megaelasia* sp. “Serra do Mar N SP”, *M. boticariana*, *M. cf. jordanensis*, and *M. apuana*, distributed mainly in the East Atlantic basin (**Figure 31** and **Figure 32**). *Megaelasia goeldii* (GB = 20) is distributed exclusively in the East Atlantic basin and composed of seven specimens from Rio de Janeiro. This clade presented seven unambiguous phenotypic transformations: absence of external vocal sac (Ch. 01: 1 → 0), undeveloped preaxial fringe on finger II in females (Ch. 14: 0 → 1), undeveloped postaxial fringe on finger II in females (Ch. 18: 0 → 1), developed metatarsal fold (Ch. 86: 1 → 2), dorsolateral light tubercles (Ch. 95: 0 → 1), conspicuous supratympanic fold (Ch. 101: 1 → 2),

and loss of melanophores on dorsal skin (Ch. 119: 1 → 0). This species was recovered as sister of all other *Megaelosia*.

The single specimen of *Megaelosia massarti* from Itanhaém, SP, Southeast Atlantic basin, was recovered as sister taxon of *M. boticariana* + *Megaelosia* sp. “Serra do Mar N SP”. The two specimens of *M. boticariana* (GB = 33) from Serra da Mantiqueira, East Atlantic basin, were recovered as sister group of three terminals from Serra do Mar of North São Paulo (Ubatuba and Boracéia, São Paulo; GB = 26), on the intercession of Paraná River and East Atlantic basins.

One tadpole from Pinhadomanhaga, East Atlantic basin, identified as *M. cf. jordanensis* and is sister group of *M. apuana*. The 16 specimens of *M. apuana* (GB = 9) formed a monophyletic group from East Atlantic basin. The species of *M. apuana* are distributed in three smaller clades: (1) *M. apuana* Domingos Martins (GB = 13), composed of two specimens from the type locality (Domingos Martins, ES); (2) *M. apuana* Caparaó ES (GB = 1), composed of six specimens from Espírito Santo side of the Parque do Caparaó and two specimens from Simonésia, Minas Gerais; and (3) *M. apuana* Caparaó MG (GB = 1), composed of six specimens from the section of the Parque do Caparaó located in the state of Minas Gerais. Clade of Domingos Martins was recovered as sister group of the two clades of Caparaó.

The clade composed of all species of *Megaelosia*, except *M. goeldii*, is supported by the following unambiguous phenotypic transformations: postaxial fringe on finger II in females surpass subarticular tubercle (Ch. 17: 2 → 3), preaxial fringe on finger III in females is along all finger (Ch. 21: 3 → 4), preaxial fringe on finger IV in females surpass proximal subarticular tubercle (Ch. 29: 5 → 6), presence of cloacal tubercles (Ch. 91: 0 → 1), iridophores on gular skin (Ch. 123: 0 → 1), absence

of melanophores on gular skin (Ch. 124: 1 → 0), and absence of posteromedial longitudinal dark stripe on gular skin (Ch. 125: 1 → 0).

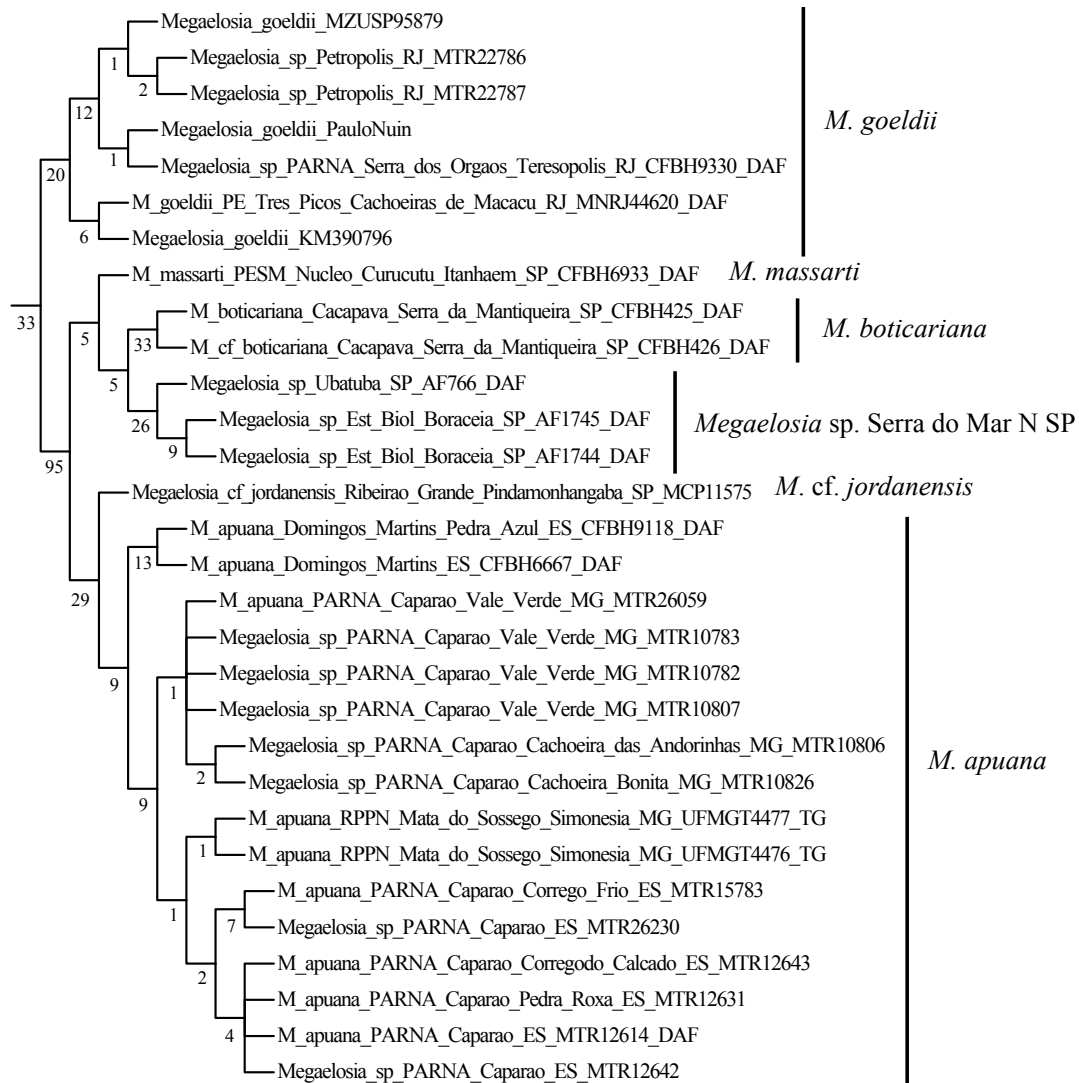


Figure 31. Strict consensus of 713 most parsimonious trees (32.405 steps) showing the relationship within the genus *Megaelosia*. Numbers under branches correspond to Goodman-Bremer support values.

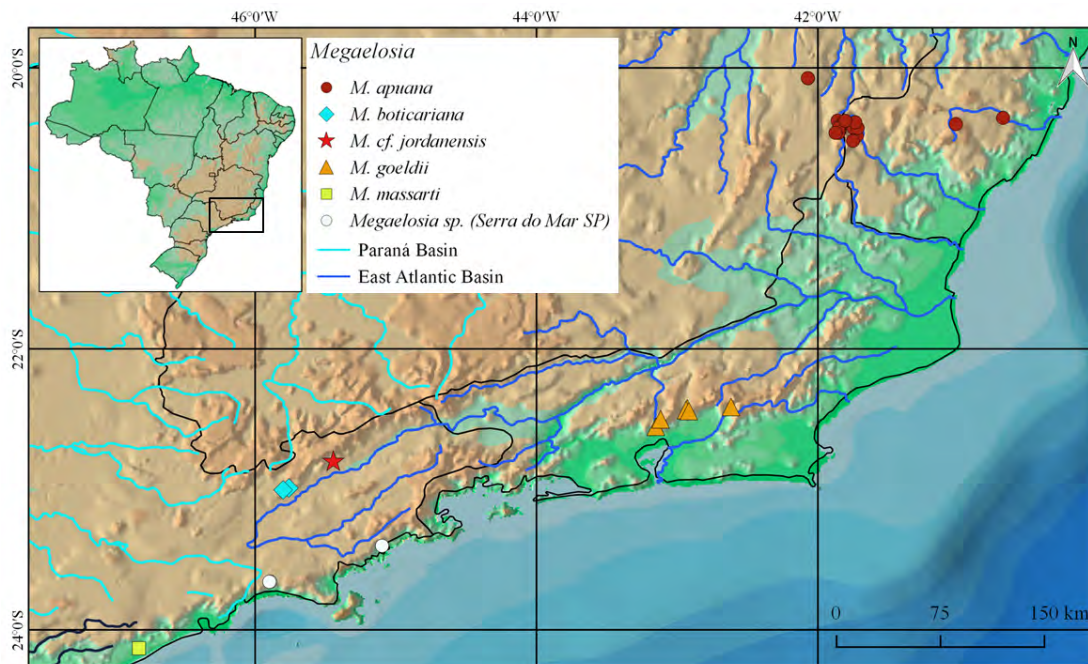


Figure 32. Distribution of *Megaelosia*.

### Relationship within *Hylodes*

The 23 known species of *Hylodes* plus unidentified terminals are distributed in 32 lineages, divided in five major clades: (1) “South” clade (GB = 64) is composed of seven subclades (*H. meridionalis* RS, *H. aff. meridionalis* “SC”, *Hylodes* sp. “Joinville SC”, *H. heyeri*, *Hylodes* sp. “Florianópolis SC”, and *H. perplicatus*), distributed in Southern Brazil (Rio Grande do Sul, Santa Catarina, and Paraná) and south of the state of São Paulo. This is the sister clade of all 26 remaining species of *Hylodes* sampled presently; (2) “Serra do Mar – no spine” clade (GB = 16) is composed of *H. charadranaetes*, *H. dactylocinus*, *H. cardosoi*, *Hylodes* sp. “Juquitiba SP”, *H. nasus*, *H. asper*, and *H. aff. asper* “SP”; (3) “Serra do Mar – spine” clade (GB = 41) is composed of *H. fredii*, *H. pipilans*, *Hylodes* sp. “Itanhém SP”, *Hylodes* sp. “Rio Claro RJ”, *Hylodes* sp. “Paranapiacaba SP”, *Hylodes* sp. “Bocaina – RJ/SP”, and *H. phyllodes*; (4) “MG/ES” clade (GB = 19) is composed of *H. otavioi*, *H. uai*, *H.*

*lateristrigatus* + *H. babax* 1, and *H. lateristrigatus* + *H. babax* 2; and (5) “Serra da Mantiqueira” clade (GB = 28) is composed of *H. ornatus*, *H. regius*, *H. magalhaesi*, *H. japi*, *H. glaber*, *H. sazimai*, *H. amnicola*, and *H. perere*. The relationships among these clades are (“Serra do Mar – no spine” (“Serra do Mar – spine” (“MG/ES”, “Serra da Mantiqueira”))).

The “South” clade (**Figure 33** and **Figure 34**) is distributed exclusively in the Southeast Atlantic basin and composed of six lineages: *H. meridionalis* (GB = 22) is composed of 11 terminals from Rio Grande do Sul plus individuals Praia Grande, on the border of the states of Santa Catarina and Rio Grande do Sul. *Hylodes* aff. *meridionalis* “SC” (GB = 30) is composed of 10 specimens from Santa Catarina (excluding Praia Grande). *Hylodes* sp. “Joinville SC” (GB = 1) is composed of two specimens from Joinville, sister group of *H. heyeri*. *Hylodes heyeri* (GB = 11) is composed of eight terminals from Paraná and south of São Paulo. *Hylodes* sp. “Florianópolis SC” (GB = 25) is composed of four specimens from Florianópolis, Sto Amaro da Imperatriz, and Águas Mornas, Santa Catarina. Finally, *H. perplicatus* (GB = 77) is composed of 11 terminals from Santa Catarina and South of Paraná. The “South” clade was supported by two unambiguous phenotypic transformations, the portion medial of *m. intermandibularis* with raphe (Ch. 139: 1 → 0) and elliptic nostril shape in tadpoles (Ch. 270: 0 → 1).

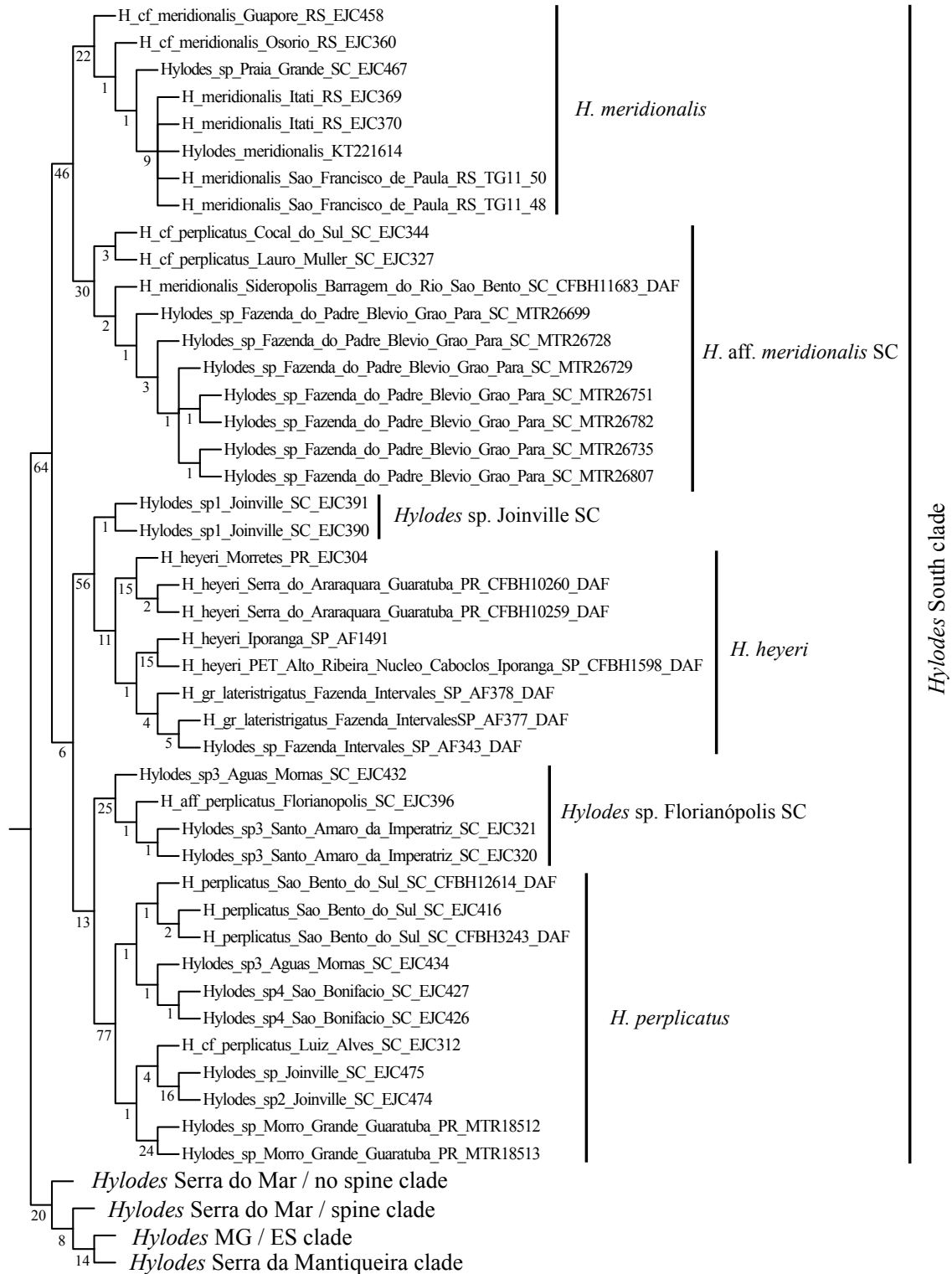


Figure 33. Strict consensus of 713 most parsimonious trees (32,405 steps), showing the relationship within *Hylodes* South clade. Numbers under branches correspond to Goodman-Bremer support values.



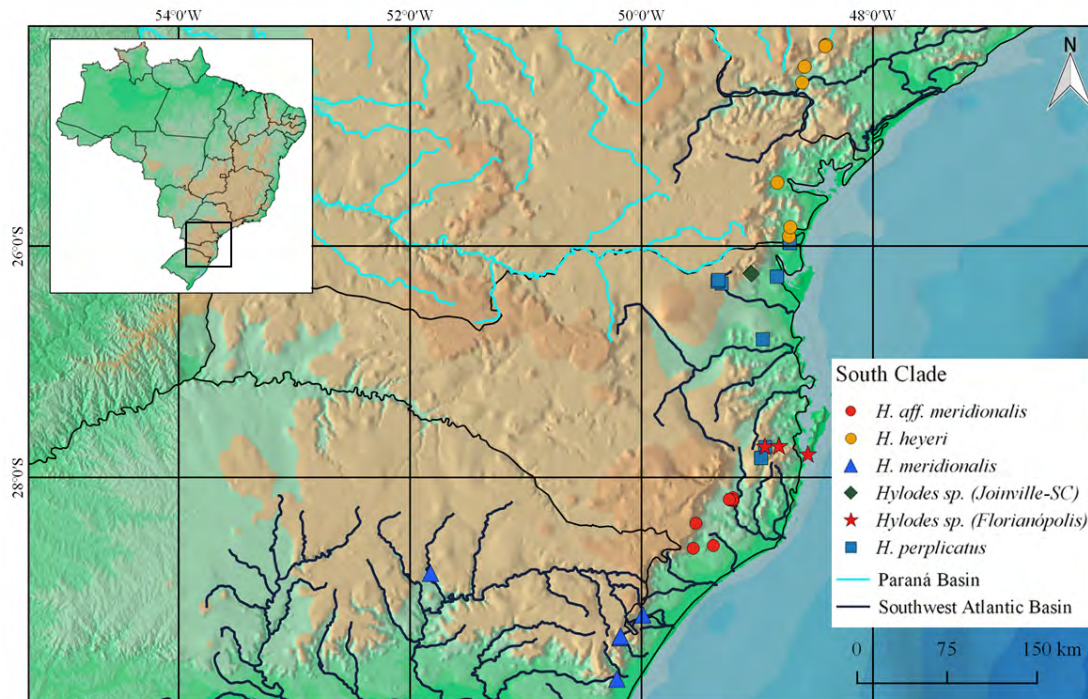


Figure 34. Distribution of *Hylodes* ‘South’ clade.

The “Serra do Mar – no spine” clade (**Figure 35** and **Figure 36**) is distributed in three basins: East Atlantic, Southeast Atlantic, and Paraná River. This clade is composed of (*H. charadranaetes* (*H. dactylocinus*, *H. cardosoi*) ((*Hylodes* sp. “JQUITIBA”, *H. nasus*) (*H. asper* “RJ”, *H. aff. asper* “SP”))). *Hylodes charadranaetes* (GB = 16) is represented by two specimens, including one topotype from Cachoeira de Macacu, RJ, East Atlantic basin. *Hylodes dactylocinus* (GB = 63) is composed of four specimens from Juréia, SP, Southeast Atlantic basin. *Hylodes cardosoi* (GB = 56) is composed of two specimens from Guaraqueçaba, PR, and five specimens from Guapiara, Miracatu, and Intervals, SP; this species occurs in the Paraná River and Southeast Atlantic basins. *Hylodes* sp. “JQUITIBA SP” (GB = 99) is composed of two specimens from JQUITIBA, Southeast Atlantic basin, sister group of *H. nasus* (GB = 73), with three terminals from Floresta da Tijuca, RJ, East Atlantic basin. *Hylodes asper* (GB = 36) is composed of five specimens from Itaguaí, Duque de Caxias,

Teresópolis, and Cachoeira de Macacu, state of Rio de Janeiro state, East Atlantic basin. This lineage was recovered as sister of *H. aff. asper* SP (GB = 14), composed of nine specimens from Serra do Mar (North of São Paulo) and Parati, Rio de Janeiro, occurring in the East Atlantic and Paraná River basins.

Unambiguous phenotypic transformations for the “Serra do Mar / no spine” clade were postaxial undeveloped postaxial fringe on finger II in females (Ch. 18: 0 → 1), preaxial fringe on finger III in males reach or surpass subarticular tubercle (Ch. 19: 4 → 2&3), and unpigmented testis (Ch. 128: 1 → 0).

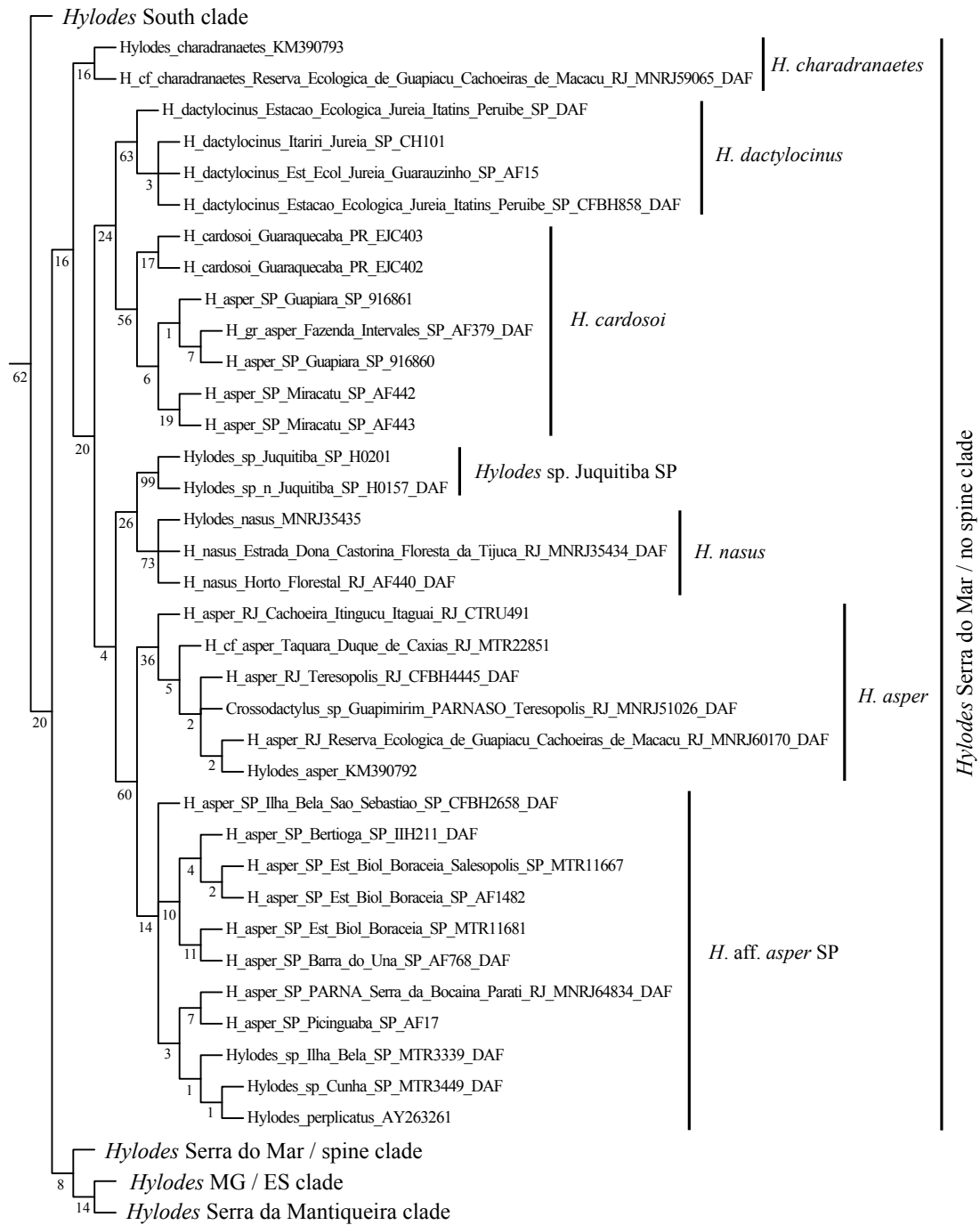


Figure 35. Strict consensus of 713 most parsimonious trees of 32.405 steps: relationship within *Hylodes* Serra do Mar / no spine clade. Numbers under branches are Goodman-Bremer support values.

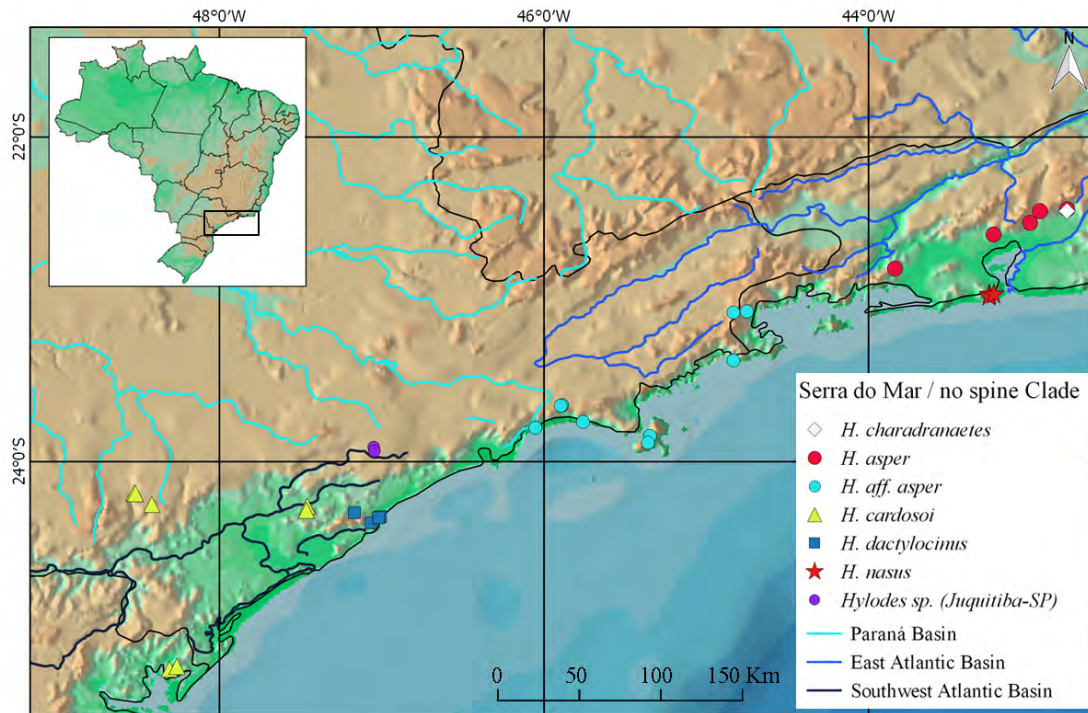


Figure 36. Distribution of *Hylodes* ‘Serra do Mar / no spine’ clade.

The “Serra do Mar – spine” clade (**Figure 37** and **Figure 38**) is composed of three currently valid species of *Hylodes* that have nuptial excrescences modified in spines (*H. fredii*, *H. pipilans*, and *H. phyllodes*). However, under nominal *H. phyllodes*, I recognize six distinct lineages. Altogether, the “Serra do Mar – spine” clade comprises ((*H. fredii*, *H. pipilans*) (*Hylodes* sp. “Itanhaém SP” (*Hylodes* sp. “Lídice RJ” (*Hylodes* sp. “Paranapiacaba SP” (*Hylodes* sp. “Bocaina” (*H. aff. phyllodes* “Ubatuba”, *H. phyllodes*)))))). This clade is distributed in three basins: East Atlantic, Southwest Atlantic, and Paraná River basins. *Hylodes fredii* (GB = 27) is composed of two topotypes from Ilha Grande, Angra dos Reis, RJ. *Hylodes pipilans* (GB = 11) is composed of nine specimens from Serra dos Órgãos and surroundings, RJ, East Atlantic basin. The *Hylodes phyllodes* (GB = 12) is composed of 10 specimens from north of the state of São Paulo (including the type locality Boracéia), Paraná River basin. The lineages *Hylodes* sp. “Itanhaém SP” (GB = 100) and *Hylodes*

sp. “Lídice RJ” (GB = 49) are composed of two specimens each, sampled from two localities that gave the name to each group; these lineages occur in the Southeast Atlantic and East Atlantic river basins, respectively. *Hylodes* sp. “Paranapiacaba SP” (GB = 21) is composed of two specimens from Paranapiacaba (Paraná River basin) and Intanhém (Southwest Atlantic basin). *Hylodes* sp. “Bocaina” (GB = 49) is composed of two specimens from Bocaina and Picinguaba, São Paulo, East Atlantic basin, and *Hylodes* sp. “Ubatuba” represented by a single specimen from Praia Vermelha, Ubatuba, SP, East Atlantic basin.

Unambiguous phenotypic transformations for the “Serra do Mar / spine” clade were nuptial excrescences on finger II of males (Ch. 05: 0 → 1) and absence of tadpoles nostril pigmentation (Ch. 273: 1 → 0).

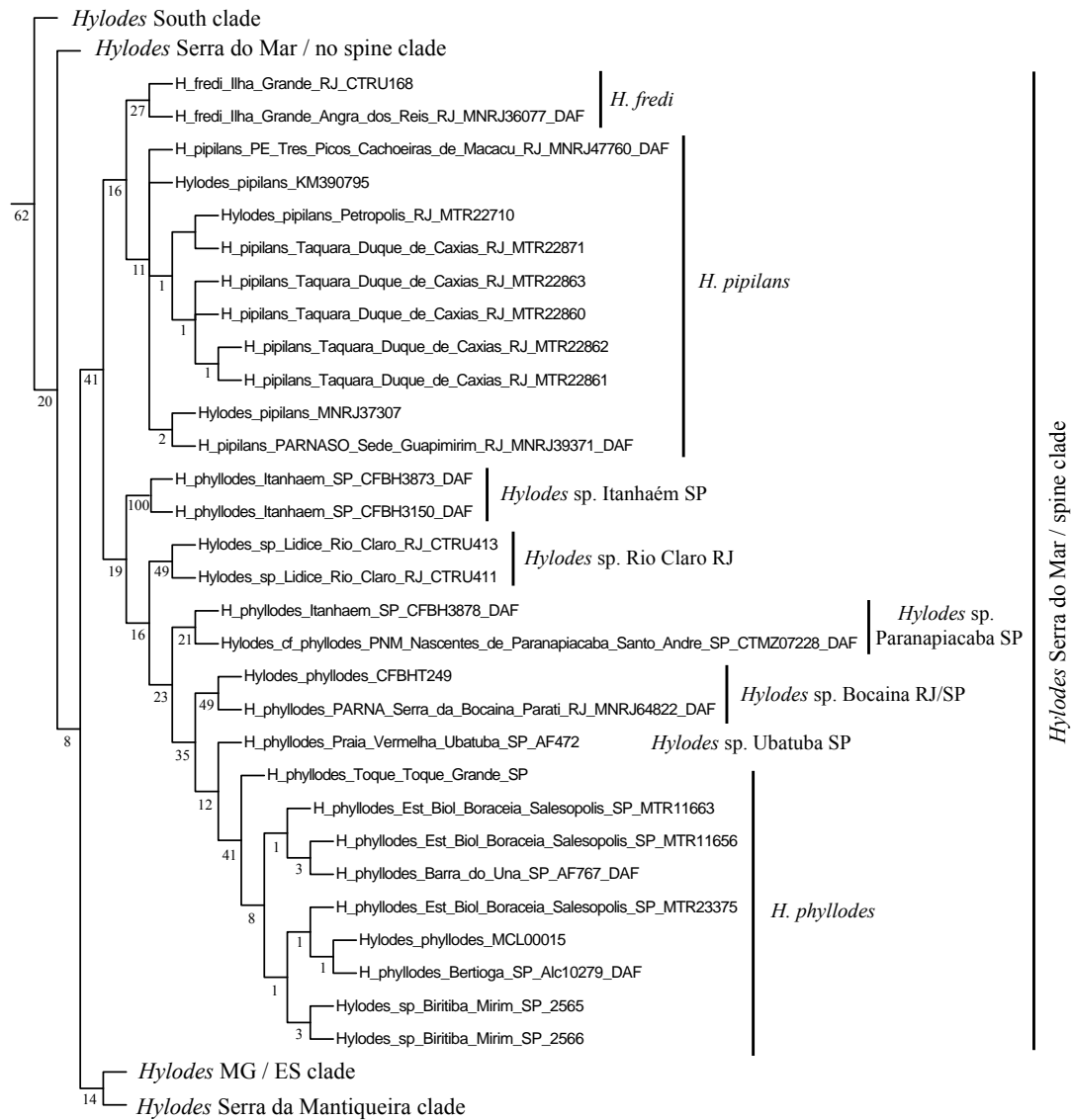


Figure 37. Strict consensus of 713 most parsimonious trees (32,405 steps), showing the relationship within *Hylodes* Serra do Mar / spine clade. Numbers under branches correspond to Goodman-Bremer support values.



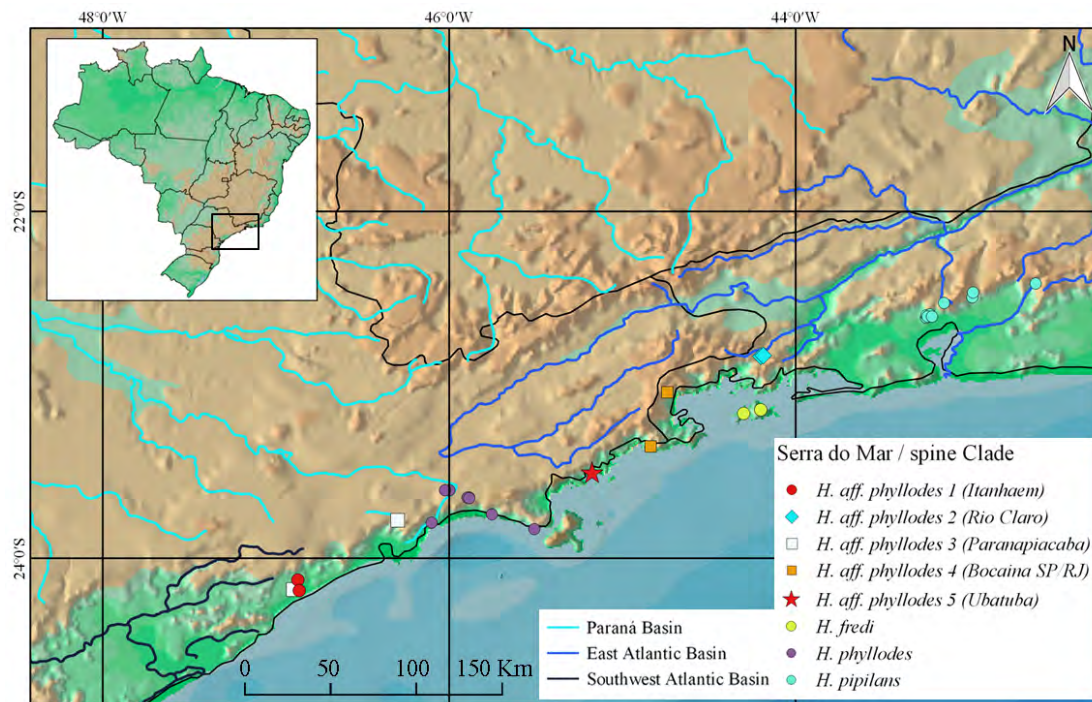


Figure 38. Distribution of Hylodes ‘Serra do Mar / spine’ clade.

The “MG/ES” clade (**Figure 39** and **Figure 40**) is composed of ((*H. otavioi*, *H. uai*) (*H. lateristrigatus* + *H. babax* 1, *H. lateristrigatus* + *H. babax* 2)) from East Atlantic and São Francisco River basins. *Hylodes otavioi* is represented by a single specimen from Morro do Pilar, MG, East Atlantic basin. *Hylodes uai* (GB = 19) is composed of six terminals from the state of Minas Gerais, East Atlantic and São Francisco River basins. The lineages *H. lateristrigatus* + *H. babax* 1 (GB = 16) is represented by three terminals, and *H. lateristrigatus* + *H. babax* 2 (GB = 6) by seven terminals, all of them previous from the states of Minas Gerais and Espírito Santo, East Atlantic basin.

Unambiguous phenotypic transformations for the “MG / ES” clade were preaxial fringe on finger III in males surpass subarticular tubercle (Ch. 19: 4 → 3), complete obliquolateral stripe (Ch. 110: 0 → 1), and free exocciptals (Ch. 173: 0 → 1).

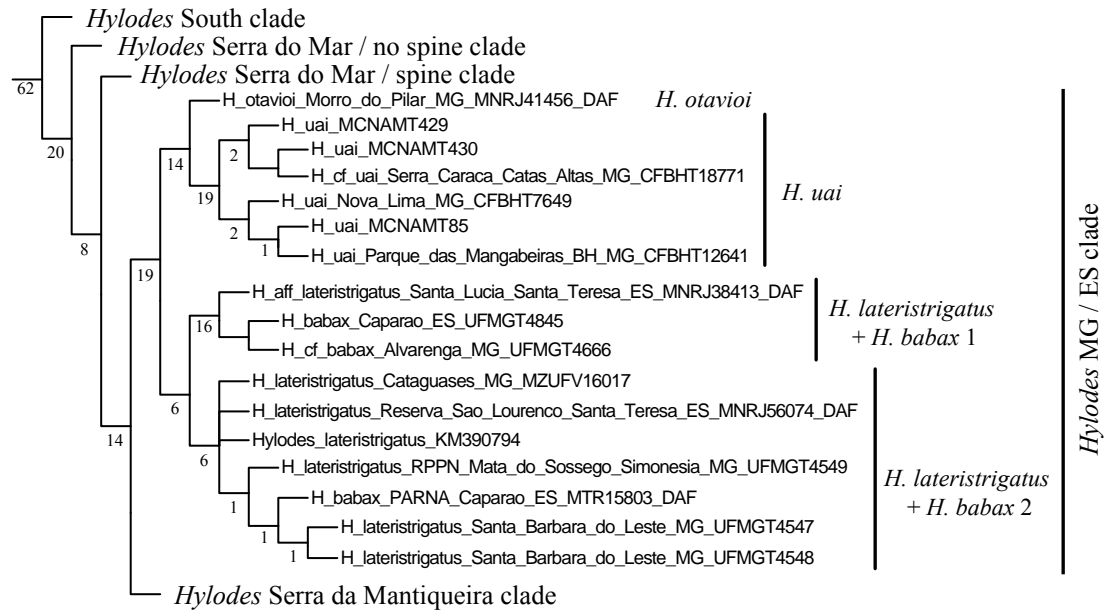


Figure 39. Strict consensus of 713 most parsimonious trees (32,405 steps), showing the relationship within *Hylodes* MG / ES clade. Numbers under branches correspond to Goodman-Bremer support values.

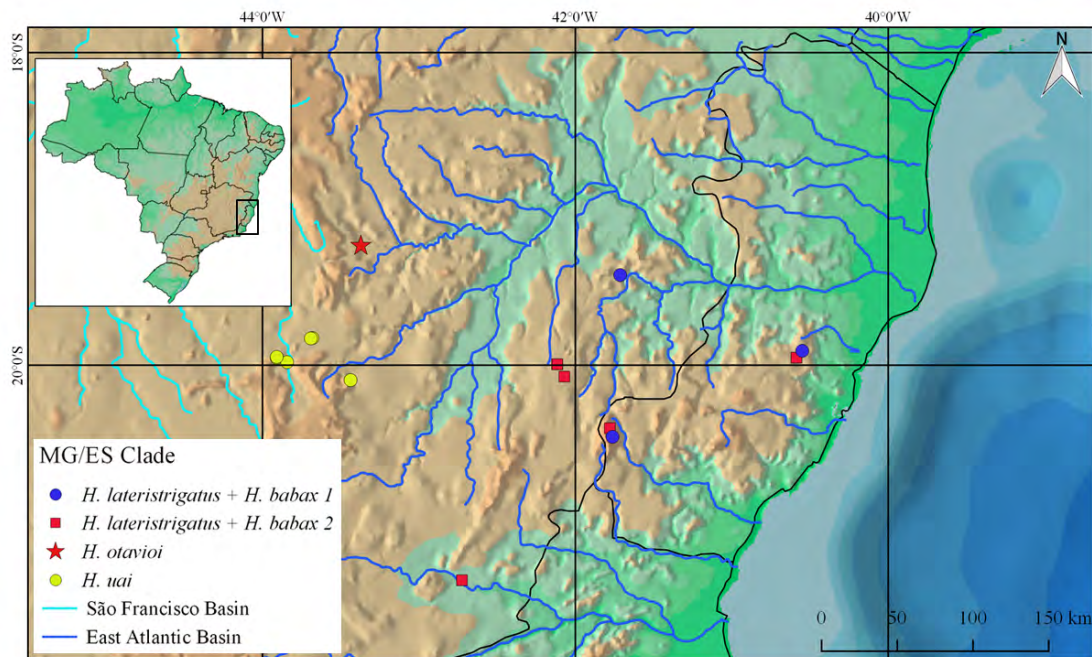


Figure 40. Distribution of *Hylodes* ‘MG / ES’ clade.

The “Serra da Mantiqueira” clade (**Figure 41** and **Figure 42**) is distributed throughout the Serra da Mantiqueira, in the intercession of Paraná River and East



Atlantic basins. It is composed of *H. ornatus*, *H. regius*, *H. japi*, *H. glaber*, *H. sazimai*, *H. amnicola*, and *H. perere*. The species *H. ornatus* and *H. regius* are represented by a single specimen each, from Parque Nacional do Itatiaia, Itamontes, Minas Gerais, East Atlantic basin. *Hylodes magalhaesi* (GB = 26) is composed of five terminals from Campos de Jordão, SP, Paraná River basin. The clade (*H. ornatus* (*H. regius*, *H. magalhaesi*)) is sister group of all remaining species of the “Serra da Mantiqueira” clade. *Hylodes japi* (GB = 41) is composed of six terminals from Jundiaí, SP, Paraná River basin, sister group of *H. glaber* (GB = 34). The latter lineage is composed of three terminals from Campos do Jordão, SP, one from Monte Verde, MG (Paraná River basin), one from Serra da Cantareira, SP (Paraná River basin), and two from Itatiaia, RJ (East Atlantic basin). The clade *H. japi* + *H. glaber* is the sister group of (*H. sazimai* (*H. amnicola* + *H. perere*)). *Hylodes sazimai* (GB = 16) is composed of three specimens from Campinas, Paraná River basin, sister group of *H. amnicola* + *H. perere*. *Hylodes amnicola* (GB = 27) is composed of three terminals from Ibitipoca, MG, East Atlantic basin. This lineage is the sister group of *H. perere* (GB = 41), composed of six terminals from Santa Bárbara do Monte Verde, Minas Gerais, East Atlantic basin. The single unambiguous phenotypic transformation recovered for the “Serra da Mantiqueira” clade is the anterior edge of scapula not concave (Ch. 267: 0 → 1).

The major clade composed of (Serra do Mar / no spine (Serra do Mar / spine (MG/ES, Serra da Mantiqueira))) is supported by the following unambiguous phenotypic transformations: tympanic membrane evident (Ch. 04: 1 → 2), developed preaxial fringe on finger IV in males (Ch. 28: 1 → 2), developed postaxial fringe on finger IV in males (Ch. 32: 1 → 2), weak posterodorsal dark outline on tympanum (Ch. 126: 0 → 1), two insertion points of the postaxial branch of the *m. extensor*

*digitorum comunis longus* (Ch. 163: 0 → 1), caput profundus III absent (Ch. 164: 1 → 0), wide contact between alary process and pars dentalis (Ch. 181: 0 → 1), and U-shape of the anterior region of esophageal process of cricoid cartilage (Ch. 219: 0 → 1).

The single unambiguous phenotypic transformations for the clade (Serra do Mar / spine (MG/ES, Serra da Mantiqueira)) was postaxial fringe on finger III in females reaches subarticular tubercle (Ch. 25: 2 → 1). Finally, the clade MG / ES + Serra da Mantiqueira presented three unambiguous phenotypic transformations: complete dorsolateral stripe (Ch. 107: 0 → 1), undeveloped omosternum (Ch. 256: 1 → 0), and posterior edge of sternum not expanded (Ch. 265: 1 → 0).

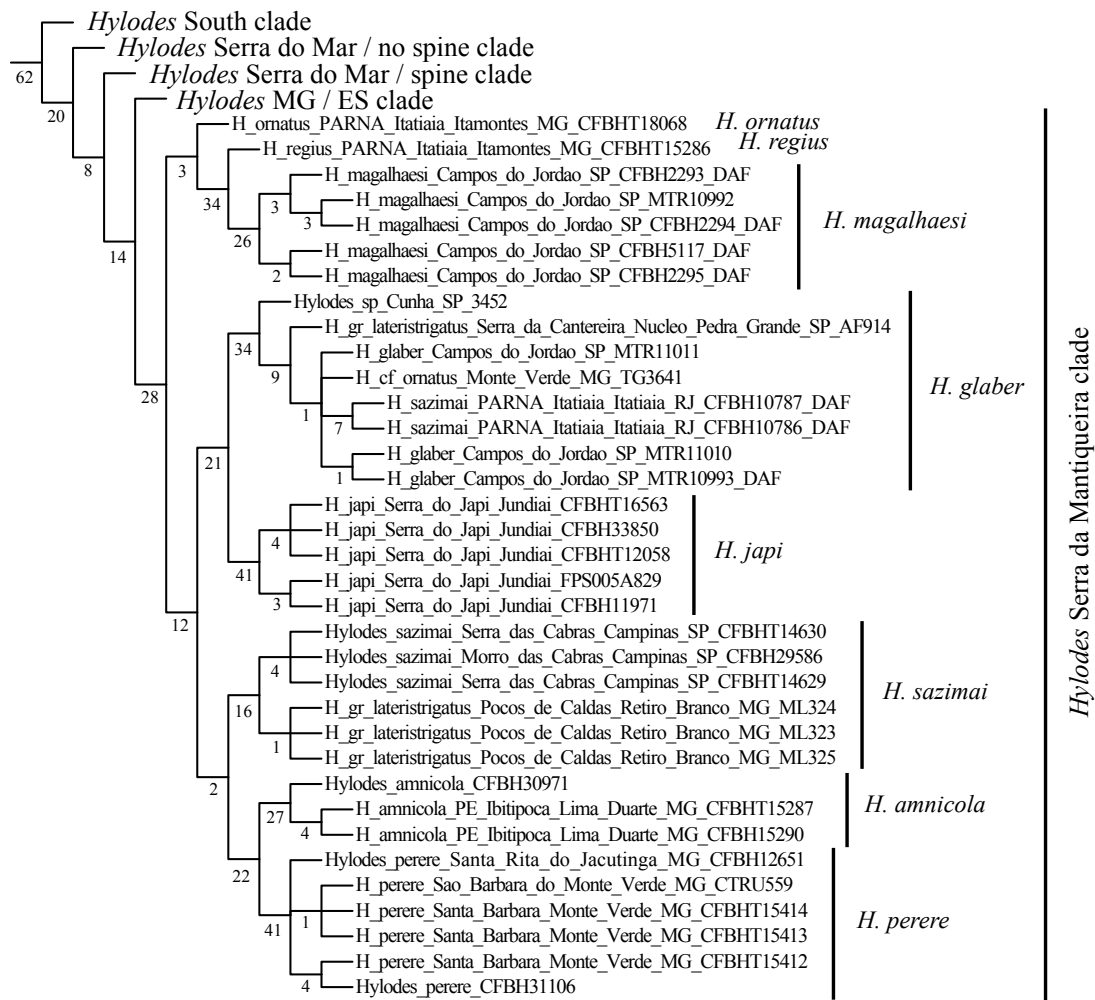


Figure 41. Strict consensus of 713 most parsimonious trees (32,405 steps), showing the relationship within *Hylodes* Serra da Mantiqueira clade. Numbers under branches correspond to Goodman-Bremer support values.

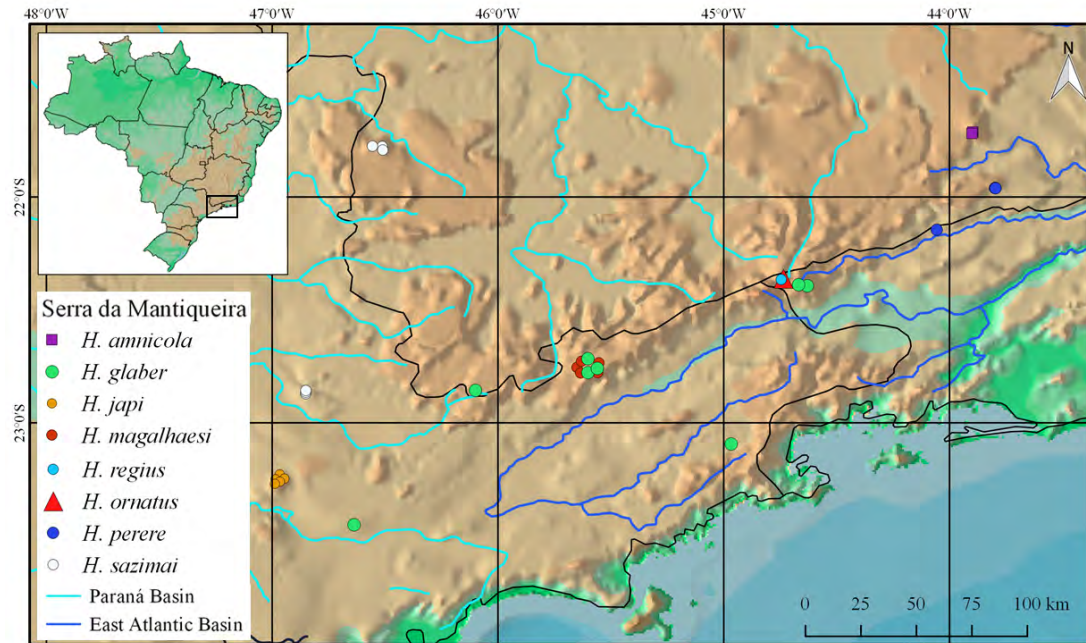


Figure 42. Distribution of *Hylodes* ‘Serra da Mantiqueira’ clade.

## DISCUSSION

### PHENETIC SPECIES GROUPS OF *HYLODES* AND *CROSSODACTYLUS*

Caramaschi and Sazima (1985) recognized three species groups in *Crossodactylus*, the *C. gaudichaudii* group, until Pimenta *et al.*'s (2014, 2015) revisions including *C. aeneus*, *C. bokermanni*, *C. caramaschii*, *C. cyclopinus*, *C. dantei*, *C. gaudichaudii*, and *C. lutzorum*; the *C. trachystomus* group, including *C. dispar*, *C. grandis*, and *C. trachystomus*; and the monospecific group of *C. schmidti*. Pimenta *et al.* (2014, 2015) questioned the validity of these groups and discouraged the use this classification for *Crossodactylus*. Although Pimenta *et al.*'s arguments were not supported by phylogenetic evidence, the phylogenetic relationships of

*Crossodactylus* recovered in my analysis confirmed that those authors were correct in their claims.

Heyer (1982) proposed four species groups in *Hylodes*, as follows: two monospecific groups, *H. glaber* group and *H. mertensi* group; *H. nasus* group, nowadays including *H. nasus*, *H. asper*, *H. cardosoi*, and *H. dactylocinus*; and *H. lateristrigatus* group, currently including *H. lateristrigatus*, *H. perplicatus*, *H. meridionalis*, *H. magalhaesi*, *H. ornatus*, *H. regius*, *H. babax*, *H. vanzolini*, *H. otavioi*, *H. charadranaetes*, *H. phyllodes*, *H. sazimai*, *H. heyeri*, *H. uai*, *H. amnicola*, *H. fredii*, *H. pipilans*, *H. perere*, and *H. japi*. Heyer's (1982) groups have not been tested phylogenetically; yet, they have been broadly employed in the taxonomic literature of *Hylodes* until presently (e.g., de Sá *et al.* 2015). My phylogenetic results only support the *H. nasus* group as proposed by Heyer (1982): (1) *Hylodes asper*, *H. cardosoi*, *H. dactylocinus*, and *H. nasus* grouped together forming a monophyletic clade; (2) *H. meridionalis*, *H. perplicatus*, and *H. heyeri* were found to be closely related; (3) *H. glaber* was placed embedded in a clade that included several representatives of Heyer's *H. lateristrigatus* group; and (4) *H. charadranaetes* was recovered as sister group of the clade composed of species originally allocated in the *H. nasus* group.

In view of the absence of phylogenetic support for most phenetic groupings of *Crossodactylus* and *Hylodes* proposed in previous decades, I advocate for the complete abolishment of these arrangements.

## COMMENTS REGARDING SOME LINEAGES

### *Crossodactylus trachystomus*

*Crossodactylus* specimens from the state of Minas Gerais were not recovered in the same clade. These specimens were distributed in six different lineages composing the *Crossodactylus* MG and *Crossodactylus* SE / NE clades. The most unexpected result regards the allocation of specimens of *C. trachystomus* in two sister lineages, *C. trachystomus* 1 and *C. trachystomus* 2, distributed mainly in Serra do Cipó (Santana do Riacho, MG) and Serra do Caraça (Catas Altas, MG), respectively; these lineages are sympatric in the region of Conceição do Mato Dentro, Minas Gerais. These results suggest the existence of two cryptic species under nominal *C. trachystomus*.

Pimenta *et al.* (2015) designated *C. bokermanni* as a junior synonym of *C. trachystomus*. I strongly suggest a detailed revision of all material referred to as *C. trachystomus*, especially those previously identified as *C. bokermanni*.

### *Megaelosia goeldii*

Pyron and Wiens (2011) recovered *Megaelosia goeldii* clustered with species of *Hylodes*. In the unpublished phylogeny of Fabri (2013), the genus *Megaelosia* was found to be paraphyletic, with *M. goeldii* recovered as sister group of *Hylodes*. Both studies only employed molecular evidence. In contrast, my analysis reconstructed the relationships of hylodids using total evidence (molecules + morphology) and recovered *Megaelosia* as a monophyletic genus, with *M. goeldii* positioned as sister of all other sampled congeners. This result rekindles the question raised by de Sá *et al.* (2014): “...in practical terms, do non-molecular characters matter?” These authors stated that their 156 morphological characters (approx. 3,5% of their total evidence

matrix) had a strong impact on their results, affecting support values and relationship within some clades significantly. de Sá *et al.* (2014) concluded that, clearly, non-molecular evidence mattered.

Results from a preliminary analysis employing exclusively the molecular data set gathered by myself (results not shown) agree with the topology recovered by Fabri (2013). Although this preliminary analysis was not intensive (24h using 8 CPU's – total of 192h/CPU's), it can still be interpreted as evidence that the monophyly of the genus *Megaelosia* is in great part supported by morphological data. Thus, my results corroborate the findings of de Sá *et al.* (2014), and I answer 'yes' to their question “*do non-molecular characters matter?*”

### ***Hylodes asper***

Specimens allocated under nominal *Hylodes asper* were recovered in two sister lineages. This result was expected based on an unpublished revision of *Hylodes*' tadpoles based on external morphology (Montesinos *et al.*, unpub. data; **Figure 43**).

During the examination of 15 lots of tadpoles of *H. asper* from five localities in the State of Rio de Janeiro (including the type locality) and two in the State of São Paulo, Southeastern Brazil, two morphotypes were consistently identified. Larvae from the municipalities of Teresópolis, Guapimirim, and Itaguaí, State of Rio de Janeiro, have nostrils with limits white and a dorsal, leaf-shaped intumescence, and tail with few round spots of moderate size, while larvae from the municipalities of Paraty, State of Rio de Janeiro, and Ubatuba and Santo André, State of São Paulo, have the limits of their nostrils decorated with a strongly marked (sometimes incomplete) dark ring and lacking an expanded dorsal intumescence, besides tail with enlarged round spots densely distributed (**Figure 43A-F**).

The present analysis included specimens from Itaguaí, Duque de Caxias, Guapimirim, Teresópolis, Cachoeira de Macacu, and Parati in the state of Rio de Janeiro, and Picinguaba, Ilha Bela, Cunha, Salesópolis, Barra do Una, and Bertioga in the state of São Paulo (**Figure 43G**). The results found here corroborate my previous findings based on external larval morphology. Although adult specimens from populations located in the states of Rio de Janeiro (plus Paraty) and São Paulo are indistinct, the geographically structured morphological variation of their tadpoles and clearly distinct molecular profile support their separation into two different species. The type locality of *H. asper* is Serra dos Orgãos, Rio de Janeiro; thus, the distribution of *H. asper* should be restricted to the state of Rio de Janeiro, plus Paraty in the state of São Paulo. All other populations from the state of São Paulo, excluding Paraty, should be allocated under a new name.



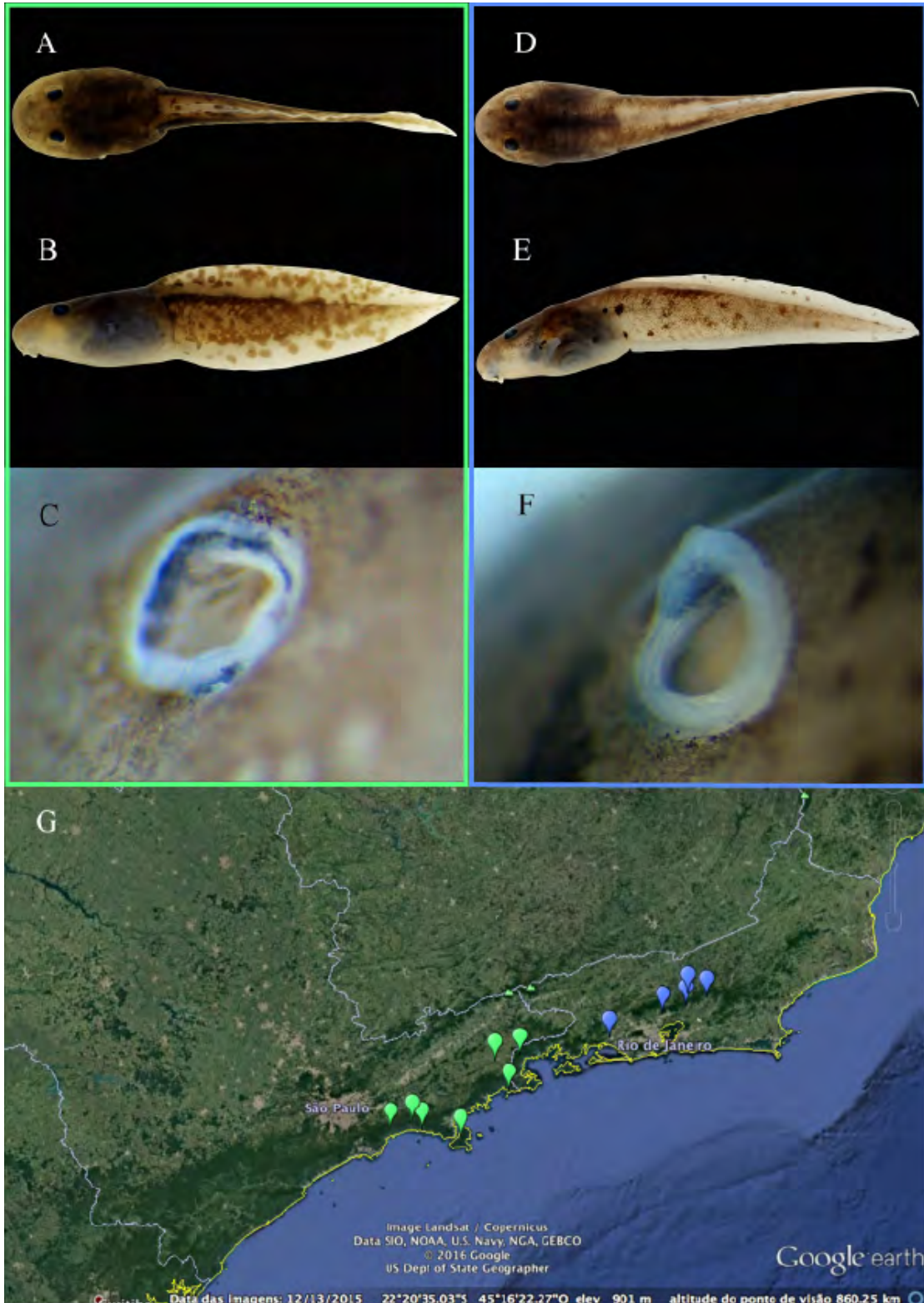


Figure 43. Morphological variation and distribution of two sets of populations currently allocated under nominal *H. asper*. (A-C) morphology of tadpoles from the state of São Paulo (green outline); (D-F) morphology of tadpoles from the state of Rio de Janeiro (blue outline); (G) distribution of *H. asper*, green dots for specimens from São Paulo and blue dots for specimens from Rio de Janeiro.

### ***Hylodes lateristrigatus* and *Hylodes babax***

*H. lateristrigatus* and *H. babax* could not be distinguished based on the topological arrangement of the populations sampled. Two clades included samples that have been associated to both nominals: (1) *H. lateristrigatus* + *H. babax* 1 with specimens from Santa Teresa (ES), Parque Nacional do Caparaó (ES), and Alvarenga (MG); (2) *H. lateristrigatus* + *H. babax* 2 composed of specimens from Santa Teresa (ES), Parque Nacional do Caparaó (ES), Simonésia (MG), Santa Bárbara do Leste (MG), and Cataguases (MG). The geographic distribution of representatives of these clades is shown in **Figure 44**. Both clades comprised specimens from Parque Nacional do Caparaó, type-locality of *H. babax*, and no topotypes of *H. lateristrigatus* from Serra do Órgãos, Teresópolis, RJ, were available for analysis. A more refined geographic sampling and rigorous analysis of specimens throughout the distribution of both species is needed to elucidate three major questions: (1) Which of these clades actually corresponds to *H. lateristrigatus*?; (2) Is *H. babax* a junior synonym of *H. lateristrigatus*?; (3) Do these clades represent distinct cryptic taxa?"

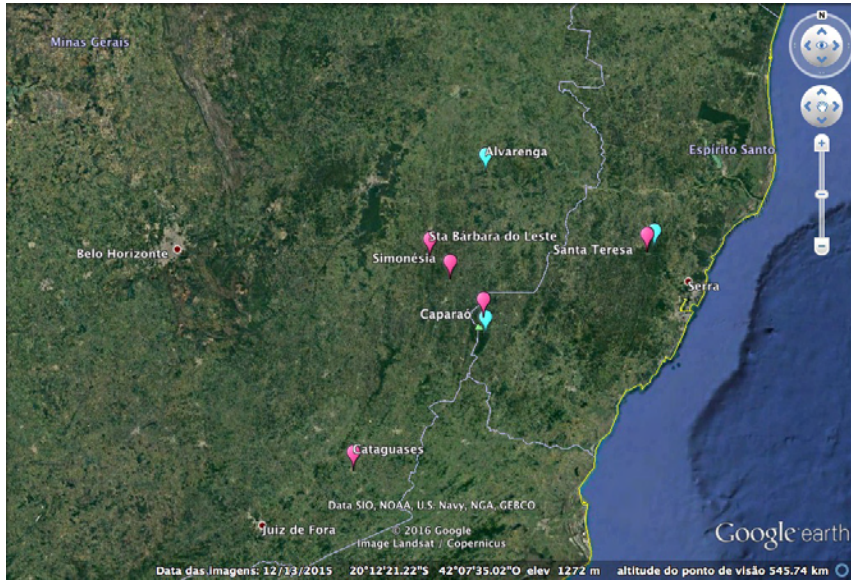


Figure 44. Distribution of *H. lateristrigatus* + *H. babax* 1, in blue, and *H. lateristrigatus* + *H. babax* 2, in pink.

### ***Hylodes glaber* and *Hylodes sazimai***

Five specimens identified as *H. sazimai* were included in the present analysis, three from Serra das Cabras, located in Campinas, state of São Paulo (same municipality that comprises its type locality), and two from Parque Nacional do Itatiaia, Itatiaia, state of Rio de Janeiro. This species was recovered as polyphyletic, and specimens from Itatiaia clustered with specimens of *H. glaber*. *Hylodes glaber* is only known from its type locality, Parque Nacional do Itatiaia, Itamontes, state of Minas Gerais, but it has not been collected since 1976 (Rocha *et al.* 2004). However, three specimens recently collected in Campos do Jordão, state of São Paulo, were associated to this nominal.

Two issues regarding *H. glaber* are: (1) I was not able to check any voucher of this species, and (2) specimens from the type locality were not included in my phylogenetic analysis. Consequently, the phylogenetic position of *H. glaber* remains questionable and additional data is needed to confirm its identity and distribution

range. My results indicate that specimens from Itaitiaia, RJ, identified as *H. sazimai* may represent *H. glaber*. If so, *H. glaber* should be considered a widely distributed species, ranging from Itaitiaia, RJ, to Monte Verde, MG, Campos do Jordão, Cunha, and Serra da Cantareira, SP. Unfortunately, the identity of this population will remain questionable until *H. glaber* be properly defined taxonomically. Furthermore, my results confirmed that the specimens of *H. sazimai* from Itaitiaia, RJ, have been misidentified. Thus, at this point, I can only state that the specimens from Itaitiaia do not correspond to *H. sazimai*.

## EVOLUTION OF SOME PHENOTYPIC CHARACTERS

### **Vocal sac**

The vocal sac structure and its association with the *interhyoideus* muscle were reported in eight character: (1) the occurrence of an external vocal sac (Ch.01); (2) the condition of the external vocal sac (Ch.02); (3) the position of the external vocal sac (Ch.03); (4) the presence of medial interruption of the *M. interhyoideus* (Ch.143); (5) the type of this interruption (Ch.144); (6) the *M. interhyoideus* condition (Ch.145); (7) the relationship between *M. interhyoideus* and the vocal sac (Ch.149); and (8) the interruption of internal vocal sac (Ch.150).

All species of *Hylodes* observed here have a modified portion of their skin that form double pouches that hold an internal vocal sac that projects through the *m. interhyoideus*; exception is *H. glaber* that lack a modified external vocal sac. This modified portion of the skin presents a two-fold thickness reduction and higher content of elastic fibers than non-modified gular skin. The external paired vocal sac was reported to four species of *Megaelosia* (*M. apuana* [Pombal *et al.* 2003],

*Megaelosia lutzae* [Izecksohn and Gouvêa 1987], *Megaelosia boticariana*, and *Megaelosia massarti* [Giaretta *et al.* 1993]). In contrast, there is no external evidence for an internally paired vocal sacs in *Crossodactylus*. Their gular skin is homogenous in thickness, vessel and glandular content, pigmentation, and fiber composition of the dermis. The modification of the skin seems to be exclusive to the clade *Megaelosia* + *Hylodes*.

In *Crossodactylus*, bilaterality is only evident externally when the frog is vocalizing. I codified the condition of the vocal sac mostly based on preserved specimens; thus, *Crossodactylus* species were codified as having “external vocal sac absent”. The only exception was *C. schmidti* that was reported by V. Caldart (pers. comm; **Figure 3A**) with a paired and subgular vocal sac. Also, other authors reported subtle bilobular expansions for *C. boulengeri* (Pimenta *et al.*, 2008), *C. caramaschii* (Bastos and Pombal, 1995), *C. cyclopinus* (Nascimento *et al.* 2005), and *C. dispar* (Pimenta, 2014). Although my character coding could be masking the presence of this structure in *Crossodactylus*, the external condition revealed in *C. schmidti* and the information from literature allowed me to confirm the presence of a paired external vocal sac in this genus.

The presence of paired vocal sacs contrasts with the condition found in all groups with which hylodids have been related to in recent phylogenetic analyses. Members of Alsodidae, Aromobatidae, Batrachylidae, Bufonidae, Cycloramphidae, Dendrobatidae, Odontophrynidae, and Rhinodermatidae all have externally simple, subgular sacs, when present (Boulenger, 1882; Burton, 1998; Cei, 1980; Grant *et al.*, 2006; Liu, 1935; Lynch, 1971; Tyler 1971a, 1974a). The presence of paired lateral vocal sacs was reported in species of *Crossodactylus*, *Hylodes* and *Megaelosia*. Thus, this character represents a putative morphological synapomorphy for Hylodidae.

The vocal sac mucosa in frogs originate bilaterally and, in the majority of species, fuse in the midline during early stages of post-metamorphic life (Inger and Greenberg 1956, Tyler 1975). Nevertheless, as described originally by McAlister (1959) for the genus *Spea*, both evaginations of the buccal cavity can remain disconnected in adults, thus resulting in ‘internally bilateral’ vocal sacs. An internal disconnection (*i.e.*, the double internal vocal sac) was found in all studied species of *Crossodactylus* and *Hylodes*.

The internal structure of the paired vocal sac of hylodids is particular in that the diverticulum is not entirely covered by submandibular musculature. Instead, the paired vocal sac passes ventrally through an opening in each contralateral *m. interhyoideus*. The examination of male juveniles and subadults suggests that the opening of the muscle occurs earlier than ventral projection of the vocal sac. This internal structure of hylodids does not resemble the structure of any other anuran described up until now. All species for which the myology and internal anatomy of paired vocal sacs has been described share the condition of having the vocal sac externally covered by the *m. interhyoideus* (Inger 1956, Tyler 1971, 1974). Consequently, the opening of the *m. interhyoideus* by the projection of vocal sacs described here is only present in Hylodidae.

Therefore, regarding the vocal sac structure, I recognize three putative synapomorphies to Hylodidae: (1) external double vocal sac; (2) disconnection of the internal vocal sac (two sacs); and (3) opening on *m. interhyoideus* through the diverticulum pass.

### **Fringe on fingers**

The fringes on fingers were codified regarding their extension (*i.e.*, longitudinal growth) and expansion (*i.e.*, lateral growth). Both fringe growths reveal a useful character system to distinguish major clades within Hylodidae. Eight characters concerning the extension of the fringe in males were recognized as synapomorphic for Hylodidae (the extension on preaxial and postaxial side of fingers II, III, IV, and V). The extension of the postaxial fringe on finger II and IV and preaxial fringe on finger V in females were recognized as synapomorphic for the clade joining *Hylodes* and *Megaelosia*.

Several small clades in all hylodid genera were also supported by the extension or expansion of these fringes. The clade joining *Crossodactylus* South / SP and *Crossodactylus* MG presented the synapomorphies expansion of skin on postaxial side of the finger II and III of males. *Hylodes* Serra do Mar / no spine clade was supported by undeveloped postaxial fringe on finger II in females and preaxial fringe on finger III in male that reaches or surpasses the subarticular tubercle. The preaxial fringe on finger II was recovered as synapomorphy of *Hylodes* ES / MG clade. A developed postaxial fringe on finger IV in males is a synapomorphy of the clade joining all *Hylodes*, except the *Hylodes* South clade. Postaxial fringe on finger III in females that reaches the subarticular tubercle supported the clade (*Hylodes* Serra do Mar / spine (*Hylodes* SE / NE clade, *Hylodes* Mantiqueira)). The clade that join all *Megaelosia*, except *M. goeldii* was supported by postaxial fringe on finger II in females surpassing the subarticular tubercle, preaxial fringe on finger III in females present along all finger, and preaxial fringe on finger IV in female surpassing the proximal subarticular tubercle. Finally, undeveloped preaxial and postaxial fringes on finger II in females support *M. goeldii*.

Interesting issues regarding the evolution of this character system were: (1) “preaxial fringe on finger III in males” (Ch. 19) that are present along all fringe in Hylodidae (Ch. 19: 0 → 4) and reduced its extension independently in two distinct clades, Serra do Mar / no spine (Ch. 19: 4 → 2&3) and MG / ES clades (Ch. 19: 4 → 3); (2) “postaxial fringe on finger II in females” (Ch. 17) reaches the subarticular tubercle in the clade *Hylodes* + *Megaelosia* (Ch. 17: 1 → 2) and increased in the clade joining all *Megaelosia*, except *M. goeldii* (Ch. 17: 2 → 3).

### **Paired scutes on finger**

Most species of Hylodidae present paired scutes atop of the digital discs, present in all genera. In some species, mainly in *Crossodactylus*, these scutes were codified as absent or inconspicuous. Grant *et al.* (2006) reported that “*all species of dendrobatids have distinctive paired dermal scutes atop digital discs*”; however these authors affirm that the scutes can be inconspicuous in some digits, especially the first and last digits.

Noble (1926) cited the sharing of this character between Hylodidae and Dendrobatidae. Latter, that author used this character to hypothesize that dendrobatids arose from *Crossodactylus* (Noble 1931). Griffiths (1959) states that these structures are “really glandulo-muscular organs and probably function to facilitate adhesion to foliage”; however, there are no evidence to support Griffiths’ thesis and their functional significance remains unknown (Grant *et al.* 2006).

Of all outgroup species analyzed in this study, only those from Dendrobatoidea present the paired dorsal scute. Thus, these structures was recovered as synapomorphy (Ch. 43: 0 → 1) for the clade (Hylodidae (*Thoropa milliaris*, Dendrobatoidea), with reversion for the inconspicuous or absent state (Ch. 43: 1 → 0) in the clade joining



*Crossodactylus* South / SP and *Crossodactylus* MG clades. Unfortunately, I did not check specimens of *T. milliaris*; however, Grant *et al.* (2006) codified this character as absent for that species. If so, this condition represents a reversal in *Thoropa milliaris*.

### **Testis**

Partially pigmented testis was recovered as a synapomorphy of Hylodidae (Ch. 128: 0 → 1), with a reversion for unpigmented testis in *Hylodes* Serra do Mar / no spine clade. No synapomorphies were recovered for *Crossodactylus* (possible reason given in ‘Results’ section); however, all species of *Crossodactylus* have a totally pigmented testis (state 2), except *C. trachystomus* that exhibits a partially pigmented testis.

Canedo (2008) suggested that the testis variably pigmented observed in *Hylodes* is unique among hylodids. That author described the testis of the other genera as largely pigmented in *Crossodactylus* and unpigmented in *Megaelosia*. Unfortunately, I did not receive permission to dissect any male specimen of *Megaelosia* (only one female specimen of *M. goeldii* was dissected); thus, the unpigmented condition observed by Canedo (2008) could not be confirmed in *Megaelosia*.

Grant *et al.* (2006) states that testis pigmentation in dendrobatids increases ontogenetically, with the mesorchia of juveniles being invariably entirely unpigmented (white) and melanosis beginning medially and eventually covering the testis entirely, forming either a dark reticulum or a solid dark color. The authors also comment that polymorphism among adults is rare. In the present analysis, only adults were observed and few specimens of each species were analyzed; however, all partially pigmented testis observed showed pigmentation approximately in the middle

of the testis. My results are consistent with those of Grant *et al.* (2006); however, within Hylodidae, the pigmentation of testis seems to have clear phylogenetic signal; pigmented testis is the ancestral condition for Hylodidae (present in *Crossodactylus*), with loss of pigmentation (partially or totally) in *Hylodes* and *Megaelasia*.

### **The *intermandibularis* muscle**

I codified six characters regarding the muscle *intermandibularis*: its relationships with *m. submentalis* (position and degree of overlap); presence of raphe or aponeurosis on the medial portion of the muscle; occurrence, type, and condition of apical supplementary elements.

The *m. intermandibularis* overlapping the posterolateral region of *m. submentalis* and the presence of apical supplementary elements of *m. intermandibularis* were recovered as synapomorphies of the clade (*Thoropa milliaris* (Dendrobatoidea, Hylodidae)).

The presence of anteromedial supplementary elements was recovered as a synapomorphy of Hylodidae. Another synapomorphy for this family was the state '*m. intermandibularis* overlaps the posterolateral region of *m. submentalis*'. Additionally, the states '*m. intermandibularis* overlaps all posterior edge' and 'only medially posterior edge of *m. submentalis*' were recovered as synapomorphies of *Hylodes*. More internally, the presence of raphe on the *m. intermandibularis* was recovered as a synapomorphy of the *Hylodes* South clade.

My analysis revealed the importance of the *m. intermandibularis* for hylodid systematics. Similar conclusions were achieved by Tyler (1971) with respect to the phylogenetic importance of the superficial gular musculature (*i.e.*, *m. submentalis*, *m. intermandibularis*, and *m. interhyoideus*) for the distantly related Hylidae. Taking into

account the putative synapomorphies regarding the association of vocal sac and *m. interhyoideus* (discussed above), the superficial musculature of the gular region of hylodids is clearly highly informative, even though this family is at least 15 times less diverse than Hylidae.

### **Zygomatic ramus of squamosal**

I codified five characters related with zygomatic ramus of squamosal: condition, shape of the anterior edge, orientation, length, and width. This structure has been regarded as informative for Hylodidae since Lynch (1971), who employed, among other characters, the morphology of the zygomatic ramus of the squamosal to diagnose all three hylodid genera: (1) moderate length, pointed, widely separated from maxilla, and otic ramus slightly shorter than zygomatic *ramus* as diagnostic characters in *Crossodactylus*; (2) short, truncated, widely separated from maxilla, and otic *ramus* as long as zygomatic *ramus* diagnostic characters in *Hylodes*; and (3) long, expanded, in broad contact with maxilla diagnostic character in *Megaelosia*.

Although Lynch (1971) analyzed only one species of each hylodid genus (*Crossodactylus gaudichaudii*, *Hylodes asper*, and *Megaelosia goeldii*), my analysis based on a much larger taxon sampling partially corroborate his findings. On one hand, I confirmed the presence of a long zygomatic *ramus* of squamosal in broad contact with maxilla in *Megaelosia*; otic *ramus* as long as zygomatic *ramus* in *Hylodes*; and zygomatic *ramus* with truncate anterior edge in most *Hylodes* species. On the other hand, the otic *ramus*, of the squamosal was found to be as long as the zygomatic *ramus*, in *Crossodactylus*, while Lynch (1971) reported a shorter otic *ramus*). Similarly, a truncate anterior edge of the zygomatic *ramus* was observed in *Hylodes* and *Crossodactylus*, and a pointy edge was mainly observed among outgroup

species, while Lynch (1971) reported a pointy edge of the zygomatic *ramus* in *C. gaudichaudii*.

Two characters codified in the present analysis were not reported by Lynch (1971): orientation and width of zygomatic *ramus*. All hylodid species have the zygomatic *ramus* of squamosal anteriorly oriented; anteroventral orientation of this structure was only found in two unrelated clades from southeastern and southern Brazil: the first includes *C. caramaschii*, *C. aff. camaschii* SP, and *Crossodactylus* sp. Paraná East, and the second all species of the *Hylodes* 'South' clade, except *H. meridionalis* and *H. aff. meridionalis* SC. The zygomatic *ramus* of the squamosal wider than otic *ramus* was recovered as a synapomorphy of *Hylodes* + *Megaelosia* (Ch. 202: 2 → 0), whereas the opposite condition, *i.e.*, zygomatic *ramus* narrower than otic *ramus*, was predominant in *Crossodactylus*.

Although Lynch (1971) has not performed a cladistics in his study of Leptodactyloids, my results confirmed the importance of the squamosal *rami* for hylodid systematics and added two novel characters that proved highly informative.

### **Tadpoles**

Amphibian larvae are potentially as informative for systematics and evolutionary studies as individuals in mature stages (Orton 1952, 1953; Lannoo 1987; Haas 2003; Candiote 2007; Candiote and Altig 2010). Despite three quarters of the existing frogs species have the tadpole stage during some period of their development, only one third of these larvae is known (McDiarmid and Altig 1999). Even smaller is the fraction of species whose larvae have been adequately described, illustrated, and diagnosed. The difficulty in recognizing anurans in larval stage to the species level likely explains the reduced number of species with known larvae.

Additionally, the morphology of anuran larvae was thought to be highly adaptive to their environment and, thus, poorly reflecting the phylogenetic relationships among species. However, several papers have shown that tadpole characters contain phylogenetic signals (Haas 1996, 1997, 2003; Larson and de Sá 1998; de Sá and Swart 1999; Maglia *et al.* 2001; Grosjean *et al.* 2015). Characters of tadpoles are complementary to those of adults and useful to resolve taxonomic and phylogenetic problems in cases where adult characters alone have been insufficient to distinguish species. In the present work, larval characters were essential for the detection of two distinct lineages allocated under nominal *H. asper*.

I included 23 larval characters in my phylogenetic analysis, resulting in several character states that were recovered as unambiguous synapomorphies at some level, from family relationships to lineages. Within this range, I highlight several important results: (1) cloacal tube on the right side of the body (Ch. 278: 0 → 1) recovered as synapomorphy for the clade with *Thoropa milliliaris*, Dendrobatoidea, and Hylodidae; (2) presence of ventral lateral line (Ch. 285: 0 → 1) and presence of supernumerary papillae (Ch. 291: 0 → 1) as synapomorphies for Hylodidae; (3) absence of nostril ornamentation as synapomorphy for *Hylodes* (Ch. 271: 1 → 0); (4) elliptic nostril was recovered as synapomorphy for *Hylodes* 'South' clade (Ch. 270: 0 → 1); and (5) dorsal fin originating before to the final portion of the body in *H. amnicola* (Ch. 286: 1 → 0). Thus, the results found in present study reinforce the importance of the inclusion of larval characters on systematics studies.

## CURRENT DISTRIBUTION PATTERN

Hylodids are distributed in five main river basins of South America: East Atlantic, Southeast Atlantic, Paraná River, São Francisco River, and North-Northeast Atlantic. Parsimony analysis of endemism (PAE) detected five areas of endemism based on the distribution of hylodids. The first area of endemism identified by PAE, East Atlantic basin, is supported by 29 species. It comprises the eastern portion of the the state of Bahia, the states of Espírito Santo and Rio de Janeiro, east of Minas Gerais, and the northeastern portion of the state of São Paulo. This area was nested in a larger area of endemism composed of the East Atlantic + São Francisco river basins, supported by two endemic species. The São Francisco basin is the only area that lacks exclusive lineages of hylodids. The only two hylodids species occurring in that area, *C. trachystomus* 2 and *H. uai*, can be additionally found in the East Atlantic basin.

Southeast Atlantic basin is the third area of endemism detected by PAE. This area comprises the eastern portion of the states of São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, and harbours 12 endemic species. The fourth area is the Paraná River basin, which encompasses a broad area covering the western portion of the states of Rio Grande do Sul, Santa Catarina, Paraná, and São Paulo, state of Mato Grosso do Sul, and southern portion of the states of Minas Gerais, Tocantins, and Mato Grosso; this basin was supported by six endemic species. The third and fourth areas of endemism detected by PAE are nested in the last area of endemism, named ‘Southeast Atlantic + Paraná River’, supported by five species. Appendix 04 reports absence and presence of hylodid’s lineages for each area.

The optimization of the distribution hylodid species over my trimmed phylogenetic tree (*i.e.*, lineages tree) revealed the likely origin of Hylodidae in the

East Atlantic basin, where the most part of the taxonomic diversity of this family found currently. Subsequent biogeographic events responsible for the presence of hylodid species in adjacent river basins occurred subsequently and affected all three hylodid genera. A general pattern observed in this preliminary analysis suggests that allopatric speciation likely took place in the Southeast Atlantic and Paraná River basins throughout a more recent phase of the diversification history of Hylodidae (**Figure 45**).

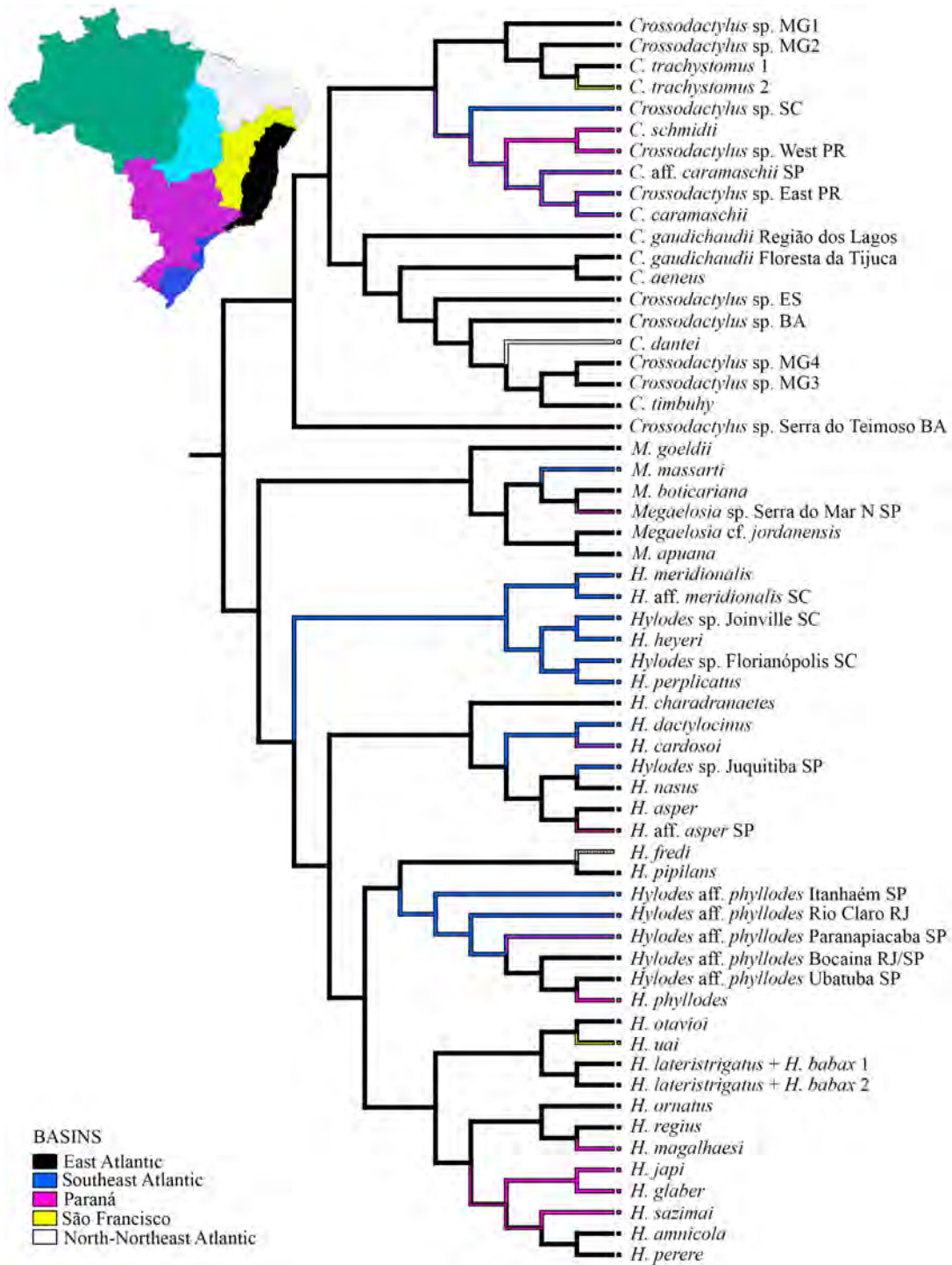


Figure 45. Optimization of the main basins of Brazil on the Hylodidae tree generated in this study.



## CONSERVATION ISSUES AND ADVANCES FOR THE HYLODIDAE EVOLUTION COMPREHENSIVE

Hylodidae is currently composed of 46 species; however, approximately one fifth of these species have not been collected from decades. The IUCN Red List of Threatened Species analyzed 40 species (approximately 87%) of Hylodidae and most of them (28 species) were listed as “Deficient Data” (DD), even though they acknowledged that many have not been collected for several years (*e.g.*, *C. dispar*, *H. babax*, and *H. glaber*; IUCN 2016). Endemic to the Atlantic Rain Forest, hylodids are extremely vulnerable to deforestation (Laia and Rocha 2012). The fragmentation of their forested habitat is probably one of the main reasons that behind the vanishing of numerous populations of hylodid species throughout their distribution.

Besides habitat fragmentation, other factors should be influencing the decline and/or disappearance of some species of Hylodidae, such as global warming and related diseases. For *Hylodes asper* and *Hylodes phyllodes*, local extinctions have been attributed to climate change (Heyer *et al.* 1988, Bertoluci and Heyer 1995). *Batrachochytrium dendrobatidis* (Bd) is a fungus that causes chytridiomycosis, affecting several species of anurans worldwide. Recent studies revealed that Bd has been present in Atlantic Rain Forest for at least a century (Rodriguez *et al.* 2014), and documented its association to several species of Hylodidae. Rodriguez *et al.* (2014) also reported a high prevalence of Bd in riparian species (see Fig. 5 in Rodriguez *et al.* 2014), indicating that the extreme association of hylodids with rivulets might somehow facilitate the spread of Bd among these frogs.

The fast decline of hylodid species and the absence of basic biological information for most representatives of this group is worrisome. The huge number of

putative new species detected presently reinforces the necessity of additional studies focused on these lineages. Recently developed laboratory protocols and technologies are expected to facilitate the collection of data useful for delimiting hylodid species, such as DNA extraction from museum species (fixed in formalin) and production of sequence data through Next Generation Sequencing (NGS) techniques (Ruane and Austin 2017). Applying these methodologies in the near future, I hope to be able to cover the complete Hylodidae's phylogeny for a better comprehension of this intriguing family.

## CONCLUSION

- *Thoropa milliliaris* 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.

## 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.

## 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 especificidade 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.

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## APPENDICES

Appendix 01. Outgroup Genbank accession number and sequences produced in this study for each loci.

OUTGROUP	H1 (12S / 16S)	COI	Cytb	RAG	28S	H3	Rhod	Tyr
<b>Allophrynidae</b>								
<i>Allophryne ruthveni</i>	AY843564		AY843786	AY844361			AY844538	KC604076
<b>Alsodidae</b>								
<i>Eupsophus calcaratus</i> MACN39079	JX204201	JX203918	JX203986				JX204132	KC593365
<b>Aromobatidae</b>								
<i>Allobates zaparo</i> USNM546405	DQ502026	DQ502752	DQ502455	DQ503305	DQ502955	DQ502301	DQ503192	HQ290940
<i>Anomaloglossus roraima</i> CPI10217	DQ502259		DQ502691	DQ503394		DQ502392		
<i>Aromobates nocturnus</i> AMNH-A130041	DQ502154	DQ502859	DQ502590		DQ502996	DQ502357	DQ503243	
<i>Mannophryne trinitatis</i> MVZ199828	DQ502131	DQ502838	DQ502562	DQ503345		DQ502347	DQ503236	
<i>Rheobates palmatus</i> MUJ5003	AH015828	DQ502925	DQ502694				DQ503271	DQ503172
<b>Batrachylidae</b>								
<i>Batrachyla leptopus</i> MACN38008	AY843572	JX203910	AY843794	AY844369	AY844204	DQ284119	AY844546	AY844028
<b>Brachycephalidae</b>								
<i>Ischnocnema parva</i> MNRJ51356	JX267379							JX267787
<b>Bufonidae</b>								
<i>Atelopus flavescens</i> BPN726	DQ283259					DQ284282	DQ283928	
<i>Amazophrynella minuta</i> MJH7095	DQ502120	DQ502828	AY843804	DQ503337		DQ284096	AY844555	
<i>Melanophryniscus klappenbachi</i>	AY843699		AY843944	AY844478	AY844306	DQ284060	DQ283765	
<i>Rhinella pygmaea</i> CFBH2894	KP685229		KP685013				KP685180	
<i>Rhinella sp.</i> DAF11.101	This study		This study				This study	
<b>Centrolenidae</b>								
<i>Nymphargus bejaranoi</i>	AY843576		AY843798	AY844372	AY844208		AY844549	AY844029
<i>Vitreorana eurygnatha</i>	AY843595		AY843814	AY844383	AY844217		AY844567	
<b>Ceratophryidae</b>								
<i>Ceratophrys cornuta</i> CFBH20082	KP295608	KP295688		KP295589			KP295708	KP295668
<i>Chacophrys pierottii</i> MACN47251	KP295621		KP295737	KP295597			KP295716	KP295677
<i>Lepidobatrachus laevis</i> MACN43499	KP295631	KP295699	KP295699	KP295599			KP295720	KP295681
<b>Craugastoridae</b>								
<i>Pristimantis fenestratus</i> MTR37091	Targino_2016				Targino_2016			

**Cycloramphidae**

<i>Cycloramphus boraceiensis</i> CFBH5757	DQ283097	DQ502856	DQ502588	DQ503357	DQ283498	DQ284147	DQ283813	DQ282924
<i>Thoropa miliaris</i> CFBH3239	DQ283331	DQ502874	DQ502607			DQ502369		
<i>Zachaenus parvulus</i> CFBH10120	KC593362							

**Dendrobatidae**

<i>Adelphobates quinquevittatus</i> OMNH36665	DQ502063	DQ502785	DQ502494		DQ502966	DQ502313	DQ503203	
<i>Ameerega trivittata</i>	DQ502021	DQ502744	DQ502449			DQ502298		DQ503145
<i>Colostethus panamensis</i>	DQ502172	DQ502875	DQ502608		DQ503010	DQ502370		
<i>Dendrobates tinctorius</i> UTA-A56495	DQ502248	DQ502918	DQ502680	DQ503387	DQ503028	DQ502384	DQ503266	
<i>Epipedobates anthonyi</i>	DQ502151	DQ502853	DQ502584			DQ502355		
<i>Hyloxalus bocagei</i> OMNH34070	DQ502038	DQ502764	DQ502469	DQ503314	DQ502961	DQ502308	DQ503199	
<i>Minyobates steyermarki</i>	DQ371310 / DQ371321		DQ371340					
<i>Oophaga lehmanni</i> CWM19050	DQ502034	DQ502761	DQ502465	DQ503310	DQ502957	DQ502304	DQ503195	
<i>Phyllobates terribilis</i> AMNH-A118566	DQ502157	DQ502861	DQ502593	DQ503358	DQ502999	DQ502360	DQ503244	
<i>Ranitomeya ventrimaculata</i> OMNH36666	DQ502071	DQ502793	DQ502502	DQ503320	DQ502969	DQ502316	DQ503206	DQ503148
<i>Silverstoneia nubicola</i> SIUC7652	DQ502161	DQ502863	DQ502596	DQ503359	DQ503000		DQ503245	

**Eleutherodactylidae**

<i>Eleutherodactylus cooki</i> USNM326784	EF493539					GQ 345213		EF493455
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**Hemiphractidae**

<i>Flectonotus sp.</i> CFBH5720	AY843589		AY843809	AY844379	AY844215		AY844562	AY844038
<i>Hemiphractus helioi</i>	AY843594		AY843813	AY844382		DQ284084	AY844566	

**Hylidae**

<i>Dendropsophus minutus</i> MACN33799	AY549345	KJ933672	AY843883	AY844432	DQ283456	DQ284046	DQ283758	AY844089
<i>Bokermannohyla sp.</i> DAF11.056	This study		This study	This study		This study	This study	

**Leptodactylidae**

<i>Leptodactylus fuscus</i> AMNH-A139088	DQ283404				DQ283716	DQ284385	DQ284015	
<i>Paratelmatobius sp.</i> CFBHT240	DQ283098				DQ283499	DQ284148	DQ283814	DQ282925
<i>Physalaemus cuvieri</i>	AY843729		AY843975	AY844499	AY844330		AY844717	

**Odontophrynidae**

<i>Proceratophrys avelinoi</i> JF1947	DQ283038					DQ284065	DQ283769	DQ282903
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**Rhinodermatidae**

<i>Rhinoderma darwini</i>	FJ882754						AY364403	
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**Telmatobiidae**

<i>Telmatobius jahuira</i> AMNH-A165110	DQ283040	DQ502743	DQ502448				DQ283770	
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Appendix 02. Hylodidae Genbank accession number and sequences produced in this study for each loci.

INGROUP	H1	COI	Cytb	RAG	28S	H3	Rhod	Tyr
<b><i>Crossodactylus aeneus</i></b>								
<i>Crossodactylus aeneus</i> KM390791	KM390791							
<i>C. aeneus</i> Barreira RJ CFBHT4476 DAF11.059	This study		This study	This study		This study	This study	
<i>C. aeneus</i> Riacho prox Rio Soberbo PARNASO RJ MNRJ37311 DAF11.115	This study	This study	This study	This study	This study		This study	This study
<i>C. aeneus</i> Riacho prox Rio Soberbo PARNASO RJ MNRJ37312 DAF11.118	This study	This study	This study	This study				This study
<i>C. aeneus</i> Sítio Dona Ana Barreira Guapimirim RJ MNRJ44585 DAF11.135	This study	This study	This study					
<i>C. aeneus</i> PE Três Picos Cachoeiras de Macacu RJ MNRJ47763 DAF11.147	This study	This study	This study					
<i>C. gaudichaudii</i> Ilha Grande Angra dos Reis RJ MNRJ38750 DAF11.121	This study		This study	This study	This study		This study	This study
<i>C. gaudichaudii</i> Ilha Grande Angra dos Reis RJ MNRJ38752 DAF11.125	This study	This study	This study	This study			This study	This study
<i>Crossodactylus</i> sp. Cacaria RJ CTRU441 RM03	This study		This study	This study	This study	This study	This study	
<i>Crossodactylus</i> sp. Ilha Grande RJ MTR15541 DAF11.030	This study		This study	This study		This study	This study	
<i>Crossodactylus</i> sp. Taquara Duque de Caxias RJ MTR22864 RM55	This study		This study					
<i>Crossodactylus</i> sp. Taquara Duque de Caxias RJ MTR22865 RM56	This study		This study					
<i>Crossodactylus</i> sp. Taquara Duque de Caxias RJ MTR22866 RM57	This study	This study	This study	This study	This study	This study	This study	This study
<i>Crossodactylus</i> sp. Taquara Duque de Caxias RJ MTR22870 RM58	This study		This study					
<i>Crossodactylus</i> sp. Petrópolis RJ MTR22740 RM45	This study		This study					
<i>Crossodactylus</i> sp. Petrópolis RJ MTR22741 RM46	This study	This study	This study	This study	This study	This study	This study	This study
<i>Crossodactylus</i> sp. Petrópolis RJ MTR22774 RM47	This study	This study	This study				This study	This study
<b><i>Crossodactylus caramaschii</i></b>								
<i>C. caramaschii</i> Ribeirão Grande SP AF520 DAF11.020	This study		This study	This study	This study	This study	This study	
<i>C. caramaschii</i> Ribeirão Grande SP AF521 DAF11.028	This study		This study	This study	This study	This study	This study	
<i>C. caramaschii</i> PET Alto Ribeira SP CFBH3093 DAF11.088	This study		This study	This study		This study	This study	
<i>C. caramaschii</i> Núcleo Caverna do Diabo Eldorado Paulista SP CTMZ02130 DAF11.102	This study	This study	This study	This study			This study	
<i>C. caramaschii</i> Núcleo Caverna do Diabo Eldorado Paulista SP CTMZ02131 DAF11.103	This study		This study	This study			This study	
<i>C. caramaschii</i> Núcleo Caverna do Diabo Eldorado Paulista SP CTMZ02255 DAF11.106	This study		This study	This study			This study	
<i>C. caramaschii</i> Núcleo Caverna do Diabo Eldorado Paulista SP CTMZ02079 DAF11.107	This study		This study	This study			This study	
<i>C. caramaschii</i> Núcleo Caverna do Diabo Eldorado Paulista SP CTMZ02640 DAF11.109	This study		This study	This study			This study	
<i>C. cf. caramaschii</i> Fazenda Intervalles SP AF374 DAF11.005	This study		This study					
<i>C. cf. caramaschii</i> Fazenda Intervalles SP AF373 DAF11.015	This study		This study			This study		
<i>Crossodactylus</i> sp. PET Alto Ribeira sp. AF71 DAF11.018	This study		This study			This study		
<i>Crossodactylus</i> sp. PET Alto Ribeira Iporanga SP CFBH430 DAF11.057	This study		This study			This study		
<i>Crossodactylus</i> sp. PET Alto Ribeira Núcleo Santana Iporanga SP CFBH431 DAF11.067	This study		This study	This study	This study	This study	This study	This study
<b><i>Crossodactylus dantei</i></b>								
<i>C. dantei</i> Fazenda da Bananeira Est Eco Murici Murici AL MUFAL10734 RM89	This study		This study		This study	This study	This study	This study
<i>C. dantei</i> Mata da Bananeira Est Eco Murici Murici AL MUFAL11075 RM95	This study		This study			This study	This study	This study

**Crossodactylus gaudichaudii 1 (Região dos Lagos)**

<i>C. gaudichaudii</i> Espraiado Maricá RJ MNRJ73527 DAF11.152	This study	This study	This study	This study				This study
<i>C. gaudichaudii</i> Espraiado Maricá RJ MNRJ73068 DAF11.143	This study	This study	This study	This study			This study	This study
<i>C. gaudichaudii</i> Serra dos Gaviões Cachoeira de Macacu RJ MNRJ53524 DAF11.153	This study							
<i>C. gaudichaudii</i> Serra dos Gaviões Cachoeira de Macacu RJ MNRJ53524 DAF11.154	This study	This study	This study	This study			This study	This study
<i>C. gaudichaudii</i> Saquarema RJ MNRJ76774 DAF11.156	This study	This study	This study	This study			This study	This study
<i>C. gaudichaudii</i> Serra dos Gaviões Cachoeira de Macacu RJ MNRJ53525 DAF11.157	This study							
<i>Crossodactylus</i> sp. Morro de São João Casimiro de Abreu RJ MNRJ40701 DAF11.138	This study		This study	This study				

**Crossodactylus gaudichaudii 2 (Floresta da Tijuca)**

<i>C. gaudichaudii</i> Estrada Dona Castorina PARNA Tijuca RJ MNRJ40552 DAF11.130	This study		This study	This study			This study	This study
<i>C. gaudichaudii</i> Estrada Dona Castorina PARNA Tijuca RJ MNRJ40553 DAF11.134	This study		This study	This study				This study
<i>C. gaudichaudii</i> PARNA Floresta da Tijuca RJ MNRJ74088 DAF11.146	This study		This study	This study			This study	This study
<i>C. gaudichaudii</i> Bom Retiro PARNA Floresta da Tijuca RJ MNRJ74089 DAF11.150	This study		This study	This study			This study	This study

**Crossodactylus schmidti**

<i>Crossodactylus schmidti</i> MLPA1414	AY843579	DQ502738	AY843801	AY844375	AY844210	DQ284050	AY844552	AY844031
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**Crossodactylus timbuhy**

<i>C. timbuhy</i> Santa Teresa ES UFMGT3379 RM127	This study		This study	This study	This study	This study	This study	This study
<i>C. timbuhy</i> Santa Teresa ES UFMGT2486 RM128	This study		This study	This study	This study	This study	This study	This study
<i>Crossodactylus</i> sp. Sítio Penha Briel Santa Teresa ES RBF1249 RM06	This study		This study		This study	This study	This study	This study
<i>Crossodactylus</i> sp. Sítio Irmã Vulpi Santa Teresa ES RBF1094 RM07	This study		This study	This study		This study	This study	This study
<i>Crossodactylus</i> sp. Sítio Penha Briel Santa Teresa ES RBF1259 RM08	This study		This study	This study		This study	This study	
<i>Crossodactylus</i> sp. Sítio Penha Briel Santa Teresa ES RBF1252 RM09	This study		This study	This study				
<i>Crossodactylus</i> sp. REBIO Augusto Ruschi Santa Teresa ES CFBH12401 DAF11.092	This study			This study		This study	This study	
<i>Crossodactylus</i> sp. REBIO Augusto Ruschi Santa Teresa ES CFBH12367 DAF11.097	This study	This study	This study	This study			This study	

**Crossodactylus trachystomus 1 (Serra do Caraça)**

<i>C. trachystomus</i> Catas Altas MG UFMGT9346 DAF11.112	This study		This study	This study	This study		This study	
<i>C. trachystomus</i> Conceição do Mato Dentro MG ML289 RM18	This study		This study				This study	
<i>C. trachystomus</i> Conceição do Mato Dentro MG ML290 RM19	This study			This study	This study	This study		This study
<i>Crossodactylus</i> sp. Caraça Catas Altas MG MNRJ38316 DAF11.116	This study	This study	This study	This study	This study		This study	This study
<i>Crossodactylus</i> sp. Banho do Belchior RPPN Serra do Caraça Catas Altas MG MNRJ38474 DAF11.120	This study	This study	This study					This study
<i>Crossodactylus</i> sp. Riacho Cascudos RPPN Serra do Caraça Catas Altas MG MNRJ38476 DAF11.124	This study	This study	This study	This study			This study	This study
<i>Crossodactylus</i> sp. RPPN Serra do Caraça Catas Altas MG MNRJ38477 DAF11.128	This study	This study	This study	This study				

<b><i>Crossodactylus trachystomus</i> 2 (Serra do Cipó)</b>							
<i>C. trachystomus</i> Conceição do Mato Dentro MG ML291 RM20	This study			This study			
<i>C. trachystomus</i> MCNAMT628 RM100	This study				This study	This study	This study
<i>C. trachystomus</i> Serra do Cipó Santana do Riacho MG MNRJ38465 DAF11.119	This study	This study	This study	This study	This study		This study
<i>C. trachystomus</i> Serra do Cipó Santana do Riacho MG MNRJ39982 DAF11.126	This study	This study	This study	This study			This study
<i>C. trachystomus</i> Serra do Cipó Santana do Riacho MG MNRJ41459 DAF11.132	This study	This study	This study	This study			This study
<i>C. trachystomus</i> Serra do Cipó MG MTR20327 DAF11.159	This study	This study	This study	This study			This study
<i>C. trachystomus</i> Serra do Cipó MG MTR20345 DAF11.160	This study	This study	This study	This study			This study
<b><i>Crossodactylus</i> sp. Serra do Teimoso BA</b>							
<i>Crossodactylus</i> sp. Serra do Teimoso BA MTR5841 DAF11.010	This study	This study	This study	This study			This study
<b><i>Crossodactylus</i> sp. MG1</b>							
<i>C. aff. caramaschii</i> Caratinga MG UFMGT4681 RM130	This study					This study	This study
<i>Crossodactylus</i> sp. Itamarati de Minas MG MZUFV16674 RM136	This study		This study	This study	This study	This study	This study
<b><i>Crossodactylus</i> sp. MG2</b>							
<i>Crossodactylus</i> sp. Olho D'água MG MZUFV15605 TG15-02	This study					This study	This study
<i>Crossodactylus</i> sp. Olho D'água MG MZUFV15606 TG15-05	This study					This study	This study
<b><i>Crossodactylus</i> sp. SC</b>							
<i>C. aff. gaudichaudii</i> Águas Mornas SC EJC435 RM116	This study	This study	This study	This study	This study	This study	
<i>C. caramaschii</i> São Bento do Sul SC UMFGT15956 DAF11.111	This study		This study	This study	This study		This study
<b><i>Crossodactylus</i> sp. PR West</b>							
<i>Crossodactylus</i> sp. Ortigueira PR IIH128 DAF11.021	This study			This study			This study
<i>Crossodactylus</i> sp. Apucarantina PR AF436 DAF11.001	This study	This study	This study			This study	This study
<i>Crossodactylus</i> sp. Apucarantina PR AF437 DAF11.007	This study	This study	This study	This study		This study	This study
<i>Crossodactylus</i> sp. Reserva Indígena de Mococa Ortigueira PR CFBH11181 DAF11.099	This study	This study	This study		This study		This study
<i>Crossodactylus</i> sp. Ourinhos SP UF7631 DAF11.046	This study	This study	This study	This study		This study	This study
<i>Crossodactylus</i> sp. Ourinhos SP UF7632 DAF11.051	This study						
<i>Crossodactylus</i> sp. Pinhalão PR IIH010 DAF11.037	This study	This study	This study			This study	This study
<i>Crossodactylus</i> sp. Pinhalão PR AF1334 DAF11.041	This study	This study	This study	This study		This study	This study
<i>Crossodactylus</i> sp. Wenceslau Bras PR IIH212 DAF11.042	This study	This study	This study	This study		This study	This study
<i>Crossodactylus</i> sp. Wenceslau Bras PR H017 DAF11.045	This study	This study	This study	This study		This study	This study
<b><i>Crossodactylus</i> sp. PR East</b>							
<i>C. caramaschii</i> Balsa Nova PR MNRJ73989 DAF11.145	This study			This study	This study		This study
<i>Crossodactylus</i> sp. Mananciais da Serra Piraquara PR MNRJ40200 DAF11.133	This study	This study	This study	This study			This study
<i>Crossodactylus</i> sp. Cascata da Professorinha Campo Magro PR MNRJ40199 DAF11.129	This study	This study	This study	This study			This study
<i>Crossodactylus</i> sp. Fazenda Morro Alto Ponta Grossa PR MNRJ40207 DAF11.137	This study			This study	This study		This study

**Crossodactylus aff. caramaschii SP**

<i>C. caramaschii</i> Parque Estadual Carlos Botelho Sete Barras SP CTMZ04569 DAF11.110	This study				This study	This study		This study
<i>C. caramaschii</i> Parque Estadual Carlos Botelho São Miguel Arcaño SP CTMZ02352 DAF11.108					This study			This study
<i>C. cf caramaschii Itanhaém SP CFBH5302 DAF11.089</i>	This study	This study	This study	This study	This study	This study	This study	This study
<i>C. cf caramaschii Itanhaém SP CFBH5303 DAF11.091</i>	This study	This study	This study	This study	This study	This study	This study	This study
<i>C. cf caramaschii Itanhaém SP CFBH7925 DAF11.094</i>	This study	This study	This study	This study	This study	This study	This study	This study
<i>Crossodactylus caramaschii Itanhaém SP CFBHT06917</i>	KJ961569	KJ961549						
<i>Crossodactylus caramaschii</i> Pilar do Sul CFBH5415	AY263235							
<i>C. caramaschii</i> Juquitiba SP H0154 DAF11.048	This study	This study	This study	This study	This study	This study	This study	This study
<i>C. caramaschii</i> Juquitiba SP H0184 DAF11.052	This study	This study	This study	This study	This study	This study	This study	
<i>C. caramaschii Ribeirão Grande SP Alc8679 DAF11.017</i>	This study						This study	
<i>C. caramaschii</i> Piedade SP H532 DAF11.043	This study	This study	This study	This study	This study	This study		
<i>Crossodactylus</i> sp. Piedade SP ITH0276 DAF11.024	This study	This study	This study	This study	This study	This study	This study	
<i>Crossodactylus</i> sp. Juquitiba SP AF1332 DAF11.026	This study		This study	This study	This study	This study	This study	
<i>Crossodactylus</i> sp. Piedade SP ITH0330 DAF11.029	This study	This study	This study	This study		This study	This study	
<i>Crossodactylus</i> sp. Juquitiba SP AF1320 DAF11.040	This study	This study	This study	This study	This study	This study	This study	
<i>Crossodactylus</i> sp. Piedade SP H0072 DAF11.047	This study	This study	This study	This study	This study	This study	This study	This study
<i>Crossodactylus</i> sp. Quilombo Caucaia do Alto SP UF8450 DAF11.050	This study	This study	This study	This study	This study	This study	This study	
<i>Crossodactylus</i> sp. Quilombo Caucaia do Alto SP AF1603 DAF11.053	This study	This study	This study	This study	This study	This study	This study	

**Crossodactylus sp. ES**

<i>Crossodactylus</i> sp. Bom Jesus ES CTRU586 RM04	This study		This study		This study	This study	This study	This study
<i>Crossodactylus</i> sp. Bom Jesus ES CTRU615 RM05	This study		This study	This study	This study	This study	This study	
<i>Crossodactylus</i> sp. Sítio Recanto da Mata Muniz Freire ES CFBH10799 DAF11.058	This study			This study	This study	This study	This study	
<i>Crossodactylus</i> sp. nov Sítio Recanto da Mata Muniz Freire ES CFBH10800 DAF11.063	This study		This study			This study	This study	
<i>Crossodactylus</i> sp. nov Muniz Freire Sítio Recanto da Mata ES CFBH10801 DAF11.068	This study	This study	This study	This study	This study	This study	This study	
<i>Crossodactylus</i> sp. Muniz Freire ES CFBH11960 DAF11.093	This study		This study			This study	This study	
<i>Crossodactylus</i> sp. Muniz Freire ES CFBH11961 DAF11.096	This study		This study				This study	
<i>Crossodactylus</i> sp. REBIO Duas Bocas Cariacica ES MNRJ39465 DAF11.123	This study		This study	This study			This study	This study
<i>Crossodactylus</i> sp. Sítio Waichert Biriricas ES RBF806 RM10	This study		This study	This study		This study	This study	

**Crossodactylus sp. BA**

<i>Crossodactylus</i> sp. Serra Bonita Camacan BA MTR15911 TG16-28	This study	This study	This study		This study	This study		This study
<i>Crossodactylus</i> sp. Serra Bonita BA MTR16259 DAF11.008	This study	This study	This study			This study	This study	
<i>Crossodactylus</i> sp. Serra das Lontras BA MTR16321 DAF11.003	This study	This study		This study		This study	This study	
<i>Crossodactylus</i> sp. Serra das Lontras BA MTR16320 DAF11.006	This study	This study	This study	This study		This study	This study	
<i>Crossodactylus</i> sp. Serra do Teimoso BA MTR6021 DAF11.012	This study	This study	This study	This study	This study	This study	This study	
<i>Crossodactylus</i> sp. Serra Bonita BA MTR16243 DAF11.014	This study	This study	This study	This study	This study	This study	This study	



<i>Crossodactylus</i> sp. Serra da Onca BA MTR16654 DAF11.016	This study		This study	This study		This study		
<i>Crossodactylus</i> sp. Serra da Onca BA MTR16655 DAF11.019	This study	This study	This study	This study	This study	This study	This study	
<i>Crossodactylus</i> sp. Fazenda Unacau BA AF916 DAF11.035	This study	This study	This study	This study	This study	This study	This study	This study
<i>Crossodactylus</i> sp. RPPN Serra Bonita Camacan BA CFBH9400 DAF11.095	This study		This study	This study	This study	This study	This study	
<i>Crossodactylus</i> sp. RPPN Serra Bonita Camacan BA CFBH9401 DAF11.098	This study	This study	This study					This study
<i>Crossodactylus</i> sp. RPPN Serra do Teimoso Jussari BA MNRJ44952 DAF11.136	This study		This study	This study				This study This study
<b><i>Crossodactylus</i> sp. MG3</b>								
<i>Crossodactylus</i> sp. CatÁguas MG MZUFV16493 RM134	This study		This study	This study	This study	This study	This study	This study
<i>Crossodactylus</i> sp. Marliéria MG MZUFV16650 RM135	This study		This study	This study	This study	This study	This study	This study
<i>Crossodactylus</i> sp. Marliéria MG MZUFV15374	This study		This study	This study	This study	This study	This study	This study
<i>Crossodactylus</i> sp. Marliéria MG MZUFV15373	This study	This study			This study	This study	This study	This study
<b><i>Crossodactylus</i> sp. MG4</b>								
<i>Crossodactylus</i> sp. Córrego dos Bizicas Ipanema MG UFMGT4637 RM126	This study		This study	This study	This study	This study	This study	This study
<i>Crossodactylus</i> sp. Bom Jesus do Galho MG UFMGT4550 TG	This study		This study		This study			
<i>Crossodactylus</i> sp. Bom Jesus do Galho MG UFMGT4551 TG	This study				This study	This study		This study
<i>Crossodactylus</i> sp. Bom Jesus do Galho MG UFMGT4552 TG	This study		This study		This study	This study	This study	This study
<i>Crossodactylus</i> sp. RPPN Feliciano Miguel Abdala Caratinga MG UFMGT4535 TG	This study			This study	This study	This study		
<i>Crossodactylus</i> sp. Bom Jesus do Galho MG UFMGT4553 TG	This study		This study	This study	This study			
<b><i>Hylodes amnicola</i></b>								
<i>H. amnicola</i> Parque Estadual Ibitipoca Lima Duarte MG CFBHT15290	KJ961576	KJ961556						
<i>Hylodes amnicola</i> CFBH30971	KJ961575	KJ961555						
<i>H. amnicola</i> Parque Estadual Ibitipoca Lima Duarte MG CFBHT15287 RM84	This study	This study	This study	This study	This study	This study	This study	
<b><i>Hylodes asper</i> RJ</b>								
<i>H. asper</i> Cachoeira Itinguçu Itaguá RJ CTRU491 RM12	This study	This study	This study	This study	This study	This study	This study	This study
<i>H. asper</i> Teresópolis RJ CFBH14029 DAF11.076	This study		This study	This study		This study	This study	This study
<i>H. asper</i> Res. Ecol. de Guapiaçu Cachoeiras de Macacu RJ MNRJ60170 DAF11.158	This study		This study	This study			This study	This study
<i>H. cf. asper</i> Taquara Duque de Caxias RJ MTR22851 RM50	This study		This study	This study		This study	This study	This study
<b><i>Hylodes aff. asper</i> SP</b>								
<i>H. asper</i> Est. Biol. da Boracéia SP MTR11681 RM29	This study	This study	This study					
<i>H. asper</i> Est. Biol. da Boracéia Salesópolis SP MTR11667 RM41	This study	This study	This study	This study	This study	This study	This study	
<i>H. asper</i> Est. Biol. da Boracéia SP AF1482 RM72	This study	This study	This study	This study	This study	This study	This study	This study
<i>H. asper</i> Picinguaba SP AF17 RM75	This study	This study	This study		This study	This study	This study	
<i>H. asper</i> Barra do Una SP AF768 DAF11.036	This study		This study			This study	This study	
<i>H. asper</i> Bertioga SP IIH211 DAF11.044	This study	This study	This study	This study		This study	This study	
<i>H. asper</i> Ilha Bela São Sebastião SP CFBH10430 DAF11.073	This study	This study	This study			This study	This study	This study
<i>H. asper</i> PARNA Serra da Bocaina Parati RJ MNRJ64834 DAF11.148	This study	This study	This study	This study			This study	This study
<i>Hylodes</i> sp. Cunha SP MTR3449 DAF11.022	This study	This study	This study	This study		This study	This study	
<i>Hylodes</i> sp. Ilha Bela SP MTR3339 DAF11.025	This study	This study	This study			This study		

***Hylodes cardosoi***

<i>H. cardosoi</i> Guaraqueçaba PR EJC402 RM108	This study	This study		This study	This study	This study	This study	
<i>H. cardosoi</i> Guaraqueçaba PR EJC403 RM111	This study	This study		This study	This study	This study	This study	This study
<i>H. asper</i> Guapiara SP 916860 RM70	This study		This study					
<i>H. asper</i> Guapiara SP 916861 RM71	This study	This study	This study	This study	This study	This study	This study	This study
<i>H. asper</i> Miracatu SP AF442 RM76	This study		This study		This study	This study	This study	
<i>H. asper</i> Miracatu SP AF443 RM77	This study	This study	This study					
<i>H. gr. asper</i> Fazenda Intervalles SP AF379 DAF11.013	This study		This study			This study		

***Hylodes charadranaetes***

<i>Hylodes charadranaetes</i> KM390793	KM390793							
<i>H. cf. charadranaetes</i> Res. Ecol. Guapiaçu Cach. de Macacu RJ MNRJ59065 DAF11.155	This study	This study	This study					This study

***Hylodes dactylocinus***

<i>H. dactylocinus</i> Est. Ecol. da Jureia Guaraúzinho SP AF15 RM74	This study	This study	This study		This study	This study	This study	This study
<i>H. dactylocinus</i> Itariri Jureia SP CH101 RM80	This study	This study	This study		This study	This study		This study
<i>H. dactylocinus</i> Est. Ecol. Jureia Itatins Núcleo Arpoador Peruipe SP CFBH7181 DAF11.074	This study		This study					This study
<i>H. dactylocinus</i> Est. Ecol. Jureia Itatins Núcleo Arpoador Peruipe SP CFBH7182 DAF11.077	This study		This study					This study

***Hylodes fredei***

<i>H. fredei</i> Ilha Grande Angra dos Reis RJ CTRU168 RM11	This study		This study	This study	This study	This study	This study	
<i>H. fredei</i> Ilha Grande Angra dos Reis RJ MNRJ36077 DAF11.114	This study		This study	This study	This study		This study	This study

***Hylodes glaber***

<i>H. glaber</i> Campos do Jordão SP MTR11010 RM31	This study	This study	This study	This study	This study	This study	This study	This study
<i>H. glaber</i> Campos do Jordão SP MTR11011 RM32	This study		This study					
<i>H. glaber</i> Campos do Jordão SP MTR10993 DAF11.049	This study	This study	This study	This study		This study	This study	
<i>H. sazimai</i> PARNA Itatiaia Itatiaia RJ CFBHT10786 DAF11.078	This study		This study			This study	This study	
<i>H. sazimai</i> PARNA Itatiaia Itatiaia RJ CFBHT10787 DAF11.080	This study		This study					
<i>H. cf. ornatus</i> Chalé Fazenda Vale da Mata Monte Verde MG TG3641 RM132	This study		This study	This study	This study	This study	This study	This study
<i>Hylodes</i> sp. Cunha SP 3452 RM17	This study	This study	This study	This study	This study	This study	This study	This study
<i>H. gr. lateristrigatus</i> Serra da Cantareira Núcleo Pedra Grande SP AF914 RM79	This study	This study	This study		This study	This study	This study	

***Hylodes heyeri***

<i>H. heyeri</i> Iporanga SP AF1491 RM73	This study		This study	This study	This study	This study	This study	This study
<i>H. heyeri</i> Morretes PR EJC304 RM121	This study		This study		This study	This study	This study	This study
<i>H. heyeri</i> PET Alto Ribeira Núcleo Caboclos Iporanga SP CFBH8280 DAF11.075	This study		This study				This study	
<i>H. heyeri</i> Faz. Creminacio Serra do Araraquara Guaratuba PR CFBH21315 DAF11.079	This study		This study				This study	
<i>H. heyeri</i> Faz. Creminacio Serra do Araraquara Guaratuba PR CFBH21316 DAF11.082	This study		This study				This study	This study
<i>H. gr. lateristrigatus</i> Fazenda Intervalles SP AF378 DAF11.002	This study		This study				This study	
<i>H. gr. lateristrigatus</i> Fazenda Intervalles SP AF377 DAF11.009	This study		This study				This study	This study
<i>Hylodes</i> sp. Fazenda Intervalles SP AF343 DAF11.011	This study		This study				This study	This study

***Hylodes japi***

H. japi Serra do Japi Jundiá SP CFBH33850	KJ961574	KJ961554						
H. japi Serra do Japi Jundiá SP FPS005A829	KJ961573	KJ961553						
H. japi Serra do Japi Jundiá SP CFBHT12058	KJ961572	KJ961552						
H. japi Serra do Japi Jundiá SP CFBHT11971	KJ961571	KJ961551						
H. japi Regiao da Ermida Serra do Japi Jundiá SP CFBH33850 RM91	This study		This study	This study	This study	This study	This study	This study

***Hylodes lateristrigatus + Hylodes babax 1***

H. babax PARNA Caparaó Santa Marta Ibitirama ES UFMG17258 RM129	This study				This study	This study	This study	This study
H. cf. babax Cachoeira Véu de Noiva Alvarenga MG UFMG16987 RM131	This study		This study		This study	This study	This study	This study
H. aff. lateristrigatus REBio Santa Lúcia Santa Teresa ES MNRJ38413 DAF11.117	This study	This study	This study	This study			This study	This study

***Hylodes lateristrigatus + Hylodes babax 2***

<i>Hylodes lateristrigatus</i>	KM390794							
H. lateristrigatus CatÁguas MG MZUFV16017 RM133	This study				This study	This study	This study	
H. lateristrigatus RPPN Mata do Sossego Simonésia MG UFMG13071 TG15.01	This study		This study		This study	This study	This study	
H. lateristrigatus Córrego dos Ferreiras Sta Barbara do Leste MG UFMG13069 TG15.09	This study		This study		This study	This study		
H. lateristrigatus Córrego dos Ferreiras Sta Barbara do Leste MG UFMG13070 TG15.11	This study					This study		
H. lateristrigatus Reserva São Lourenco Santa Teresa ES MNRJ56074 DAF11.141	This study	This study	This study					This study
H. babax PARNA Caparaó ES MTR15803 DAF11.031	This study	This study	This study			This study	This study	

***Hylodes magalhaesi***

H. magalhaesi Campos do Jordão SP MTR10992 RM30	This study	This study	This study	This study	This study	This study	This study	This study
H. magalhaesi Campos do Jordão SP CFBH9920 DAF11.060	This study	This study	This study			This study	This study	
H. magalhaesi Campos do Jordão SP CFBH9921 DAF11.062	This study	This study	This study	This study		This study	This study	
H. magalhaesi Campos do Jordão SP CFBH9922 DAF11.064	This study		This study				This study	
H. magalhaesi Campos do Jordão SP CFBHT5117 DAF11.066	This study	This study	This study			This study	This study	

***Hylodes meridionalis***

H. meridionalis Itati RS EJC370 RM102	This study		This study	This study	This study	This study	This study	This study
H. meridionalis Itati RS EJC369 RM115	This study		This study		This study	This study	This study	This study
H. meridionalis Arroio Humaitá São Francisco de Paula RS TG11.48	This study		This study	This study			This study	
H. meridionalis Arroio Humaitá São Francisco de Paula RS TG11.50	This study		This study				This study	
H. cf. meridionalis Guapore RS EJC458 RM109	This study	This study		This study	This study	This study	This study	This study
H. cf. meridionalis Osorio RS EJC360 RM117	This study	This study	This study	This study	This study	This study	This study	
<i>Hylodes</i> sp. Praia Grande SC EJC467 RM104	This study		This study	This study	This study	This study	This study	This study

***Hylodes aff. meridionalis SC***

H. meridionalis Barragem do Rio São Bento Siderópolis SC CFBH24278 DAF11.069	This study		This study						
H. cf. <i>perplicatus</i> Lauro Muller SC EJC327 RM112	This study		This study		This study	This study	This study		
H. cf. <i>perplicatus</i> Cocal do Sul SC EJC344 RM114	This study	This study	This study	This study	This study	This study	This study	This study	This study
Hylodes sp. Fazenda do Padre Blévio Grão Pará SC MTR26699 RM63	This study		This study						
Hylodes sp. Fazenda do Padre Blévio Grão Pará SC MTR26728 RM64	This study	This study	This study	This study	This study	This study	This study	This study	This study
Hylodes sp. Fazenda do Padre Blévio Grão Pará SC MTR26729 RM65	This study		This study						
Hylodes sp. Fazenda do Padre Blévio Grão Pará SC MTR26735 RM66	This study		This study						
Hylodes sp. Fazenda do Padre Blévio Grão Pará SC MTR26751 RM67	This study	This study	This study						
Hylodes sp. Fazenda do Padre Blévio Grão Pará SC MTR26782 RM68	This study		This study						
Hylodes sp. Fazenda do Padre Blévio Grão Pará SC MTR26807 RM69	This study		This study						

***Hylodes nasus***

H. nasus Tijuca Rio de Janeiro RJ MNRJ35435	KJ961577	KJ961557							
H. nasus Rio de Janeiro Horto Florestal RJ AF440 DAF11.034	This study		This study	This study		This study			
H. nasus Estrada Dona Castorina Floresta da Tijuca RJ MNRJ35434 DAF11.113	This study	This study	This study	This study				This study	This study

***Hylodes ornatus***

H. ornatus PARNA Itatiaia Itamontes MG CFBH34905 RM92	This study		This study	This study	This study	This study	This study		
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***Hylodes otavioi***

H. otavioi Morro do Pilar MG MNRJ41456 DAF11.131	This study		This study	This study				This study	This study
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***Hylodes perere***

Hylodes <i>perere</i> Santa Bárbara do Monte Verde MG CFBH31106	KJ961581	KJ961561							
H. <i>perere</i> RPPN Ovídio Antônio Pires Santa Rita do Jacutinga MG CFBHT12651	KJ961580	KJ961560							
H. <i>perere</i> Sta Barbara do Monte Verde MG CTRU559 RM83	This study	This study	This study		This study	This study	This study	This study	This study
H. <i>perere</i> Sta Barbara do Monte Verde MG CFBH31106 RM86	This study	This study	This study		This study	This study	This study	This study	This study
H. <i>perere</i> Sta Barbara do Monte Verde MG CFBH31107 RM87	This study	This study	This study		This study	This study	This study	This study	This study
H. <i>perere</i> Sta Barbara do Monte Verde MG CFBH31108 RM88	This study	This study			This study	This study	This study	This study	This study

***Hylodes perplicatus***

H. perplicatus São Bento do Sul SC EJC416 RM101	This study	This study	This study	This study	This study	This study	This study		
H. perplicatus Rio Vermelho São Bento do Sul SC CFBH22008 DAF11.061	This study		This study			This study	This study		
H. perplicatus São Bento do Sul SC CFBH3243 DAF11.071	This study		This study	This study		This study			This study
H. cf. <i>perplicatus</i> Luiz Alves SC EJC312 RM124	This study		This study		This study	This study	This study	This study	This study
Hylodes sp. Morro Grande Guaratuba PR MTR18512 RM43	This study	This study	This study	This study	This study	This study	This study	This study	This study
Hylodes sp. Morro Grande Guaratuba PR MTR18513 RM44	This study	This study	This study					This study	This study
Hylodes sp. Joinville SC EJC475 RM103	This study	This study	This study	This study	This study	This study	This study	This study	This study
Hylodes sp.2 Joinville SC EJC474 RM106	This study	This study	This study	This study	This study	This study			This study
Hylodes sp.4 São Bonifácio SC EJC427 RM118	This study	This study	This study		This study	This study	This study	This study	This study
Hylodes sp.4 São Bonifácio SC EJC426 RM122	This study	This study			This study	This study	This study	This study	This study
Hylodes sp.3 Águas Mornas SC EJC434 RM125	This study	This study	This study	This study	This study	This study	This study	This study	

***Hylodes phyllodes***

<i>H. phyllodes</i> Est. Biol. da Boracéia Salesópolis SP MTR11656 RM33	This study	This study	This study					
<i>H. phyllodes</i> Est. Biol. da Boracéia Salesópolis SP MTR11663 RM40	This study	This study	This study	This study	This study	This study	This study	This study
<i>H. phyllodes</i> Praia Vermelha Ubatuba SP AF472 RM78	This study	This study	This study		This study	This study	This study	
<i>H. phyllodes</i> Barra do Una SP AF767 DAF11.033	This study	This study	This study	This study	This study	This study	This study	
<i>H. phyllodes</i> Bertioga SP Alc10279 DAF11.054	This study	This study	This study	This study	This study	This study	This study	
<i>H. cf. phyllodes</i> Toque toque Grande São Sebastião SP sem tombo RM82	This study	This study	This study	This study	This study	This study	This study	This study
<i>Hylodes</i> sp. Biritiba Mirim SP 2565 RM34	This study	This study	This study	This study	This study	This study	This study	This study
<i>Hylodes</i> sp. Biritiba Mirim SP 2566 RM38	This study		This study					
<i>Hylodes phyllodes</i> Est. Biol. da Boracéia Salesópolis SP MTR23375 RM60	This study		This study					
<i>Hylodes phyllodes</i> MCL 00015	DQ502171	DQ502873	DQ502606	DQ503367	DQ503009	DQ502368	DQ503253	

***Hylodes pipilans***

<i>H. pipilans</i> Serra dos Orgãos Teresópolis RJ MNRJ37307	KJ961582	KJ961562						
<i>Hylodes pipilans</i> KM390795	KM390795							
<i>H. pipilans</i> Taquara Duque de Caxias RJ MTR22860 RM51	This study	This study	This study	This study		This study	This study	This study
<i>H. pipilans</i> Taquara Duque de Caxias RJ MTR22861 RM52	This study		This study					
<i>H. pipilans</i> Taquara Duque de Caxias RJ MTR22862 RM53	This study	This study	This study					
<i>H. pipilans</i> Taquara Duque de Caxias RJ MTR22863 RM54	This study		This study					
<i>H. pipilans</i> Taquara Duque de Caxias RJ MTR22871 RM59	This study	This study	This study	This study	This study	This study	This study	
<i>H. pipilans</i> Petrópolis RJ MTR22710 RM137	This study							
<i>H. pipilans</i> PARNASO Sede Guapimirim RJ MNRJ39371 DAF11.122	This study		This study					This study
<i>H. pipilans</i> PE Três Picos Cachoeiras de Macacu RJ MNRJ47760 DAF11.144	This study		This study					

***Hylodes sazimai***

<i>H. sazimai</i> Serra das Cabras Campinas SP CFBHT14630	KJ961585	KJ961565						
<i>H. sazimai</i> Morro das Cabras Campinas SP CFBH29586	KJ961584	KJ961564						
<i>H. sazimai</i> Serra das Cabras Campinas SP CFBHT14629	KJ961583	KJ961563						
<i>H. gr. lateristrigatus</i> Poços de Caldas Retiro Branco MG ML323 RM21	This study		This study					
<i>H. gr. lateristrigatus</i> Poços de Caldas Retiro Branco MG ML324 RM22	This study		This study	This study	This study	This study	This study	This study
<i>H. gr. lateristrigatus</i> Poços de Caldas Retiro Branco MG ML325 RM23	This study		This study					

***Hylodes regius***

<i>H. regius</i> PARNA Itatiaia Parte Alta Itamontes MG CFBH30970 RM81	This study	This study		This study	This study	This study	This study	This study
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***Hylodes uai***

<i>H. uai</i> Parque das Manguabeiras Belo Horizonte MG CFBH22818 RM93	This study	This study	This study		This study	This study	This study	This study
<i>H. uai</i> Nova Lima MG CFBHT7649 RM94	This study	This study	This study	This study	This study	This study	This study	This study
<i>H. uai</i> Parque das Manguabeiras Belo Horizonte MG MCNAM11327 RM96	This study		This study		This study	This study	This study	This study
<i>H. uai</i> Serra da Piedade Caete MG MCNAMT429 RM98	This study	This study	This study	This study	This study	This study	This study	This study
<i>H. uai</i> Serra da Piedade Caete MG MCNAMT430 RM99	This study	This study	This study		This study	This study	This study	This study
<i>H. cf. uai</i> Serra do Caraça Catas Altas MG CFBH38103 RM90	This study		This study		This study	This study	This study	This study

<b><i>Hylodes</i> sp. Joinville SC</b>							
<i>Hylodes</i> sp.1 Joinville SC EJC390 RM105	This study		This study	This study	This study	This study	This study
<i>Hylodes</i> sp.1 Joinville SC EJC391 RM120	This study		This study		This study	This study	This study
<b><i>Hylodes</i> sp. Florianópolis SC</b>							
<i>Hylodes</i> sp.3 Águas Mornas SC EJC432 RM113	This study		This study		This study	This study	This study
<i>H. aff. perplicatus</i> Florianópolis SC EJC396 RM123	This study	This study		This study	This study	This study	This study
<i>Hylodes</i> sp.3 Santo Amaro da Imperatriz SC EJC320 RM107	This study				This study	This study	This study
<i>Hylodes</i> sp.3 Santo Amaro da Imperatriz SC EJC321 RM110	This study		This study		This study	This study	This study
<b><i>Hylodes</i> sp. Juquitiba SP</b>							
<i>Hylodes</i> sp.n. Juquitiba SP H0157 DAF11.038	This study		This study	This study		This study	This study
<i>Hylodes</i> sp. Juquitiba SP H0201 RM16	This study	This study	This study	This study	This study	This study	This study
<b><i>Hylodes</i> sp. Itanhaém SP</b>							
<i>H. phyllodes</i> Itanhaém SP CFBHT3150 DAF11.081	This study	This study	This study			This study	This study
<i>H. phyllodes</i> Itanhaém SP CFBHT3873 DAF11.083	This study	This study	This study	This study		This study	This study
<b><i>Hylodes</i> sp. Rio Claro RJ</b>							
<i>Hylodes</i> sp. Lídice Rio Claro RJ CTRU411 RM01	This study			This study	This study	This study	This study
<i>Hylodes</i> sp. Lídice Rio Claro RJ CTRU413 RM02	This study		This study		This study	This study	This study
<b><i>Hylodes</i> sp. Paranapiacaba SP</b>							
<i>H. phyllodes</i> Itanhaém SP CFBHT3878 DAF11.085	This study	This study	This study	This study		This study	This study
<i>H. cf. phyllodes</i> PNM Nascentes de Paranapiacaba Santo André SP CTMZ07228 DAF11.100	This study	This study	This study	This study	This study		This study
<b><i>Hylodes</i> sp. Bocaina RJ/SP</b>							
<i>H. phyllodes</i> Picinguaba Ubatuba SP CFBHT249	DQ283096		DQ502587			DQ284146	DQ283812 DQ282923
<i>H. phyllodes</i> PARNA Serra da Bocaina Parati RJ MNRJ64822 DAF11.142	This study	This study	This study	This study			This study This study
<b><i>Megaelosia apuana</i></b>							
<i>M. apuana</i> Domingos Martins ES CFBH10811 DAF11.084	This study	This study	This study	This study		This study	This study
<i>M. apuana</i> Pedra Azul Domingos Martins ES CFBHT9118 DAF11.090	This study	This study				This study	This study
<i>M. apuana</i> PARNA Caparaó Pedra Roxa ES MTR12631 RM35	This study		This study	This study	This study	This study	This study
<i>M. apuana</i> PARNA Caparaó Córrego do Calçado ES MTR12643 RM37	This study		This study				
<i>M. apuana</i> PARNA Caparaó Córrego Frio ES MTR15783 RM39	This study		This study				
<i>Megaelosia</i> sp. PARNA Caparaó ES MTR12642 RM36	This study	This study	This study		This study	This study	This study
<i>Megaelosia</i> sp. PARNA Caparaó ES MTR26230 RM62	This study		This study				
<i>M. apuana</i> PARNA Caparaó ES MTR12614 DAF11.023	This study	This study	This study			This study	This study
<i>M. apuana</i> RPPN Mata do Sossego Simonésia MG UFMG5736 TG15.04	This study		This study		This study		
<i>M. apuana</i> RPPN Mata do Sossego Simonésia MG UFMG5738 TG15.07	This study		This study		This study	This study	



Appendix 03. Phenotypic matrix extracted from Mesquite. Different colors represent different states of characters.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
Taxon \ Character																								
1	<i>C_aeneus</i>	0	?	?	2	1	1	0&1	2	1	1	1	0	0	?	1	1	2	0	4	1	3	0	
2	<i>C_caramaschii</i>	0	?	?	2	1	1	1&2	0&2	0&1	1	2	0	1	0	2	0	2	0	2	0	2	0	
3	<i>C_dantei</i>	0	?	?	1	1	1	0	2	1	0	1	?	0	2	?	0	?	4	?	2	1	?	
4	<i>C_gaudichaudii</i>	0	?	?	2	1	1	1	2	1	1	1	?	1	0	1	?	1	0	4	?	4	0	
5	<i>C_schmidti</i>	1	1	0	2	1	1	1	3&4	1	0&1	1	?	?	?	0	?	?	2	?	?	?	?	
6	<i>C_timbuhy</i>	0	?	?	2	1	1	1	1&2&3	1	0	0	?	0	?	0	?	0	?	1	0	4	0	
7	<i>C_trachystomus</i>	0	?	?	2	1	1	1	2&3	1	0&1	0	?	0	?	1	0	0	?	4	0	2	?	
8	<i>H_amicola</i>	1	1	1	2	0	?	?	?	0	?	1	0	?	?	2	0	?	?	4	1	?	?	
9	<i>H_asper_RJ</i>	1	1	1	1&2	0	?	?	?	0	?	1&2	0	?	1	2	2	?	1	4	2	?	1	
10	<i>H_asper_SP</i>	1	1	1	2	0	?	?	?	0	?	1	?	1	0	4	1	2	0	3	1	3	1	
11	<i>H_babax</i>	1	1	1	2	0	?	?	?	0	?	0	?	?	?	2	2	?	?	2	2	?	?	
12	<i>H_cardosoi</i>	1	1	1	2	0	?	?	?	0	?	0	?	0	?	2	2	2	1	2	2	2	1	
13	<i>H_charadranaetes</i>	1	1	1	2	0	?	?	?	0	?	2	?	0	?	2	?	2	1	2	1	4	1	
14	<i>H_dactylocinus</i>	1	1	1	2	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	2	1	
15	<i>H_fredi</i>	1	1	1	2	1	1	0	5	0	?	0	?	0	?	2	1	1	0	2	1	1	0	
16	<i>H_glaber</i>	1	1	1	1	0	0	?	?	0	?	2	0	?	0	3	0	?	0	4	0	?	0	
17	<i>H_heyeri</i>	1	1	1	2	0	?	?	?	0	?	1	0	?	?	2	1	?	?	4	1	?	?	
18	<i>H_japi</i>	1	1	1	1	0	?	?	?	0	?	?	2	?	1	?	2	?	1	?	2	?	1	
19	<i>H_lateristrigatus</i>	1	1	1	1&2	0	?	?	?	0	?	2	0	?	?	2	1	?	?	3	1	?	?	
20	<i>H_magalhaesi</i>	1	1	1	2	0	?	?	?	0	?	0	?	1	0	2	2	2	0	2	2	2	0	
21	<i>H_meridionalis</i>	1	1	1	1	0	?	?	?	0	?	1&2	?	2	0	2	?	2	0	4	?	2	0	
22	<i>H_nasus</i>	1	1	1	1&2	0	?	?	?	0	?	?	?	2	1	?	?	2	1	?	?	3	1	
23	<i>H_ornatus</i>	1	1	1	1&2	0	?	?	?	0	?	2	0	2	0	2	0	2	0	4	0	1	0	
24	<i>H_otavioi</i>	1	1	1	2	0	?	?	?	0	?	?	?	2	?	1	?	2	?	1	?	2	?	1
25	<i>H_perere</i>	1	1	1	2	0	?	?	?	0	?	?	?	1	?	?	?	1	?	?	2	2	?	1
26	<i>H_perplicatus</i>	1	1	1	1	0	?	?	?	0	?	1	?	2	0	2	?	2	0	4	?	2	0	
27	<i>H_phylloides</i>	1	1	1	2	1	1	0	5	0	?	2	?	?	?	1&2	?	?	?	4	1	?	1	
28	<i>H_pipilans</i>	1	1	1	2	1	1	0	5	0	?	2	0	2	0	2	0	2	0	4	0	3	0	
29	<i>H_regius</i>	1	1	1	1	0	?	?	?	0	?	3	0	?	?	2	1	?	?	3	1	?	?	
30	<i>H_sazimai</i>	1	1	1	2	0	?	?	?	0	?	1	0	?	?	2	0	?	?	4	1	?	?	
31	<i>H_uai</i>	1	1	1	1	0	?	?	?	0	?	?	?	0	?	1	?	2	?	3	?	3	?	
32	<i>M_apuana</i>	1	1	1	1	0	?	?	?	0	?	?	?	2	0	?	?	3	0	?	?	4	1	
33	<i>M_boticariana</i>				1	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	
34	<i>M_goeldii</i>	0			1	0	?	?	?	0	?	?	?	2	1	?	?	2	1	?	?	3	1	
35	<i>M_massarti</i>	1	1	1	1	0	?	?	?	0	?	?	?	2	0	?	?	3	0	?	?	4	0	
36	<i>Leptodactylus_fuscus</i>	1	0	0	2	0	?	?	?	0	?	0	?	0	?	0	?	0	?	0	?	0	?	
37	<i>Hemiphractus_johnsoni</i>	0				0	?	?	?	?	0	?	?	?	?	0	?	?	?	0	?	?	?	
38	<i>Physalaemus_cuvieri</i>	1	0	0	0&1	0	?	?	?	0	?	0	?	0	?	0	?	0	?	0	?	0	?	
39	<i>Amereega_trivitatta</i>	1				0	?	?	?	?	?	0	?	?	?	0	?	?	?	0	?	?	?	
40	<i>Pristimantis_fenestratus</i>	?	?	?	1	?	?	?	?	0	?	?	?	?	?	?	0	?	?	?	?	0	?	
41	<i>Dendropsophus_minutus</i>	1	0	0	1	0	?	?	?	0	?	?	?	?	?	?	0	?	?	?	?	0	?	
42	<i>Cycloramphus_brasiliensis</i>	0				0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	
43	<i>Rhinella_major</i>	1	0	0		1	0	?	?	?	?	0	?	?	?	0	?	?	0	?	?	?	?	
44	<i>Vitreorana_eurygnatha</i>	1	0	0		0	?	?	?	0	?	?	?	?	?	0	?	?	0	?	?	0	?	
45	<i>Ceratophrys_cornuta</i>				0	?	?	?	?	?	0	?	?	?	?	0	?	?	0	?	?	?	?	
46	<i>Rheobates_palmatus</i>	0	?	?	1	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	
47	<i>Allophryne_ruthveni</i>				1	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	



	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Taxon \ Character																							
1 C_aeneus	1	1	2	0	4	1	4	0	2	1	0	3	1	2	0	3	1	2	0	0&1	1	2	
2 C_caramaschii	1	0	0		4	0	4	0	4	0	2	0	1	0	2	0	2	0	4	0	0	1	2
3 C_dantei	3		1	0	5		4	1	1		0	1		1	1	6		2	1	0	1		
4 C_gaudichaudii	1	1	2	0	5	1	5	0	2	1	0	1	1	1	0	3	1	5	0	1	1	2	
5 C_schmidti	0				4				1							2				0	1		
6 C_timbuhy	0		0		5	0	6	0	1	0	5	0	1	0	3	0	2	0	2	0	0&1	1	2
7 C_trachystomus	2	0			4	0	5		1	0	2		0		0		5	0	0		0	1	2
8 H_amicola	2	1	1		5	1			4	1			5	1			5	1			1	1	2
9 H_asper_RJ	1&2	2		1	4	2		1	4	2		1	4	2		1	4&5	2		1	1	1	1&2
10 H_asper_SP	1	1	2	1	4	2	5	1	4	2	4	1	5	2	5	1	4	2	4	1	1	1	1
11 H_babax	3	2			5	2			4	2			5	2			5	2			1	1	2
12 H_cardosoi	2	2	1	2	5	2	4	1	5	2	4	1	4	2	2	1	5	2	4	1	1	1	1&2
13 H_charadraetaes	1	1	2	1	4	1	5	1	1	1	4	1	4	1	4	1	5	1	5	1	1	1	1&2
14 H_dactylocinus		2		1		2		1		2		1		2		1		2		1	1	1	2
15 H_fredi	2	1	1	0	5	2	5	0	5	2	0		5	2	2	0	4	2	2	0	1	1	2
16 H_glaber	2	0		0	4	1		1	4	1		1	5	1		1	4	1		1	1	1	1
17 H_heyeri	2	1			5	1			4	1			4	1			4	1	1	1	1	1	1&2
18 H_japi	2		1		5	2		1		2		1		2		1		2		1	0&1	1	2
19 H_lateristrigatus	2	1			5	2			4	2			4	2			4	2			1	1	2
20 H_magalhaesi	1	2	1	0	5	2	5	0	3&4	2	4	0	3&4	2	1	0	5	2	4	0	1	1	2
21 H_meridionalis	2		2	0	5	1	5	0	4		4	1	5		5	1	4&5		4	1	1	1	1
22 H_nasus			2	1		1	4	1		1	2	1		1	2	1		1	2	1	1	1	1
23 H_ornatus	2	0	1	0	4	1	5	0	4	1	4	0	4	1	5	0	4	1	3	0	1	1	2
24 H_otavioi		2		1		2		1		2		1		2		1		2		1	1	1	2
25 H_perere	1	2		1	4	2		1	4	2		1	4	2		1	4	2		1	1	1	2
26 H_perplicatus	2		2	0	4		5	0	4		4	0	4		2	0	4		5	0	1	1	2
27 H_phylloides	2	1		1	2&6	2		1	2&4	2		1	2&5	2		1	1&6	2		1	1	1	1
28 H_pipilans	2	0	1	0	5	2	5	0	4	2	1	0	5	2	4	0	5	2	5	0	1	1	2
29 H_regius	2	1			5	2			4	2			4	2			5	2			1	1	1
30 H_sazimai	2	1			5	2			4	2			4	2			5	2			1	1	2
31 H_uai	2				4		4		4		4		4				4		5		1	1	2
32 M_apuana			2	1			6	1			5	1			4	1			5	1	0	1	
33 M_boticariana																					1		
34 M_goeldii			2	1			5	1			4	1			4	1			4	1	1		
35 M_massarti			2	0			6	0			4	0			4	0			4	0	1		
36 Leptodactylus_fuscus	0		0		0		0		0		0		0		0		0		0		0	0	
37 Hemiphractus_johnsoni	0				0				0				0				0				0	0	
38 Physalaemus_cuvieri	0		0		0		0		0		0		0		0		0		0		0		
39 Amereega_trivitatta	0				0				0			0			0						1	0	
40 Pristimantis_fenestratus			0				0					0					0				0		
41 Dendropsophus_minutus			0				0					0					0				0	1	
42 Cycloramphus_brasiliensis	0								0			0					0				0	1	
43 Rhinella_major	0				0				0			0					0				0	0&1	
44 Vitreorana_eurygnatha			0																		0	1	
45 Ceratophrys_cornuta	0				0				0			0					0				0	1	
46 Rheobates_palmatius																					1		
47 Allophryne_ruthveni																					0		

	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67
Taxon \ Character																						
1 C_aeneus	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1
2 C_caramaschii	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1
3 C_dantei	1	1	1	?	1	1	1	?	1	1	1	?	1	1	1	?	1	1	1	?	1	1
4 C_gaudichaudii	1	?	1	2	1	?	1	2	1	?	1	2	1	?	1	2	1	?	1	2	1	?
5 C_schmidti	1	?	1	?	1	?	1	?	1	?	1	?	1	?	1	?	1	?	1	?	1	?
6 C_timbuhy	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1
7 C_trachystomus	1	?	1	2	1	?	1	2	1	?	1	2	1	?	1	2	1	?	1	2	1	?
8 H_amicola	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1
9 H_asper_RJ	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1
10 H_asper_SP	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
11 H_babax	?	?	1	2	?	?	1	2	?	?	1	2	?	?	1	2	?	?	1	2	?	?
12 H_cardosoi	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1
13 H_charadranaetes	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1
14 H_dactylocinus	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1
15 H_fredi	1	0	1	2	1	0	1	2	1	0	1	2	1	0	1	2	1	0	1	2	1	0
16 H_glaber	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
17 H_heyeri	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1
18 H_japi	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1
19 H_lateristrigatus	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1
20 H_magalhaesi	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1
21 H_meridionalis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
22 H_nasus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
23 H_ornatus	0&1	0	1	2	1	0	1	2	1	0	1	2	1	0	1	2	1	0	1	2	1	0
24 H_otavioi	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1
25 H_perere	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1
26 H_perplicatus	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1
27 H_phyllodes	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
28 H_pipilans	1	0	1	2	1	0	1	2	1	0	1	2	1	0	1	2	1	0	1	2	1	0
29 H_regius	?	?	1	1	?	?	1	1	?	?	1	1	?	?	1	1	?	?	1	1	?	?
30 H_sazimai	?	?	1	2	?	?	1	2	?	?	1	2	?	?	1	2	?	?	1	2	?	?
31 H_uai	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1
32 M_apuana	1	2	1	?	1	2	1	?	1	2	1	?	1	2	1	?	1	2	1	?	1	2
33 M_boticariana	1	?	?	?	1	?	?	?	1	?	?	?	1	?	?	?	1	?	?	?	1	?
34 M_goeldii	1	2	?	?	1	2	?	?	1	2	?	?	1	2	?	?	1	2	?	?	1	2
35 M_massarti	1	2	?	?	1	2	?	?	1	2	?	?	1	2	?	?	1	2	?	?	1	2
36 Leptodactylus_fuscus	0	?	0	?	0	?	0	0	?	0	?	0	?	0	?	0	?	0	?	0	?	0
37 Hemiphractus_johnsoni	?	?	0	?	?	?	0	0	?	?	0	?	?	?	0	?	?	?	0	?	?	?
38 Physalaemus_cuvieri	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
39 Amereega_trivitatta	?	?	0	?	?	?	0	0	?	?	0	?	?	?	0	?	?	?	0	?	?	?
40 Pristimantis_fenestratus	0	?	?	?	0	?	?	?	0	?	?	?	0	?	?	?	0	?	?	?	0	?
41 Dendropsophus_minutus	1	?	1	?	1	?	1	?	1	?	1	?	1	?	1	?	1	?	1	?	1	?
42 Cycloramphus_brasiliensis	?	?	1	?	?	?	1	?	?	?	1	?	?	?	1	?	?	?	1	?	?	?
43 Rhinella_major	?	?	0&1	?	?	?	0&1	?	?	?	0&1	?	?	?	0&1	?	?	?	0&1	?	?	?
44 Vitreorana_eurygnatha	1	?	1	?	1	?	1	?	1	?	1	?	1	?	1	?	1	?	1	?	1	?
45 Ceratophrys_cornuta	?	?	1	?	?	?	1	?	?	?	1	?	?	?	1	?	?	?	1	?	?	?
46 Rheobates_palmatus	1	?	?	?	1	?	?	?	1	?	?	?	1	?	?	?	1	?	?	?	1	?
47 Allophryne_ruthveni	1	?	?	?	1	?	?	?	1	?	?	?	1	?	?	?	1	?	?	?	1	?



	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88
Taxon \ Character																					
1 C_aeneus	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	2	0	0&1	0
2 C_caramaschii	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	1	0	1	0&1
3 C_dantei	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	0	0	1
4 C_gaudichaudii	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	1	0	1	0
5 C_schmidti	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	0	1	0
6 C_timbuhy	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	1&2	0	1	0
7 C_trachystomus	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	1	0	1	0
8 H_amicola	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	1	0	1	0
9 H_asper_RJ	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	2	1	0	1	1
10 H_asper_SP	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	0	1	1
11 H_babax	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	0	1	0	1
12 H_cardosoi	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	2	2	0	0&1	0&1
13 H_charadraetaes	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	1&2	1	0	1	0
14 H_dactylocinus	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	2	0	1	1
15 H_fredi	1	2	1	0	1	2	1	0	1	2	1	0	1	2	1	0	2	1	0	1	0
16 H_glaber	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1&2	1	0	0&1	0
17 H_heyeri	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	1	1&2	1	1	2	1	0	1	0
18 H_japi	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	1	0	1	0
19 H_lateristrigatus	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1&2	1	0	1	0
20 H_magalhaesi	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	1	0	0&1	0
21 H_meridionalis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0
22 H_nasus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1&2	0	1	0
23 H_ornatus	1	2	0&1	0	1	2	1	0	1	2	1	0	1	2	1	0	2	1	0	0&1	0
24 H_otavioi	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	1	0	1	1
25 H_perere	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	1	0	1	0
26 H_perplicatus	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	1	0	1	0
27 H_phyllodes	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1&2	1	0	1	0
28 H_pipilans	1	2	1	0	1	2	1	0	1	2	1	0	1	2	1	0	2	1	0	1	0
29 H_regius	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	0	1	0	1
30 H_sazimai	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	1	0	1	0
31 H_uai	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	1	0	1	0
32 M_apuana	1	1	1	2	1	1	1	2	1	1	1	1	1	1	2	1	2	1&2	1	0	1
33 M_boticariana	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	0	1
34 M_goeldii	1	1	1	2	1	1	1	2	1	1	1	1	1	1	1	2	1	2	1	0	1
35 M_massarti	1	1	1	2	1	1	1	2	1	1	1	1	1	1	1	2	1	2	0	1	0
36 Leptodactylus_fuscus	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0
37 Hemiphractus_johnsoni	0	1	1	1	0	1	1	1	0	1	1	1	0	1	1	1	0	0	0	0	1
38 Physalaemus_cuvieri	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0&1	0	1
39 Amereega_trivitatta	0	1	1	1	0	1	0	1	0	1	0	1	0	1	0	1	0	0	0	1	1
40 Pristimantis_fenestratus	1	1	0	1	1	0	1	1	0	1	1	1	0	1	1	1	0	0	0	0	0
41 Dendropsophus_minutus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
42 Cycloramphus_brasiliensis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0&1	1	0	1	1
43 Rhinella_major	0&1	1	1	1	0&1	1	1	1	0&1	1	1	1	0&1	1	1	1	0	0	0	0	0
44 Vitreorana_eurygnatha	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
45 Ceratophrys_cornuta	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
46 Rheobates_palmatus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0
47 Allophryne_ruthveni	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1



	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108
Taxon \ Character																				
1 C_aeneus	0	1	0&1	1	0	1	0&1	0&1	0	1	0	0&1	0&1&2	1	1	1	0&1	0&1	0	0
2 C_caramaschii	0	1	0&1	1	0&1	0	0	0&1	0	1	0	0	1	1	0	1	0&1	0&1	0	0&1
3 C_dantei	0	1	0	1	0	0	0	0	0	1	0	0	2	1	1	1	1	0	0	0
4 C_gaudichaudii	0	1	0&1	0&1	0	0	0&1	1	0	1	0	0	1&2	1	7	0&1	0&1	0&1	0	0
5 C_schmidti	0	1	0&1	0&1	0	1	0&1	0&1	0	1	0	0	1&2	1	0	0&1	0&1	0&1	0	0
6 C_timbuhy	0	1	0&1	0&1	0	0	0&1	0&1	0	1	0	0&1	1	0&1	1	1	0&1	1	0	0
7 C_trachystomus	0	1	0&1	1	0&1	1	0&1	0&1	0	1	0	0&1	1&2	1	0	0&1	0&1	0&1	0	0
8 H_amicola	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1
9 H_asper_RJ	0	1	0&1	0&1	0	0	0&1	0&1	0	1	0	0	1&2	0&1	0	0&1	0&1	0	0	0
10 H_asper_SP	0	1	0&1	1	0	1	1	0&1	0	1	0	0	2	1	0	0&1	0	0	0	0&1
11 H_babax	0	0&1	0&1	1	0	0	0&1	0	1	0	1	0&1	1	0	1	1	0&1	0	0	0
12 H_cardosoi	0	1	0&1	1	0	1	0&1	1	0	1	0	0&1	2	1	0	0&1	0	0	0	0
13 H_charadranaetes	0	1	0	1	0	0	0	0	0	1	0	1	1&2	1	0	0&1	0&1	1	0	0&1
14 H_dactylocinus	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0	1	1	0	0	0
15 H_fredi	0	1	1	1	0	0	1	0	0	1	0	1	2	1	0	1	1	0	0	1
16 H_glaber	0	1	0&1	0	0	0	0&1	0	1	0	0&1	2	0&1	0&1	0&1	0	0	0	0	0
17 H_heyeri	0	1	0	1	0	0	0&1	0	0	1	1	1	1&2	1	1	1	0&1	0&1	0	0
18 H_japi	0	0&1	0	1	0	1	0&1	0&1	0	0	0	1	1	1	0	1	1	0	0	0&1
19 H_lateristrigatus	0	1	0	0&1	0	0	0	0&1	0	1	1	0	1&2	1	0	0&1	1	0&1	1	0&1
20 H_magalhaesi	0	1	0&1	0&1	0	0	0	0&1	0	0	0	1	1	1	0	1	1	1	0&1	0
21 H_meridionalis	0	1	1	1	0	0	1	0	0	1	1	0	1	1	0	1	1	1	1	0
22 H_nasus	0	1	0	1	0	0&1	1	0&1	0	1	1	0	2	1	1	1	0&1	0	0	0
23 H_ornatus	0	0&1	0&1	1	0	0	0&1	0	1	0	1	1&2	1	1	1	0&1	0&1	0&1	0	0
24 H_otavioi	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0
25 H_perere	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	0&1	1	1	0	0
26 H_perplicatus	0	1	0&1	1	0	0&1	0	0	0	1	0	1	1&2	0&1	0	1	0&1	0&1	0	0&1
27 H_phylodes	0	1	0	0&1	0	0	0	0	0	0	0	0	1&2	1	0	1	0&1	1	0	0
28 H_pipilans	0	1	0	1	0	0	0	0	0	1	0	1	2	1	0	1	1	0	0	0
29 H_regius	0	1	1	1	0	0	1	0	0	1	0	1	2	1	0	1	0	0	0	0
30 H_sazimai	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0
31 H_uai	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0
32 M_apuana	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
33 M_boticariana	0	1	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0
34 M_goeldii	0	1	0	0	0	0&1	1	1	0	0	0	0	2	0	0	0	0	0	0	0
35 M_massarti	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
36 Leptodactylus_fuscus	0	1	0&1	0	0	0&1	0&1	0&1	0	0	0	0&1	2	1	0	1	0&1	0&1	0	0&1
37 Hemiphractus_johnsoni	1	0&1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
38 Physalaemus_cuvieri	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0&1	1	0&1	1	0
39 Amerega_trivitatta	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0&1
40 Pristimantis_fenestratus	0	1	0	0	0	0	1	1	0	0	0	0&1	1	0	0	0&1	0	0	0	0
41 Dendropsophus_minutus	0	1	0	0	0	0	1	0	0	0	0	0	0&1	1	0	1	0	1	0	0
42 Cycloramphus_brasiliensis	0	1	0&1	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0
43 Rhinella_major	1	1	0&1	1	1	0	0&1	1	1	0	0	0	2	0	0	1	0	0	0	0
44 Vitreorana_eurygnatha	0	1	0&1	0	0	0	1	0&1	0	0	0	1	1	1	0	0	0	0	0	0
45 Ceratophrys_cornuta	1	1	0	0	0	0	1	0	0	0	0	1	2	0	0	1	0	0	0	0
46 Rheobates_palmatus	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0&1
47 Allophryne_ruthveni	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0



	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	
Taxon \ Character																				
1 C_aeneus	0	?	0	?	0	1	0&1	1&2	0	0	1	1	0	0&1	0	0&1	1	0&1	1	
2 C_caramaschii	0&1	0	0&1	0	0&1	0&1	0	3&4	0	0	0&1	0	0	0&1	0	0&1	0&2	0&1&2	0&1	
3 C_dantei	0	?	1	0	0	0	?	?	1	0	1	0	0	1	0	1	1	1	0	
4 C_gaudichaudii	0&1	0&1	0&1	0	0&1	0&1	0	1&2	0	0	0&1	0	0	0&1	0	0&1	0&1	0&2	0&2	
5 C_schmidti	0&1	0	0	?	0	1	0&1	3&4	0	1	0&1	0&1	0	0&1	0&1	1	0&1&2	0&1	0&1	
6 C_timbuhy	0	?	0&1	0	0	1	0&1	3&4	0	0&1	0&1	0&1	0	0&1	0	0&1	1&2	1&2	0&1	
7 C_trachystomus	0&1	0	0&1	1	0&1	0&1	1	4	0&1	0&1	0&1	1	0&1	0&1	0	0&1	0&2	0&1	0&1	
8 H_amicola	0	?	0	?	0	1	0	2	0	1	1	1	1	1	0	1	1	0	2	
9 H_asper_RJ	0&1	0	0	?	0	1	0	3	0	0&1	0&1	1	0	0&1	0	0&1	0	0&2	1	
10 H_asper_SP	0	?	0	?	0	1	0	3	0	0	1	0&1	0	0&1	0	0&1	0&1	0&1	0&1&2	
11 H_babax	0&1	1	0	?	0&1	0&1	1	?	0	0&1	0&1	1	1	0&1	0&1	0&1	0&2	0&1	1&2	
12 H_cardosoi	0&1	0	0	?	0&1	1	0&1	3	0&1	0&1	1	1	0&1	0	0&1	0&1	0&1&2	1&2	0&1	
13 H_charadranaetes	0	?	0	?	0&1	0&1	0	3	0	1	0&1	1	0	1	0	1	2	0&2	2	
14 H_dactylocinus	0	?	0	?	0	0	?	?	0	1	1	0	0	0	0	1	2	0	1	
15 H_fredi	1	0	0	?	1	1	1	1	0	1	1	1	0	1	0	1	2	0	0	
16 H_glaber	0&1	0	0	?	0&1	0&1	0	2	0&1	0&1	0&1	0&1	1	0&1	1	0&1	0&1	0	0&1	
17 H_heyeri	0&1	1	0	?	0	0&1	0	1&2	0	0&1	0&1	1	1	0&1	1	0&1	2	0&2	1&2	
18 H_japi	1	0&1	0	?	0&1	1	0&1	2	0	0	1	1	0	1	0	1	0&1	0&1	0&1	
19 H_lateristrigatus	0&1	1	0&1	0	0&1	0&1	1	?	0	0	0&1	1	0	1	0	0&1	2	0&1	2	
20 H_magalhaesi	0	?	0	?	1	1	0&1	0&1	0&1	0&1	1	1	0&1	1	0&1	1	0	1&2	2	
21 H_meridionalis	0	?	0	?	0	0	?	?	1	1	1	1	0	1	0	1	0	0	1	
22 H_nasus	0	?	0	?	1	1	0&1	3&4	0	0&1	0&1	1	0&1	1	0&1	1	0&2	2	2	
23 H_ornatus	0&1	0&1	0&1	0	1	0&1	0&1	2&3	0	0&1	0&1	0&2	0&1	0&1	0&1	0&1&2	0&1	1&2		
24 H_otavioi	1	1	?	?	?	0	?	?	0	1	1	?	?	1	?	1	?	?	?	
25 H_perere	1	?	0	?	?	1	0&1	4	0	?	1	?	?	1	?	1	2	2	?	
26 H_perplicatus	0&1	0&1	0	?	0	1	0&1	3	0	0&1	0	1	0	1	0	1	0&1	0&1	0&1	
27 H_phylloides	0	?	0	?	0&1	0&1	1	2&3	0&1	1	0&1	1	0&1	1	0&1	1	2	2	2	
28 H_pipilans	1	0	0	?	1	1	1	?	0	0	1	0	0	1	0	1	2	1	1	
29 H_regius	1	0	0	?	1	0	?	?	0	1	0	0	1	1	1	1	2	2	2	
30 H_sazimai	0	0	0	?	1	1	1	3	?	1	1	1	0	1	0	1	1	2	2	
31 H_uai	0	?	0	?	0	1	1	3	0	1	1	1	0	1	0	1	0	2	2	
32 M_apuana	0	?	0	?	0	1	1	?	0	0	1	1	1	0	1	0	0	0	0	
33 M_boticariana	0	?	0	?	0	0	?	?	0	0	1	1	1	0	1	0	0	0	0	
34 M_goeldii	0	?	0	?	0	0&1	0	4&5	0	0&1	0	0	0	1	0	1	1&2	0	0	
35 M_massarti	0	?	0	?	0	0	?	?	0	0	0	?	0	1	1	0	0	0	0	
36 Leptodactylus_fuscus	0	?	0	?	1	1	1	?	0	0	1	1	0	0	0	0&1	0	2	0&1	
37 Hemiphractus_johnsoni	0	?	0&1	0	1	1	0&1	?	0	1	0	0	1	0	1	0	0	2	0	
38 Physalaemus_cuvieri	0	?	0&1	1	1	1	0	?	0	?	?	0&1	0&1	1	0	0	0	0	0	
39 Amereega_trivitatta	0	?	0	?	0	0	?	?	0	0	0	?	0&1	0&1	1	0	0	0	0	
40 Pristimantis_fenestratus	0&1	0	0	?	0	0	?	?	0	0	0	?	0&1	0&1	1	1	0	1&2	0	
41 Dendropsophus_minutus	0&1	0	0	?	0&1	0	?	?	0	0	0	2	0	0	0	0	0	0	0	
42 Cycloramphus_brasiliensis	0&1	0	0	?	0&1	0	?	?	0	1	0	0&1	0&1	0&1	0	0&1	0&1	0	0	
43 Rhinella_major	0&1	0	0	?	0	0	?	?	0	0	0	?	0	0&1	0	0&1	0	0&2	0	
44 Vitreorana_eurygnatha	0	?	0	?	0	0	?	?	0&1	0	1	0	0	0	0	0	0	0	0	
45 Ceratophrys_cornuta	0	?	1	1	0	1	0	?	0	?	?	?	0	0	1	0	0	1	0	
46 Rheobates_palmatus	0&1	0	0	?	0	0	?	?	0	0&1	0	1	0	0	0	0	0	0	0	
47 Allophryne_ruthveni	0	?	1	1	1	0	?	?	1	0	0	2	0	0	1	0	0	2	0	



	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	
Taxon \ Character																				
1 C_aeneus	0&2	1&2	0	0&1	2	1	0	0&2	0&1	0&1	1	0	1	0	0	0&1	0&1	0	0	
2 C_caramaschii	2	2	1	1	1&2	0	?	0	1	0	1	0	1	0	?	0	?	0	0	
3 C_dantei	2	1	0	1	1	1	1	0	?	1	?	0	1	0	1	1	?	0	0	
4 C_gaudichaudii	1&2	2&3	0	0	1&2	0&1	0	0	0&2	1	?	1	1	0	0&1	0&1	1	0	0	
5 C_schmidti	2	2	?	1	1	1	0	2	2	1	?	1	1	0	1	1	0	0	0	
6 C_timbuhy	2	1	?	0	1	1	0	0	1	1	?	1	1	0	?	0	?	0	0	
7 C_trachystomus	1	2	0	1	1&2	1	0	0&2	0&2	0&1	1	0	1	0	1	0&1	1	0	0	
8 H_amnicola	2	1	?	1	?	?	?	0	1	1	?	0	1	0	0	1	1	0	0	
9 H_asper_RJ	0	0&1	?	0	1&2	0&1	0	1&2	2	1	2	1	1	0	1	0&1	1	0	0	
10 H_asper_SP	0	1	1	0	1&2	1	0	0&2	1	1	?	1	1	0	1	0&1	1	0	0	
11 H_babax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
12 H_cardosoi	0&1	1&2	0	0&1	1&2	0&1	0&1	0&1&2	1&2	0&1	0&1&2	0&1	1	0	0	0&1	0&1	0	0	
13 H_charadranaetes	0	1	?	1	2	0	?	0&1	1&2	0	2	1	1	0	0	1	0	0	?	
14 H_dactylocinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
15 H_fredi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
16 H_glaber	0	2	0	0	2	0&1	0	1&2	1&2	0&1	0	0	1	0	?	1	0	0	0	
17 H_heyeri	?	?	?	1	1	?	?	0	2	1	?	0	1	0	1	1	0	0	0	
18 H_japi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
19 H_lateristrigatus	0	0	?	1	1	1	0	1	2	0	0	1	1	0	?	1	1	0	0	
20 H_magalhaesi	2	1	?	1	1	1	0	0	2	0	2	0	1	0	0	1	0	0	0	
21 H_meridionalis	1	1	?	?	2	0	?	0	2	0	2	0	1	0	?	1	1	0	0	
22 H_nasus	?	?	0&1	1	1	1	0	1	1	0	0	1	1	0	?	1	1	0	0	
23 H_ornatus	?	?	0	1	2	1	0	1	2	0	0	?	1	0	?	0	?	0	0	
24 H_otavioi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
25 H_perere	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
26 H_perplicatus	1	2	0	1	2	1	0	1&2	2	0&1	0	0&1	1	0	0&1	0&1	0	0	0	
27 H_phyllodes	2	1	?	1	1&2	0&1	0	0	1	0	0	1	1	0	0	0&1	0	0	0	
28 H_pipilans	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
29 H_regius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
30 H_sazimai	2	2	?	?	?	?	?	0	1	0	0	1	1	0	1	1	1	0	0	
31 H_uai	?	?	0	0	2	1	0	0	2	0	2	0	1	0	1	1	1	0	?	
32 M_apuana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
33 M_boticariana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
34 M_goeldii	?	?	0	1	1	0	?	2	2	0	1	1	0	?	?	0	?	0	0	
35 M_massarti	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	
36 Leptodactylus_fuscus	0	2	0	0	1	1	0&1	1	0	0	2	0	0	?	?	1	0	0&1	0&1	
37 Hemiphractus_johnsoni	0	0&1	?	0	0&1	0&1	0	0&2	0	2	?	0&1	0	?	?	1	0	0	0	
38 Physalaemus_cuvieri	1	0	0	1	0	1	0	1	0	0	1	1	1	1	?	1	0	0&1	1	
39 Amereega_trivitatta	0	2&3	?	1	1	0&1	?	1	0	0	1	0	1	0&1	?	1	0	1	1	
40 Pristimantis_fenestratus	?	?	0	0&1	0&2	1	0	1&2	0	0&1	1	1	0&1	1	?	0	?	0	0	
41 Dendropsophus_minutus	0	2	0&1	0	1&2	1	0	0	0	0	2	1	0	?	?	?	?	0&1	0&1	
42 Cycloramphus_brasiliensis	0	1&2	?	0&1	1	0&1	0	2	1&2	0	2	0&1	0	?	?	1	0&1	1	1&2	
43 Rhinella_major	0	1&2	?	0&1	1	0	?	1	0	0&1	2	1	0	?	?	1	0	0	0	
44 Vitreorana_eurygnatha	0	0	0&1	0	0	0&1	1	2	1	0&1	2	1	0	?	?	1	1	0&1	0&2	
45 Ceratophrys_cornuta	0	?	?	0	1	1	0	?	0	2	?	1	0	?	?	0	?	1	0	
46 Rheobates_palmatus	0	?	0&1	1	0&2	1	0	0	0	0	1	0&1	1	1	?	0	?	0	0	
47 Allophryne_ruthveni	?	?	1	0	1	0	?	0	2	0	1	?	0	?	?	?	?	?	?	



	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168
Taxon \ Character																						
1 C_aeneus	0	0&1	0&1	1	1	0	?	0	0	0&1	0	0	0	0	0	1	1	1	?	1	1	2
2 C_caramaschii	0	0	1	?	1	0	0	0	0	0	?	0	0	0	0	0	0	1	1	1	1	2
3 C_dantei	1	?	1	1	1	0	?	0	0	1	1	0	0	0	0	1	1	0	1	1	1	2
4 C_gaudichaudii	0	0	0&1	1	1	0&1	0	0	0&1	0&1	0	0	0	0&1	0	0&1	0	1	?	1	1	2
5 C_schmidti	0	0	1	1	1	0	?	0	0	0	1	0	0	0	0	1	1	1	?	1	1	2
6 C_timbuihy	0	0	1	?	1	1	0	0	0	1	?	0	0	1	0	0	0	1	1	1	1	2
7 C_trachystomus	0&1	0	0	?	1	0&1	0&1	0	0	0&1	1	0	0	1	0	0	0&1	1	?	1	1	2
8 H_amicola	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	?	?	2
9 H_asper_RJ	0	0&1	1	1	1	0&1	0&1	0&1	0&1	1	?	0	0	0&1	0	0	0&1	0	1	1	1	2
10 H_asper_SP	0&1	0	0&1	1	1	1	0	0&1	0	1	0	0	0	0	0	0	0&1	0	?	1	1	2
11 H_babax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12 H_cardosoi	0&1	0	0&1	1	1	1	0	0&1	0&1	1	0	0	0	0	0	0	0&1	0	?	1	1	2
13 H_charadranaetes	0	1	1	1	1	1	0&1	0	1	1	1	0	0	1	0	0	0&1	0	?	0	1	2
14 H_dactylocinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
15 H_fredi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
16 H_glaber	0	0	0&1	?	1	0&1	0	1	0&1	0&1	?	0	0	0	0	0	0	0	1	1	1	2
17 H_heyeri	1	0	1	1	1	1	1	0	0	1	1	0	0	1	0	1	0	0	?	1	1	2
18 H_japi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19 H_lateristrigatus	0	0	1	?	1	1	0	0	1	1	?	0	0	0	0	0	1	0	1	1	1	?
20 H_magalhaesi	0	0	1	1	1	1	1	0	0	1	1	0	0	2	0	0	0	1	0	1	1	2
21 H_meridionalis	1	0	0	?	1	1	0	1	0	1	1	0	0	2	0	0	0	1	0	1	1	0&2
22 H_nasus	0	0	0	?	1	0&1	0	1	0	1	?	0	0	0	0	0	1	0	1	1	1	1&2
23 H_ornatus	0	0	0	?	1	1	0	1	0	1	?	0	0	0	0	0	1	1	1	1	1	2
24 H_otavioi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
25 H_perere	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26 H_perplicatus	0	0	0&1	1	1	1	0	0&1	0&1	0&1	0	0	0	0&1	0	0	0&1	1	?	1	1	2
27 H_phylloides	1	0	1	1	1	1	0&1	0	1	1	1	0	0	0	0	0&1	1	0	?	1	1	1&2
28 H_pipilans	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
29 H_regius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
30 H_sazimai	0	0	1	1	1	1	1	0	1	1	1	0	0	?	0	0	1	0	0	1	1	2
31 H_uai	1	1	0	1	1	1	1	1	1	1	1	0	0	?	0	?	?	?	?	1	1	2
32 M_apuana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
33 M_boticariana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
34 M_goeldii	0	0	0	0	1	0	?	0	0	0	?	0	0	0	1	0	0	?	?	?	?	?
35 M_massarti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
36 Leptodactylus_fuscus	0	0&2	0	?	1	1	0	0&1	0	0	?	0	0	0	0	0	0	?	?	?	?	2
37 Hemiphractus_johnsoni	0	0	0&1	?	1	0	?	0	0	?	1	1	1&2	1	0	0	1	0	0	0	0	0&2
38 Physalaemus_cuvieri	0	0&3	0	?	1	0&1	0	1	0	1	?	0	0	1	0	0	0	?	?	?	?	2
39 Amereega_trivitatta	0	2&3	0	?	1	0&1	0	1	0	2	?	0	0	0	0	0	0	?	?	?	?	2
40 Pristimantis_fenestratus	0	0	0	?	0&1	1	1	1	0&1	0	?	0	0	0&1	1	0	0	?	?	?	?	0
41 Dendropsophus_minutus	0	0&2	0	?	0	1	0	1	0	0&1	?	1	1	0	1	0	0	?	?	?	?	2
42 Cycloramphus_brasiliensis	0&1	2&3	0	?	1	1	1	0	1&2	?	0	0	0	0	0	0	0	?	?	?	?	0
43 Rhinella_major	0	0	0	?	0	0&1	0	1	0	2	0	?	1	0	2	0	0	0	?	?	?	0&2
44 Vitreorana_eurygnatha	0	0&1	0	?	0	0&1	0	0&1	0&1	0	?	1	0	0&1	0	0	0	?	?	?	?	1&2
45 Ceratophrys_cornuta	1	2	0	?	1	1	1	0	2	1	?	1	0	2	0	0	0	1	0	0	0	2
46 Rheobates_palmatus	0	0	0	?	1	1	0	1	0	0	?	0	1	0	1	0	1	?	?	?	?	2
47 Allophryne_ruthveni	?	?	0	?	0	0	1	0	2	0	?	1	0	1	1	0	0	1	0	0	0	2



	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187
Taxon \ Character																			
1 C_aeneus	1&2&3	0&1&2	0&1	0&1	0&1	0&1	0&1	0&1	0	?	0	0&1	1	0	1	0	0&1	0	
2 C_caramaschii	2	0&1	0&1	0	0	0&1	0	1	0	?	0	0	0	0&1	0&1	0	0	0	
3 C_dantei	1	1	0	0&1	1	0	1	0&1	0	1	0	0	0&1	0	0	1	0	0&1	0
4 C_gaudichaudii	2&3	0&1&3	0&1&3	0&1	0&1	0&1	0&1	0	1	0	0	0&1	0&1	0&1	0&1	0	0&1	0	
5 C_schmidti	3	1	0	0	0	0	1	1	0	1	0	0	0	1	0	1	0	1	0
6 C_timbuhy	?	1	?	?	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?
7 C_trachystomus	1&2	1&3	0	0&1	0&1	0&1	0&1	0	1	0	0	0	0&1	0	0&1	0	0&1	0	
8 H_amicola	3	1	1	0	0	1	1	1	0	1	1	0	0	1	0	1	1	1	1
9 H_asper_RJ	3	0&3	0	0&1	0&1	0&1	0&1	0&1	0	1	1	0	1	1	0	1	0	0	1
10 H_asper_SP	2	0	1	0	0	0&1	1	1	0	1	1	0	0	?	1	1	0	1	1
11 H_babax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12 H_cardosoi	1&2&3	0&1&2	0&1	0&1	0&1	0&1	0&1	0	1	1	0	1	1	0	1	0	0&1	0&1	
13 H_charadranaetes	3	1	1	0	0	1	1	1	0	1	0	0	1	1	1	1	0	1	1
14 H_dactylocinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
15 H_fredi	1&2	1	1	0	0	1	0	1	0	1	1	0	1	1	0	1	0	1	1
16 H_glaber	1&2	1	0	0&1	0&1	0	0	0	0	1	1	0	0	1	0&1	0&1	0	0	1
17 H_heyeri	3	1	0	0	0	1	1	1	0	1	1	0	0	1	0	1	0	1	1
18 H_japi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19 H_lateristrigatus	0	1	1	0	1	1	0	?	0	?	?	?	?	?	?	?	?	?	?
20 H_magalhaesi	2	0	1	0	0	0	1	1	1	1	1	0	0	1	0	1	0	1	1
21 H_meridionalis	2&3	0&1	0	0&1	0&1	1	1	1&2	0	1	1	0	0&1	1	0	1	0&1	1	1
22 H_nasus	2	0&1	0	0&1	0&1	1	0&1	1	0	1	1	0	1	1	0&1	1	0	0	1
23 H_ornatus	1	1	0	0	0	1	1	1	0	?	?	0	1	?	?	?	0	?	0
24 H_otavioi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
25 H_perere	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26 H_perplicatus	1&3	0&2	0	0&1	0&1	0	0&1	0&1	0&1	1	?	0	0	1	0	1	0&1	1	1
27 H_phylloides	1&3	0&1	0	0	0	0&1	0&1	1	0	1	1	0	1	0&1	0	1	0&1	0&1	1
28 H_pipilans	1	1	1	0	0	1	0	1	0	1	?	0	1	1	0	1	0	0&1	1
29 H_regius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
30 H_sazimai	2	1	1	0	0	1	1	1	0	1	1	0	0	1	0	1	0	1	1
31 H_uai	2	1&3	1	0&1	1	1	0&1	1	0&1	1	1	0	1	1	0&1	1	0&1	1	1
32 M_apuana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
33 M_boticariana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
34 M_goeldii	3	1	0	1	1	0	0	2	0	1	1	1	0	1	1	0	0	1	0
35 M_massarti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
36 Leptodactylus_fuscus	0	3	0&1	0&1	0	0	1	2	0	1	?	1&2	0&1	0	0&1	1	1	0&1	1
37 Hemiphractus_johnsoni	3	1	0	0	0&1	0	0	2	0	1	?	2	0&1	0	1	1	1	1	1
38 Physalaemus_cuvieri	3	3	0	1	1	0	0&1	0	0	1	?	?	?	?	?	?	?	?	?
39 Amereega_trivitatta	2&3	1	0	0	0	0	0	1	0	?	?	?	?	?	?	?	?	?	?
40 Pristimantis_fenestratus	3	3	0	0&1	0&1	0	1	0&1	0	1	?	0	1	0&1	0	1	0	1	1
41 Dendropsophus_minutus	2&3	1&3	0&2	1	1	1	0&1	0&2	0&1	?	?	2	0	0	0&1	1	0	1	0&1
42 Cycloramphus_brasiliensis	2	1	2	0	0	0	0&1	0&1	0	1	?	2	0	0&1	1	0	1	0	1
43 Rhinella_major	0	3	2	0	0&1	0	0	2	0	1	?	?	?	?	?	1	1	0&1	1
44 Vitreorana_eurygnatha	3	1	1&2	0&1	0&1	0&1	1	1&2	0&1	1	?	1&2	1	0	0	1	1	1	0
45 Ceratophrys_cornuta	1	?	1	1	1	0	0	2	0	1	?	2	1	0	1	1	1	0	1
46 Rheobates_palmatus	2	1	0	0&1	0&1	0&1	1	0&1	0	1	?	0	0&1	0	0&1	1	1	1	0
47 Allophryne_ruthveni	1	1	2	0	0	1	0	1	0	0	?	2	0	0	0	1	1	1	1



	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204
Taxon \ Character																	
1 C_aeneus	1	0&1	0&1&2	0&2	0	2	0	0&1	0&1&2	0&1	2	1&2	0&1	0&1&2	1&2	1	1
2 C_caramaschii	1	0	1	1	0	2	0	0&1	1	0	2	2	1	1&2	2	0&1	1
3 C_dantei	1	0	0	1	1	2	1	0	1	2	2	1	1	1	2	1	1
4 C_gaudichaudii	0&1	0&1	0&1&2	0&1	0&1	1&2	0	0&1	1	0&1	2	2	0&1	0&1&2	0&2	0&1	0&1
5 C_schmidti	0	0	1	2	1	2	0	0	1	0	2	1	0	1	1	0	1
6 C_timbuhy	?	?	?	?	?	?	1	0	1	0	0	?	?	?	?	?	?
7 C_trachystomus	1	0	0&1	0	0	?	0&1	0&1	1	0	2	1&2	0	1&2	2	0&1	1
8 H_amicola	0	1	?	2	0	?	1	0	1	0	2	1	0	1	0	1	1
9 H_asper_RJ	0	1	1	0&2	0&1	2	0&1	0&1	0	0	2	1	0	1&2	0&2	0&1	1
10 H_asper_SP	0	1	0&1	1&2	0&1	2	0&1	0&1	1	0	2	0	0	2	2	1	0
11 H_babax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12 H_cardosoi	0	1	0&1&2	0&1	1	1&2	0&1	0&1	0&1	0&2&3	2	1	0	1&2	1&2	0&1	0&1
13 H_charadranaetes	0	1	2	2	1	?	1	?	0	0	2	1	0	1	1	1	1
14 H_dactylocinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
15 H_fredi	0	1	2	?	0	2	?	0	?	?	2	1	?	2	0&2	0&1	1
16 H_glaber	0	1	2	1	0	2	0	1	1	0&3	2	1&2	0	1	2	1	1
17 H_heyeri	0	1	2	0	1	2	1	0	2	3	2	1	1	2	0	1	1
18 H_japi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19 H_lateristrigatus	?	1	0	?	1	2	0	1	0	3	?	?	?	?	?	0	1
20 H_magalhaesi	0	1	?	1	0	?	1	0	1	0	2	1	1	1	0	1	1
21 H_meridionalis	0	1	2	0	0&1	2	1	0	0	0	2	1	0	1&2	0&1&2	0&1	1
22 H_nasus	0	1	0&1	0	0	2	0	0&1	0	0	2	1	0	2	2	0	1
23 H_ornatus	0	1	1	0	0	2	0	1	1	2	?	?	?	?	?	?	?
24 H_otavioi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
25 H_perere	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26 H_perplicatus	0	1	0&2	2	0&1	2	0&1	0&1	0	0	2	2	1	1	0	1	1
27 H_phyllodes	0	1	1&2	2	0&1	2	1	0&1	0	0	2	1	0	1&2	0&1	0&1	0&1
28 H_pipilans	0	1	1	1	0	2	?	0&1	?	?	2	1	0	1	0	0&1	1
29 H_regius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
30 H_sazimai	0	1	?	2	0	?	1	0	1	0	2	1	0	1	0	1	1
31 H_uai	0	1	0&1	1&2	0&1	2	1	0	1	1	2	1&2	0&1	0&2	1	1	1
32 M_apuana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
33 M_boticariana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
34 M_goeldii	0	1	1	0	0	2	1	1	0	1	3	0	1	0	0	1	1
35 M_massarti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
36 Leptodactylus_fuscus	0	1	0	?	1	2	0	0&1	0&2	0	2	1&2	0&1	0	0&1	?	0&1
37 Hemiphractus_johnsoni	?	1	1	0	1	2	0	0	0&1	0	2	1	0	2	2	?	0&1
38 Physalaemus_cuvieri	?	?	?	?	0	2	0&1	1	0	0&1	1&2	0&2	0&1	2	2	1	1
39 Amereega_trivitatta	?	?	1	0&1	0	2	1	0&1	0	0&3	2	2	1	0	2	1	?
40 Pristimantis_fenestratus	0&1	1	0&1	1	1	2	0	1	1	1	2	1	0&1	2	1	1	1
41 Dendropsophus_minutus	0	1	0&1	0	0	1&2	1	0&1	0	0	2	1&2	0&1	0	0	1	0&1
42 Cycloramphus_brasiliensis	0	1	1&2	1	1	2	0	0&1	0&2	0&1	2	2	0	0&1	0	1	0&1
43 Rhinella_major	?	0	1	0&1	0&1	2	0&2	0&1	1&2	1&3	0	?	?	2	2	0	1
44 Vitreorana_eurygnatha	0	0	1	0	0	0	0&1	0	0&1	3	2	1&2	0&1	1&2	2	0&1	1
45 Ceratophrys_cornuta	?	0	?	?	1	2	0	1	2	3	?	?	?	?	?	?	?
46 Rheobates_palmatus	1	0	1	0&1	0	1&2	1	0	1	0&3	2	1	0	2	1&2	1	1
47 Allophryne_ruthveni	?	0	1	0	0	1	1	0	0	1	2	1	1	2	2	1	1



	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220	221	222	223	224
Taxon \ Character																				
1 C_aeneus	1	0&1	1&2	1	1	1	1	0	0&1	0	2	1&2	?	?	?	0	0&1	1&2	0&1&2	0
2 C_caramaschii	1	0&2	0&2	?	1	?	0	0	0	2	0	1	0	0	0	0&1	1&2	0	0&1	
3 C_dantei	1	0&2	0&2	?	0	1	0	?	1	?	1&2	1&2	?	?	?	0	1	0&1	0&1	1
4 C_gaudichaudii	0&1	0&1	0&1&2	1	1	0	?	?	?	?	?	?	?	?	?	0	0&1	1	0&1	1
5 C_schmidti	0	0	2	1	?	?	?	0	2	1	2	2	0	0&1	?	0	1	1	0	1
6 C_timbuhy	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
7 C_trachystomus	0&1	1	1&2	1	1	1	1	0	1	0	1	2	0	0	0	0	1	1	0	0
8 H_amicola	1	1	1	1	1	1	1	0	2	1	1	2	0	1	1	0	0	1	0	0
9 H_asper_RJ	1	1&2	0&2	1	1	1	1	0	2	1	2	2	0	0	0	0	1	1	0	0
10 H_asper_SP	1	1	0&1	1	1	1	1	0	2	0	2	2	0	0	1	0	1	2	0	1
11 H_babax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12 H_cardosoi	0&1	1&2	2	1	?	?	?	0	2	0	?	?	0	0	1	0	0&1	2	0&2	0
13 H_charadranaetes	1	1	1	1	?	?	?	0	2	0	?	?	0	1	1	0	1	1	0	1
14 H_dactylocinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
15 H_fredi	0	1&2	2	?	?	?	0	1	1	2	1	1	?	?	?	0	0	1&2	1&2	0&1
16 H_glaber	1	1	2	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17 H_heyeri	1	1	2	1	1	1	1	0	2	1	?	?	?	?	?	0	1	2	0	0
18 H_japi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19 H_lateristrigatus	?	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
20 H_magalhaesi	1	1	1	1	0	0	?	0	2	0	?	?	0	1	1	0	1	1	0	0
21 H_meridionalis	1	0&1	0&2	1	?	?	1	0	0&1	0&1	1	?	1	1&2	0	0	0&1	0&1&2	0&1&2	0&1
22 H_nasus	1	1&2	2	1	1	1	1	0	0&1	0&1	0&1	1	?	?	?	0	0&1	0&1	1&2	0
23 H_ornatus	?	2	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
24 H_otavioi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
25 H_perere	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26 H_perplicatus	1	1&2	2	1	0	1	1	0	2	1	1	2	?	?	?	0	1	2	0	1
27 H_phylloides	1	1&2	1&2	1	0	1	1	0	1&2	1&2	1&2	0&1	?	?	?	0	0&1	1	0&1	1
28 H_pipilans	1	0&1	0&2	?	?	?	1	0	2	2	1&2	0&1	0&1	1	1&2	0	1	1&2	0&1	0
29 H_regius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
30 H_sazimai	1	1	1	?	?	?	1	0	2	0	2	2	?	?	?	0	1	1	0	0
31 H_uai	1	0&2	1	1	1	1	1	0	1&2	1&2	1	1	?	?	?	0	0&1	1&2	0&2	0&1
32 M_apuana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
33 M_boticariana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
34 M_goeldii	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	2	0
35 M_massarti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
36 Leptodactylus_fuscus	0	0	0&1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
37 Hemiphractus_johnsoni	0	1&2	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
38 Physalaemus_cuvieri	?	0&2	1&2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
39 Amereega_trivitatta	?	?	?	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
40 Pristimantis_fenestratus	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
41 Dendropsophus_minutus	0&1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
42 Cycloramphus_brasiliensis	0&1	0&1	0&1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
43 Rhinella_major	?	1&2	0&2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
44 Vitreorana_eurygnatha	0	0	1&2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
45 Ceratophrys_cornuta	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
46 Rheobates_palmatus	0&1	0	1&2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
47 Allophryne_ruthveni	?	0	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

		225	226	227	228	229	230	231	232	233	234	235	236	237	238	239	240	241	242	243	244	245
Taxon \ Character																						
1	C_aeneus	0&2	2	0	2	2	0&1	0	1&2	0	0	0&1	0	0	0	1	0	2	0&1	0&1	0	0
2	C_caramaschii	2	2	0	1&2	2	0	0	1	?	0	0	0	0	0	1	0	2	0&1	1	0	0
3	C_dantei	1&2	1&2	0	1	2	1	0	1&2	0	0	?	0	0	0	0&1	0	2	0&1	1	0	0
4	C_gaudichaudii	1&2	1&2	0	1&2	1&2	0	0	1	0	0	0&1	0	0	0	1	0	2	0&1	0&1	0	0
5	C_schmidti	2	1	?	1	2	0	0	1	?	0	0	0	0	0	1	0	2	0	1	0	0
6	C_timbuhy	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
7	C_trachystomus	2	2	0	1	2	1	0	1	?	0	0	1	0	0	1	0	2	0	1	0	0
8	H_amnicola	1	1	?	2	2	1	0	2	0	0	0	0	0	0	1	0	2	1	1	0	0
9	H_asper_RJ	2	2	0	1	2	0	0	2	0	0	1	?	0	0	0	0	2	0	1	0	0
10	H_asper_SP	?	1	?	?	2	0	?	1	?	?	?	?	0	?	?	2	1	1	0	0	0
11	H_babax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12	H_cardosoi	2	2	0&1	2	2	1	0	2	0	0	1	?	0	1	?	0	2	0&1	1	0	0
13	H_charadranaetes	2	1	?	2	2	0	0	1	?	0	0	0	0	0	1	0	2	0	1	0	0
14	H_dactylocinus	?																				
15	H_fredi	1&2	2	0&1	2	2	1	0&1	1&2	0	0&1	0	0	0	0	1	0	2	0	1	0	0
16	H_glaber	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17	H_heyeri	2	2	0	2	2	1	0	2	0	0	1	?	0	0	0	0	2	1	1	0	0
18	H_japi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19	H_lateristrigatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
20	H_magalhaesi	1	2	0	1	2	0	0	1	?	0	0	0	0	0	1	0	2	0	1	0	0
21	H_meridionalis	1&2	2	0&1	1&2	2	1	0	1&2	0&1	0	1	0	0	0	0&1	0	2	0&1	1	0	0
22	H_nasus	1	1&2	0	1&2	2	0&1	0	2	0&1	0	1	?	0	0	0	0	2	0	1	0	0
23	H_ornatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
24	H_otavioi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
25	H_perere	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26	H_perplicatus	2	2	0	1	2	1	0	2	0	0	1	?	0	0	0	0	2	0	1	0	0
27	H_phylloides	2	1&2	0	1&2	2	0&1	0	1	0	0	0	0	0	0	1	0	2	0&1	1	0	0
28	H_pipilans	0&1&2	2	0&1	2	2	0&1	0	2	0&1	0	1	?	0	0	1	0	2	0&1	1	0	0
29	H_regius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
30	H_sazimai	1	1	?	2	2	1	0	2	0	0	0	0	0	0	1	0	2	0	1	0	0
31	H_uai	0&2	2	0&1	1&2	2	0&1	0	1	?	0	0	1	0	0	1	0	2	0	1	0	0
32	M_apuana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
33	M_boticariana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
34	M_goeldii	?	2	1	?	2	1	0	1	?	0	1	?	0	1	?	0	2	1	1	0	0
35	M_massarti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
36	Leptodactylus_fuscus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
37	Hemiphractus_johnsoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
38	Physalaemus_cuvieri	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
39	Amereega_trivitatta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
40	Pristimantis_fenestratus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
41	Dendropsophus_minutus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
42	Cycloramphus_brasiliensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
43	Rhinella_major	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
44	Vitreorana_eurygnatha	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
45	Ceratophrys_cornuta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
46	Rheobates_palmatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
47	Allophryne_ruthveni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?



		246	247	248	249	250	251	252	253	254	255	256	257	258	259	260	261	262	263	264	265	266	267	268	269
Taxon \ Character																									
1	C_aeneus	1	0&2	1	0	0	1	1	1	1	1	0	2	1	1	1	1	0	1	1	1	3	0		
2	C_caramaschii	1	1	1	0	0	1	1	1	1	1	0	2	0		0	0		0	0					
3	C_dantei	1	1&2	1	0	0	1	1	1	1	1		0	1	1	2	1	1	0	0	1	0			
4	C_gaudichaudii	0&1	0&1	1	0	0	1	1	1	1	1		0	1	1	1	1	1			1	0	3	0	
5	C_schmidti	1	3	0	0	0	1	2	1	1	1	0	2	1	1	0	1	1	0	1	1	0			
6	C_timbuhy																								
7	C_trachystomus	0		0	0	0	1	1	1	1	1	0	0	1	1	2	1	0	0	1	1	0			
8	H_amicola	0	0	1	0	0	0	2	1	1	1	0	0	1	1	0	1	1	0	0	1	1			
9	H_asper_RJ	1	0	1	0	0	0	2	1	1	1	1	0	0	1	1	0	1	1	1	1	0	1		
10	H_asper_SP	0	3	0	0	0	1	3	0	1	1	1	0	0	0	1	0	0	0	1	1	0	1	3	0
11	H_babax																								0
12	H_cardosoi	1	0	1	0	0	0	2	1	1	1		2	1	1	0	1	1	0		0	0			
13	H_charadranaetes	1	0	1	0	0	0	2	1	1	1	0	2	1	1	1	1	1	0	1	0	0			
14	H_dactylocinus																								1
15	H_fredi	1	0&1	1	0	0	1	2	1	1															0
16	H_glaber																								3
17	H_heyeri	1	0	1	0	0	0	2	1	1	1	1	1	2	1	1	0	1	2	0	1	1	1		0
18	H_japi																								0
19	H_lateristrigatus																								0
20	H_magalhaesi	1	0	1	0	0	0	1	1	1	1	0	2	0	1	1	0	1	1			0	1		0
21	H_meridionalis	0&1	0	1	0	0	1	2&3	0	1	1										0	1			0
22	H_nasus	1	0&1	1	0	0	1	3	1	1	0	1	2	2	0	0	0	0	0	1	0	0	1	2	0
23	H_ornatus																								0
24	H_otavioi																								0
25	H_perere																								0
26	H_perplicatus	1	0	1	0	0	1	2	1	1	1	1	0	0	0&1	1	0	1	2	0	1	0	0		0
27	H_phylloides	1	0	1	0	0	1	1&2	1	1			2	1	1	1	1	1	0		0	0		3	0
28	H_pipilans	1	0	1	0	0	1	2&3	1	1		1	0	1	0	0	0	1	0	1	1	0	1		0
29	H_regius																								
30	H_sazimai	1	0	1	0	0	0	2	1	1	1	0	0	0	1	1	0	1	1			0	1		0
31	H_uai	1	0	1	0	0	0&1	2	1	1	1	0	0	0	0	1	0	1	1		0	0	0		0
32	M_apuana																								0
33	M_boticariana																								5
34	M_goeldii							1																	0
35	M_massarti																								4
36	Leptodactylus_fuscus							0																	1
37	Hemiphractus_johnsoni							0																	
38	Physalaemus_cuvieri							0																	0
39	Amereega_trivitatta							1																	2
40	Pristimantis_fenestratus							0																	7
41	Dendropsophus_minutus							0																	
42	Cycloramphus_brasiliensis							0																	3
43	Rhinella_major							0																	
44	Vitreorana_eurygnatha							0																	0
45	Ceratophrys_cornuta							0																	
46	Rheobates_palmatus							1																	2
47	Allophryne_ruthveni							0																	0



		270	271	272	273	274	275	276	277	278	279	280	281	282	283	284	285	286	287	288	289	290	291	292
Taxon \ Character																								
1	C_aeneus	0	0	?	?	?	?	2	1	1	1	1	0	0	1	1	0	0	1	1	?	?	1	?
2	C_caramaschii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
3	C_dantei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
4	C_gaudichaudii	0	1	?	?	?	?	?	?	1	1	1	1	0	1	1	1	0	1	1	?	?	1	?
5	C_schmidti	0	?	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	1	1	?	?	1	0
6	C_timbuhy	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
7	C_trachystomus	0	1	?	?	?	?	?	?	1	1	1	1	1	0	1	1	1	0	1	1	?	?	1
8	H_amicola	0	0	?	0	?	1	2	1	1	1	1	1	1	1	1	1	0	1	?	1	2	1	?
9	H_asper_RJ	0	1	1	0	?	1	2	0	1	1	1	1	1	1	1	1	1	1	?	1	2	1	?
10	H_asper_SP	0	0&1	0&1	1	0&1	1	2	0	1	1	1	1	1	1	1	1	1	1	?	1	2	1	1
11	H_babax	0	0	?	0	?	1	2	0	1	1	1	1	1	1	1	1	1	0	1	2	1	?	
12	H_cardosoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
13	H_charadraetaes	0&1	0	?	0	?	1	2	0	1	1	1	1	1	1	1	1	1	0	1	2	1	?	
14	H_dactylocinus	0&1	0	?	1	0&1	1	2	1	1	1	1	1	1	1	1	1	1	0	1	2	1	1	
15	H_fredi	0	0&1	0	0	?	1	2	1	1	1	1	1	1	1	1	1	1	0	1	2	1	?	
16	H_glaber	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17	H_heyeri	0&1	0&1	0	0	?	1	2	1	1	1	1	1	1	1	1	1	1	0	1	2	1	?	
18	H_japi	0	?	?	?	?	1	2	?	1	?	?	?	?	?	?	?	?	1	?	1	2	?	
19	H_lateristrigatus	0&1	0	?	0	?	1	2	1	1	1	1	1	1	1	1	1	1	0	1	2	1	?	
20	H_magalhaesi	0	1	0	1	0	1	2	1	1	1	1	1	1	1	1	1	1	0	1	2	1	?	
21	H_meridionalis	1	0	?	1	1	1	2	1	1	1	1	1	1	1	1	1	2	1	0	1	2	1	?
22	H_nasus	0&1	0	?	1	0&1	1	2	1	1	1	1	1	1	1	1	1	1	0	1	2	1	?	
23	H_ornatus	0	1	0	1	0	1	2	0&1	1	1	1	1	1	1	1	1	1	0	1	2	1	?	
24	H_otavioi	0	0	?	1	1	1	2	0	1	1	1	1	1	1	1	1	1	?	1	2	1	?	
25	H_perere	0	0	?	1	1	1	2	1	1	1	1	1	1	1	1	1	1	0	1	2	1	?	
26	H_perplicatus	1	0	?	1	0	1	2	0	1	?	?	?	?	?	?	0	1	?	1	2	1	?	
27	H_phylloides	0&1	0	?	0	?	1	2	0	1	1	1	1	1	1	1	1	1	?	1	2	1	?	
28	H_pipilans	0	0	?	?	?	?	?	?	1	1	1	1	?	1	1	1	1	0	?	?	?	1	
29	H_regius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
30	H_sazimai	0	0	?	1	0	1	2	?	1	1	1	1	0	1	1	1	1	?	1	2	1	?	
31	H_uai	0&1	0	?	1	0	1	2	1	1	1	1	1	1	1	1	1	1	0	1	2	1	?	
32	M_apuana	0	1	?	?	?	?	?	?	1	1	1	1	1	1	1	1	0	1	0	1	2	1	?
33	M_boticariana	?	?	?	?	?	?	2	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
34	M_goeldii	0	1	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	0	?	?	?	1	?
35	M_massarti	?	?	?	?	?	?	2	?	1	1	1	1	1	1	1	1	1	?	1	2	1	?	?
36	Leptodactylus_fuscus	0	1	?	?	?	?	?	?	1	0	1	0	1	1	0	0	0	0	?	?	?	0	?
37	Hemiphractus_johnsoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
38	Physalaemus_cuvieri	0	?	?	?	?	?	?	?	0	1	1	1	1	1	1	0	1	1	0	?	?	0	?
39	Amereega_trivitatta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
40	Pristimantis_fenestratus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
41	Dendropsophus_minutus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
42	Cycloramphus_brasiliensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
43	Rhinella_major	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
44	Vitreorana_eurygnatha	1	1	?	?	?	?	?	?	0	1	1	1	1	1	1	0	0	0	0	?	?	1	?
45	Ceratophrys_cornuta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
46	Rheobates_palmatus	0	0	?	?	?	?	?	?	1	1	1	1	1	1	1	0	1	1	0	?	?	0	?
47	Allophryne_ruthveni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 5. Occurrence of Hylodidae's lineages on each drainage basin.

		1	2	3	4	5
		Parana basin	Southwest basin	Sao Francisco basin	East basins	North-Northeast Atlatl
Taxon \ Character						
1	Crossodactylus sp Serra do Teimoso BA	0	0	0	1	0
2	Crossodactylus sp MG 1	0	0	0	1	0
3	Crossodactylus sp MG 2	0	0	0	1	0
4	C trachystomus 1	0	0	0	1	0
5	C trachystomus 2	0	0	1	1	0
6	Crossodactylus sp SC	0	1	0	0	0
7	C schmidti	1	0	0	0	0
8	Crossodactylus sp West PR	1	0	0	0	0
9	Crossodactylus sp East PR	1	1	0	0	0
10	C caramaschii	1	1	0	0	0
11	C aff caramaschii SP	1	1	0	0	0
12	C gaudichaudii Regiao dos Lagos	0	0	0	1	0
13	C gaudichaudii Floresta da Tijuca	0	0	0	1	0
14	C aeneus	0	0	0	1	0
15	Crossodactylus sp ES	0	0	0	1	0
16	Crossodactylus sp BA	0	0	0	1	0
17	C dantei	0	0	0	0	1
18	Crossodactylus sp MG 3	0	0	0	1	0
19	Crossodactylus sp MG 4	0	0	0	1	0
20	C timbuiy	0	0	0	1	0
21	M goeldii	0	0	0	1	0
22	M massarti	0	1	0	0	0
23	M boticariana	0	0	0	1	0
24	Megaelosia sp Serra do Mar N SP	1	0	0	1	0
25	M cf jordanensis	0	0	0	1	0
26	M apuana	0	0	0	1	0
27	H meridionalis	0	1	0	0	0
28	H aff meridionalis SC	0	1	0	0	0
29	Hylodes sp Joinville SC	0	1	0	0	0
30	H heyeri	0	1	0	0	0
31	Hylodes sp Florianopolis SC	0	1	0	0	0
32	H perplicatus	0	1	0	0	0
33	H charadraetes	0	0	0	1	0
34	H dactylocinus	0	1	0	0	0
35	H cardosoi	1	1	0	0	0
36	Hylodes sp Juiquitiba SP	0	1	0	0	0
37	H nasus	0	0	0	1	0
38	H asper	0	0	0	1	0
39	H aff asper SP	1	0	0	1	0
40	H fredii	?	?	?	?	?
41	H pipilans	0	0	0	1	0
42	H aff phyllodes Itanhaem SP	0	1	0	0	0
43	H aff phyllodes Rio Claro RJ	0	1	0	0	0
44	H aff phyllodes Paranapiacaba SP	1	1	0	0	0
45	H aff phyllodes Bocaina RJ/SP	0	0	0	1	0
46	H aff phyllodes Praia Vermelha SP	0	0	0	1	0
47	H phyllodes	1	0	0	0	0
48	H otavioi	0	0	0	1	0
49	H uai	0	0	1	1	0
50	H lateristrigatus + H babax 1	0	0	0	1	0
51	H lateristrigatus + H babax 2	0	0	0	1	0
52	H ornatus	0	0	0	1	0
53	H regius	0	0	0	1	0
54	H magalhaesi	1	0	0	0	0
55	H japi	1	0	0	0	0
56	H glaber	1	0	0	1	0
57	H sazimai	1	0	0	0	0
58	H amnicola	0	0	0	1	0
59	H perere	0	0	0	1	0