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## Phylogenetic systematics of egg-brooding frogs (Anura: Hemiphractidae) and the evolution of direct development

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## Abstract

Egg-brooding frogs (Hemiphractidae) are a group of 105 currently recognized Neotropical species, with a remarkable diversity of developmental modes, from direct development to free-living and exotrophic tadpoles. Females carry their eggs on the back and embryos have unique bell-shaped gills. We inferred the evolutionary relationships of these frogs and used the resulting phylogeny to review their taxonomy and test hypotheses on the evolution of developmental modes and bell-shaped gills. Our inferences relied on a total evidence parsimony analysis of DNA sequences of up to 20 mitochondrial and nuclear genes (analyzed under tree-alignment), and 51 phenotypic characters sampled for 83% of currently valid hemiphractid species. Our analyses rendered a well-resolved phylogeny, with both Hemiphractidae (sister of Athesphatana) and its six recognized genera being monophyletic. We also inferred novel intergeneric relationships [*(Cryptobatrachus, Flectonotus)*, (*Stefania, (Fritziana, (Hemiphractus, Gastrotheca))*)], the non-monophyly of all species groups previously proposed within *Gastrotheca* and *Stefania*, and the existence of several putative new species within *Fritziana* and *Hemiphractus*. Contrary to previous hypotheses, our results support the most recent common ancestor of hemiphractids as a direct-developer. Free-living aquatic tadpoles apparently evolved from direct-developing ancestors three to eight times. Embryos of the sister taxa *Cryptobatrachus* and *Flectonotus* share a pair of single gills derived from branchial arch I, while embryos of the clade including the other four genera have two pairs of gills derived from branchial arches I and II respectively. Furthermore, in *Gastrotheca* the fusion of the two pairs of gills is a putative synapomorphy. We propose a revised taxonomy concordant with our optimal topologies.

**Key words:** *Cryptobatrachus*, *Flectonotus*, *Fritziana*, *Gastrotheca*, gills, *Hemiphractus*, Neotropics, parsimony, *Stefania*, taxonomy, total evidence, tree-alignment

## Introduction

Anuran systematics has experienced considerable progress in the last decade due to the ever-increasing amounts of molecular data and taxon sampling (e.g., Darst & Cannatella 2004; Faivovich *et al.* 2005; Frost *et al.* 2006; Grant *et al.* 2006; Roelants *et al.* 2007; Guayasamin *et al.* 2008; Hedges *et al.* 2008; Pyron & Wiens 2011). This growth of evidence allowed for more severe testing of hypotheses previously constructed on the basis of relatively small datasets. In many cases, the results of independent studies based on somewhat different sets of characters and taxa, and using different optimization criteria, converged on the same or relatively similar solutions, suggesting that evidence for inferred relationships was unambiguous and immune to different assumption sets. Such is the case of Nobleobatrachia, a clade including roughly 50% of all known species of anurans and the vast majority of Neotropical frogs (Frost *et al.* 2006). In many other cases, however, poorly resolved or incongruous relationships among studies (e.g., Frost *et al.* 2006; Roelants *et al.* 2007; Pyron & Wiens 2011) suggest that stronger tests based on more evidence and rigorous analyses are necessary to recover well-resolved relationships or, at least, to elucidate the causes of incongruence (e.g., Padial *et al.* 2014). As explained below, one of the most notable and yet unresolved cases in anuran systematics concerns the position and inter-relationships of egg-brooding frogs.

The name "egg-brooding frogs" informally refers to all species of non-aquatic Neotropical frogs in which females carry their eggs on their backs<sup>1</sup>, either inside a pouch, hence the common name marsupial frogs, or exposed on the dorsum (Fig. 1). Egg brooding frogs are placed in the family Hemiphractidae Peters, 1862, currently containing 105 recognized species belonging to six genera (Frost 2014): *Cryptobatrachus*, *Flectonotus*, *Fritziana*, *Gastrotheca*, *Hemiphractus*, and *Stefania*. Most species of egg-brooding frogs inhabit Neotropical lowland or montane rainforest, with a few species known from humid high-elevation Andean grasslands or the rocky summits of the tepuis of the Guiana Shield. Thus, there are species of egg-brooding frogs in all major humid terrestrial biomes of the Neotropics including Central America (Costa Rica and Panama), Chocó and Darién (Colombia, Ecuador, and Panama), the Andes (from Venezuela and northern Colombia to northern Argentina), the Caribbean coastal mountains (Colombia, Venezuela, and the islands of Trinidad and Tobago), the Amazonian lowlands (Bolivia, Brazil, Colombia, Ecuador, and Peru), the Guiana Shield (Brazil, Guyana, and Venezuela), and the Atlantic Forest (Brazil).

Besides the remarkable adaptations that egg-brooding frogs have evolved to carry eggs on their backs, many species in this group undergo development without a free-living larval phase. This trait has been observed in species of *Cryptobatrachus*, *Hemiphractus*, and *Stefania*. Contrarily, development in frogs of the genera *Flectonotus* and *Fritziana* involves a free-living tadpole. In the genus *Gastrotheca* some species are direct-developers while others have aquatic larvae. Such unusual variation in developmental modes led some researchers to point at *Gastrotheca* as the only group of anurans in which free-living tadpoles had re-evolved from ancestors with direct-development (Duellman & Hillis 1987; Duellman *et al.* 1988; Wiens *et al.* 2007).

Regardless of their developmental mode, all species of egg-brooding frogs for which the character has been studied have embryos with unique bell-shaped gills (Noble 1927; del Pino & Escobar 1981). Also, many species of egg-brooding frogs present ornamented skulls (*i.e.*, exostosis of some of its dorsal surfaces), which form spectacular shapes in species of the genus *Hemiphractus* (e.g., Trueb 1974; Mendelson *et al.* 2000). Species of the genus *Hemiphractus* also have tooth-like structures ("fangs") on their mandibles associated with a carnivorous diet (Trueb 1974; Sheil *et al.* 2001)—most frogs are insectivorous—and *Gastrotheca guentheri* is the only anuran known to have mandibular teeth (Boulenger 1882).

Due to the uniqueness of some of their characteristics and the exceptional possibilities they provide to study the evolution of the biphasic life cycle of amphibians, egg-brooding frogs have received considerable attention. Multiple aspects of their biology have been studied in detail, such as their development (e.g., del Pino & Escobar 1981; del Pino *et al.* 2007), tadpole and adult morphology (Wassersug & Duellman 1984; Tyler & Duellman 1995), and systematics (e.g., Duellman & Hillis 1987; Duellman *et al.* 1988; Mendelson *et al.* 2000; Duellman *et al.* 2011a). However, and as explained below, despite many recent efforts to elucidate the phylogenetic relationships of egg-brooding frogs, recent studies show conflicting results, to the point that even the monophyly of the family is still contested.

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1. The term marsupial frogs has been used interchangeably with egg-brooding frogs (e.g., Duellman *et al.* 1988; Mendelson *et al.* 2000). We use the former term for species which females have a dorsal pouch (*i.e.*, species of the genera *Flectonotus* and *Gastrotheca*), in accordance with its more restricted original definition (Duellman & Maness 1980).



**FIGURE 1.** Representatives of the supraspecific taxa of Hemiphractidae recognized in this study. (a) A female of *Cryptobatrachus remotus* from Venezuela carrying on its back its recently hatched froglets, embryos undergo direct development (photo by FJMR-R); (b) A gravid female of *Flectonotus pygmaeus* from Venezuela carrying its eggs on a pouch on its back formed by two longitudinal flaps of skin that are adherent middorsally, endotrophic tadpoles hatch from the eggs and complete their development in water (photo by Mauricio Rivera-Correa); (c) An adult of *Fritziaria goeldi* from Brazil (photo by JPP); (d) An adult female of the terrestrial *Hemiphractus scutatus* from Colombia (photo by SC-F); (e) An adult male of *Hemiphractus proboscideus* from Peru (photo by Giuseppe Gagliardi-Urrutia); (f) A female of *Stefania ginesi* from Venezuela carrying its eggs on its back, embryos undergo direct development and hatch as froglets (photo by FJMR-R); (g) A female of *Gastrotheca albolineata* from Brazil carrying its eggs inside an enclosed pouch with a posterior opening, embryos undergo direct development and emerge from the pouch as froglets (photo by JPP); (h) A female of *Gastrotheca marsupiata* from Peru (photo by JMP); (i) A female of *Gastrotheca megacephala* from Brazil (photo by JPP); (j) An adult male of *Gastrotheca walkeri* from Venezuela (photo by FJMR-R).



FIGURE 1. (Continued)

**The phylogenetic relationships of egg-brooding frogs.** After a long history of taxonomic changes (see Frost 2014), the monophyly of egg-brooding frogs, as the subfamily Hemiphraactinae within Hylidae, came to be accepted although rarely tested (e.g., Noble 1927, 1931; Duellman & Hoogmoed 1984; Silva 1998; Mendelson *et al.* 2000; Burton 2004). Molecular analyses have been nonetheless inconclusive about the monophyly and phylogenetic position of this taxon. The first analysis of hemiphraetid relationships based on mtDNA sequences analyzed under parsimony, maximum likelihood (ML), and Bayesian approaches (BA), refuted their monophyly and did not find them closely related to Hylidae (Darst & Cannatella 2004). Faivovich *et al.* (2005), using a different method (parsimony under tree-alignment), also retrieved egg-brooding frogs as non-monophyletic and distantly related to Hylidae. Shortly after, Wiens *et al.* (2005) published a complementary study of hylid phylogenetics, with only partially overlapping taxon and character sampling with respect to previous studies. Their analyses, based on different permutations of data partitions, number of taxa, and optimization criteria were inconclusive. Under BA, egg-brooding frogs were recovered as monophyletic in most cases except for the analyses of mitochondrial genes alone and the 12S alone. Under parsimony, egg-brooding frogs were non-monophyletic in all cases except on the basis of phenotypic data alone or when a dataset with fewer taxa was analyzed<sup>2</sup>. Also, both parsimony and BA of phenotypic data recovered egg-brooding frogs as a clade within hylids, while all other datasets retrieved them as distantly related to hylids regardless of the optimization criterion. Frost *et al.* (2006), as part of their analysis of the relationships of extant amphibians and using the same method and taxon sampling of egg-brooding frogs but a somewhat different character sampling than Faivovich *et al.* (2005), also retrieved egg-brooding frogs as non-monophyletic and distributed in three clades to which they assigned the rank of family: Amphignathodontidae for *Fritziana* (as *Flectonotus* in their study) and *Gastrotheca*; Cryptobatrachidae for *Cryptobatrachus* and *Stefania*; and Hemiphractidae for *Hemiphraactus*. Two subsequent studies found conflicting results regarding the monophyly of hemiphractids (Wiens *et al.* 2006, 2007). Wiens *et al.* (2006: Supp. data) recovered egg-brooding frogs as non-monophyletic under parsimony analysis of DNA sequences, while Wiens *et*

2. Because Wiens *et al.* (2005) did not show their parsimony topologies, non-monophyly is inferred from the absence of support values in the relevant clades according to the legends of their Figs 2, 3, 4, 5, and 8.

*al.* (2007) found egg-brooding frogs monophyletic under BA of DNA sequences. One key difference between the two studies by Wiens *et al.* (2006, 2007) is that Wiens *et al.* (2007) excluded *Cryptobatrachus* from their results.

In an attempt to explain the disagreement of previous studies, Guayasamin *et al.* (2008) pointed out that inferences based on parsimony or mitochondrial genes alone recovered egg-brooding frogs as non-monophyletic (Darst & Cannatella 2004; Faivovich *et al.* 2005; Wiens *et al.* 2006: Supp. data; Frost *et al.* 2006; Guayasamin *et al.* 2008) or monophyletic with weak support (Wiens *et al.* 2005), while inferences based on datasets including nuclear genes under a Bayesian approach yielded a highly supported clade of egg-brooding frogs (Wiens *et al.* 2005, 2007; Guayasamin *et al.* 2008). According to this pattern, differences among studies could be explained by the effect that different assumptions of methods (parsimony versus probabilistic inferences) had on molecular datasets with different rates of character evolution. However, the compared studies also differed in the number of taxa and characters sampled, the exhaustiveness of tree searches, method of alignment, model parameters, as well as modes of presenting data (e.g., strict consensus trees versus single optimal trees or majority rule consensus). Thus, many alternative factors provided appealing explanations but none of these were tested. Furthermore, a key and yet overlooked aspect in this discussion was that all the studies that recovered a monophyletic Hemiphractidae lacked at least the taxon *Cryptobatrachus*. Nevertheless, Guayasamin *et al.* (2008) returned all egg-brooding frogs to Hemiphractidae and this taxonomy has prevailed since then. Most subsequent studies dealing directly or indirectly with the relationships of egg-brooding frogs that recovered a monophyletic Hemiphractidae also lacked at least *Cryptobatrachus* (e.g., Heinicke *et al.* 2009; Duellman *et al.* 2011a; Fisher-Reid & Wiens 2011; Pyron & Wiens 2011; Wiens 2011; Wiens & Morrill 2011; Gomez-Mestre *et al.* 2012; Blackburn & Duellman 2013). As such, no complete test of the monophyly of the group was ever performed. A recent analysis of Brachycephaloidea that included 13 outgroup species of the six genera of hemiphractids (Padial *et al.* 2014) found hemiphractids as monophyletic using the same methods as Faivovich *et al.* (2005) or Frost *et al.* (2006) but not under ML or parsimony when the alignment of DNA sequences was based on similarity. Therefore, it remains unclear whether disagreements among studies were due to artifacts or assumptions of methods, differences in taxon and character sampling, the mere shortcomings of heuristic searches, or any other of the many methodological differences among studies.

Besides the monophyly of egg-brooding frogs, other problems persist at both higher and lower levels. The position of egg-brooding frogs remains uncertain even in analyses that recovered a monophyletic Hemiphractidae, with some studies supporting a sister relationship with Brachycephaloidea (Wiens *et al.* 2007; Heinicke *et al.* 2009; Padial *et al.* 2014) while other studies (Pyron & Wiens 2011; Fouquet *et al.* 2013) found them as the sister group of Athesphatanura. Also, the taxon sampling of previous studies of egg-brooding frogs was not exhaustive with regard to available evidence, hampering a strong test of their monophyly and the intergeneric relationships of the whole group. Thus, what is still missing is a thorough analysis of the phylogenetic relationships of egg-brooding frogs that includes all evidence used by previous studies plus additional characters and taxa.

**The evolution of developmental modes.** Egg-brooding frogs exhibit a remarkable pattern of developmental modes. Available phylogenies with a dense taxon sampling of egg-brooding frogs (Wiens *et al.* 2007; Blackburn & Duellman 2013) suggest that, within *Gastrotheca*, there are closely related species with drastically different developmental modes. For example, the direct developer *G. nicefori* is nested within a clade of six species that have a free-living and feeding tadpole. However, there are also contrasting differences at deep nodes, with all species of *Flectonotus* and *Fritziana* having free-living tadpoles while species of the closely related *Hemiphractus* are direct-developers (Wiens *et al.* 2007; Blackburn & Duellman 2013).

Although previous studies investigated the evolution of developmental modes in egg-brooding frogs (Duellman & Hillis 1987; Duellman *et al.* 1988; Mendelson *et al.* 2000; Wiens *et al.* 2007; Gomez-Mestre *et al.* 2012), both the ambiguity of phylogenetic relationships and the absence of key taxa have precluded a strong test of the evolution of direct development. Wiens *et al.* (2007) suggested that the presence of a free-living tadpole in some species of *Gastrotheca* evolved a single time from a direct-developing ancestor but they found this optimization to be very sensitive to different assumptions. Gomez-Mestre *et al.* (2012) inferred that the most recent common ancestor (MRCA) of egg-brooding frogs had a free-living tadpole and that direct-development evolved multiple times from it, rejecting the hypothesis of the re-evolution of a tadpole stage from a direct-developing ancestor. Relevant is that both Wiens *et al.* (2007) and Gomez-Mestre *et al.* (2012) excluded *Cryptobatrachus*, and *Cryptobatrachus* and *Fritziana*, respectively. In summary, what is lacking is a robust test where all relevant taxa and characters under scrutiny are included as evidence to infer the evolutionary history of the group.

**Goals of this study.** The main goal of this study is to test previous hypotheses of phylogenetic relationships of egg-brooding frogs. To do so, and given the complexity and diversity of previous results based on disparate and non-overlapping datasets, we have gathered DNA sequences of all species available in GenBank and generated new sequences for key taxa. Furthermore, we combined this molecular data with phenotypic characters used in previous studies. In addition, we test the hypothesis that in some species of egg-brooding frogs a free-living tadpole re-evolved from an ancestor with direct development (Wiens *et al.* 2007) and discuss the evolution of other remarkable characters such as bell-shaped external gills.

## Material and methods

**Optimality criterion and nucleotide homology.** We chose the criterion of parsimony (unweighted) so that our phylogenetic inferences minimize *ad hoc* assumptions and maximize falsifiability and explanatory power of evidence (Wiley 1975; Farris 1983; Farris *et al.* 2001; Kluge 2001a, b, 2009; Kluge & Grant 2006; Grant & Kluge 2009). We applied parsimony to tree-alignment (Sankoff 1975; Sankoff & Rousseau 1975; Sankoff *et al.* 1976; Wheeler 1996) to infer the minimum number of transformation events needed to explain observed differences (including indels) in DNA sequences (Grant & Kluge 2004; 2009; Kluge & Grant 2006; Wheeler *et al.* 2006; Grant & Kluge 2009; Padial *et al.* 2014).

**Taxon sampling.** Our primary goals, testing the monophyly of Hemiphractidae and the phylogenetic relationships of as many species of egg-brooding frogs as possible, required careful design of taxon sampling. It was necessary to include a broad representation of outgroup taxa, whose character variation may bring to test the monophyly and sister relationship of egg-brooding frogs as inferred by previous studies, and as many species of egg-brooding frogs as possible.

To test the monophyly of egg-brooding frogs within Nobleobatrachia, we included representatives of all currently used families within this clade following the taxonomy outlined in Frost (2014). We selected specific outgroup terminals trying to maximize character coverage (*i.e.*, homologous sequences available from Genbank and phenotypic characters sampled by Mendelson *et al.* 2000) and phylogenetic structure according to the trees of the two most densely sampled anuran phylogenies (Frost *et al.* 2006; Pyron & Wiens 2011) (see Appendix 1 for a detailed explanation of outgroup selection). The identification of outgroup terminals was updated according to Blotto *et al.* (2013), Fouquet *et al.* (2013), Padial *et al.* (2014), and Faivovich *et al.* (2014). Among outgroups, we included a particularly dense taxon sampling for Brachycephaloidea (50 terminals with representatives of all genera with sequences available in GenBank) and Athesphatanura (71 terminals representing all 14 families currently recognized). Additionally, we added six non-Nobleobatrachian anurans of which *Heleophryne purcelli* was used as the root. All in all, our dataset included 127 outgroup terminals (Appendix 1).

Our final dataset includes 96 terminals of egg-brooding frogs representing 83% of currently recognized species and all past and present recognized genera and infrageneric groups, as well as species from all major ecoregions in which these anurans occur. Information on the specimens used in this study is listed in Appendices 1 and 2.

Fifteen ingroup terminals could be identified only to the genus level. *Cryptobatrachus* sp. KU 204000 is a cleared-and-stained specimen studied by Mendelson *et al.* (2000) and is only coded for phenotypic data. *Fritziana* sp. MNRJ 44592, *Fr. aff. fissilis* sp. 1 CFBH 5726, *Fr. aff. fissilis* sp. 2 MNRJ 44622, and *Fr. aff. fissilis* sp. 3 (labeled *Fritziana cf. fissilis* by Duellman *et al.* 2011a) likely represent four new species of *Fritziana* according to Duellman *et al.* (2011a) and our own results. *Gastrotheca* sp. A QCAZ 22635, *G. sp. B* QCAZ 21105, *G. sp. C* QCAZ 47299, *G. sp. D* QCAZ 42725, and *G. sp. E* QCAZ 21213 were considered to be representatives of five new species by Blackburn & Duellman (2013). Analyses of DNA sequences of three genes from 27 samples of *Gastrotheca* from Bolivia (results not shown, De la Riva, Padial, and Castroviejo-Fisher, unpublished results) revealed three non-sister lineages for which there are available names but correspondences between species names and populations remain unclear. For example, specimens of the species that we herein labelled *G. sp. 2* have been previously identified as *G. cf. marsupiata* (Faivovich *et al.* 2005), *G. piperata* (Duellman & Köhler 2005), and *G. lauzuricae* (Blackburn & Duellman 2013). This is not surprising as examination of voucher specimens (including type material) of *G. lauzuricae*, *G. piperata*, and *G. splendens*, as well as the current synonyms *Hylodes coeruleomaculatus* and *Nototrema bolivianum*, indicate that diagnostic morphological characters that are purported to provide evidence of divergence among some species are polymorphic and shared among species (De la Riva,



Padial, and Castroviejo-Fisher, unpublished results). On the other hand, some characters that might support the validity of some species were neglected. Furthermore, given that these three lineages occur in sympatry, assigning specimens to available species remains challenging. Because the necessarily deep analysis of the alpha taxonomy and nomenclature of Bolivian *Gastrotheca* was beyond the scope of this study, we refer to these three species from Bolivia as *G. sp. 1* IDIR 4073 (MNCN/ADN 576), *G. sp. 2* for specimens *G. cf. marsupiata* MNK 5286 of Faivovich *et al.* (2005) [which was re-determined as *G. piperata* by Duellman & Köhler (2005)] and *G. lauzuricae* CBG 1020 (MNCN/ADN 9529) of Blackburn & Duellman (2013), and *G. sp. 3* for specimens ZFMK 66954 (MNCN/ADN 25033) and MNCN 43052. Finally, *Stefania* aff. *evansi* ROM 44254 and *S. sp.* IRSNB 15853 are considered new species following Kok *et al.* (2012).

We also updated the identification of three terminals. *Cryptobatrachus* sp. JDL 14865 of Darst & Cannatella (2004) is *C. fuhrmanni* (J.D. Lynch in litt. to W.E. Duellman, the latter in litt. to SC-F). The relevant tissue is most likely from the specimen now catalogued as KU 204892 and not KU 204292 as suggested by Schmid *et al.* (2013 "2012"); according to a search on HerpNET2 on 4 January 2014, the voucher KU 204292 is a specimen of *Anaxyrus terrestris* from Jasper, South Carolina. *Flectonotus* sp. CFBH 5726<sup>3</sup> of Faivovich *et al.* (2005) is a species of *Fritziana* following Duellman *et al.* (2011a) and Teixeira *et al.* (2012); our comparisons of DNA sequences with other species of *Fritziana* in GenBank and our own sequences suggest it is a new species. *Gastrotheca fissipes* JLG 90 of Faivovich *et al.* (2005) is the subsequently named *G. megacephala* following Izecksohn *et al.* (2009), Teixeira *et al.* (2012) and Blackburn & Duellman (2013).

Seven species are represented by more than one terminal because preliminary comparisons of DNA sequences and subsequent phylogenetic analyses showed large divergences and, in some cases, non-sister relationships. These redundant terminals were *Cryptobatrachus fuhrmanni* JDL 14865 and MHUA A 5160, *Gastrotheca excubitor* MUSM 26280 and KU 173171, *G. griswoldi* MHNSM 20588 and KU 181701, *G. nicefori* KU 181071 and MHUA A 5716, *G. riobambae* KU 178468 and UIMNH 94580, *Hemiphractus scutatus* JMP 2150 and RWM 10453, and *H. fasciatus* MVUP 1927, CHP 6397, EVACC 207, EVACC 065, EVACC 061, and CHP 6670.

For 21 terminals (*Cryptobatrachus remotus*, *Flectonotus fitzgeraldi*, *Fl. pygmaeus*, *Fritziana fissilis*, *Gastrotheca cornuta*, *G. dunni*, *G. ernestoi*, *G. marsupiata*, *G. megacephala*, *G. microdiscus*, *G. nebulanastes*, *G. pseustes*, *G. sp. 2*, *G. sp. 3*, *G. testudinea*, *Hemiphractus bubalus*, *H. fasciatus* sp. 1, *H. fasciatus* sp. 2, *H. helioi*, *Stefania evansi*, and *S. scalae*) sequences from different individuals of the same species were merged to construct a single complete composite sequence for the combined analyses. In this way we reduced the number of terminals, amount of missing data, number of possible optimal trees, and the potential effect of wildcards. We only applied this approach after checking for compliance to the following criteria: specimens were found as sister terminals in our own exploratory phylogenetic analyses as well as in the literature (Duellman *et al.* 2011a; Blackburn & Duellman 2013; Crawford *et al.* 2013) and, when sisters, the uncorrected proportional genetic distances (p-distances) between shared mitochondrial DNA fragments were <1%.

Similarly, molecular data from different specimens of the same species were sometimes available (e.g., there are in GenBank DNA sequences of ND1 for seven specimens of *Stefania evansi*). We used the same criteria mentioned above to exclude redundant specimens sampled for overlapping data.

**Molecular data.** We downloaded all DNA sequences of egg-brooding frogs deposited in GenBank prior to May 31, 2013. After discarding markers that were available only for one species (e.g., the sequence of VegT mRNA was only available for *Gastrotheca riobambae*) we were left with complete or partial sequences of the following 20 mitochondrial and nuclear genes: tRNAPhe, 12S rRNA, tRNAVal, two non-overlapping fragments of the 16S rRNA, tRNALeu, NADH dehydrogenase subunit 1 (ND1), cytochrome oxidase I (COI), cytochrome b (cytb), 28S rRNA, proto-oncogene cellular myelocytomatosis exons 2 (C-MYC 2) and 3 (C-MYC 3), chemokine receptor 4 (CXCR4), histone (H3a), proopiomelanocortin A (POMC), two non-overlapping fragments of the recombination activating gene 1 (RAG1), rhodopsin exon 1 (Rho), seven in absentia homolog 1 (SIAH), solute carrier family 8 member 1 (SLC8A1), solute carrier family 8 member 3 (SLC8A3), and tyrosinase (Tyr). We also produced 168 new sequences representing 15 genes from 23 specimens of 19 species of egg-brooding frogs (Appendix 2). Amplification, sequencing, and editing protocols follow those of Guayasamin *et al.* (2008). Primers not listed in Guayasamin *et al.* (2008) are presented in Appendix 3.

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3. The voucher code of this specimen was reported by Faivovich *et al.* (2005) as CFBH 5720 but the correct code is CFBH 5726 (C.F.B. Haddad in litt. to J.M. Padial).

**Phenotypic data.** The backbone of the phenotypic data used in this study is the 51 phenotypic characters for 28 egg-brooding frog species and five hyloid outgroups analyzed by Mendelson *et al.* (2000). We refer the reader to Mendelson *et al.* (2000) for detailed descriptions of the phenotypic characters. Prior to integrating the phenotypic dataset into our study, we updated the identification of some terminals of Mendelson *et al.* (2000). *Gastrotheca fissipes* KU 193298 is *G. megacephala* following Izecksohn *et al.* (2009), Teixeira *et al.* (2012), and Blackburn & Duellman (2013). *Gastrotheca excubitor* KU 173218 is a paratype of *G. nebulanastes* following Duellman *et al.* (2011b). *Hemiphractus johnsoni* KU 153436 is a paratype of *H. helioi* according to Sheil & Mendelson (2001). *Stefania evansi* KU 167671–74, 181122–24 are *S. scale* according to Señaris *et al.* (1997 "1996").

As noted above, we found that sequences of different specimens of *Cryptobatrachus fuhrmanni*, *Gastrotheca excubitor*, *G. griswoldi*, *G. riobambae*, *Hemiphractus fasciatus*, and *H. scutatus* can be highly divergent and in some cases non-sister terminals (see Results), suggesting the existence of more than one species under those names. Therefore, matching phenotypic data and DNA sequences under a single terminal involved some uncertainty. We assigned the phenotypic characters of *C. fuhrmanni* KU 169378 to the terminal *C. fuhrmanni* JDL 14865 because both specimens come from the northern part of the Cordillera Oriental of Colombia, while specimen *C. fuhrmanni* MHUA A 5160 comes from the Cordillera Central of Colombia. We assigned the phenotypic characters of *G. excubitor* (KU 146840–41 and KU 164088–89) to the terminal *G. excubitor* KU 173171 on the basis of the geographic proximity and the fact that the specimens were identified by W. E. Duellman, one of the authors of the original description of *G. excubitor* Duellman and Fritts, 1972. We assigned the phenotypic characters of *G. griswoldi* (KU 138232 and KU 146844–5) to the terminal *G. griswoldi* KU 181701 because all these specimens come from near the type locality in Junín, Peru, while *G. griswoldi* MHNSM 20588 is from Huánuco, Peru. Phenotypic data for *G. riobambae* (KU 99126, KU 99128–29, KU 138575–76, and KU 148543–44) were assigned to the terminal *G. riobambae* KU 178468 because all specimens were collected within the known distribution of the species (Frenkel *et al.* 2010), while *G. riobambae* UIMNH 94580 comes from San Rafael, Azuay, Ecuador, which is in the lowlands of the Pacific coast of Ecuador near the Gulf of Guayaquil and outside the known distribution of *G. riobambae*. The phenotypic observations of *H. fasciatus* are based on specimens KU 93509–10 from Darién, Panama, were assigned to *H. fasciatus* sp. 1 because specimens of this terminal also come from Darién, Panama, while specimens of terminals *H. fasciatus* sp. 2 and sp. 3 come from Chepo and Coclé, Panama, respectively. Lastly, the phenotypic observations of *H. scutatus* KU 129752 were assigned to *H. scutatus* JMP 2150 because this specimen is closest to the type locality, Rio Solimões, Amazonas, Brazil (see Hoogmoed & Gruber 1983; Glaw & Franzen 2006).

We updated Mendelson's *et al.* (2000) phenotypic dataset with the observations of del Pino & Escobar (1981) on gills and of Sheil *et al.* (2001) for *Hemiphractus*. Also, characters 41, 46, and 47 of Mendelson *et al.* (2000) were modified as described below.

Character 41. Pouch type. Mendelson *et al.* (2000) coded our states 1 and 2 as the same character state (*i.e.*, 41—1 dorsolateral folds of skin); however, the descriptions of del Pino (1980), Duellman & Gray (1983), Duellman *et al.* (2011a), and our own observations allow clear distinction between the folds present in females of *Flectonotus* and *Fritziana*. Accordingly, we code Character 41 as follows:

0—Pouch absent.

1—Lateral skin folds not adherent middorsally.

2—Pouch formed by two longitudinal flaps of skin that are adherent middorsally over the eggs, forming an enclosed pouch.

3—Enclosed pouch with a posterior opening.

Character 46. State of development of young at hatching. We recognize the same character states as in Mendelson *et al.* (2000) but we included new information from Duellman *et al.* (2011a) and Schmid *et al.* (2013 "2012").

Character 47. Deposition of eggs. Mendelson *et al.* (2000) recognized three character states (0—eggs in water; 1—eggs on dorsum; 2—eggs on leaves). In the context of our study, we preferred to include more character states to better represent the diversity known within anurans:

0—Aquatic eggs deposited in water.

1—Terrestrial eggs (*i.e.*, not in water) deposited in a nest.

- 2—Terrestrial eggs, arboreal.
- 3—Terrestrial eggs deposited on substrate (e.g., rocks, burrows, ground).
- 4—Terrestrial eggs on dorsum.
- 5—Aquatic eggs deposited in a nest.

Because we were particularly interested in the evolution of direct development in Nobleobatrachia, we augmented (whenever possible) our observations of character 46 to all ingroup and outgroup taxa. We obtained additional information on life history modes of egg-brooding frogs from Wiens *et al.* (2007), Blackburn & Duellman (2013), and citations therein, and for outgroup taxa from references cited in Appendix 4.

**Phylogenetic analyses.** To be able to incorporate into the tree-alignment analysis all homologous (as defined by primers and sequencing) DNA sequences with different lengths due to missing data, each marker has to be independently prealigned and divided into putatively homologous sections (Wheeler *et al.* 2006). To do so we used MAFFT v7 (Kato & Standley 2013) under the "auto" strategy and default parameters to generate the prealignments. The resulting multiple sequence alignments were visualized in SE-AL v2.0a11 (<http://tree.bio.ed.ac.uk/software/seal/>) and modified so that: (i) clear artifacts created by the alignment program were corrected (*i.e.*, the end and/or the beginning of shorter fragments within a gene were sometimes placed at the corresponding end or beginning of the whole alignment by the program and we placed them at the beginning or end of the corresponding sequence); and (ii) outgroup sequences were not longer than the longest egg-brooding frog sequence for that marker (*i.e.*, sequences of outgroups were trimmed when necessary). The prealignments of each marker were used to divide them into shorter contiguous fragments without missing data also using SE-AL v2.0a11. This strategy generated putatively homologous fragments where length variation among DNA sequences is only due to insertions and/or deletions of nucleotides, a requisite for tree-alignment analysis in POY (Wheeler *et al.* 2006). Fragment partitions were located in conserved regions (no gaps and few or none nucleotide substitutions) according to the multiple sequence alignments.

We employed parsimony analyses as implemented in POY 5.1.1 (Varón *et al.* 2010; Wheeler *et al.* 2014) with equal weights for all transformations (including insertion/deletion events) and all characters coded as non-additive (except those indicated otherwise by Mendelson *et al.* 2000). The DNA sequence fragments described above were analyzed under direct optimization (Wheeler 1996). Searches were conducted using the automated "search" function, which attempts as many builds (*i.e.*, Wagner trees), swaps [*i.e.*, tree bisection–reconnection (TBR) branch swapping], ratchets (Nixon 1999), and tree-fusings (Goloboff 1999) as possible within the specified time. We stored the shortest and unique trees of each search, allowing the parallel processors to exchange trees and add the pool of selected best and unique trees to the subsequent interactions of the command (Varón *et al.* 2010). Five consecutive 48-hour searches followed by a final search of 240 hours (totalling 480 hours) were implemented in parallel at the American Museum of Natural History Cluster Enyo, using 32 processors. The resulting shortest trees were submitted to a final round of swapping using iterative pass optimization (Sankoff *et al.* 1976; Wheeler 2003a) in POY. As we have observed that POY 5.1.1 does not always report all the equally parsimonious trees, the optimal alignment resulting from iterative pass optimization was converted to a data matrix (Wheeler 2003b) and driven searches were conducted in TNT (Goloboff *et al.* 2008a; equal costs for all transformations, non-additive characters but those indicated by Mendelson *et al.* 2000, gaps treated as fifth state) until a stable strict consensus was reached at least five times. In this way, we assessed whether additional equally parsimonious trees were supported by evidence derived from the tree-alignment matrix.

We calculated Goodman-Bremer (GB) values (Goodman *et al.* 1982; Bremer 1988; see Grant & Kluge 2008a) for each supported clade in TNT using the optimal tree-alignment matrix and the parameters specified in the bremer.run macro (available at <http://www.zmuc.dk/public/phylogeny/tnt/>), which begins by searching for trees *N* steps longer than the optimum (10 random addition sequence Wagner builds and TBR swapping saving two trees per replicate) for suboptimal trees using inverse constraints for each node of the most parsimonious tree. Swapping of each constrained search was limited to 20 minutes and constrained searches were repeated three times. We calculated jackknife (JK) frequencies from 1000 pseudoreplicates searched with 100 RAS + TBR and a maximum of 10 trees saved per replicate, gaps treated as fifth state, and removal probability of 0.36 ( $\sim e^{-1}$ ), which purportedly renders jackknife and bootstrap values comparable (Farris *et al.* 1996). We caution that, as in analyses of similarity-alignment matrices, the resulting clade frequencies are conditional on this particular alignment and not the data themselves. Given that the tree-alignment matrix is derived from the optimal tree, the resulting clade frequencies are expected to be higher than would be obtained from matrices aligned according to different guide trees (e.g., a

UPGMA or neighbor-joining tree, as in MAFFT and CLUSTAL, respectively). Padial *et al.* (2014) corroborated this expectation for JK but found higher GB values in a similarity-aligned matrix than by resampling the tree-alignment matrix for the same sequence data.

## Results

Tree searches of the complete dataset in POY yielded 23 most parsimonious trees (79567 steps). A final round of swapping using iterative pass optimization on these trees further reduced the cost (79313 steps). The implied alignment contains 18349 molecular transformation series that combined with the 51 phenotypic characters yielded a static dataset of 18400 transformation series (all alignments are available from [https://drive.bitcasa.com/send/DIDPyZKS1pzh7NkMHbC3Ki\\_DCyD1zHDk4gd\\_VXMpatjY](https://drive.bitcasa.com/send/DIDPyZKS1pzh7NkMHbC3Ki_DCyD1zHDk4gd_VXMpatjY)). Tree searches of this static dataset in TNT found 63 most parsimonious trees (Fig. 2).

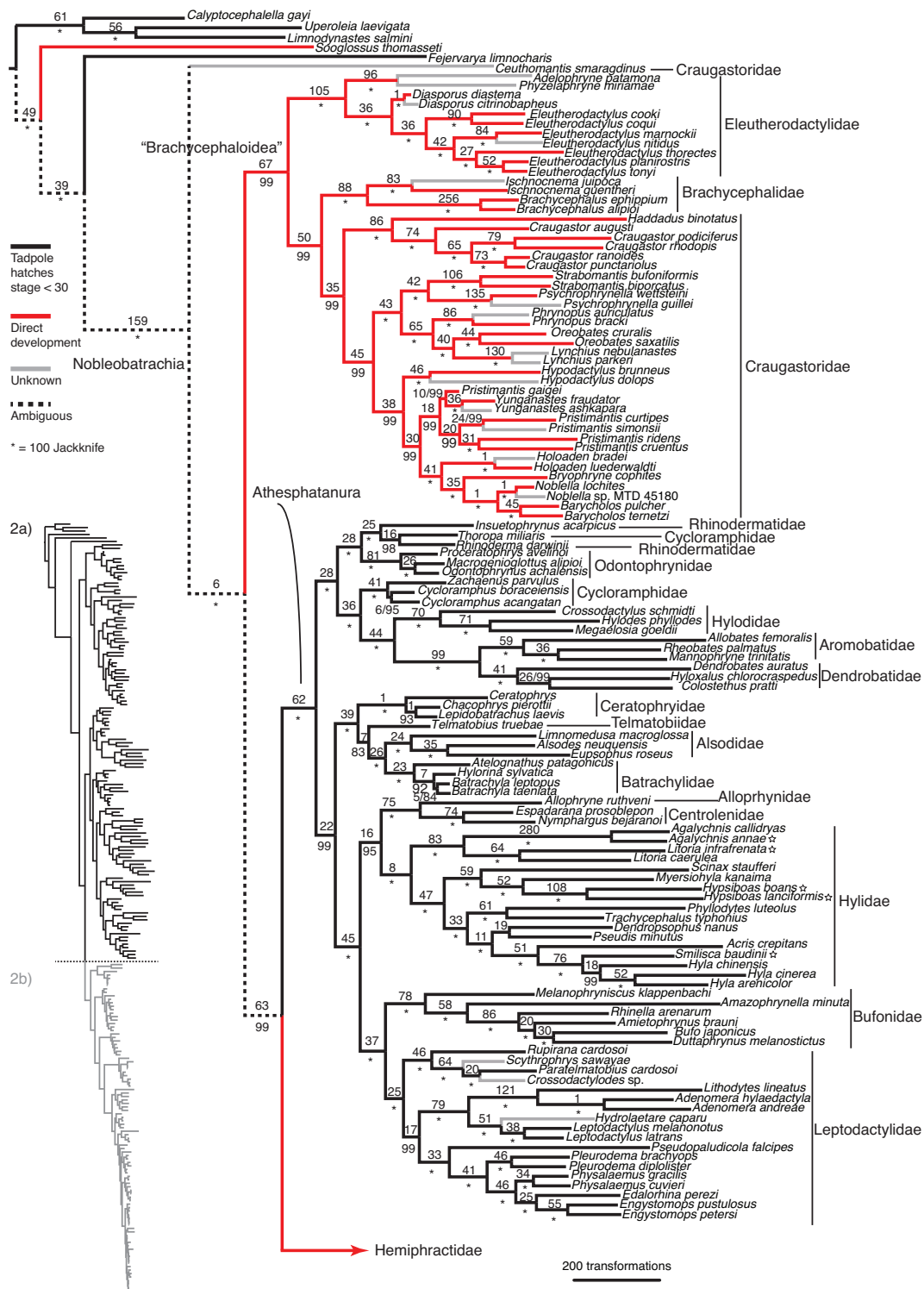
Egg-brooding frogs were recovered as a natural group (GB = 1; JK = 99) nested within Nobleobatrachia (GB = 159; JK = 100) and sister of all other frog families within Nobleobatrachia except those of Brachycephaloidea (GB = 63; JK = 99). We recovered *Ceuthomantis smaragdinus* as the sister taxon of all other nobleobatrachians, therefore rendering a non-monophyletic Brachycephaloidea and Craugastoridae. The families Alsodidae, Aromobatidae, Batrachylidae, Bufonidae, Centrolenidae, Ceratophryidae, Dendrobatidae, Hylidae, Hylodidae, Leptodactylidae, and Odontophryidae were recovered as monophyletic while Cycloramphidae and Rhinodermatidae were recovered as non-monophyletic because our optimal trees placed *Thoropa miliaris* as the sister of *Rhinoderma darwinii*. The families Allophryniidae and Telmatobiidae were represented by just one terminal each. Given the diversity of Nobleobatrachia, it is obvious that our taxon sampling was not designed to evaluate all the internal relationships of its different families or the relationships among them. Consequently, our results outside of egg-brooding frogs should not be interpreted as tests of previous hypotheses of relationships based on denser taxon sampling (e.g., Padial *et al.* 2014, for Brachycephaloidea).

Within egg-brooding frogs all genera were recovered as monophyletic. Nevertheless, we obtained some unexpected relationships. The first split separates a clade (GB = 4; JK = 98) containing *Cryptobatrachus* + *Flectonotus*, which is a novel sister relationship. The relationships within *Cryptobatrachus* are not resolved in the strict consensus.

*Stefania* (GB = 51; JK = 99) was inferred as the sister taxon of a clade containing *Gastrotheca*, *Fritziana*, and *Hemiphractus* (GB = 8; JK = 99), which is another novel sister relationship (GB = 8; JK = 98). Within *Stefania* neither the *S. evansi* nor the *S. goini* species groups are monophyletic. A clade formed by *S. ginesi* and *S. satelles* forms the sister group of the remaining species. Within the latter clade, *S. schuberti* is sister of the other species, which are arranged in three main clades. One clade includes *S. ayangannae*, *S. coxi*, *S. riveroi*, and *S. sp.* [a putative new species according to Kok *et al.* (2012)]. The second contains *S. riae*, *S. roraimae*, and *S. woodleyi*. The third clade includes *S. evansi*, *S. scalae*, and *S. aff. evansi* [another putative new species according to Kok *et al.* (2012)].

*Fritziana* (GB = 77; JK = 100) is recovered as the sister of *Gastrotheca* and *Hemiphractus* (GB = 29; JK = 99), which is another novel sister relationship. The relationships among members of *Fritziana* are pectinate, with *F. goeldii* as the sister of the remaining species. *Fritziana fissilis* was recovered paraphyletic with respect to *F. ohausi*, and there are large genetic divergences among the seven terminals (genetic p-distances of 532 bp of the marker 16S rRNA = 5.7–12.1%).

*Hemiphractus* (GB = 17; JK = 100) was inferred to be the sister group of *Gastrotheca* (GB = 17; JK = 100), also a novel sister relationship. We obtained *H. helioi* as sister of the other species. *Hemiphractus bubalus*, *H. johnsoni*, and *H. proboscideus* are sister of a clade that contains *H. scutatus*, represented by two terminals with large genetic distances (genetic p-distances between 491 bp of the marker 16S rRNA = 8.2%), and *H. fasciatus*, represented by three terminals with relatively large nucleotide disparity (genetic p-distances between 533 bp of the marker 16S rRNA = 2.5–5.7%).



**FIGURE 2.** Phylogenetic relationships of egg-brooding frogs and outgroups inferred from parsimony analysis of phenotypic characters and DNA sequences under direct optimization. This topology reflects one of the 63 most parsimonious trees (tree costs = 79313 steps) with the evolution of direct development shown by the color of branches. Numbers above and below branches, or separated by a slash, represent Goodman-Bremer values and jackknife proportions respectively and black dots on nodes indicate collapsed clades in the strict consensus. A skeletal topology, with the magnified section marked in black, is shown on the left side. White stars indicate taxa represented in the phenotypic dataset of Mendelson *et al.* (2000) and black stars indicate taxa only represented by phenotypic data from Mendelson *et al.* (2000). (a) Relationships among outgroups; we cropped the root (*Heleophryne purcelli*) for ease of representation. (b) Relationships among egg-brooding frogs showing the taxonomy proposed in this work; terminals without a voucher code indicate that sequences from different individuals of the same species were joined to construct a single composite sequence.

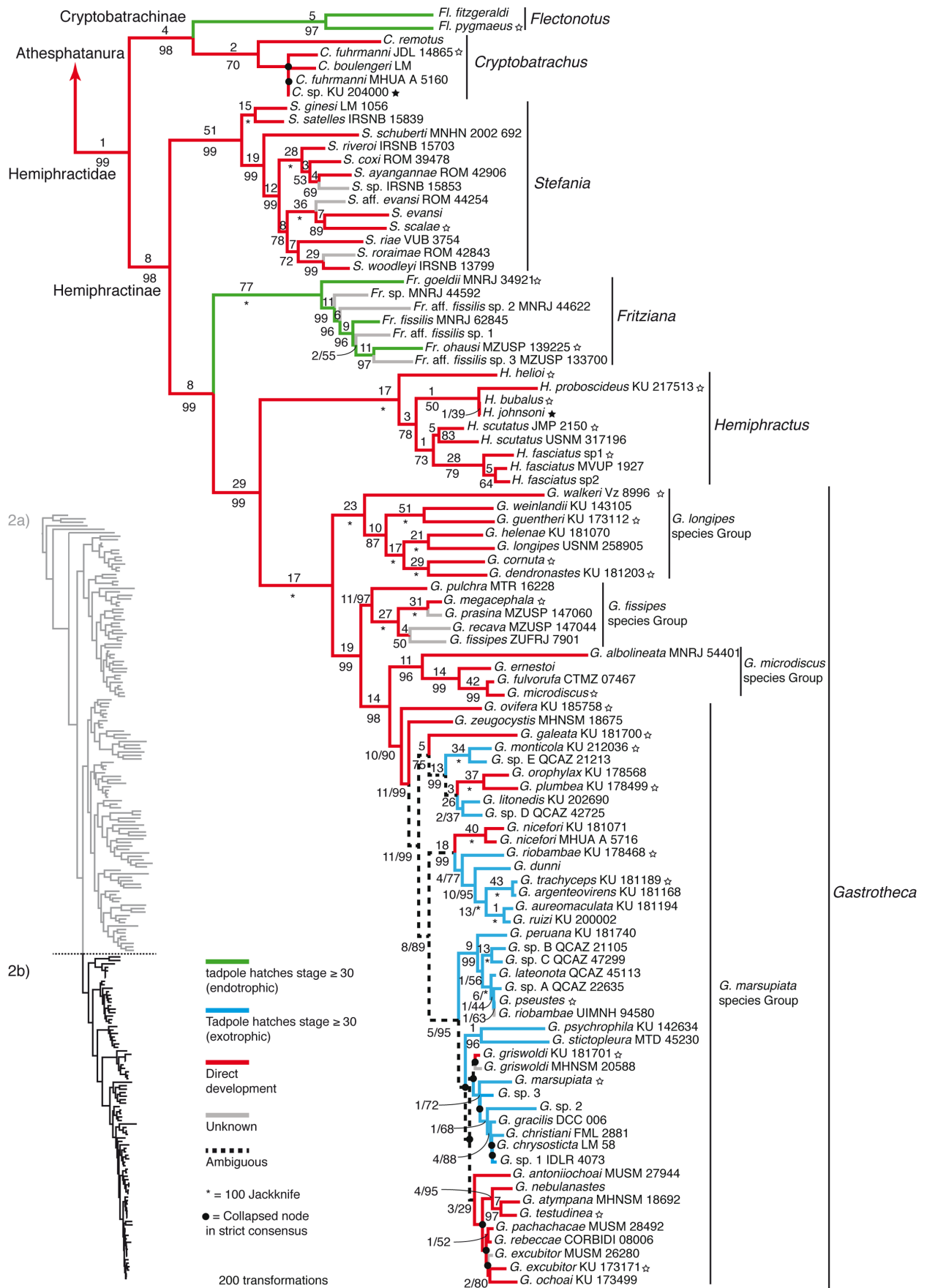


FIGURE 2. (Continued)

Within *Gastrotheca* we recovered a clade (GB = 23; JK = 100) that contains *G. walkeri*, of the *G. williamsoni* group of Schmid *et al.* (2013 "2012"), as the sister taxon of a clade that includes species of the *G. longipes* group (GB = 10; JK = 87) *sensu* Schmid *et al.* (2013 "2012"), referred to as the Northwest South American clade by Blackburn & Duellman (2013). This clade is the sister group of a clade that includes the rest of species in the genus. Within this latter clade, we recovered a clade (GB = 11; JK = 97) with five species from the Atlantic Forest of Brazil, followed in succession by a second clade (GB = 11; JK = 96) of species from the Atlantic Forest, by *G. ovifera*, and by *G. zeugocystis*, which is the sister species of all the remaining sampled species, which in turn are part of the following three main clades.

The first clade partially corresponds to the *Gastrotheca plumbea* group of Schmid *et al.* (2013 "2012"), also called the Northern Andes clade by Blackburn & Duellman (2013), but includes *G. galeata* (GB = 5; JK = 75) and excludes *G. argenteovirens*, *G. aureomaculata*, *G. dunni*, *G. nicefori*, *G. riobambae*, *G. ruizi*, and *G. trachyceps*. The second clade contains part of the *G. plumbea* group of Schmid *et al.* (2013 "2012") (*G. argenteovirens*, *G. aureomaculata*, *G. dunni*, *G. nicefori*, *G. riobambae*, *G. ruizi*, and *G. trachyceps*) and two sister samples of nominal *G. nicefori* with marked genetic divergences (genetic p-distances between 417 bp of the marker 12S rRNA = 3.8% and between 492 bp of the marker 16S rRNA = 1.2%). *Gastrotheca riobambae* is paraphyletic, with terminal KU 178468 not being closely related to *G. riobambae* UIMNH 94580, which belongs to the third clade. The third clade, partially matches the content of the *G. marsupiata* group of Schmid *et al.* (2013 "2012"), called the Central Andes clade by Blackburn & Duellman (2013), but with the exclusion of *Gastrotheca zeugocystis* (GB = 5; JK = 95). Within this clade, the terminal *G. riobambae* UIMNH 94580 mentioned above is the sister of *G. pseustes*, with genetic p-distances between 399 bp of the marker 16S rRNA = 0.5%, and was collected at a locality where *G. pseustes* has been found (Ron & Frenkel, 2010). Also within this clade, the samples identified in GenBank as *Gastrotheca griswoldi* (MHNSM 20588 and KU 181701) are not sister terminals in all most parsimonious trees and *G. excubitor* (KU 173171 and MUSM 26280) is paraphyletic.

## Discussion

Our analyses of combined molecular and phenotypic characters recovered the monophyly of egg-brooding frogs and corroborated the monophyly of all genera. No other study has included as many species and characters as ours, nor has any other study combined all previous phenotypic and molecular data used so far to infer the relationships of this group. As such, our analyses provide a more robust test of the monophyly of egg-brooding frogs and their internal relationships. Below, we discuss alternative explanations for the differences found among previous studies concerning the monophyly and phylogenetic position of Hemiphractidae. We also discuss how our novel hypothesis of relationships bears on the evolution of several phenotypic traits in egg-brooding frogs, with emphasis on direct-development. At the end, we provide a section with a revised taxonomy.

**The monophyly of egg-brooding frogs.** Different studies inferred hemiphractids as non-monophyletic on the basis of DNA sequences or DNA sequences combined with phenotypic data analyzed under different optimality criteria [Darst & Cannatella 2004 (parsimony, ML, BA); Faivovich *et al.* 2005 (parsimony); Wiens *et al.* 2005 (parsimony, but not BA); Frost *et al.* 2006 (parsimony); Wiens *et al.* 2006: Supp. data (at least parsimony<sup>4</sup>)]. This was interpreted as the result of long-branch attraction (LBA) and/or predominance of fast evolving mitochondrial genes (presumably assuming "saturation" and high levels of homoplasy) biasing parsimony analysis (Wiens 2007; Wiens *et al.* 2007; Guayasamin *et al.* 2008). Missing from the argument was that the datasets analyzed under probabilistic methods and used to support the monophyly of egg-brooding frogs lacked key taxa. For example, Wiens *et al.* (2007) removed *Cryptobatrachus* from their analyses because of its unstable position and Guayasamin *et al.* (2008) did not include *Cryptobatrachus*. Padial *et al.* (2014) challenged the hypothesis that LBA and "saturation" of mitochondrial genes was biasing parsimony analysis because they found a monophyletic Hemiphractidae using parsimony under tree-alignment with a dataset that included taxa missing in previous analyses (e.g., *Cryptobatrachus* and *Fritziana*). It could be argued that increasing taxon sampling provided the conditions to break long branches in the parsimony analyses of Padial *et al.* (2014); however, they only included 13 species of hemiphractids that were represented by DNA sequences dominated by mtDNA genes obtained from previously published studies. Relevant is that Padial *et al.* (2014) found that neither ML nor parsimony analyses

4. Wiens *et al.* (2006) neither showed nor discussed hemiphractid relationships inferred from their BA.

recovered the monophyly of hemiphractids when DNA sequences were aligned using conventional methods based on structural similarity. One could be inclined to conclude that the method of alignment (*i.e.*, similarity versus tree-alignment) was the key factor explaining the contradictory results of Padial *et al.* (2014). However, neither Faivovich *et al.* (2005) nor Frost *et al.* (2006) recovered a monophyletic Hemiphractidae, in spite of using the same method of tree-alignment as and comparable tree searches to Padial *et al.* (2014).

We conclude that we face a complex case, in which one cannot tell apart, by mere comparison of the results of previous studies, the potential effects that non-mutually exclusive factors—such as differences in taxon and character sampling, optimality criteria, exhaustiveness of tree searches, treatment of indels, data partition schemes, model selection, and alignment parameters—could have on the incongruence observed among different studies regarding the monophyly of hemiphractids. However, rather than trying to single out the causes of incongruence among studies, we have focused on the analysis of available evidence. The strength of our study is that we revisited all previous phylogenetic hypotheses by building a dataset in a cumulative and constructive approach (*i.e.*, adding data to what others have generated). Thus, our tree summarizes the state of understanding of hemiphractid evolutionary relationships.

**The phylogenetic position of Hemiphractidae.** During most of their taxonomic history, species of egg-brooding frogs were thought to be part of Hylidae (e.g., Duméril & Bibron 1841; Boulenger 1904; Peracca 1914; Miranda-Ribeiro 1920; Noble 1927, 1931) or related to them (e.g., Peters 1862), while species now included in *Hemiphractus* and even some species of *Cryptobatrachus* were instead placed in Cystignathidae (e.g., Gravenhorst 1825; Duméril & Bibron 1841; Günther 1859 "1858"; Cope 1866; Ruthven 1916) (see Frost 2014, for a detailed account of nomenclatural changes). Lutz (1968) considered most egg-brooding frogs to form a clade, her hylid subfamily Opisthodelphinae, leaving *Hemiphractus scutatus* outside of this group because of its reduced digital discs. Although she provided the first explicit phylogenetic hypothesis of their relationships, her non-quantitative hypothesis has largely been ignored (but see Mendelson *et al.* 2000). For several decades most studies (e.g., Trueb 1970, 1974; Duellman 1970; Mendelson *et al.* 2000) followed Noble's (1927, 1931) conclusion that hemiphractids were hylids<sup>5</sup>. This notion was increasingly questioned in the late 1990s and early 2000s. Silva (1998) and Burton (2004), using phenotypic data, retrieved egg-brooding frogs as monophyletic and the sister of Phyllomedusinae in a clade with a basal polytomy including Allophryniidae + Centrolenidae, Hylinae + Pseudinae, and Pelodyadinae, rendering Hylidae as non-monophyletic. Haas (2003), in his analysis of anuran relationships primarily based on larval morphology, also recovered egg-brooding frogs as neither the sister of nor included within Hylidae. Molecular phylogenies also started to challenge the hypothesis that egg-brooding frogs were hylids, although taxon sampling was still limited to one or two species of hemiphractids (Ruvinsky & Maxson 1996; Austin 2002; Darst & Cannatella 2004). It was the study of Faivovich *et al.* (2005) that decisively challenged this long-standing hypothesis and formalized their results transferring egg-brooding frogs to "Leptodactylidae". Wiens *et al.* (2005) recovered hemiphractids as a clade within hylids when analyzing phenotypic data only, while their more explanatory analyses combining molecular and phenotypic data retrieved the groups as distantly related. Frost *et al.* (2006), as part of their broader analysis of extant amphibians, also retrieved egg-brooding frogs as non-monophyletic and distributed in three clades, none of them closely related to hylids.

Nonetheless, although the previous view of hemiphractids as hylids started to be abandoned, the phylogenetic position of hemiphractids (and their monophyly, see above) remained unclear. Wiens *et al.* (2005) were the first to suggest a sister relationship between reciprocally monophyletic Hemiphractidae and Brachycephaloidea. Later, Heinicke *et al.* (2009) analyzed two datasets of DNA sequences from up to 17 genes from representatives of 13 genera of Brachycephaloidea, three genera of hemiphractids (*Hemiphractus*, *Stefania*, and *Flectonotus*) and representatives of all other families of Nobleobatrachia of Frost *et al.* (2006) and recovered Brachycephaloidea and Hemiphractidae as sister taxa, a clade which they named Orthobatrachia. The monophyly of Orthobatrachia has indeed been questioned by several subsequent studies with larger taxon and character sampling (Pyron & Wiens 2011; Fouquet *et al.* 2013: Fig. 2; Zhang *et al.* 2013; but see Padial *et al.* 2014). Schmid *et al.* (2013 "2012") did not endorse the results of those studies that refuted the monophyly of Orthobatrachia and constrained their topology to support their claims about the evolution of direct development. Our analyses nonetheless recovered Hemiphractidae as the sister group of Athesphatanura, supporting the results of Pyron & Wiens (2011) and Fouquet

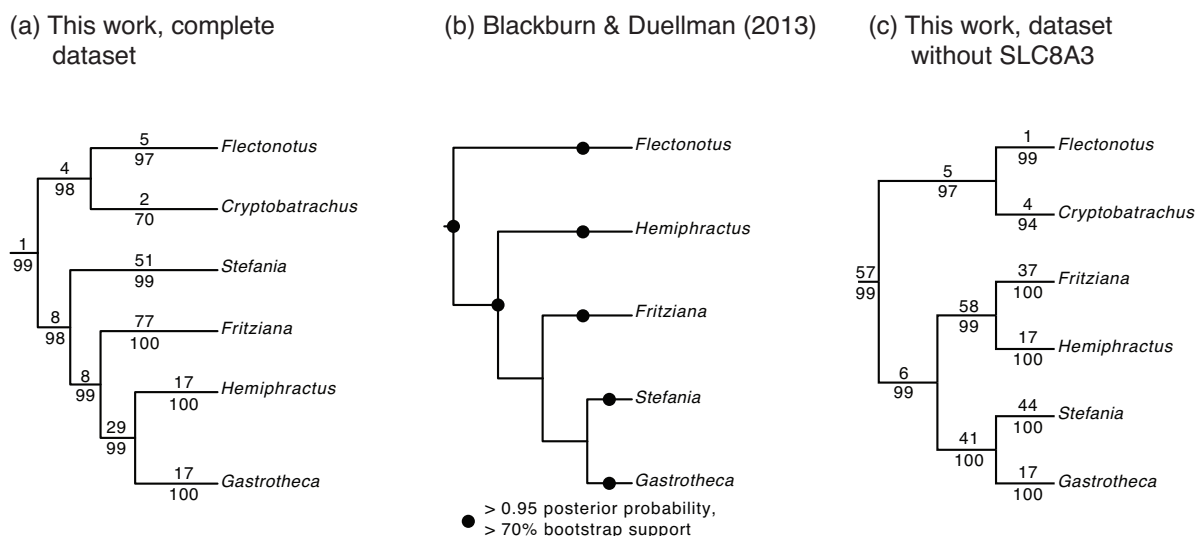
5. Noble (1927, 1931) did not mention either of the then recently-named taxa *Flectonotus* (Miranda-Ribeiro, 1926) and *Fritziana* (as *Fritzia* by Miranda-Ribeiro, 1920) even though these genera had been noted in their original descriptions to share with the other marsupial frogs the transport of eggs in a specialized pouch in the dorsum of females.



*et al.* (2013: Fig. 2). As explained below, these findings have important implications for understanding the evolution of reproductive modes in hemiphractids and other groups (Athesphatanura and Brachycephaloidea). However, due to our limited sampling of taxa outside Hemiphractidae, the sister relationships of the group remain to be tested in the context of a larger analysis of Nobleobatrachia.

**Phylogenetic relationships within Hemiphractidae.** The monophyly of the six currently recognized genera was corroborated by our results. However, the relationships among hemiphractid genera recovered by our analyses (Fig. 3a) differ from those of previous studies (e.g., Wiens *et al.* 2007; Duellman *et al.* 2011a; Fisher-Reid & Wiens 2011; Pyron & Wiens 2011; Gomez-Mestre *et al.* 2012; Blackburn & Duellman 2013) that consistently recovered the relationships depicted in Figure 3b. As discussed in the previous section, the aforementioned studies differ from ours in analytical approach and sampling. Also, several clades among our optimal topologies received low support (specially GB values but not exclusively). For example, Hemiphractidae, Cryptobatrachinae, and Hemiphractinae are supported by GB = 1, 4, and 8 respectively. Also the genus *Cryptobatrachus* is supported by GB = 2 and JK = 70. Both optimal and expected support measures (Wheeler 2010) are often interpreted, prospectively, as indicative of clade stability—*i.e.*, relationships with high support are expected to be recovered in future studies based on additional samples (e.g., Siddall 2002; Hovenkamp 2004, 2009; Guayasamin *et al.* 2009; Vences *et al.* 2013).

Misfortune during our parsimony searches presented us with an illustrative example that contradicts this expectation. By mistake, we performed the same parsimony analyses presented herein but on a dataset that lacked the marker SLC8A3. This marker contains up to 1132 bp of relatively low variability (e.g., no indels and 321 parsimony informative characters according to a similarity alignment) and it was sampled only for 47 taxa (13 of them hemiphractids). The results of the analyses of the two datasets differed markedly (Fig. 3a, c), both in topology and clade support, and the only relationships among hemiphractid genera that did not change were the less supported (*i.e.*, Cryptobatrachinae and Hemiphractinae). These results are not surprising as clade support values are not a measure of the power of additional evidence to overturn a hypothesis of relationships (Brower 2006; Grant & Kluge 2007, 2008b; Goloboff *et al.* 2008b; Wheeler 2010).



**FIGURE 3.** Summary of different hypothesis of phylogenetic relationships among hemiphractid genera indicating support; numbers above and below branches represent Goodman-Bremer values and jackknife proportions respectively. (a) Topology obtained from the parsimony total evidence analysis performed in this work (see Material and methods for details). (b) Topology obtained from maximum likelihood and Bayesian analyses of DNA sequences of 16S, ND1, POMC, and RAG1 by Blackburn & Duellman (2013). (c) Topology obtained from the parsimony analysis performed in this work but excluding the marker SLC8A3 from our dataset. See main text for discussion.

Branch length between several sister terminals is minimal and deserve discussion. Differentiation between the pairs of sister species *Cryptobatrachus fuhrmanni* and *C. sp.*, and *Hemiphractus bubalus* and *H. johnsoni* is due to the fact that both *C. sp.* and *H. johnsoni* were only sampled for phenotypic characters. Given that most phenotypic characters included in our study are variable at the genus level (Mendelson *et al.* 2000), it is no surprise that only very few differences are observed between sister species. Within the *Gastrotheca marsupiata* species group (*sensu*

this work) there are several cases of remarkably short branches between sister terminals putatively belonging to different species. This could indicate taxonomic issues (e.g., synonyms), misidentification of samples (from specimens to tubes), contamination of samples, or actual low molecular divergence. Potential taxonomic issues and possible misidentifications are discussed in the Systematics section.

**Evolution of direct development.** Our results support the MRCA of hemiphractids as a direct-developer (Fig. 2). Free-living aquatic tadpoles evolved within hemiphractids from direct development at least two different times and a maximum of eight. These surprising results constitute the first empirical evidence of the evolution of a free-living tadpole from a direct-developer ancestor in anurans. The results of Mendelson *et al.* (2000) were ambiguous due to a basal polytomy, and the results of Wiens *et al.* (2007: 1892 and Fig. 1) and Gomez-Mestre *et al.* (2012: Fig. S2)—both using ML character reconstruction with a model with different rates of change between character states—recovered the MRCA of egg-brooding frogs as having a tadpole, with direct development evolving several times from it. However, Wiens *et al.* (2007) and Gomez-Mestre *et al.* (2012) favored a sub-optimal character reconstruction arguing that their own optimal solution was misleading. This sub-optimal solution implied that, within *Gastrotheca*, the free-living tadpole of various species evolved from a common ancestor with direct development. Our results also suggest that the diversification of Athesphatanura, the largest radiation in Nobleobatrachia both in terms of diversity of species and phenotypes, may have been coupled with a shift in the MRCA from direct-development to free-living tadpoles. Contrarily, the ancestors of both Nobleobatrachia and Athesphatanura + Hemiphractidae were inferred by Gomez-Mestre *et al.* (2012) as having a free-living tadpole. Limitations in taxon sampling hamper, nonetheless, an adequate test of this hypothesis. Regardless, our results highlight, once more, the importance of taxon sampling in the reconstruction of character evolution.

What constitutes "direct development" is important here inasmuch as this term has been differently defined through the literature (Altig & Johnston 1989; Hanken 2003, and references therein) since it was first coined by F.M. Balfour in the nineteenth century for ontogeny from which the larval stage has been lost (according to Hall 2000). In anurans, the term has been applied to frogs that go through a free-living (*i.e.*, outside the egg capsule) but truncated endotrophic larval stage, to frogs that have no discernible larval morphology and appear to develop directly from gastrula to froglet. For example, all species of *Breviceps* for which the character is known have an embryo that hatches as an endotrophic tadpole, with apparently no mouthparts, that develops into a froglet while in a subterranean jelly nest (Channing 2001; Channing & Howel 2006; Harper *et al.* 2010)—a condition that several sources report as direct development (De Villiers 1929; McDiarmid & Altig 1999; Müller *et al.* 2007; Harper *et al.* 2010<sup>6</sup>). Given the disparity of available definitions, for purposes of this discussion we consider direct developers those species in which the embryo hatches from the egg as a fully formed, albeit miniature adult (*i.e.*, stage 46 of Gosner 1960). However, the ontogenetic trajectory of larval development within the egg capsule of nominal direct-developers should not be conflated with the notion that both larva-specific features and metamorphosis were lost during development. Detailed studies reveal that in amphibians direct development does not necessarily involve the complete loss of larval features (Wassersug & Duellman 1984; McDiarmid & Altig 1999; Blackburn 2004; Müller 2006; Kerney *et al.* 2007, 2012; Ziermann & Diogo 2013) but, rather, the loss of the ability to live outside of the egg capsule.

If we consider that a free-living larval stage evolving from a direct developing ancestor has only been inferred in hemiphractids (this study), *Desmognathus* salamanders (Chippindale *et al.* 2004), and Seychelles caecilians (San Mauro *et al.* 2014), it is remarkable that in hemiphractids this apparent re-acquisition of free-living larvae has occurred two to eight times independently. Even more outstanding is that there is no evidence of a reversal in the older, more species-rich, and closely related group, Brachycephaloidea. As suggested by Kerney *et al.* (2012), the degree of developmental repatterning and loss of larval structures might constrain the re-appearance of a free-living larval stage. While in Brachycephaloidea larval characters are more reduced or even skipped (Elinson 2013; Ziermann & Diogo 2013, and references therein), in *Gastrotheca*, species with direct development pass through basically the same early developmental stages as those with free-living tadpoles (Wassersug & Duellman 1984) and retain at least some rudiments of oral features typical of species with a free-living tadpole (this is also the case for species of *Stefania*). However, these larval characters present in the direct developing embryos of *Gastrotheca* and *Stefania* need to be studied in detail and included in a cladistic analysis in order to understand their origin.

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6. This different use of terminology might be the reason why Gomez-Mestre *et al.* (2012) also treated *Breviceps* as a possible case of a free-living tadpole evolving from a direct developing ancestor.

A scenario that also needs further investigation is the amount of yolk available to the embryo. The reversion from direct development in *Gastrotheca* can be seen as an endotrophic tadpole that remains on the mother's pouch for only some time, and only when the yolk is almost depleted is the embryo released as a free-living and feeding tadpole. This is part of the continuum that has been recognized between direct development and free-living and feeding tadpoles (McDiarmid & Altig, 1999). Within *Gastrotheca*, the evolution of a tadpole from a direct-developing ancestor has happened at least once, at the base of the Andean radiation. However, the branching pattern and distribution of the character in the most exclusive clade containing *G. galeata* KU 181700 and *G. ochoai* KU 173499 implies several equally parsimonious solutions. The basal branches of the *Gastrotheca* Andean radiation are very short and result in several polytomies in the strict consensus (Fig. 2b).

Although the re-evolution of free-living larvae from direct-developing ancestors within *Gastrotheca* has already been discussed (e.g., Duellman & Hillis 1987; Duellman *et al.* 1988; Wiens *et al.* 2007), our analysis indicates that this has happened not only in *Gastrotheca* but also in *Flectonotus* and *Fritziانا*. Contrary to what happens in species of *Gastrotheca* with a free-living larva, the sister group of *Flectonotus* has direct development (species of the genus *Cryptobatrachus*) with embryos not showing tadpole oral features (Wassersug & Duellman 1984). Tadpoles of *Flectonotus* are endotrophic and hatch at stages 38–41 of Gosner (1960) while those of *Fritziانا* are facultative exotrophic and hatch at stages 30–41 (Duellman & Maness 1980; del Pino & Escobar 1981; Duellman & Gray 1983; Weygoldt & Carvalho-e-Silva 1991; Duellman *et al.* 2011). Although tadpoles of both *Flectonotus* and *Fritziانا* lack labial teeth and papillae, those of *Flectonotus* have jaw sheaths weakly cornified and ventral velum small and present only laterally with the resulting gap equal to about half the width of the buccal floor, while those of *Fritziانا* have small and keratinized jaw sheaths and complete ventral velum in the floor of the mouth (Duellman & Gray 1983; Wassersug & Duellman 1984). Tadpoles of *Gastrotheca* are known to hatch at different stages ( $\geq 31$  of Gosner 1960), have labial teeth, papillae, keratinized jaw sheaths, complete ventral velum in the floor of the mouth, and filter rows of one filter plate overlapping the facing filter plate, so that uninterrupted gill filter rows bridge the gill slits (Wassersug & Duellman 1984). Thus, it is obvious from our cursory review of the literature that the free-living tadpole stage in *Flectonotus*, *Fritziانا* and *Gastrotheca* has been gained not only independently but also at different developmental stages and with different morphological and trophic features.

The available information on the distribution of life-history strategies allows us to make some predictions about their occurrence in other groups, in a manner similar to Smith and Wheeler's (2006) approach to venomous fishes. We predict that in all species of *Fritziانا* the embryo hatches as an aquatic tadpole. On the other hand, we expect that in females of all species of *Stefania*, Atlantic Forest *Gastrotheca*, and the species herein represented by the sample *G. excubitor* MUSM 26280, a froglet emerges from the egg capsule. With the data at hand, we cannot make an educated guess about the hatching stage of embryos in the species herein represented by the sample *G. griswoldi* MHNSM 20588.

**Evolution of external gills.** The monophyly of Hemiphraetidae is supported by the phenotypic synapomorphies of female transport of eggs in a specialized depression or sac in the dorsum and bell-shaped gills in embryos (Noble 1927; Mendelson *et al.* 2000; this work). The evolution of both characters might be related to challenges faced by terrestrial eggs, such as desiccation, predation, and gas exchange. While transport of eggs by an adult might decrease predation and water loss, the presence of expanded, non-ephemeral, and vascularized external gills in embryos have been related to enhancing gas exchange (Warkentin 2002; Nokhbatolfighahai & Downie 2008). External gills are present in the embryos of many anurans, both with aquatic and terrestrial eggs (Duellman & Trueb 1986; Nokhbatolfighahai & Downie 2008). One might expect large, vascularized, and non-ephemeral external gills in embryos of species with direct development because these eggs are usually larger than those of species with a tadpole stage (implying a proportionally smaller surface area for gas exchange) and the eggs hatch when their rate of oxygen consumption is at or near a peak (Mitchell & Seymour 2000). Interestingly, this prediction is only met by hemiphraetid embryos, while other direct-developing anurans show no external gills or they are rudimentary and ephemeral. The tail has been proposed as an alternative respiratory surface (e.g., Peters 1876; Townsend & Stewart 1985; Thibaudeau & Altig 1999; Nokhbatolfighahai *et al.* 2010). Observations on species of Brachycephaloidea (the other major radiation of direct-developing Neotropical frogs with terrestrial eggs) show a highly vascularized and expanded tail applied close to the perivitelline membrane, suggesting a role in respiratory exchange [e.g., *Craugastor augusti* (Valett & Jameson 1961 but see Townsend & Stewart 1985: 433), *Pristimantis urichi* (Nokhbatolfighahai *et al.* 2010), *Ischnocnema guentheri* (Lynn & Lutz 1946), and several

species of *Eleutherodactylus* (e.g., Sampson 1904; Noble 1925; Lynn 1942; Townsend & Stewart 1985)]. Nonetheless, external gills have been reported for a number of *Eleutherodactylus* such as *E. portoricensis* (Gitlin 1944; Townsend & Stewart 1985), *E. martinicensi* (Chibon 1960), *E. johnstonei* (Adamson *et al.* 1960), *E. planirostris* (Hughes 1959), and *E. inoptatus* Noble (1925, 1927), but in all cases the external gills are small and ephemeral, which is the norm in anurans.

Also relevant is that Gitlin (1944) reported that the external gills of *Eleutherodactylus portoricensis* are derived from the third branchial arch while in hemiphractids they derive from the first or the first and second arches (del Pino & Escobar 1981; Mendelson *et al.* 2000). Within hemiphractids, the sister taxa *Cryptobatrachus* and *Flectonotus* have a single pair of gills derived from branchial arch I, while in *Gastrotheca*, *Fritziana*, *Hemiphractus*, and *Stefania* two pairs of gills are derived from branchial arches I and II respectively (see character 43). Unfortunately, the branchial arch origin of external gills, when present in anuran embryos, is seldom reported in the literature and we could not infer the ancestral state for hemiphractids. In any case, we hypothesize that the external gills of hemiphractids are homologous to those of other Nobleobatrachia so that their unique bell shape and non-transient nature are modifications within the same transformation series.

Within the clade containing *Gastrotheca*, *Fritziana*, *Hemiphractus*, and *Stefania* further variation exists regarding the fusion of the gill stalks (character 44) and of the two pairs of bell-shaped gills (character 45). On one hand, the fusion of the gill stalks is reconstructed as a derived character within *Gastrotheca* with at least five origins (*G. christiani*, *G. galeata*, *G. guentheri*, *G. testudinea*, and the MRCA of *G. griswoldi* KU 181701 and *G. pseustes*). On the other hand, the fusion of the two pairs of bell-shaped gills has been observed in the 21 species of *Gastrotheca* where the character has been studied and in *H. fasciatus*. However, the character is unknown for *G. fissipes*, *G. megacephala*, *G. prasina*, *G. pulchra*, and *G. recava*.

## Systematics

On the basis of our results, we provide a revised taxonomy of the family Hemiphractidae. We recognized two subfamilies, six genera, and four species groups of *Gastrotheca*. Unambiguous transformations (*i.e.*, shared by all optimal trees) for the supraspecific taxa included in this section are listed in Appendix 5. Because the majority of the phenotypic characters that we analyzed have only been scored for a handful of hylid species (characters of Mendelson *et al.* 2000), their status as synapomorphies needs to be tested in a dataset with a larger representation of non-hylids nobleobatrachians. In addition to a diagnosis for all supraspecific taxa considered, we provide a characterization summarizing the main known phenotypic characteristics of each genus. A graphical summary of our taxonomy is presented in Fig. 2b.

### Family: Hemiphractidae Peters, 1862

**Immediately more inclusive taxon.** Unclear. We recovered a sister relationship with Athesphatanura (see also Pyron & Wiens 2011; Fouquet *et al.* 2013) and the more inclusive taxon would be a clade nearly equivalent to Cladophrynia (Frost *et al.* 2006) but with the inclusion of *Hemiphractus*. Other works (e.g., Heinicke *et al.* 2009; Padiál *et al.* 2014) recovered a sister relationship with Brachycephaloidea and the most inclusive taxon would be Orthobatrachia.

**Sister taxon.** Unclear. Athesphatanura (Pyron & Wiens 2011; Fouquet *et al.* 2013; this work) or Brachycephaloidea (Heinicke *et al.* 2009; Padiál *et al.* 2014).

**Content.** Cryptobatrachinae Frost, Grant, Faivovich, Bain, Haas, Haddad, de Sá, Channing, Wilkinson, Donnellan, Raxworthy, Campbell, Blotto, Moler, Drewes, Nussbaum, Lynch, Green, and Wheeler, 2006, and Hemiphractinae Peters, 1862

**Type genus.** *Hemiphractus* Wagler, 1828.

**Diagnosis.** (1) bell-shaped gills in embryos (character 42, 0→1); (2) female transport of eggs in a specialized depression or sac in the dorsum (character 47, 0→4). All unambiguous transformations are listed in Appendix 5.

A broad *m. abductor brevis plantae halluces* has been suggested as a synapomorphy (Burton 2004; Faivovich *et al.* 2005) but this character has not been included in our analysis. Direct developing has also been suggested as a

synapomorphy (Mendelson *et al.* 2000) and in our analysis the MRCA of Hemiphractidae is reconstructed as a direct developer; however, the ancestral state of the MRCA of Athesphatanura + Hemiphractidae is ambiguous and no transformation could be inferred with certainty.

**Distribution.** Neotropical lowlands and montane rainforests, with a few species known from humid high-elevation Andean grasslands and the rocky summits of the tepuis of the Guiana Shield (Argentina, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Guyana, Panama, Peru, both islands of Trinidad and Tobago, and Venezuela).

**Comments.** According to the results of Heinicke *et al.* (2009), Hemiphractidae is the sister taxon of Brachycephaloidea and they named this clade Orthobatrachia. However, all studies with denser taxon sampling of Athesphatanura and Brachycephaloidea, and similar character sampling (Pyron & Wiens 2011; Gomez-Mestre *et al.* 2012; Fouquet *et al.* 2013; this work) reject Orthobatrachia. Padial *et al.* (2014) recovered Orthobatrachia with a dense taxon sampling of Brachycephaloidea but their samples of Athesphatanura were limited to eight species of Hylidae and two species of Leptodactylidae. The phylogenetic position of Hemiphractidae remains unsolved.

**Subfamily: Cryptobatrachinae** Frost, Grant, Faivovich, Bain, Haas, Haddad, de Sá, Channing, Wilkinson, Donnellan, Raxworthy, Campbell, Blotto, Moler, Drewes, Nussbaum, Lynch, Green, and Wheeler, 2006

**Immediately more inclusive taxon.** Hemiphractidae Peters, 1862.

**Sister taxon.** Hemiphractinae Peters, 1862.

**Content.** *Cryptobatrachus* Ruthven, 1916, and *Flectonotus* Miranda-Ribeiro, 1926.

**Type genus.** *Cryptobatrachus* Ruthven, 1916.

**Diagnosis.** (1) Absence of supraorbital flange (character 36, 1→0), with the same characters state coded for *Fritziana ohausi*, *Gastrotheca griswoldi*, and *G. marsupiata*; (2) one pair of bell-shaped gills exclusively derived from branchial arch I (although this character is diagnostic from its sister taxon, it was not retrieved as a synapomorphy because the ancestral state is unknown). All unambiguous transformations are listed in Appendix 5.

**Distribution.** Northern Andes of Colombia and Venezuela (Cordilleras Oriental, Central and Occidental, Sierra de Perijá, and Cordillera de Mérida), Sierra Nevada de Santa Marta in Colombia, Cordillera de la Costa in Venezuela, and both islands of Trinidad and Tobago.

**Comments.** The sister relationship between *Cryptobatrachus* and *Flectonotus* was unexpected. Several studies assumed a sister relationship of *Cryptobatrachus* with *Stefania* (e.g., Duellman & Hoogmoed 1984; Lynch 2008; Wiens *et al.* 2007; Schmid *et al.* 2013 "2012") based on overall external similarity. Frost *et al.* (2006) recovered a sister relationship between *Cryptobatrachus* and *Stefania*, a clade to which they assigned the family rank.

### **Genus: *Cryptobatrachus* Ruthven, 1916**

**Immediately more inclusive taxon.** Cryptobatrachinae Frost, Grant, Faivovich, Bain, Haas, Haddad, de Sá, Channing, Wilkinson, Donnellan, Raxworthy, Campbell, Blotto, Moler, Drewes, Nussbaum, Lynch, Green, and Wheeler, 2006.

**Sister taxon.** *Flectonotus* Miranda-Ribeiro, 1926.

**Content** (6 species): *Cryptobatrachus boulengeri* Ruthven, 1916, *C. conditus* Lynch, 2008, *C. fuhrmanni* (Peracca, 1914), *C. pedroruizi* Lynch, 2008, *C. remotus* Infante-Rivero, Rojas-Runjaic, and Barrio-Amorós, 2009, and *C. ruthveni* Lynch, 2008.

**Type species.** *Cryptobatrachus boulengeri* Ruthven, 1916, by original designation.

**Diagnosis.** (1) ventral crest of alae of parasphenoid present (character 3, 0→1), with the same characters state coded for *Gastrotheca dendronastes*, *G. galeata*, *G. guentheri*, *G. microdiscus*, *G. plumbea*, *G. riobambae*, and *Hemiphractus*; (2) cultriform process posterior to orbitonasal foramina (character 5, 1→0), with the same characters state coded for *Stefania scalae*; (3) anteromedial process of neopalatine present (character 11, 0→1); (4) medial contact of vomers (character 17, 0→1), with the same character state coded for *Fritziana ohausi*, *G. dendronastes*, *G. guentheri*, *G. plumbea*, *G. walkeri*, *H. bubalus*, and *H. johnsoni*; (5) subarticular adhesive pads on distal subarticular tubercles of outer fingers (although this character was not included in our analysis). Because the relationships among *Cryptobatrachus* are ambiguous (a polytomy in our strict consensus tree), the transformations

reported herein are only shared among some of the optimal trees (Appendix 5). Nonetheless, at least the character states listed above in points 3 and 5 seem to be shared among all species of the genus (Lynch 2008), therefore representing unambiguous transformations regardless of the branching order within the genus.

**Characterization.** (1) one pair of bell-shaped gills derived from branchial arch I covering 25–50% of body of the embryo; (2) females carrying exposed eggs on their backs; (3) direct development; (4) embryos without oral larval features; (5) males without vocal sacs or apertures and apparently not vocalizing; (6) superficial mandibular musculature Type A of Tyler & Duellman (1995) (*i.e.*, the *m. submentalis* is of moderate size, the *m. intermandibularis* is differentiated by the presence of an apical element, the fibers of which are in contact medially, the customary sheet-like element of the *m. intermandibularis* bears a median raphe, the *m. interhyoideus* extends slightly posterior to the mandibles); (7) sphenethmoid weakly ossified anteriorly; (8) subarticular adhesive pads on distal subarticular tubercles of outer fingers; (9) ventral out-growth of the palatine growing medially until it articulates with the distal edge of the dentigerous process (del Pino & Escobar 1981; Duellman & Hoogmoed 1984; Wassersug & Duellman 1984; Tyler & Duellman 1995; Mendelson *et al.* 2000; Lynch 2008).

**Distribution.** Mountain rainforests of the northern Andes of Colombia and Venezuela (Cordilleras Oriental, Central and Occidental, and Sierra de Perijá) and Sierra Nevada de Santa Marta in Colombia.

**Comments.** The monophyly of the genus has been corroborated on the basis of phenotypic characters (Duellman & Hoogmoed 1984; Mendelson *et al.* 2000; Lynch 2008). Most molecular studies did not include DNA sequences of more than one terminal (Darst & Cannatella 2004; Faivovich *et al.* 2005; Wiens *et al.* 2005, 2006; Frost *et al.* 2006; Schmid *et al.* 2013 "2012"; Zhang *et al.* 2013). Padial *et al.* (2014) is the only exception and found that *C. boulengeri* and *C. fuhrmanni* did not form a monophyletic group. Lynch's (2008) most extensive study evaluated phenotypic characters and recognized six species, proposing the following phylogenetic relationships on the basis of morphological characters: *Stefania* (*C. nicefori*, (*C. fuhrmanni*, (*C. boulengeri*, *C. conditus*, *C. pedroruizi*, *C. ruthveni*))).

Although the genus *Cryptobatrachus* is monophyletic (Fig. 2b), its intrageneric relationships are ambiguous in our strict consensus tree (*i.e.*, a polytomy). Thus, the relationships postulated by Lynch (2008) cannot be rejected nor corroborated. According to the large genetic distances observed in the sequences of putative *C. fuhrmanni* studied here, it seems that there could be at least two species under this name. Most likely, the new species would correspond to populations from the Cordillera Oriental of Colombia, for which the name *C. fuhrmanni orientalis* Rivero, 1968 "1966" might be available. However, we refrain from taking any taxonomic action until detailed comparisons are performed. We follow Infante-Rivero *et al.* (2009 "2008") and consider *C. nicefori* Cochran and Goin, 1970 (a species only known from the holotype) as a hyline unassigned to genus ("*Hyla*" *nicefori*), although possibly in *Hyloscirtus*.

## Genus: *Flectonotus* Miranda-Ribeiro, 1926

**Immediately more inclusive taxon.** Cryptobatrachinae Frost, Grant, Faivovich, Bain, Haas, Haddad, de Sá, Channing, Wilkinson, Donnellan, Raxworthy, Campbell, Blotto, Moler, Drewes, Nussbaum, Lynch, Green, and Wheeler, 2006.

**Sister taxon.** *Cryptobatrachus* Ruthven, 1916.

**Content** (2 species): *Flectonotus fitzgeraldi* (Parker, 1934) and *F. pygmaeus* (Boettger, 1893).

**Type species.** *Nototrema pygmaeum* Boettger, 1893.

**Diagnosis.** (1) pouch formed by two longitudinal flaps of skin that are adherent middorsally over the eggs forming an enclosed pouch (character 41, 0→2); (2) endotrophic tadpoles hatching at stage  $\geq 30$  of Gosner (1960) (character 46, 3→2). All unambiguous transformations are listed in Appendix 5.

**Characterization.** (1) one pair of bell-shaped gills derived from branchial arch I covering  $\leq 25\%$  of the body of embryo; (2) females carrying eggs on their backs inside a pouch formed by two longitudinal flaps of skin that are adherent middorsally over the eggs, forming an enclosed pouch; (3) in females that are not reproductively active, flaps either meeting along the midline of the dorsum, thereby closing the dorsal pouch, or leaving a gap of 1–2 mm; (4) embryos hatching as non-feeding tadpoles at advance stage (38–41 of Gosner, 1960); (5) tadpoles with jaw sheaths weakly cornified, lacking labial teeth and papillae, and ventral velum small and present only laterally with the resulting gap equal to about half the width of the buccal floor; (6) nasal bones small, slender, widely separated medially by the sphenethmoid; (7) males producing advertisement calls and having gaping holes as vocal sac

apertures; (8) superficial mandibular musculature Type A of Tyler and Duellman (1995) (*i.e.*, the *m. submentalis* is of moderate size, the *m. intermandibularis* is a single, undifferentiated sheet bearing a median raphe, the *m. interhyoideus* extends slightly posterior to the mandibles) (del Pino & Escobar 1981; Duellman & Gray 1983; Wassersug & Duellman 1984; Tyler & Duellman 1995; Mendelson *et al.* 2000; Duellman *et al.* 2011).

**Distribution.** Restricted to the montane rainforests of the northern Cordillera Oriental of Colombia, Cordillera de Mérida and Cordillera de la Costa in Venezuela, and both islands of Trinidad and Tobago.

**Comments.** Detailed reviews are provided by Duellman & Gray (1983) and Duellman *et al.* (2011). Weygoldt & Carvalho-e-Silva (1991) accepted the tree of Duellman & Gray (1983), within which *Flectonotus* was recovered as paraphyletic with respect to *Fritziana* (see also Duellman *et al.* 2011: Fig. 1). Mendelson *et al.* (2000) recovered *Flectonotus pygmaeus* as the sister of the clade formed by *Fritziana goeldii* + *Fritziana ohausi*. In that study *Flectonotus* + *Fritziana* was supported by the synapomorphies: 1) quadratojugal not articulating with the maxilla; 2) brooding pouch formed by dorsolateral folds of skin; 3) overlap between *m. intermandibularis* and *m. submentalis*; and 4) absence of supplementary elements of *m. intermandibularis*. Nevertheless, Mendelson *et al.* (2000) could not test the monophyly of *Flectonotus* with respect to *Fritziana* because they only included *Flectonotus pygmaeus* in their analysis. Duellman *et al.* (2011), using DNA sequences of representatives of all species of both groups, found both genera to be monophyletic and not sister taxa, therefore justifying the resurrection of *Fritziana* from the synonymy of *Flectonotus*. Our results corroborate the hypothesis of Duellman *et al.* (2011).

### Subfamily: Hemiphractinae Peters, 1862

**Immediately more inclusive taxon.** Hemiphractidae Peters, 1862.

**Sister taxon.** Cryptobatrachinae Frost, Grant, Faivovich, Bain, Haas, Haddad, de Sá, Channing, Wilkinson, Donnellan, Raxworthy, Campbell, Blotto, Moler, Drewes, Nussbaum, Lynch, Green, and Wheeler, 2006.

**Content.** *Fritziana* Mello-Leitão, 1937, *Gastrotheca* Fitzinger, 1843, *Hemiphractus* Wagler, 1828, and *Stefania* Rivero, 1968

**Type genus.** *Hemiphractus* Wagler, 1828.

**Diagnosis.** (1) Posteromedial process of vomer smooth (character 12, 0→1), with a reversal in *Fritziana ohausi*, the MRCA of *Gastrotheca plumbea* and *G. testudinea*, and a transformation into a different character state in *Hemiphractus*; (2) postorbital process short (character 20, 0→1), with the same character state coded for *Cryptobatrachus fuhrmanni*, a reversal in *F. goeldii* and *G. griswoldi*, and a transformation into a different character state in *G. guentheri*, *G. megacephala*, and *Hemiphractus*; (3) zygomatic ramus long, articulating only with postorbital process of maxilla (character 39, 0→2), with transformations into different character states in *F. goeldii*, *F. ohausi*, *G. galeata*, *G. griswoldi*, *G. walkeri*, *H. bubalus*, *H. johnsoni*, *H. proboscideus*, *H. scutatus*, and *Stefania scalae*; (4) two pairs of bell-shaped gills derived from branchial arches I and II (although this character is diagnostic from its sister taxon, it was not retrieved as a synapomorphy because the ancestral state is unknown). All unambiguous transformations are in Appendix 5.

**Distribution.** Neotropical lowlands and montane rainforests with a few species known from humid high-elevation Andean grasslands and the rocky summits of the tepuis of the Guiana Shield (Argentina, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Guyana, Panama, Peru, and Venezuela).

### Genus: *Fritziana* Mello-Leitão, 1937

**Immediately more inclusive taxon.** Hemiphractinae Peters, 1862.

**Sister taxon.** An unnamed clade containing *Gastrotheca* Fitzinger, 1843 and *Hemiphractus* Wagler, 1828.

**Content** (4 species): *Fritziana fissilis* (Miranda-Ribeiro, 1920), *F. goeldii* (Boulenger, 1895), *F. ohausi* (Wandolleck, 1907), and *F. ulei* Miranda-Ribeiro, 1926.

**Type species.** *Hyla goeldii* Boulenger, 1895.

**Diagnosis.** (1) neopalatines not extending medially to ossified sphenethmoid (character 9, 1→0), with the same characters state coded for *Gastrotheca griswoldi*, *G. testudinea*, and *G. walkeri*; (2) quadratojugal not

articulating with maxilla (character 23, 0→1), with the same characters state coded for *Flectonotus pygmaeus*; (3) distal ends of alary processes diverging laterally (character 26, 0→1), with the same characters state coded for *G. marsupiata*, *G. megacephala*, and *G. walkeri*; (4) facultative endotrophic tadpoles hatching at stage  $\geq 30$  of Gosner (1960) (character 46, 3→2); (5) lateral skin folds not adherent middorsally over eggs (although this character is diagnostic from all other hemiphraetids, it was not retrieved as a synapomorphy because the ancestral state is unknown). All unambiguous transformations are listed in Appendix 5.

**Characterization.** (1) two pairs of bell-shaped gills derived from branchial arches I and II covering  $\leq 25\%$  of the embryo; (2) females of *Fritziana goeldii* and *F. ohausi* carrying eggs on their backs with lateral skin folds only bordering the eggs laterally, in some females of *F. fissilis* the lateral folds either cover the eggs middorsally but are not adherent, whereas in others the middorsal area is not covered; (3) longitudinal folds becoming apparent on the female's back only during mating; (4) embryos hatching as facultative non-feeding tadpoles at an advanced stage ( $\geq 30$  of Gosner 1960); (5) tadpoles with small and keratinized jaw sheaths, lacking labial teeth and papillae, and complete ventral velum in the floor of the mouth; (6) large nasals nearly in contact anterior to the sphenethmoid; (7) males producing advertisement calls and having gapping holes as vocal sac apertures; (8) superficial mandibular musculature Type A of Tyler & Duellman (1995) (del Pino & Escobar 1981; Duellman & Gray 1983; Wassersug & Duellman 1984; Weygoldt & Carvalho-e-Silva 1991; Tyler & Duellman 1995; Mendelson *et al.* 2000; Duellman *et al.* 2011).

**Distribution.** Endemic to the Atlantic Forest of eastern Brazil.

**Comments.** Pertinent literature is shared with *Flectonotus*. Thus, the remarks made above for *Flectonotus* apply to this genus. Duellman *et al.* (2011) inferred *F. ohausi* to be sister of the clade *F. fissilis* + *F. goeldii*. Schmid *et al.* (2013 "2012") obtained a different topology (*F. goeldii*, (*F. cf. fissilis*, (*F. fissilis* + *F. ohausi*))), in which *F. cf. fissilis* might represent a new species.

It is obvious from our molecular results that the current species diversity within *Fritziana* is vastly underestimated and that as many as four more species might be recognized. These putative new species are currently hidden under the name *Fritziana fissilis*. Careful examination of the external morphology of the preserved specimens sequenced in our study revealed that they match the description of *F. fissilis*. Furthermore, we did not find diagnostic characters among the specimens. We identified the specimen MNRJ 62845 as *Fritziana fissilis sensu stricto* because it was collected near the type locality in Município Nova Friburgo, Rio de Janeiro, Brazil but this identification should be considered tentative and revisited as more evidence becomes available. The species *Fritziana ulei* (Miranda-Ribeiro, 1926) was recently considered valid by Folly *et al.* (2014) and might be included in our analysis inasmuch as this species is only known from three specimens limiting our understanding of the variation of current diagnostic features.

## Genus: *Gastrotheca* Fitzinger, 1843

**Immediately more inclusive taxon.** An unnamed clade containing *Gastrotheca* Fitzinger, 1843 and *Hemiphraetus* Wagler, 1828.

**Sister taxon.** *Hemiphraetus* Wagler, 1828.

**Content** (68 species): *Gastrotheca abdita* Duellman, 1987, *G. aguaruna* Duellman, Barley, and Venegas, 2014, *G. albolineata* (Lutz and Lutz, 1939), *G. andaquiensis* Ruiz-Carranza and Hernández-Camacho, 1976, *G. angustifrons* (Boulenger, 1898), *G. antomia* Ruiz-Carranza, Ardila-Robayo, Lynch, and Restrepo-Toro, 1997, *G. antoniochoai* (De la Riva and Chaparro, 2005), *G. aratia* Duellman, Barley, and Venegas, 2014, *G. argenteovirens* (Boettger, 1892), *G. atympana* Duellman, Lehr, Rodríguez, and von May, 2004, *G. aureomaculata* Cochran and Goin, 1970, *G. bufona* Cochran and Goin, 1970, *G. cariniceps* Duellman, Trueb, and Lehr, 2006, *G. christiani* Laurent, 1967, *G. chrysosticta* Laurent, 1976, *G. cornuta* (Boulenger, 1898), *G. dendronastes* Duellman, 1983, *G. dumni* B. Lutz, 1977, *G. dysprosita* Duellman, 2013, *G. ernestoi* Miranda-Ribeiro, 1920, *G. espeletia* Duellman and Hillis, 1987, *G. excubitor* Duellman and Fritts, 1972, *G. fissipes* (Boulenger, 1888), *G. flamma* Juncá and Nunes, 2008, *G. fulvorufa* (Andersson, 1911), *G. galeata* Trueb and Duellman, 1978, *G. gracilis* Laurent, 1969, *G. griswoldi* Shreve, 1941, *G. guentheri* (Boulenger, 1882), *G. helenae* Dunn, 1944, *G. lateonota* Duellman and Trueb, 1988, *G. lauzuricae* De la Riva, 1992, *G. litonedis* Duellman and Hillis, 1987, *G. lojana* Parker, 1932, *G. longipes* (Boulenger, 1882), *G. marsupiata* (Duméril and Bibron, 1841), *G. megacephala* Izecksohn, Carvalho-e-Silva, and Peixoto, 2009, *G. microdiscus* (Andersson, 1910), *G. monticola* Barbour and Noble, 1920, *G. nebulanastes*



Duellman, Catenazzi, and Blackburn, 2011, *G. nicefori* Gaige, 1933, *G. ochoai* Duellman and Fritts, 1972, *G. orophylax* Duellman and Pyles, 1980, *G. ossilaginis* Duellman and Venegas, 2005, *G. ovifera* (Lichtenstein and Weinland, 1854), *G. pacchamama* Duellman, 1987, *G. pachachacae* Catenazzi and von May, 2011, *G. peruana* (Boulenger, 1900), *G. phalarosa* Duellman and Venegas, 2005, *G. phelloderma* Lehr and Catenazzi, 2011, *G. piperata* Duellman and Köhler, 2005, *G. plumbea* (Boulenger, 1882), *G. prasina* Teixeira, Vechio, Recoder, Carnaval, Strangas, Damasceno, Sena, and Rodrigues, 2012, *G. pseustes* Duellman and Hillis, 1987, *G. psychrophila* Duellman, 1974, *G. pulchra* Caramaschi and Rodrigues, 2007, *G. rebecca* Duellman and Trueb, 1988, *G. recava* Teixeira, Vechio, Recoder, Carnaval, Strangas, Damasceno, Sena, and Rodrigues, 2012, *G. riobambae* (Fowler, 1913), *G. ruizi* Duellman and Burrowes, 1986, *G. splendens* (Schmidt, 1857), *G. stictopleura* Duellman, Lehr, and Aguilar, 2001, *G. testudinea* (Jiménez de la Espada, 1870), *G. trachyceps* Duellman, 1987, *G. walkeri* Duellman, 1980, *G. weinlandii* (Steindachner, 1892), *G. williamsoni* Gaige, 1922, and *G. zeugocystis* Duellman, Lehr, Rodríguez, and von May, 2004.

**Type species.** *Hyla marsupiata* Duméril and Bibron, 1841.

**Diagnosis.** (1) Enclosed pouch with a posterior opening (character 41, 0→3); (2) presence of two fused pairs of bell-shaped gills derived from branchial arches I and II (character 45, 1→0), with the same character state coded for *Hemiphractus fasciatus*. All unambiguous transformations are listed in Appendix 5.

**Characterization.** (1) Two fused pairs of bell-shaped gills derived from branchial arches I and II (the gill stalks can be fused or not) covering most of the embryo; (2) females carrying eggs on their backs inside an enclosed pouch with a posterior opening; (3) in females that have reproduced but are not reproductively active the posterior opening is present; (4) in most species embryos go through direct development but in some species embryos hatch as feeding tadpoles at an advanced stage ( $\geq 31$  of Gosner, 1960); (5) embryos of species with direct development having oral larval features, although their quantity dramatically varies among species; (6) tadpoles having labial teeth, papillae, keratinized jaw sheaths, and complete ventral velum in the floor of the mouth, filter rows of one filter plate overlapping the facing filter plate, so that uninterrupted gill filter rows bridge the gill slits; (7) males of most species producing advertisement calls and having vocal sac apertures either absent or present as gaping holes, slits, or small orifices; (8) superficial mandibular musculature Type A or B of Tyler & Duellman (1995) (del Pino & Escobar 1981; Wassersug & Duellman 1984; Tyler & Duellman 1995; Mendelson *et al.* 2000).

**Distribution.** Lowland and mountain rainforests, and humid high grasslands of the Andes, with an ample distribution from Costa Rica through Panama and the tropical Andes to Ecuador in the Pacific and northern Argentina in the east, Cordillera de la Costa of Venezuela, and the Brazilian Atlantic Forest.

**Comments.** The literature dealing with this large genus of egg-brooding frogs is extensive and includes studies on the taxonomy (e.g., Duellman & Fritts 1972; Duellman 1974; Duellman & Hillis 1987; Duellman *et al.* 1988; Duellman & Venegas 2005; Teixeira *et al.* 2012), developmental biology (del Pino & Escobar 1981; del Pino *et al.* 2007 and references therein), and adult and tadpole morphology (e.g., Wassersug & Duellman 1984; Tyler & Duellman 1995; Haas 2003; Burton 2004). Dubois (1987 "1986") recognized three subgenera (*Gastrotheca*, *Duellmania*, and *Opisthodelphys*), an arrangement that has been largely ignored because the taxa proved to be non-monophyletic (Mendelson *et al.* 2000; Wiens *et al.* 2007), and were based on notions that did not regard monophyly as of classificatory importance. Duellman *et al.* (1988), on the basis of immunological distances, recognized four species groups (the *G. marsupiata*, *G. nicefori*, *G. ovifera*, and *G. plumbea* groups). Except for the *G. marsupiata* group, the monophyly of these groups has not been corroborated. Mendelson *et al.* (2000) included 17 species of *Gastrotheca* and rejected the monophyly of all previously suggested species groups. They also recovered *Hemiphractus* nested within *Gastrotheca*. However, Mendelson *et al.* (2000) continued to recognize both genera pending a more complete phylogenetic study. Subsequent studies (e.g., Faivovich *et al.* 2005, Wiens *et al.* 2005, 2007) have not recovered *Hemiphractus* nested within *Gastrotheca*. Wiens *et al.* (2007) found that none of the species groups of Duellman *et al.* (1988) were monophyletic, rearranged the content of the *G. marsupiata* and *G. plumbea* groups (the later including *G. nicefori*, which had formerly been placed in a monotypic group), and left all of the species of the former *G. ovifera* group plus *G. fissipes*, *G. walkeri*, and *G. galeata* unassigned to a group. Teixeira *et al.* (2012) found, on the basis on DNA sequences, that the Atlantic forest species of *Gastrotheca* do not form a monophyletic group. Subsequently, Blackburn & Duellman (2013) presented additional corroborating evidence of the non-monophyly of the Atlantic Forest species of *Gastrotheca*. Schmid *et al.* (2013 "2012") proposed five species groups (although the content of these groups was not explicitly stated), with *G. ovifera* and *G. galeata* unassigned to a group and with the following relationships (*G. fissipes* group ((*G.*

*williamsoni* group, *G. longipes* group) (*G. galeata* (*G. ovifera* (*G. plumbea* group, *G. marsupiata* group)))). However, their study presents some problems. First, the tree was inferred from a partially constrained topology (Schmid *et al.* 2013 "2012": 86) such that Hemiphractidae was monophyletic, *Eleutherodactylus* + *Diasporus* was the closest relative of Hemiphractidae, and the remaining outgroups were set to follow the results of Heinicke *et al.* (2009). Second, the species contents of the *G. longipes*, *G. marsupiata*, and *G. plumbea* groups were not explicitly stated and cannot be deduced from the publication. Third, there is evidence in the form of DNA sequences suggesting that the *G. fissipes* group, at least as formulated by Schmid *et al.* (2013 "2012"), is not monophyletic (Teixeira *et al.* 2012; Blackburn & Duellman 2013). Fourth, the monophyly of the *G. williamsoni* group was not evaluated because only *G. walkeri* was included in the phylogeny.

According to Haas (2003), the following larval characters sampled for *Gastrotheca riobambae* are potential synapomorphies of *Gastrotheca*: (1) *m. subarcualis rectus* I portion with origin from ceratobranchial III absent (Haas 35.0); (2) functional larval *m. levator mandibulae lateralis* present (Haas 56.0); (3) *ramus mandibularis* (cranial nerve V3) posterior running through the *m. levator mandibulae externus* group (Haas 65.1); (4) posterior palatoquadrate clearly concave with bulging and pronounced margin (Haas 68.1); (5) processus pseudopterygoideus long (Haas 77.2); and (6) dorsal connection from processus muscularis to commissura quadrato-orbitalis (Haas 78.2). However, some or all of these characters may be located as less inclusive levels of universality within the genus or might be shared with members of *Flectonotus* and/or *Fritziana*. None of the different subgeneric taxonomies (*i.e.*, subgenera, species groups, clades) historically proposed for *Gastrotheca* (*i.e.*, Dubois 1987 "1986"; Duellman *et al.* 1988; Wiens *et al.* 2007; Schmid *et al.* 2013 "2012"; Blackburn & Duellman, 2013) are monophyletic according to our results. Subsequently, we recognized four monophyletic species groups: *G. fissipes* species group, *G. longipes* species group, *G. marsupiata* species group, and *G. microdiscus* species group (see respective accounts for details).

It is obvious from our phylogenetic results and comparison of genetic distances that some of the identifications of DNA sequences available in the literature deserve careful examination of the voucher specimens to reassess the taxonomic identity of those samples [compare *G. excubitor* KU 173171 (Wiens *et al.* 2007) versus MUSM 26280 (Duellman *et al.* 2011b); *G. griswoldi* MHNSM 20588 (Lehr *et al.* 2005) versus KU 181701 (Wiens *et al.* 2007); *G. nicefori* KU 181071 (Wiens *et al.* 2007) versus MHUA A 5716 (this work); and *G. riobambae* KU 178468 (Wiens *et al.* 2007) versus UIMNH 94580 (Ruvinsky & Maxson 1996)]. In the case of *G. nicefori*, our sample MHUA A 5716 comes from near the type locality [Pennsylvania, Departamento Caldas, Colombia, according to the original description by Gaige (1933)], while KU 181071 comes from Venezuela (Táchira: 11 km S Delicias, 1750 m a.s.l.). The available name *Gastrotheca yacambuensis* Yústiz, 1976, could correspond to the Venezuelan populations (see also Barrio-Amorós, 1999 "1998") but we refrain from taking any taxonomic actions until more samples become available. The specimen *G. riobambae* UIMNH 94580 most likely is a misidentified specimen of *G. pseustes*, inasmuch as it was collected from a locality far from the known distribution of *G. riobambae* (Frenkel *et al.* 2010), where specimens of *G. pseustes* have been found (Ron & Frenkel 2010), the specimen is found in our analysis as sister of our sample of *G. pseustes*, and the genetic distances between the two samples = 0.5% (see Results). However, direct examination of the voucher UIMNH 94580 is needed to confirm its identification.

### ***Gastrotheca fissipes* species group**

**Immediately more inclusive taxon.** An unnamed clade containing the *Gastrotheca fissipes* species group and *G. marsupiata* species group.

**Sister taxon.** An unnamed clade containing the *Gastrotheca marsupiata* species group and the *G. microdiscus* species group.

**Content** (6 species): *Gastrotheca fissipes*, *G. flamma*, *G. megacephala*, *G. prasina*, *G. pulchra*, and *G. recava*.

**Diagnosis.** Unambiguous transformations are restricted to nucleotides (Appendix 5), inasmuch as our dataset mainly contains phenotypic characters for a single species (*G. megacephala*); however, several characters (*i.e.*, 16, 20, 22, 26, 27, 34, 35, 37, 38, 40) include transformations that are potential synapomorphies of this clade.

**Distribution.** Atlantic forest, from the State of Espírito Santo in the south to the State of Pernambuco in the north.

**Comments.** Although *Gastrotheca flamma* is not included in our phylogeny, it is tentatively assigned to this clade on overall similarity with *G. pulchra*.

### ***Gastrotheca longipes* species group**

**Immediately more inclusive taxon.** *Gastrotheca* Fitzinger, 1843.

**Sister taxon.** An unnamed clade containing all other species of *Gastrotheca*.

**Content** (12 species): *Gastrotheca andaquiensis*, *G. angustifrons*, *G. antomia*, *G. bufona*, *G. cornuta*, *G. dendronastes*, *G. guentheri*, *G. helenae*, *G. longipes*, *G. walkeri*, *G. weinlandii*, and *G. williamsoni*.

**Diagnosis.** (1) vomers with medial contact (character 17, 0→1), with the same character state coded for *Cryptobatrachus*, *Fritziana ohausi*, *Gastrotheca plumbea*, *Hemiphractus helioi*, *H. johnsoni*, and a reversal in *G. cornuta*; (2) pouch type 2 (del Pino 1980), with the same character state coded for *G. ovifera* (although this character was not included in our analysis). All unambiguous transformations are listed in Appendix 5.

**Distribution.** Lowlands and highlands of Central America (Costa Rica and Panama) and South America (Colombia, Ecuador, Peru, and Venezuela).

**Comments.** Although *Gastrotheca andaquiensis*, *G. angustifrons*, *G. antomia*, *G. bufona*, and *G. williamsoni* are not included in our phylogeny, they are tentatively assigned to this clade based on overall similarity with the other species (Duellman *et al.* 1988; Ruiz-Carranza *et al.* 1997).

### ***Gastrotheca marsupiata* species group**

**Immediately more inclusive taxon.** An unnamed clade containing the *Gastrotheca marsupiata* species group and the *Gastrotheca microdiscus* species group.

**Sister taxon.** *Gastrotheca microdiscus* species group.

**Content** (46 species): *Gastrotheca abdita*, *G. aguaruna*, *G. antoniochoai*, *G. aratia*, *G. argenteovirens*, *G. atympana*, *G. aureomaculata*, *G. cariniceps*, *G. christiani*, *G. chrysosticta*, *G. dunni*, *G. dysprositata*, *G. espeletia*, *G. excubitor*, *G. galeata*, *G. gracilis*, *G. griswoldi*, *G. lateonota*, *G. lauzuricae*, *G. litonedis*, *G. lojana*, *G. marsupiata*, *G. monticola*, *G. nebulanastes*, *G. nicefori*, *G. ochoai*, *G. orophylax*, *G. ovifera*, *G. ossilaginis*, *G. pacchamama*, *G. pachachacae*, *G. peruana*, *G. phalarosa*, *G. phelloderma*, *G. piperata*, *G. plumbea*, *G. pseustes*, *G. psychrophila*, *G. rebecca*, *G. riobambae*, *G. ruizi*, *G. splendens*, *G. stictopleura*, *G. testudinea*, *G. trachyceps*, and *G. zeugocystis*.

**Diagnosis.** (1) postchoanal process forming less than half posteromedial border of choana (character 16, 12→0), with the same character state coded for *Cryptobatrachus* sp. *Gastrotheca cornuta*, *G. guentheri*, *G. walkeri*, *Hemiphractus fasciatus*, and *H. helioi*, and a transformation into different character states in *G. galeata*, *G. excubitor*, and *G. marsupiata*; (2) occipital artery in a closed canal and opens into orbit (character 38, 12→3), with a transformation into a different character state in *G. excubitor*, *G. griswoldi*, *G. marsupiata*, *G. pseustes*, and *G. testudinea*. All unambiguous transformations are listed in Appendix 5.

**Distribution.** Highlands of Argentina, Bolivia, Colombia, Ecuador, Panama, Peru and Venezuela.

**Comments.** *Gastrotheca aguaruna*, *G. aratia* and *G. lojana* are assigned to this clade following the phylogenetic tree of Duellman *et al.* (2014). Although *G. abdita*, *G. cariniceps*, *G. dysprositata*, *G. espeletia*, *G. ossilaginis*, *G. pachachacae*, *G. phalarosa*, and *G. phelloderma* are not included in our analysis, they are tentatively assigned to this clade based on overall morphological similarity to other species of this clade and biogeographic affinities (all are high Andean species). As explained in Materials and methods (see also Duellman & De la Riva 1999) the taxonomy of Bolivian species *G. lauzuricae*, *G. piperata*, and *G. splendens* needs to be thoroughly revised.

### ***Gastrotheca microdiscus* species group**

**Immediately more inclusive taxon.** An unnamed clade containing the *Gastrotheca marsupiata* species group and the *Gastrotheca microdiscus* species group.

**Sister taxon.** *Gastrotheca marsupiata* species group.

**Content** (4 species): *Gastrotheca albolineata*, *G. ernestoi*, *G. fulvorufa*, *G. microdiscus*.

**Diagnosis.** Unambiguous transformations are restricted to nucleotides (Appendix 5).

**Distribution.** Atlantic forest biome, from the State of Espírito Santo in the north to the State of Santa Catarina in the south.

## Genus: *Stefania* Rivero, 1968

**Immediately more inclusive taxon.** Hemiphractinae Peters, 1862.

**Sister taxon.** An unnamed clade containing *Gastrotheca* Fitzinger, 1843, *Fritziana* Mello-Leitão, 1937, and *Hemiphractus* Wagler, 1828.

**Content** (19 species): *Stefania ackawaio* MacCulloch and Lathrop, 2002, *S. ayangannae* MacCulloch and Lathrop, 2002, *S. breweri* Barrio-Amorós and Fuentes-Ramos, 2003, *S. coxi* MacCulloch and Lathrop, 2002, *S. evansi* (Boulenger, 1904), *S. ginesi* Rivero, 1968, *S. goini* Rivero, 1968, *S. marahuaquensis* (Rivero, 1961), *S. neblinae* Carvalho, MacCulloch, Bonora, and Vogt, 2010, *S. oculosa* Señaris, Ayarzagüena, and Gorzula, 1997, *S. percristata* Señaris, Ayarzagüena, and Gorzula, 1997, *S. riae* Duellman and Hoogmoed, 1984, *S. riveroi* Señaris, Ayarzagüena, and Gorzula, 1997, *S. roraimae* Duellman and Hoogmoed, 1984, *S. satelles* Señaris, Ayarzagüena, and Gorzula, 1997, *S. scalae* Rivero, 1970, *S. schuberti* Señaris, Ayarzagüena, and Gorzula, 1997, *S. tamacuarina* Myers and Donnelly, 1997, and *S. woodleyi* Rivero, 1968.

**Type species.** *Hyla evansi* Boulenger, 1904.

**Diagnosis.** Unambiguous transformations are restricted to nucleotides (Appendix 5), inasmuch as the majority of phenotypic characters were coded only for *Stefania scalae*.

**Characterization.** (1) two pairs of bell-shaped gills derived from branchial arches I and II covering most of the embryo; (2) females carrying exposed eggs on their backs; (3) direct development; (4) embryos with reduced oral larval features; (5) males without vocal sacs or apertures, but at least some species vocalizing; (6) superficial mandibular musculature Types A and B of Tyler and Duellman (1995); (7) sphenethmoid well ossified anteriorly; (8) zygomatic ramus of the squamosal close to or in contact with the maxilla (del Pino & Escobar 1981; Señaris *et al.* "1997" [1996]; Duellman & Hoogmoed 1984; Wassersug & Duellman 1984; Tyler & Duellman 1995; Mendelson *et al.* 2000; Sinsch & Juraske 2006).

**Distribution.** Restricted to the rainforests and shrub areas of the uplands and highlands of the Guiana Shield in Brazil, Guyana, and Venezuela.

**Comments.** Rivero (1970) defined two species groups. Species of the *Stefania evansi* group have a head "as broad as long or longer than broad" while the head in species of the *S. goini* group is "much broader than long". Not surprisingly, giving the A and not-A definitions of these groups, Duellman & Hoogmoed (1984) recovered a monophyletic *S. goini* group, which was nested within a paraphyletic *S. evansi* group. Subsequent studies continued to recognize the two nominal groups and assigned species accordingly (e.g., Señaris *et al.* 1997 "1996"; MacCulloch & Lathrop 2002; Barrio-Amorós & Fuentes-Ramos 2003). Wiens *et al.* (2007) included DNA sequences of five species, three of the *S. goini* group (*S. coxi*, *S. ginesi*, and *S. schuberti*) and two of the *S. evansi* group (*S. evansi* and *S. scalae*) and, counter to the results of Duellman & Hoogmoed (1984), retrieved a monophyletic *S. evansi* group nested within a paraphyletic *S. goini* group. Kok *et al.* (2012) analyzed DNA sequences of the mitochondrial genes 16S and ND1 of 45 specimens of *Stefania* representing 11 nominal species and some putative new species. Their topology (a MrBayes majority-rule consensus tree) indicated that neither the *S. goini* nor the *S. evansi* groups are monophyletic. According to our results, the *Stefania evansi* and *S. goini* species groups are non-monophyletic. As reported by Kok *et al.* (2012), the samples *Stefania* aff. *evansi* and *Stefania* sp. correspond to undescribed species.

## Genus: *Hemiphractus* Wagler, 1828

**Immediately more inclusive taxon.** An unnamed clade containing *Gastrotheca* Fitzinger, 1843 and *Hemiphractus* Wagler, 1828.

**Sister taxon.** *Fritziana* Mello-Leitão, 1937.

**Content** (6 species): *Hemiphractus bubalus* (Jiménez de la Espada, 1870), *H. fasciatus* Peters, 1862, *H. helioi* Sheil and Mendelson, 2001, *H. johnsoni* (Noble, 1917), *H. proboscideus* (Jiménez de la Espada, 1870), and *H. scutatus* (Spix, 1824).

**Type species.** *Rana scutata* Spix, 1824.

**Diagnosis.** (1) Alae narrow laterally (character 2, 0→1), with the same character state coded for *Gastrotheca galeata*, *G. griswoldi*, and a reversal in *Hemiphractus scutatus*; (2) ventral crests of alae present (character 3, 0→

>1), with the same character state coded for *Cryptobatrachus*, *G. dendronastes*, *G. galeata*, *G. guentheri*, *G. microdiscus*, *G. plumbea*, and *G. riobambae*; (3) ventral ridge of neopalatine present, with rounded or sharp serrations (character 10, 1→2), with the same character state coded for *G. argenteovirens*, *G. galeata*, and *G. ovifera*; (4) posteromedial process of vomer serrated (character 12, 1→2); (5) prechoanal process forming less than half anteromedial border of choana (character 15, 2→1), with the same character state coded for *C. fuhrmanni*, *G. guentheri*, *G. marsupiata*, and *G. pseustes*, a reversal in *H. proboscideus*, and a transformation into a different character state in *H. bubalus*; (6) bifurcation of pre- and postchoanal processes posterior to level of dentigerous process (character 18, 0→2), with the same character state coded for *G. marsupiata*; (7) postorbital process long (character 20, 1→2), with the same character state coded for *G. guentheri* and *G. megacephala*; (8) broad overlap of articulation of maxilla and premaxilla from anterior view (character 21, 0→1); (9) pterygoid process of maxilla present (character 22, 0→1), with the same character state coded for *G. guentheri* and *G. megacephala*; (10) pars temporalis present (character 24, 0→1); (11) lingual process of premaxilla present (character 25, 0→1); (12) occipital crest present (character 29, 0→1), with the same character state coded for *G. dendronastes*, *G. galeata*, and *G. ovifera*; (13) squamosal crest present (character 30, 0→1), with the same character state coded for *G. argenteovirens*, *G. cornuta*, *G. dendronastes*, *G. galeata*, *G. guentheri*, and *G. ovifera*; (14) nasal crest present (character 31, 0→1), with the same character state coded for *G. galeata* and *G. guentheri* and a reversal in *H. scutatus*; (15) postorbital flange plate-like, dorsal to crista parotica (character 37, 0→2), with the same character state coded for *G. galeata* and *G. megacephala*; (16) *mm. intermandibularis* and *submentalis* separated (character 48, 1→0), with the same character state coded for *G. cornuta* and *G. guentheri*; (17) aponeurosis of *m. intermandibularis* large (character 50, 2→0), with the same character state coded for *C. sp.*, *G. guentheri*, and *G. testudinea*. All unambiguous transformations are listed in Appendix 5.

**Characterization.** (1) two pairs of bell-shaped gills (fused in *Hemiphractus fasciatus*) derived from branchial arches I and II covering most of the embryo; (2) females carrying exposed eggs on their backs; (3) direct development; (4) embryos without oral larval features; (5) males without vocal sacs or apertures and apparently not vocalizing; (6) superficial mandibular musculature Type C of Tyler & Duellman (1995) (*i.e.*, the *m. submentalis* is small, the *m. intermandibularis* is a single, undifferentiated sheet bearing a large, median aponeurosis, the *m. interhyoideus* does not extend posteriorly beyond the mandibles); (7) cultriform process of parasphenoid becoming distinctly narrow anteriorly; (8) presence of a zygomatic ridge; (9) presence of a supraorbital ridge and odontoids on the dentary and angulosplenial; (10) presence of prominent, triangular, paraoccipital processes; (11) presence of a fleshy proboscis (Trueb 1974; del Pino & Escobar 1981; Wassersug & Duellman 1984; Tyler & Duellman 1995; Mendelson *et al.* 2000; Sheil *et al.* 2001).

**Distribution.** Lowland and montane rainforests of Panama, Pacific slopes of Colombia and northwestern Ecuador, and upper Amazon Basin and Amazonian slopes of the Andes in Bolivia, Brazil, Colombia, Ecuador, and Peru.

**Comments.** Detailed taxonomic reviews can be found in Trueb (1974) and Sheil *et al.* (2001). The monophyly of the genus has been recovered on the basis of morphology and DNA sequences (Mendelson *et al.* 2000; Sheil *et al.* 2001; Wiens *et al.* 2007). However, Mendelson *et al.* (2000) found *Hemiphractus* to be nested within *Gastrotheca* but, as noted above, this arrangement has not been corroborated by DNA sequences (*e.g.*, Faivovich *et al.* 2005; Wiens *et al.* 2005, 2007; Padial *et al.* 2014). Sheil *et al.* (2001) recovered two main clades, each with three species: ((*H. helioi* (*H. fasciatus*, *H. scutatus*)) (*H. johnsoni* (*H. proboscideus*, *H. bubalus*))). Wiens *et al.* (2007) included sequences of four species and obtained a partially different topology with *H. scutatus* sister of the other three species: (((*H. proboscideus*, *H. bubalus*) *H. helioi*) *H. scutatus*).

Our topology is almost identical to that obtained by Sheil *et al.* (2001) on the basis of phenotypic characters except that in our topology *Hemiphractus helioi* is sister of all other species in the genus instead of sister of *H. fasciatus* + *H. scutatus*. Our results indicate that the samples identified as *H. fasciatus* and *H. scutatus* could correspond, in each case, to more than one species. In the case of *H. fasciatus*, we found three divergent mitochondrial lineages, a result already advanced by Crawford *et al.* (2013). The available name *H. panamensis* (Stejneger, 1917), currently placed under the synonymy of *H. fasciatus* by Trueb (1974), could correspond to one of those lineages. For *H. scutatus*, we found two divergent lineages. *Hemiphractus scutatus* currently contains the synonyms *H. boulengeri* Miranda-Ribeiro, 1926 and *H. divaricatus* Cope, 1868, considered as synonyms by Myers & Carvalho (1945) and Trueb (1974), respectively.

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## Author contributions

SC-F and DRF designed the study, SC-F, JMP, IDIR, JPPJr, FJMR-R, HRdS, and EM-M generated the data, SC-F and JMP analyzed the data, SC-F, JMP, and DRF wrote the manuscript, IDIR, JPPJr, FJMR-R, HRdS, and EM-M read and improved the manuscript.

## Authors' note

While this paper was in press, we examined the gills of the embryos of *Gastrotheca megacephala* (UESC 13685) and *G. pulchra* (UESC 8120) of the *Gastrotheca fissipes* species group. The embryos of both species were in state 46 of Gosner (1960) and have gill stalks not fused (character 44 -1) and bell-shaped gills fused distally (character 45-1). Our observation further supports the presence of two fused pairs of bell-shaped gills derived from branchial arches I and II (character 45, 1→0) as a synapomorphy for *Gastrotheca*.

**APPENDIX 1.** Terminals, voucher codes (only included for ingroup taxa), and GenBank accession numbers of DNA sequences used in this study. Acronyms follow Frost (2014) except for CBG (Centro de Biodiversidad y Genética, Cochabamba), CHP (Círculo Herpetológico de Panamá), CORBIDI (Centro de Ornitología y Biodiversidad), CTMZ (tissue collection at MZUSP), DCC (David C. Cannatella field series), EVACC (El Valle Amphibian Conservation Center), JDL (John D. Lynch field series), JLG (João Luis Gasparini field series), JMP (José M. Padial field series), LM (Linda Maxson field series), MNCN/ADN (tissue collection at MNCN), MJH (Martin J. Henzl field series), MTR (Miguel T. Rodrigues field series), MVUP (Museo de Vertebrados de la Universidad de Panamá), VUB (unknown, from Kok *et al.* 2012), Vz (unknown, from Wiens *et al.* 2007).

| Taxon*   | tRNA Phe | 12S         | tRNA Val    | 16S (1)     | 16S (2)     | tRNA Leu    | ND1         | COI      | cytb      | 28S      | C-MYC 2  |
|--|----------|-------------|-------------|-------------|-------------|-------------|-------------|----------|-----------|----------|----------|
| <i>Acris crepitans</i>                                   | —        | EF566970    | EF566970    | EF566970    | AY819491    | AY819491    | AY819491    | —        | AY843782  | AY844194 | AY819194 |
| <i>Adelophryne patamona</i>                              | —        | EU186679    | EU186679    | EU186679    | GQ345247    | GQ345247    | GQ345247    | —        | GQ345201  | GQ345136 | GQ345149 |
| <i>Adenomera andreae</i>                                 | —        | HQ290944    | HQ290944    | HQ290944    | HQ290944    | HQ290944    | HQ290944    | KC520689 | JQ321766  | —        | —        |
| <i>Adenomera hylaedactyla</i>                            | —        | KC603939    | KC603939    | KC603939    | —           | —           | —           | KC603995 | KC603967  | —        | —        |
| <i>Agalychnis amnae</i>                                  | —        | GQ366221    | GQ366221    | GQ366221    | GQ366291    | GQ366291    | GQ366291    | —        | GQ365913  | —        | EF174320 |
| <i>Agalychnis callidryas</i>                             | —        | DQ283423    | DQ283423    | DQ283423    | FJ489334    | FJ489334    | FJ489334    | FJ766570 | —         | —        | EF174321 |
| <i>Allobates femoralis</i>                               | —        | AY364543    | AY364543    | AY364543    | HQ290951    | HQ290951    | HQ290951    | DQ502811 | HQ290531  | DQ283465 | —        |
| <i>Allophryne ruthveni</i>                               | —        | AY843564    | AY843564    | AY843564    | AY819458    | AY819458    | AY819458    | —        | AY843786  | —        | AY819162 |
| <i>Alsodes neuquensis</i>                                | —        | AY843565    | AY843565    | AY843565    | JX204017    | JX204017    | JX204017    | JX203891 | AY843787  | AY844197 | —        |
| <i>Amazophrynella minuta</i>                             | —        | AY843582    | AY843582    | AY843582    | AY819462    | AY819462    | AY819462    | DQ502828 | AY843804  | —        | AY819166 |
| <i>Amietophrynus brauni</i>                              | —        | FJ882822    | FJ882822    | FJ882822    | FJ882822    | FJ882822    | —           | —        | —         | DQ283726 | —        |
| <i>Atelognathus patagonicus</i>                          | —        | AY843571    | AY843571    | AY843571    | —           | —           | —           | JX203909 | AY843793  | AY844203 | —        |
| <i>Barycholos pulcher</i>                                | —        | EU186727    | —           | EU186709    | —           | —           | —           | —        | —         | —        | —        |
| <i>Barycholos ternetzi</i>                               | —        | —           | —           | DQ283094    | —           | —           | —           | —        | —         | DQ283496 | —        |
| <i>Batrachyla leptopus</i>                               | —        | AY843572    | AY843572    | AY843572    | —           | —           | —           | —        | AY843794  | AY844204 | —        |
| <i>Batrachyla taeniata</i>                               | —        | AY578817    | —           | DQ864550    | —           | —           | —           | —        | KC603962  | —        | —        |
| <i>Brachycephalus alipioi</i>                            | —        | HQ435676    | —           | HQ435690    | —           | —           | —           | —        | HQ435703  | —        | —        |
| <i>Brachycephalus ephippium</i>                          | —        | DQ283091    | DQ283091    | DQ283091    | GQ345243    | GQ345243    | GQ345243    | —        | HQ435706  | DQ283494 | GQ345145 |
| <i>Bryophryne cophites</i>                               | —        | EF493537    | EF493537    | EF493537    | —           | —           | —           | —        | —         | —        | —        |
| <i>Bufo japonicus</i>                                    | AB303363 | AB303363    | AB303363    | AB303363    | AB303363    | AB303363    | AB303363    | AB303363 | AB303363  | —        | —        |
| <i>Calyptocephalella gayi</i>                            | —        | DQ283439    | DQ283439    | DQ283439    | AY819471    | AY819471    | AY819471    | JX298374 | JX298415  | DQ283748 | AY819175 |
| <i>Ceratophrys (C. cornuta, C. cranwelli, C. ornata)</i> | —        | DQ347035 C. | DQ347035 C. | FJ882777 C. | AY523774 C. | AY523774 C. | AY523774 C. | —        | L10983 C. | —        | —        |
| <i>Ceuthomantis smaragdinus</i>                          | —        | GQ345132    | GQ345132    | GQ345132    | GQ345132    | —           | GQ345251    | —        | GQ345206  | GQ345140 | GQ345154 |

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| Taxon*   | tRNA Phe | 12S      | tRNA Val | 16S (1)                | 16S (2)  | tRNA Leu  | ND1       | COI       | cytb     | 28S      | C-MYC 2  |
|--|----------|----------|----------|------------------------|----------|-----------|-----------|-----------|----------|----------|----------|
| <i>Chacophrys pierottii</i>                              | —        | DQ283328 | DQ283328 | DQ283328               | —        | —         | —         | —         | —        | —        | —        |
| <i>Colostethus pratti</i>                                | —        | HQ290969 | HQ290969 | HQ290969               | HQ290969 | HQ290969  | HQ290969  | DQ502865  | HQ290547 | DQ503011 | —        |
| <i>Craugastor augusti</i>                                | —        | AY326011 | AY326011 | AY326011               | —        | —         | —         | —         | —        | —        | —        |
| <i>Craugastor podiciferus</i>                            | —        | EF493360 | EF493360 | EF493360               | EF493360 | —         | —         | —         | GQ345197 | —        | AY211319 |
| <i>Craugastor punctariolus</i>                           | —        | DQ283168 | DQ283168 | DQ283168               | —        | —         | —         | FJ766667  | —        | DQ283558 | —        |
| <i>Craugastor ranoides</i>                               | —        | DQ283105 | —        | DQ283106               | —        | —         | —         | —         | DQ350246 | DQ283505 | AY211287 |
| <i>Craugastor rhodopis</i>                               | —        | DQ283317 | DQ283317 | DQ283317               | —        | —         | —         | —         | —        | DQ283648 | AY211315 |
| <i>Crossodactylodes</i> sp                               | —        | KC603957 | KC603957 | KC603958               | —        | —         | —         | KC603985  | KC603963 | —        | —        |
| <i>Crossodactylus schmidti</i>                           | —        | AY843579 | AY843579 | AY843579               | —        | —         | HQ290948  | DQ502738  | AY843801 | AY844210 | —        |
| <i>Cryptobatrachus boulengeri</i> LM                     | —        | —        | —        | —                      | AY819485 | AY819485  | AY819485  | —         | —        | —        | —        |
| <i>Cryptobatrachus fuhrmanni</i> JDL 14865               | —        | AY326050 | AY326050 | AY326050               | JX564861 | JX564861  | JX564861  | JX564861  | JX564861 | —        | —        |
| <i>Cryptobatrachus fuhrmanni</i> MHUA A 5160             | —        | KR559912 | KR270398 | KR270398 +<br>KR270414 | —        | —         | —         | —         | —        | —        | —        |
| <i>Cryptobatrachus remotus</i> MHNLS 18853 + MHNLS 17664 | —        | KR559914 | KR559914 | KR270400 +<br>KR270416 | KR138379 | KR138379  | KR138379  | —         | —        | —        | —        |
| <i>Cycloramphus acangatan</i>                            | —        | HQ634162 | —        | FJ685683               | —        | —         | —         | —         | FJ685663 | —        | —        |
| <i>Cycloramphus boraceiensis</i>                         | —        | DQ283097 | DQ283097 | AY162397               | —        | —         | —         | DQ502856  | DQ502588 | DQ283498 | —        |
| <i>Dendrobates auratus</i>                               | —        | DQ347026 | DQ347026 | AY364565               | —        | —         | HQ290980  | FJ766698  | AY843803 | AY844211 | —        |
| <i>Dendropsophus nanus</i>                               | —        | AY549346 | AY549346 | AY549346               | GQ366298 | GQ366298  | GQ366298  | —         | AY549399 | AY844271 | AY819208 |
| <i>Diasporus</i> aff <i>diastema</i>                     | —        | —        | —        | FJ784484               | —        | —         | —         | FJ766810  | —        | —        | —        |
| <i>Diasporus diastema</i>                                | —        | EU186682 | EU186682 | EU186682               | EU186682 | —         | —         | —         | GQ345200 | GQ345135 | GQ345148 |
| <i>Duttaphrynus melanostictus</i>                        | —        | AB331714 | AB331714 | FJ882791               | FJ882791 | NC 005794 | NC 005794 | NC 005794 | —        | DQ283658 | —        |
| <i>Edalorhina perezii</i>                                | —        | AY843585 | AY843585 | AY843585               | —        | —         | —         | —         | AY843807 | DQ283474 | —        |
| <i>Eleutherodactylus cooki</i>                           | —        | EF493539 | EF493539 | EF493539               | EF493539 | —         | —         | —         | HQ831648 | —        | —        |
| <i>Eleutherodactylus coqui</i>                           | —        | GQ345176 | GQ345176 | GQ345176               | —        | —         | —         | —         | EF637038 | —        | —        |
| <i>Eleutherodactylus marnockii</i>                       | —        | DQ283102 | —        | DQ283101               | —        | —         | —         | —         | —        | DQ283502 | —        |
| <i>Eleutherodactylus nitidus</i>                         | —        | EU186730 | —        | DQ283316               | —        | —         | —         | —         | —        | DQ283647 | —        |
| <i>Eleutherodactylus planirostris</i>                    | —        | DQ283107 | DQ283107 | DQ283107               | GQ345246 | GQ345246  | GQ345246  | —         | HQ831615 | DQ283629 | —        |
| <i>Eleutherodactylus thorectes</i>                       | —        | EF493384 | EF493384 | EF493384               | EF493384 | —         | —         | —         | HQ831649 | —        | —        |
| <i>Eleutherodactylus tonyi</i>                           | —        | EF493790 | —        | EF493602               | —        | —         | —         | —         | HQ831643 | —        | —        |

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| Taxon*   | tRNA Phe  | 12S       | tRNA Val  | 16S (1)                | 16S (2)   | tRNA Leu  | ND1       | COI       | cytb      | 28S      | C-MYC 2  |
|--|-----------|-----------|-----------|------------------------|-----------|-----------|-----------|-----------|-----------|----------|----------|
| <i>Engystomops petersi</i>   | —         | FJ668190  | FJ668190  | FJ668190               | —         | —         | —         | —         | —         | —        | —        |
| <i>Engystomops pustulosus</i>  | —         | DQ337242  | DQ337242  | DQ337248               | —         | —         | —         | FJ766700  | —         | —        | —        |
| <i>Espadarana prosoblepon</i>  | —         | AY843574  | AY843574  | AY843574               | —         | —         | AY286065  | FJ766592  | AY843796  | AY844206 | AY819170 |
| <i>Eupsophus roseus</i>  | —         | AY843587  | AY843587  | AY843587               | JX204054  | JX204054  | JX204054  | DQ502852  | AY843808  | —        | —        |
| <i>Fejervarya limnocharis</i>  | NC 005055 | NC 005055 | NC 005055 | NC 005055              | NC 005055 | NC 005055 | NC 005055 | NC 005055 | NC 005055 | —        | —        |
| <i>Flectonotus fitzgeraldi</i> ZSM 1610<br>2006 + KU 192399            | —         | AY819355  | KR270401  | KR270401+<br>KR270417  | AY819486  | AY819486  | AY819486  | —         | —         | —        | AY819189 |
| <i>Flectonotus pygmaeus</i> MHNLS<br>17478 + KU 184958                 | —         | DQ679232  | KR270402  | KR270402+<br>KR270418  | DQ679341  | DQ679341  | DQ679341  | —         | —         | —        | —        |
| <i>Fritziana fissilis</i> MNRJ 62845                                   | —         | KR559916  | KR270403  | KR270403 +<br>KR270419 | —         | —         | —         | —         | —         | —        | —        |
| <i>Fritziana</i> aff. <i>fissilis</i> sp. 2 MNRJ<br>44622              | —         | KR559917  | KR270404  | KR270404 +<br>KR270421 | —         | —         | —         | —         | —         | —        | —        |
| <i>Fritziana</i> aff. <i>fissilis</i> sp. 3 MZSUP<br>133700            | —         | —         | —         | JN157634               | KC844943  | KC844943  | KC844943  | —         | —         | —        | —        |
| <i>Fritziana</i> aff. <i>fissilis</i> sp. 1 CFBH<br>5726 + MZUSP 13546 | —         | AY843589  | AY843589  | AY843589               | KC844944  | KC844944  | KC844944  | —         | AY843809  | AY844215 | —        |
| <i>Fritziana goeldi</i> MNRJ 34921                                     | —         | KR559918  | KR270405  | KR270405 +<br>KR270423 | —         | —         | —         | —         | —         | —        | —        |
| <i>Fritziana ohausi</i> MZUSP 139225                                   | —         | —         | —         | JN157635               | KC844945  | KC844945  | KC844945  | —         | —         | —        | —        |
| <i>Fritziana</i> sp. MNRJ 44592  | —         | —         | KR270406  | KR270406+<br>KR270424  | —         | —         | —         | —         | —         | —        | —        |
| <i>Gastrotheca albolineata</i> MNRJ<br>54401                           | —         | KR559919  | KR270407  | KR270407+<br>KR270425  | KC844949  | KC844949  | KC844949  | —         | —         | —        | —        |
| <i>Gastrotheca antoniochoai</i><br>MUSM 27944                          | —         | —         | —         | JN157622               | KC844950  | KC844950  | KC844950  | —         | —         | —        | —        |
| <i>Gastrotheca argenteovirens</i> KU<br>181168                         | —         | DQ679233  | —         | DQ679383               | DQ679342  | DQ679342  | DQ679342  | —         | —         | —        | —        |
| <i>Gastrotheca atympana</i> MHNSM<br>18692                             | —         | DQ679234  | —         | DQ679384               | DQ679343  | DQ679343  | DQ679343  | —         | —         | —        | —        |
| <i>Gastrotheca aureomaculata</i> KU<br>181194                          | —         | DQ679235  | —         | DQ679385               | DQ679344  | DQ679344  | DQ679344  | —         | —         | —        | —        |
| <i>Gastrotheca christiani</i> FML 2881                                 | DQ679236  | DQ679236  | —         | DQ679386               | DQ679345  | DQ679345  | DQ679345  | —         | —         | —        | —        |
| <i>Gastrotheca chrysosticta</i> LM 58                                  | DQ679237  | DQ679237  | —         | DQ679387               | DQ679346  | DQ679346  | DQ679346  | —         | —         | —        | —        |
| <i>Gastrotheca</i> sp. 1 IDLR 4073<br>(MNCN/ADN 566)                   | —         | —         | —         | KR270428               | —         | —         | —         | —         | KR138416  | —        | —        |

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| Taxon*  | tRNA Phe | 12S      | tRNA Val | 16S (1)               | 16S (2)  | tRNA Leu | ND1      | COI      | cytb     | 28S | C-MYC 2  |
|---|----------|----------|----------|-----------------------|----------|----------|----------|----------|----------|-----|----------|
| <i>Gastrotheca cornuta</i> USNM<br>572472 + AMNH 107251 | —        | AY843591 | AY843591 | AY843591              | DQ679347 | DQ679347 | DQ679347 | FJ766706 | AY843811 | —   | —        |
| <i>Gastrotheca dendronastes</i> KU<br>181203            | —        | DQ679239 | —        | DQ679389              | DQ679348 | DQ679348 | DQ679348 | —        | —        | —   | —        |
| <i>Gastrotheca dummi</i> ICN 10059 +<br>MHUA A 4800     | —        | DQ679240 | —        | KR270426              | DQ679349 | DQ679349 | DQ679349 | —        | —        | —   | —        |
| <i>Gastrotheca ernestoi</i> MNRJ<br>57129 + MNRJ 64000  | KR559920 | KR559920 | KR270408 | KR270408+<br>KR270427 | KC844952 | KC844952 | KC844952 | —        | —        | —   | —        |
| <i>Gastrotheca excubitor</i> KU 173171                  | DQ679241 | DQ679241 | —        | DQ679391              | DQ679350 | DQ679350 | DQ679350 | —        | —        | —   | —        |
| <i>Gastrotheca excubitor</i> MUSM<br>26280              | —        | —        | —        | JN157623              | —        | —        | —        | —        | —        | —   | —        |
| <i>Gastrotheca fissipes</i> ZUFRJ 7901                  | —        | —        | —        | —                     | JX262925 | JX262925 | JX262925 | —        | —        | —   | JX262895 |
| <i>Gastrotheca fulvorufa</i> CTMZ<br>07467              | —        | —        | —        | KC844929              | KC844954 | KC844954 | KC844954 | —        | —        | —   | —        |
| <i>Gastrotheca galeata</i> KU 181700                    | DQ679242 | DQ679242 | —        | DQ679392              | DQ679351 | DQ679351 | DQ679351 | —        | —        | —   | —        |
| <i>Gastrotheca gracilis</i> DCC 006                     | —        | DQ679243 | —        | —                     | —        | —        | —        | —        | —        | —   | —        |
| <i>Gastrotheca griswoldi</i> KU 181701                  | —        | DQ679244 | —        | —                     | DQ679352 | DQ679352 | DQ679352 | —        | —        | —   | —        |
| <i>Gastrotheca griswoldi</i> MHNSM<br>20588             | —        | AM039716 | —        | AM039648              | —        | —        | —        | —        | —        | —   | —        |
| <i>Gastrotheca guentheri</i> KU<br>173112               | —        | DQ679245 | —        | DQ679393              | DQ679353 | DQ679353 | DQ679353 | —        | —        | —   | —        |
| <i>Gastrotheca helenae</i> KU 181070                    | DQ679246 | DQ679246 | —        | DQ679394              | DQ679354 | DQ679354 | DQ679354 | —        | —        | —   | —        |
| <i>Gastrotheca lateonota</i> QCAZ<br>45113              | —        | —        | —        | KC844923              | KC844948 | KC844948 | KC844948 | —        | —        | —   | —        |
| <i>Gastrotheca</i> sp. 2 MNK 5286 +<br>CBG 1020         | —        | AY843590 | AY843590 | AY843590              | KC844955 | KC844955 | KC844955 | —        | AY843810 | —   | —        |
| <i>Gastrotheca litonedis</i> KU 202690                  | —        | DQ679247 | —        | DQ679395              | DQ679355 | DQ679355 | DQ679355 | —        | —        | —   | —        |
| <i>Gastrotheca longipes</i> USNM<br>258905              | DQ679248 | DQ679248 | —        | DQ679396              | DQ679356 | DQ679356 | DQ679356 | —        | —        | —   | —        |
| <i>Gastrotheca marsupiata</i> KU<br>214813 + KU 214814  | AY819356 | AY819356 | —        | DQ679397              | AY819487 | AY819487 | AY819487 | —        | —        | —   | AY819190 |
| <i>Gastrotheca</i> sp. 3 ZFMK 66954 +<br>MNCN 43052     | —        | —        | —        | KR270429              | —        | —        | —        | —        | KR138417 | —   | —        |
| <i>Gastrotheca megacephala</i> JLG 90<br>+ CFBH T377    | —        | AY843592 | AY843592 | AY843592              | KC844953 | KC844953 | KC844953 | —        | —        | —   | —        |

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| Taxon*   | tRNA Phe | 12S      | tRNA Val | 16S (1)  | 16S (2)  | tRNA Leu | ND1      | COI | cytb | 28S | C-MYC 2  |
|--|----------|----------|----------|----------|----------|----------|----------|-----|------|-----|----------|
| <i>Gastrotheca microdiscus</i> CFBH T 1250 + CFBH T 3068 | —        | —        | —        | KC844932 | KC844958 | KC844958 | KC844958 | —   | —    | —   | —        |
| <i>Gastrotheca monticola</i> KU 212036                   | AY819357 | AY819357 | —        | DQ679398 | AY819488 | AY819488 | AY819488 | —   | —    | —   | AY819191 |
| <i>Gastrotheca nebulanastes</i> MUSM 27943 + MCZ 265218  | —        | —        | —        | JN157625 | KC844959 | KC844959 | KC844959 | —   | —    | —   | —        |
| <i>Gastrotheca nicefori</i> KU 181071                    | —        | DQ679249 | —        | DQ679399 | DQ679357 | DQ679357 | DQ679357 | —   | —    | —   | —        |
| <i>Gastrotheca nicefori</i> MHUA A 5716                  | —        | KR559921 | KR270409 | KR270409 | KR138380 | KR138380 | KR138380 | —   | —    | —   | —        |
| <i>Gastrotheca ochoai</i> KU 173499                      | —        | DQ679250 | —        | DQ679400 | DQ679358 | DQ679358 | DQ679358 | —   | —    | —   | —        |
| <i>Gastrotheca orophylax</i> KU 178568                   | DQ679251 | DQ679251 | —        | DQ679401 | DQ679359 | DQ679359 | DQ679359 | —   | —    | —   | —        |
| <i>Gastrotheca ovifera</i> KU 185758                     | —        | DQ679252 | —        | —        | DQ679360 | DQ679360 | DQ679360 | —   | —    | —   | —        |
| <i>Gastrotheca pachachacae</i> MUSM 28492                | —        | —        | —        | JN157620 | —        | —        | —        | —   | —    | —   | —        |
| <i>Gastrotheca peruana</i> KU 181740                     | DQ679253 | DQ679253 | —        | DQ679402 | DQ679361 | DQ679361 | DQ679361 | —   | —    | —   | —        |
| <i>Gastrotheca plumbea</i> KU 178499                     | DQ679254 | DQ679254 | —        | DQ679403 | DQ679362 | DQ679362 | DQ679362 | —   | —    | —   | —        |
| <i>Gastrotheca prasina</i> MZUSP 147060                  | —        | JX262891 | —        | —        | JX262922 | JX262922 | JX262922 | —   | —    | —   | JX262899 |
| <i>Gastrotheca pseustes</i> QCAZ 42862 + TNHC 62492      | —        | AY326051 | AY326051 | AY326051 | KC844962 | KC844962 | KC844962 | —   | —    | —   | —        |
| <i>Gastrotheca psychrophila</i> KU 142634                | DQ679255 | DQ679255 | —        | DQ679404 | DQ679363 | DQ679363 | DQ679363 | —   | —    | —   | —        |
| <i>Gastrotheca pulchra</i> MTR 16228                     | —        | JX262894 | —        | —        | —        | —        | —        | —   | —    | —   | JX262898 |
| <i>Gastrotheca rebecca</i> CORBIDI 08006                 | —        | —        | —        | KC844937 | KC844963 | KC844963 | KC844963 | —   | —    | —   | —        |
| <i>Gastrotheca recava</i> MZUSP 147044                   | —        | JX262890 | —        | —        | JX262921 | JX262921 | JX262921 | —   | —    | —   | JX262903 |
| <i>Gastrotheca riobambae</i> KU 178468                   | —        | DQ679256 | —        | DQ679405 | DQ679364 | DQ679364 | DQ679364 | —   | —    | —   | —        |
| <i>Gastrotheca riobambae</i> UIMNH 94580                 | —        | U39974   | —        | U39976   | —        | —        | —        | —   | —    | —   | —        |
| <i>Gastrotheca ruizi</i> KU 200002                       | —        | DQ679257 | —        | DQ679406 | DQ679365 | DQ679365 | DQ679365 | —   | —    | —   | —        |
| <i>Gastrotheca</i> sp. A QCAZ 22635                      | —        | —        | —        | KC844935 | KC844961 | KC844961 | KC844961 | —   | —    | —   | —        |
| <i>Gastrotheca</i> sp. B QCAZ 21105                      | —        | —        | —        | KC844939 | KC844965 | KC844965 | KC844965 | —   | —    | —   | —        |
| <i>Gastrotheca</i> sp. C QCAZ 47299                      | —        | —        | —        | KC844934 | KC844960 | KC844960 | KC844960 | —   | —    | —   | —        |

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| Taxon*   | tRNA Phe | 12S      | tRNA Val | 16S (1)               | 16S (2)  | tRNA Leu | ND1      | COI      | cytb     | 28S      | C-MYC 2  |
|--|----------|----------|----------|-----------------------|----------|----------|----------|----------|----------|----------|----------|
| <i>Gastrotheca</i> sp. D QCAZ 42725                                | —        | —        | —        | KC844938              | KC844964 | KC844964 | KC844964 | —        | —        | —        | —        |
| <i>Gastrotheca</i> sp. E QCAZ 21213                                | —        | —        | —        | KC844922              | KC844947 | KC844947 | KC844947 | —        | —        | —        | —        |
| <i>Gastrotheca stictopleura</i> MTD 45230                          | DQ679258 | DQ679258 | —        | DQ679407              | DQ679366 | DQ679366 | DQ679366 | —        | —        | —        | —        |
| <i>Gastrotheca testudinea</i> QCAZ 16444 + CBG 774                 | —        | —        | —        | KR270430              | KC844966 | KC844966 | KC844966 | —        | KR559927 | —        | —        |
| <i>Gastrotheca trachyceps</i> KU 181189                            | DQ679259 | DQ679259 | —        | DQ679408              | DQ679367 | DQ679367 | DQ679367 | —        | —        | —        | —        |
| <i>Gastrotheca walkeri</i> Vz 89–96                                | —        | DQ679260 | —        | DQ679409              | DQ679368 | DQ679368 | DQ679368 | —        | —        | —        | —        |
| <i>Gastrotheca weinlandii</i> KU 143105                            | DQ679261 | DQ679261 | —        | DQ679410              | DQ679369 | DQ679369 | DQ679369 | —        | —        | —        | —        |
| <i>Gastrotheca zeugocystis</i> MHNSM 18675                         | —        | DQ679262 | —        | DQ679411              | —        | —        | —        | —        | —        | —        | —        |
| <i>Haddadus binotatus</i>  | —        | EF493361 | EF493361 | EF493361              | EF493361 | —        | —        | —        | GQ345198 | DQ283493 | GQ345147 |
| <i>Heleophryne purcelli</i>  | —        | AY843593 | AY843593 | AY843593              | —        | —        | AY948755 | —        | AY843812 | AY844216 | —        |
| <i>Hemiphractus bubalus</i> KU 143107 + KU 178588                  | —        | DQ679263 | —        | DQ679412              | DQ679370 | DQ679370 | DQ679370 | —        | —        | GQ345134 | —        |
| <i>Hemiphractus fasciatus</i> MVUP 1927                            | —        | —        | —        | FJ784476              | —        | —        | —        | FJ766707 | —        | —        | —        |
| <i>Hemiphractus fasciatus</i> sp1 CHP 6397 + EVACC 207 + EVACC 065 | —        | —        | —        | KC014933              | KC844967 | KC844967 | KC844967 | KC014710 | —        | —        | —        |
| <i>Hemiphractus fasciatus</i> sp2 EVACC 061 + CHP 6670             | —        | —        | —        | KC129342              | KC844968 | KC844968 | KC844968 | KC014706 | —        | —        | —        |
| <i>Hemiphractus helioi</i> MHNCP 9063 + MJH 3689                   | —        | AY843594 | AY843594 | AY843594              | —        | —        | —        | —        | AY843813 | —        | —        |
| <i>Hemiphractus proboscideus</i> KU 217513                         | AY819358 | AY819358 | —        | DQ679413              | AY819489 | AY819489 | AY819489 | —        | —        | —        | AY819192 |
| <i>Hemiphractus scutatus</i> JMP 2150 (MNCN/ADN 46913)             | —        | KR559923 | KR270411 | KR270411+<br>KR270432 | —        | —        | —        | KR559926 | —        | —        | —        |
| <i>Hemiphractus scutatus</i> USNM 317196                           | —        | DQ679264 | —        | DQ679414              | DQ679371 | DQ679371 | DQ679371 | —        | —        | —        | —        |
| <i>Holoaden bradei</i>   | —        | EF493378 | —        | EF493366              | EF493366 | —        | —        | —        | —        | —        | —        |
| <i>Holoaden luederwaldti</i>                                       | —        | EU186728 | —        | EU186710              | —        | —        | —        | —        | —        | —        | —        |
| <i>Hydrolaetare caparu</i>   | —        | KC603953 | KC603953 | KC603954              | —        | —        | —        | KC603988 | KC603975 | —        | —        |
| <i>Hyla arenicolor</i>   | —        | EF566960 | EF566960 | EF566960              | AY819494 | AY819494 | AY819494 | —        | AY843824 | —        | AY819197 |

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| Taxon*                               | tRNA Phe | 12S                    | tRNA Val | 16S (1)                | 16S (2)  | tRNA Leu | ND1      | COI      | cytb     | 28S      | C-MYC 2  |
|--------------------------------------|----------|------------------------|----------|------------------------|----------|----------|----------|----------|----------|----------|----------|
| <i>Hyla chinensis</i>                | —        | AY458593               | AY458593 | AY458593               | AY458593 | AY458593 | AY458593 | AY458593 | AY458593 | —        | DQ055761 |
| <i>Hyla cinerea</i>                  | —        | AY680271               | AY680271 | AY680271               | AY819498 | AY819498 | AY819498 | FJ226785 | AY843846 | AY844241 | AY819201 |
| <i>Hylodes phyllodes</i>             | —        | DQ283096               | DQ283096 | DQ502171               | —        | —        | —        | DQ502873 | DQ502606 | DQ503009 | —        |
| <i>Hylorina sylvatica</i>            | —        | JX204222               | JX204222 | JX204222               | —        | —        | —        | —        | —        | —        | —        |
| <i>Hyloxalus chlorocraspedus</i>     | —        | DQ502080               | DQ502080 | DQ502080               | —        | —        | —        | DQ502800 | DQ502511 | DQ502975 | —        |
| <i>Hypodactylus brunneus</i>         | —        | EF493357               | EF493357 | EF493357               | GQ345248 | GQ345248 | GQ345248 | —        | GQ345203 | GQ345138 | GQ345151 |
| <i>Hypodactylus dolops</i>           | —        | EF493394               | EF493394 | EF493394               | EF493394 | —        | —        | —        | —        | —        | —        |
| <i>Hypsiboas boans</i>               | —        | AY843610               | AY843610 | AY843610               | AY819496 | AY819496 | AY819496 | —        | AY843835 | AY844231 | AY819199 |
| <i>Hypsiboas lanciformis</i>         | —        | AY843636               | AY843636 | AY843636               | AY819543 | AY819543 | AY819543 | —        | AY843870 | AY844258 | —        |
| <i>Insuetophrynus acarpicus</i>      | —        | JX204223               | JX204223 | JX204223               | —        | —        | —        | JX203938 | AY691185 | —        | —        |
| <i>Ischnocnema guentheri</i>         | —        | EF493533               | EF493533 | EF493533               | EF493533 | —        | —        | —        | GQ345196 | —        | —        |
| <i>Ischnocnema juipoca</i>           | —        | DQ283093               | DQ283093 | DQ283093               | —        | —        | —        | —        | —        | DQ283495 | —        |
| <i>Lepidobatrachus laevis</i>        | —        | DQ283152               | DQ283152 | DQ283152               | AY819475 | AY819475 | AY819475 | —        | —        | DQ283543 | AY819179 |
| <i>Leptodactylus melanonotus</i>     | —        | AY943224 +<br>FJ882762 | FJ882762 | AY943224 +<br>FJ882762 | —        | —        | AY948760 | —        | —        | —        | AY337266 |
| <i>Leptodactylus latrans</i>         | —        | AY843688               | AY843688 | AY843688               | —        | —        | —        | —        | AY843934 | AY844302 | —        |
| <i>Limnodynastes salmini</i>         | —        | AY326071               | AY326071 | AY326071               | —        | —        | —        | —        | —        | —        | —        |
| <i>Limnomedusa macroglossa</i>       | —        | AY843689               | AY843689 | AY843689               | —        | —        | —        | —        | AY843935 | —        | —        |
| <i>Lithodytes lineatus</i>           | —        | AY326012               | AY326012 | AY326012               | HQ290949 | HQ290949 | HQ290949 | KC604003 | JQ321833 | AY844303 | —        |
| <i>Litoria caerulea</i>              | —        | AY326038               | AY326038 | AY326038               | AY819531 | AY819531 | AY819531 | AY883980 | AY843938 | —        | AY819234 |
| <i>Litoria infrafrenata</i>          | —        | AY843694               | AY843694 | AY843694               | GQ366302 | GQ366302 | GQ366302 | FJ952337 | AY843940 | AY844304 | —        |
| <i>Lynchiurus nebulanastes</i>       | —        | EU186704               | EU186704 | EU186704               | —        | —        | —        | —        | —        | —        | AY819320 |
| <i>Lynchiurus parkeri</i>            | —        | EU186705               | EU186705 | EU186705               | —        | —        | —        | —        | —        | —        | —        |
| <i>Macrogenioglottus alipioi</i>     | —        | KC593360               | KC593360 | KC593360               | KC593353 | KC593353 | KC593353 | —        | FJ685665 | —        | —        |
| <i>Mannophryne trinitatis</i>        | —        | EU342504               | EU342504 | DQ502131               | —        | —        | —        | DQ502838 | DQ502562 | —        | —        |
| <i>Megaelosia goeldii</i>            | —        | DQ283072               | DQ283072 | DQ283072               | —        | —        | —        | DQ502839 | DQ502563 | —        | —        |
| <i>Melanophryniscus klappenbachi</i> | —        | AY843699               | AY843699 | AY843699               | —        | —        | —        | DQ502739 | AY843944 | AY844306 | —        |
| <i>Myersiophyla kanaima</i>          | —        | AY843634               | AY843634 | AY843634               | GQ366307 | GQ366307 | GQ366307 | —        | AY843868 | —        | —        |
| <i>Noblella lochites</i>             | —        | EU186699               | EU186699 | EU186699               | —        | —        | —        | —        | —        | —        | —        |
| <i>Noblella</i> sp. MTD 45180        | —        | AM039714               | —        | AM039646               | —        | —        | —        | —        | —        | —        | —        |

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| Taxon*                             | tRNA Phe | 12S      | tRNA Val | 16S (1)                | 16S (2)  | tRNA Leu | ND1      | COI      | cytb     | 28S      | C-MYC 2  |
|------------------------------------|----------|----------|----------|------------------------|----------|----------|----------|----------|----------|----------|----------|
| <i>Nymphargus bejaranoi</i>        | —        | AY843576 | AY843576 | AY843576               | —        | —        | —        | —        | AY843798 | AY844208 | EU663314 |
| <i>Odontophrynus achalensis</i>    | —        | DQ283248 | DQ283248 | DQ283248               | —        | —        | —        | —        | —        | DQ283611 | —        |
| <i>Oreobates cruralis</i>          | —        | EU186666 | EU186666 | EU186666               | EU186666 | —        | —        | —        | —        | —        | —        |
| <i>Oreobates saxatilis</i>         | —        | JF809931 | —        | JF809962               | —        | —        | —        | —        | —        | —        | —        |
| <i>Paratelmatobius cardosoi</i>    | —        | EU224404 | EU224404 | EU224404               | —        | —        | —        | —        | —        | —        | —        |
| <i>Phrynopus auriculatus</i>       | —        | EF493708 | EF493708 | EF493708               | —        | —        | —        | —        | —        | —        | —        |
| <i>Phrynopus bracki</i>            | —        | EF493709 | EF493709 | EF493709               | EF493709 | —        | —        | —        | GQ345202 | GQ345137 | GQ345150 |
| <i>Phyllodytes luteolus</i>        | —        | AY843721 | AY843721 | AY843721               | GQ366314 | GQ366314 | GQ366314 | —        | AY843966 | AY844324 | —        |
| <i>Physalaemus cuvieri</i>         | —        | AY843729 | AY843729 | AY843729               | JX204060 | JX204060 | JX204060 | —        | AY843975 | AY844330 | AY819181 |
| <i>Physalaemus gracilis</i>        | AY943229 | AY943229 | —        | AY943242               | AY943242 | —        | —        | —        | —        | DQ283728 | —        |
| <i>Phyzelaphryne miriamae</i>      | —        | EU186689 | EU186689 | EU186689               | EU186689 | —        | —        | —        | —        | —        | —        |
| <i>Pleurodema brachyops</i>        | —        | AY843733 | AY843733 | AY843733               | —        | —        | —        | —        | AY843979 | —        | —        |
| <i>Pleurodema diplolister</i>      | —        | JQ937187 | JQ937187 | JQ937187               | —        | —        | —        | KC603986 | KC603981 | —        | —        |
| <i>Pristimantis cruentus</i>       | —        | EF493697 | EF493697 | EF493697 +<br>FJ784557 | FJ882747 | FJ882747 | FJ882747 | FJ766786 | —        | —        | —        |
| <i>Pristimantis curtipes</i>       | —        | EF493513 | EF493513 | EF493513               | AY819473 | AY819473 | AY819473 | —        | —        | —        | AY819177 |
| <i>Pristimantis gaigeae</i>        | —        | —        | —        | FJ784490               | —        | —        | —        | FJ766792 | —        | —        | AY211290 |
| <i>Pristimantis ridens</i>         | —        | EF493355 | EF493355 | EF493355               | EF493355 | —        | —        | FJ766808 | —        | —        | AY211306 |
| <i>Pristimantis simonsii</i>       | —        | EU186665 | EU186665 | EU186665               | EU186665 | —        | —        | —        | —        | —        | AY819321 |
| <i>Proceratophrys avelinoi</i>     | —        | DQ283038 | DQ283038 | DQ283038               | —        | —        | —        | —        | FJ685671 | —        | —        |
| <i>Pseudis minutus</i>             | —        | —        | AY843739 | —                      | GQ366339 | GQ366339 | GQ366339 | —        | AY843985 | AY844336 | —        |
| <i>Pseudopaludicola falcipes</i>   | —        | AY843741 | AY843741 | AY843741               | —        | —        | —        | KC520684 | KC593350 | —        | —        |
| <i>Psychrophrynella guillei</i>    | —        | AY843720 | AY843720 | AY843720               | —        | —        | —        | —        | —        | AY844323 | —        |
| <i>Psychrophrynella wettsteini</i> | —        | EU186696 | EU186696 | EU186696               | GQ345250 | GQ345250 | GQ345250 | —        | —        | GQ345139 | GQ345153 |
| <i>Rheobates palmatus</i>          | —        | EU342508 | EU342508 | EU342508               | HQ290967 | HQ290967 | HQ290967 | DQ502925 | HQ290545 | —        | —        |
| <i>Rhinella arenarum</i>           | —        | AY843573 | AY843573 | AY843573               | JX204061 | JX204061 | JX204061 | —        | AY843795 | AY844205 | —        |
| <i>Rhinoderma darwini</i>          | —        | AY364357 | —        | AY364378               | —        | —        | AY523783 | DQ502858 | DQ502589 | DQ283654 | —        |
| <i>Rupirana cardosoi</i>           | —        | KC603955 | KC603955 | KC603956               | —        | —        | —        | KC603987 | KC603964 | —        | —        |
| <i>Scinax staufferi</i>            | —        | AY843761 | AY843761 | AY843761               | GQ366340 | GQ366340 | GQ366340 | —        | AY844006 | —        | —        |
| <i>Scythrophrys sawayae</i>        | —        | EU224417 | EU224417 | EU224417               | —        | —        | —        | —        | —        | DQ283500 | —        |

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| Taxon*   | tRNA Phe | 12S      | tRNA Val | 16S (1)                | 16S (2)  | tRNA Leu | ND1                    | COI      | cytb     | 28S      | C-MYC 2  |
|--|----------|----------|----------|------------------------|----------|----------|------------------------|----------|----------|----------|----------|
| <i>Smilisca baudinii</i>   | —        | AY843762 | AY843762 | AY843762               | DQ388762 | DQ388762 | DQ388762               | —        | AY844007 | —        | DQ388738 |
| <i>Sooglossus thomasseti</i>   | —        | DQ283452 | DQ283452 | DQ283452               | —        | —        | —                      | —        | AY341742 | DQ283755 | —        |
| <i>Stefania</i> aff. <i>evansi</i> ROM 44254                                     | —        | —        | —        | JQ742195               | —        | —        | JQ742366               | —        | —        | —        | —        |
| <i>Stefania</i> <i>ayangannae</i> ROM 42906                                      | —        | —        | —        | JQ742212               | —        | —        | JQ742380               | —        | —        | —        | —        |
| <i>Stefania coxi</i> ROM 39478   | —        | DQ679265 | —        | DQ679415               | DQ679372 | DQ679372 | JQ742350 +<br>DQ679372 | —        | —        | —        | —        |
| <i>Stefania evansi</i> AMNH A 164211<br>+ ROM 39450 + ROM 39451 +<br>IRSNB 14586 | —        | AY819359 | AY843767 | AY843767               | AY819490 | AY819490 | AY819490               | —        | —        | AY844353 | AY819193 |
| <i>Stefania ginesi</i> LM 1056   | DQ679266 | DQ679266 | —        | DQ679417               | DQ679373 | DQ679373 | DQ679373               | —        | —        | —        | —        |
| <i>Stefania riae</i> VUB 3754  | —        | —        | —        | JQ742172               | —        | —        | JQ742343               | —        | —        | —        | —        |
| <i>Stefania riveroi</i> IRSNB 15703  | —        | —        | —        | JQ742177               | —        | —        | JQ742348               | —        | —        | —        | —        |
| <i>Stefania roraimae</i> ROM 42843   | —        | —        | —        | JQ742214               | —        | —        | JQ742276               | —        | —        | —        | —        |
| <i>Stefania satelles</i> IRSNB 15839   | —        | —        | —        | JQ742175               | —        | —        | JQ742346               | —        | —        | —        | —        |
| <i>Stefania scalae</i> KU 181122 +<br>MHNLS 17152                                | —        | DQ679267 | DQ679267 | KR270413 +<br>KR270434 | DQ679374 | DQ679374 | JQ742362 +<br>DQ679374 | —        | —        | —        | —        |
| <i>Stefania schuberti</i> MNHN 2002<br>692                                       | —        | AY843768 | AY843768 | AY843768               | —        | —        | —                      | —        | AY844013 | AY844354 | —        |
| <i>Stefania</i> sp. IRSNB 15853  | —        | —        | —        | JQ742181               | —        | —        | JQ742352               | —        | —        | —        | —        |
| <i>Stefania woodleyi</i> IRSNB 13799   | —        | —        | —        | JQ742185               | —        | —        | JQ742356               | —        | —        | —        | —        |
| <i>Strabomantis biporcatus</i>   | —        | EU186691 | EU186691 | EU186691               | GQ345249 | GQ345249 | GQ345249               | —        | GQ345204 | —        | GQ345152 |
| <i>Strabomantis bufoniformis</i>   | —        | DQ283165 | DQ283165 | DQ283165               | —        | —        | —                      | FJ766635 | —        | DQ283555 | —        |
| <i>Telmatobius truebae</i>   | AY819348 | AY819348 | —        | DQ679378               | AY819478 | AY819478 | AY819478               | —        | —        | —        | AY819182 |
| <i>Thoropa miliaris</i>  | —        | DQ283331 | DQ283331 | DQ283331               | —        | —        | —                      | DQ502874 | FJ685662 | —        | —        |
| <i>Trachycephalus typhonius</i>  | —        | AY549362 | AY549362 | AY549362               | GQ366341 | GQ366341 | GQ366341               | --       | EU034077 | AY844322 | AY819217 |
| <i>Uperoleia laevigata</i>   | —        | DQ283221 | DQ283221 | DQ283221               | —        | —        | —                      | —        | —        | —        | —        |
| <i>Yunganastes ashkapara</i>   | —        | FJ438807 | —        | EU192233 +<br>FJ438796 | —        | —        | —                      | —        | —        | —        | —        |
| <i>Yunganastes fraudator</i>   | —        | JF809938 | —        | FJ539065               | —        | —        | —                      | —        | —        | —        | —        |
| <i>Zachaenus parvulus</i>  | —        | KC593362 | KC593362 | KC593362               | —        | —        | —                      | —        | —        | —        | —        |

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## APPENDIX 1. (Continued)

| Taxon*   | C-MYC 3  | CXCR4                           | H3a      | POMC                          | RAG1 (1)                        | RAG1 (2) | Rho                             | SIAH     | SLC8A1                          | SLC8A3                          | Tyr                             |
|--|----------|---------------------------------|----------|-------------------------------|---------------------------------|----------|---------------------------------|----------|---------------------------------|---------------------------------|---------------------------------|
| <i>Acris crepitans</i>                                   | AY819268 | EF107468                        | DQ284107 | AY819109                      | EF107304 +<br>AY844358          | —        | AY844533                        | AY844762 | EF107244                        | EF107403                        | AY844019                        |
| <i>Adelophryne patamona</i>                              | GQ345167 | GQ345185                        | GQ345215 | GQ345262                      | GQ345280 +<br>GQ345296          | EU186751 | GQ345302                        | GQ345312 | GQ345233                        | GQ345331                        | EU186772                        |
| <i>Adenomera andreae</i>                                 | —        | —                               | —        | KC604061                      | KC604015 +<br>KC604037          | —        | KC604094                        | —        | HQ290704                        | —                               | KC520698                        |
| <i>Adenomera hylaedactyla</i>                            | —        | —                               | DQ284093 | KC604063                      | KC604017 +<br>KC604039          | —        | KC604095                        | —        | —                               | —                               | JN691529                        |
| <i>Agalychnis annae</i>                                  | —        | GQ365977                        | —        | EF158394                      | EF174311                        | —        | —                               | GQ366159 | —                               | —                               | GQ366198                        |
| <i>Agalychnis callidryas</i>                             | —        | AB612054                        | DQ284401 | EF158395                      | AY323765                        | EF493362 | AY844537                        | AY844765 | AB612055                        | —                               | DQ283018                        |
| <i>Allobates femoralis</i>                               | —        | —                               | DQ502325 | HQ290831                      | DQ503327                        | —        | DQ503215                        | DQ503077 | HQ290711                        | —                               | HQ290891                        |
| <i>Allophryne ruthveni</i>                               | AY819242 | —                               | —        | AY819077                      | EU663432                        | —        | AY844538                        | AY844766 | —                               | —                               | —                               |
| <i>Alsodes neuquensis</i>                                | —        | —                               | DQ284118 | —                             | AY844362                        | —        | AY844539                        | AY844767 | —                               | —                               | —                               |
| <i>Amazophrynella minuta</i>                             | AY819246 | DQ306496                        | DQ284096 | AY819081                      | DQ158346 +<br>DQ503337          | —        | AY844555                        | —        | —                               | —                               | EF364362                        |
| <i>Amietophryne brauni</i>                               | —        | DQ306514                        | —        | DQ158279                      | EF107331                        | —        | DQ284021                        | DQ282873 | EF107272                        | EF107435                        | DQ283011                        |
| <i>Atelognathus patagonicus</i>                          | —        | —                               | —        | —                             | AY844368                        | —        | AY844545                        | AY844773 | —                               | —                               | AY844027                        |
| <i>Barycholos pulcher</i>                                | —        | —                               | —        | —                             | —                               | EU186744 | —                               | —        | —                               | —                               | EU186765                        |
| <i>Barycholos ternetzi</i>                               | —        | —                               | DQ284144 | —                             | —                               | —        | DQ283810                        | —        | —                               | —                               | DQ282921                        |
| <i>Batrachyla leptopus</i>                               | —        | —                               | DQ284119 | —                             | AY844369                        | —        | AY844546                        | AY844774 | —                               | —                               | AY844028                        |
| <i>Batrachyla taeniata</i>                               | —        | —                               | —        | KC604075                      | KC604007                        | —        | —                               | —        | —                               | —                               | —                               |
| <i>Brachycephalus alipioi</i>                            | —        | —                               | —        | —                             | —                               | HQ435718 | —                               | —        | —                               | —                               | HQ435732                        |
| <i>Brachycephalus ephippium</i>                          | GQ345162 | GQ345180                        | GQ345212 | GQ345256                      | GQ345275 +<br>GQ345290          | EU186761 | DQ283808                        | DQ282673 | GQ345228                        | GQ345326                        | DQ282919                        |
| <i>Bryophryne cophites</i>                               | —        | —                               | —        | —                             | —                               | EF493423 | —                               | —        | —                               | —                               | EF493508                        |
| <i>Bufo japonicus</i>                                    | —        | AB612061                        | —        | JN653306                      | AB612057                        | —        | —                               | —        | AB612062                        | —                               | AB612059                        |
| <i>Calyptocephalella gayi</i>                            | —        | EF107495                        | DQ284415 | AY819090                      | AY583337                        | —        | DQ284036                        | DQ282893 | EF107275                        | EF107440                        | JX298244                        |
| <i>Ceratophrys (C. cornuta, C. cranwelli, C. ornata)</i> | —        | AY364188 C.<br><i>cranwelli</i> | —        | AY819091 C.<br><i>cornuta</i> | AY364218 C.<br><i>cranwelli</i> | —        | AY364399 C.<br><i>cranwelli</i> | —        | AY523718 C.<br><i>cranwelli</i> | AY948886 C.<br><i>cranwelli</i> | DQ347168 C.<br><i>cranwelli</i> |
| <i>Ceuthomantis smaragdinus</i>                          | GQ345169 | GQ345190                        | GQ345220 | GQ345267                      | GQ345285                        | —        | GQ345305                        | GQ345317 | GQ345238                        | GQ345336                        | —                               |
| <i>Chacophrys pierottii</i>                              | —        | —                               | —        | —                             | —                               | —        | —                               | —        | —                               | —                               | —                               |
| <i>Colostethus pratti</i>                                | —        | —                               | DQ502362 | HQ290847                      | DQ503361                        | —        | DQ503247                        | DQ503112 | HQ290727                        | —                               | HQ290907                        |
| <i>Craugastor augusti</i>                                | AY211289 | —                               | DQ284291 | —                             | —                               | —        | DQ283935                        | DQ282786 | —                               | —                               | DQ282963                        |

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| Taxon*  | C-MYC 3              | CXCR4    | H3a      | POMC     | RAG1 (1)               | RAG1 (2) | Rho      | SIAH     | SLC8A1   | SLC8A3   | Tyr      |
|---|----------------------|----------|----------|----------|------------------------|----------|----------|----------|----------|----------|----------|
| <i>Craugastor podiciferus</i>                               | GQ345164<br>AY211319 | GQ345182 | —        | GQ345258 | GQ345277 +<br>GQ345292 | EF493450 | —        | —        | GQ345230 | GQ345328 | EF493481 |
| <i>Craugastor punctariolus</i>                              | —                    | —        | DQ284206 | —        | —                      | —        | DQ283862 | —        | —        | —        | —        |
| <i>Craugastor ranoides</i>                                  | AY211287             | —        | DQ284154 | —        | —                      | —        | DQ283820 | —        | —        | —        | DQ282928 |
| <i>Craugastor rhodopis</i>                                  | AY211315             | —        | DQ284317 | —        | —                      | —        | DQ283960 | DQ282808 | —        | —        | DQ282968 |
| <i>Crossodactylodes</i> sp                                  | —                    | —        | —        | KC604048 | KC604011 +<br>KC604033 | —        | KC604105 | —        | —        | —        | KC604077 |
| <i>Crossodactylus schmidti</i>                              | —                    | —        | DQ284050 | HQ290828 | DQ503298               | —        | —        | AY844780 | HQ290708 | —        | AY844031 |
| <i>Cryptobatrachus boulengeri</i> LM                        | —                    | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Cryptobatrachus fuhrmanni</i> JDL<br>14865               | —                    | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Cryptobatrachus fuhrmanni</i><br>MHUA A 5160             | —                    | —        | —        | KR270358 | KR138418               | —        | —        | —        | —        | —        | —        |
| <i>Cryptobatrachus remotus</i><br>MHNLS 18853 + MHNLS 17664 | —                    | KR138404 | —        | KR270360 | KR138419               | KR138394 | —        | —        | KR138381 | KR270375 | KR270387 |
| <i>Cycloramphus acangatan</i>                               | —                    | —        | —        | —        | HQ634170 +<br>FJ685703 | —        | —        | —        | —        | —        | —        |
| <i>Cycloramphus boraceiensis</i>                            | —                    | —        | DQ284147 | —        | DQ503357               | —        | DQ283813 | DQ282675 | —        | —        | DQ282924 |
| <i>Dendrobates auratus</i>                                  | —                    | AY364184 | DQ284072 | HQ290857 | EU325909               | —        | AY364395 | AY844781 | AY948823 | AY948879 | DQ347160 |
| <i>Dendropsophus nanus</i>                                  | AY819282             | GQ365985 | DQ284051 | AY819123 | AY844437               | —        | AY844634 | AY844852 | —        | —        | —        |
| <i>Diasporus aff diastema</i>                               | —                    | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Diasporus diastema</i>                                   | —                    | GQ345184 | GQ345214 | GQ345261 | GQ345279 +<br>GQ345295 | EU186752 | —        | GQ34531  | GQ345232 | GQ345330 | EU186773 |
| <i>Duttaphrynus melanostictus</i>                           | —                    | DQ306508 | DQ284324 | DQ158317 | EU712821               | —        | AF249097 | DQ282815 | AY948805 | AY948851 | —        |
| <i>Edalorhina perezi</i>                                    | —                    | —        | DQ284095 | —        | —                      | —        | AY844558 | AY844784 | —        | —        | —        |
| <i>Eleutherodactylus cooki</i>                              | GQ345166             | —        | GQ345213 | HQ831999 | HQ831830 +<br>GQ345294 | EF493413 | —        | GQ345310 | —        | —        | EF493455 |
| <i>Eleutherodactylus coqui</i>                              | —                    | EF107500 | —        | —        | EF107341               | —        | —        | —        | EF107282 | EF107445 | —        |
| <i>Eleutherodactylus marnockii</i>                          | —                    | EF107463 | DQ284151 | —        | EF107300               | EF493399 | DQ283817 | DQ282677 | EF107238 | EF107388 | EF493476 |
| <i>Eleutherodactylus nitidus</i>                            | —                    | —        | DQ284316 | —        | —                      | —        | DQ283959 | DQ282807 | —        | —        | —        |
| <i>Eleutherodactylus planirostris</i>                       | —                    | —        | DQ284294 | HQ831975 | HQ831774               | EF493396 | DQ283937 | DQ282788 | —        | —        | DQ282964 |
| <i>Eleutherodactylus thorectes</i>                          | —                    | —        | —        | HQ832000 | HQ831831               | EF493416 | —        | —        | —        | —        | EF493473 |
| <i>Eleutherodactylus tonyi</i>                              | —                    | —        | —        | HQ831994 | HQ831824               | —        | —        | —        | —        | —        | —        |
| <i>Engystomops petersi</i>                                  | —                    | —        | —        | —        | GQ375543               | —        | FJ668238 | —        | —        | —        | —        |
| <i>Engystomops pustulosus</i>                               | —                    | EF107462 | —        | —        | EF107299               | —        | —        | —        | EF107237 | EF107387 | —        |

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| Taxon*   | C-MYC 3  | CXCR4    | H3a      | POMC     | RAG1 (1) | RAG1 (2) | Rho      | SIAH     | SLC8A1   | SLC8A3   | Tyr      |
|--|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
| <i>Espadarana prosoblepon</i>  | AY819250 | AY364193 | —        | AY819085 | EU663453 | —        | AY364404 | AY844776 | AY948834 | AY948896 | —        |
| <i>Eupsophus roseus</i>  | —        | —        | DQ284120 | KC604074 | KC604032 | —        | AY844560 | AY844786 | —        | —        | AY844036 |
| <i>Fejervarya limnocharis</i>  | —        | AB277307 | DQ284356 | AB526646 | —        | AB277335 | DQ458271 | AY844787 | AB277321 | AB526674 | EU980027 |
| <i>Flectonotus fitzgeraldi</i> ZSM 1610<br>2006 + KU 192399            | AY819265 | GQ345177 | —        | KR270361 | DQ679274 | KR138395 | —        | —        | GQ345224 | GQ345322 | KR270388 |
| <i>Flectonotus pygmaeus</i> MHNLS<br>17478 + KU 184958                 | —        | —        | —        | DQ679310 | DQ679275 | —        | —        | —        | —        | —        | —        |
| <i>Fritziana fissilis</i> MNRJ 62845                                   | —        | KR138406 | —        | —        | —        | —        | —        | —        | KR138384 | —        | KR270389 |
| <i>Fritziana</i> aff. <i>fissilis</i> sp. 2 MNRJ<br>44622              | —        | KR138407 | —        | KR270362 | KR138422 | KR138396 | —        | —        | KR138385 | KR270377 | KR270390 |
| <i>Fritziana</i> aff. <i>fissilis</i> sp. 3 MZSUP<br>133700            | —        | —        | —        | JN157627 | KC844990 | —        | —        | —        | —        | —        | —        |
| <i>Fritziana</i> aff. <i>fissilis</i> sp. 1 CFBH<br>5726 + MZUSP 13546 | —        | —        | —        | JN157628 | AY844379 | —        | AY844562 | AY844788 | —        | —        | AY844038 |
| <i>Fritziana goeldi</i> MNRJ 34921                                     | —        | KR138408 | —        | KR270363 | —        | —        | —        | —        | KR138386 | KR270378 | KR270391 |
| <i>Fritziana ohausi</i> MZUSP 139225                                   | —        | —        | —        | JN157629 | KC844991 | —        | —        | —        | —        | —        | —        |
| <i>Fritziana</i> sp. MNRJ 44592  | —        | KR138409 | —        | KR270364 | —        | —        | —        | —        | —        | KR270379 | —        |
| <i>Gastrotheca albolineata</i> MNRJ<br>54401                           | —        | KR138410 | —        | KR270365 | KR138423 | KR138397 | —        | —        | KR138387 | KR270380 | KR270392 |
| <i>Gastrotheca antoniihoai</i><br>MUSM 27944                           | —        | —        | —        | KC844972 | KC844993 | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca argenteovirens</i> KU<br>181168                         | —        | —        | —        | DQ679311 | —        | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca atympana</i> MHNSM<br>18692                             | —        | —        | —        | DQ679312 | DQ679276 | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca aureomaculata</i> KU<br>181194                          | —        | —        | —        | —        | DQ679277 | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca christiani</i> FML 2881                                 | —        | —        | —        | DQ679313 | DQ679278 | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca chrysosticta</i> LM 58                                  | —        | —        | —        | —        | DQ679279 | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca</i> sp. 1 IDLR 4073<br>(MNCN/ADN 566)                   | —        | —        | —        | —        | —        | —        | KR270372 | —        | —        | —        | —        |
| <i>Gastrotheca cornuta</i> USNM<br>572472 + AMNH 107251                | —        | —        | —        | DQ679314 | DQ679280 | —        | —        | —        | —        | —        | AY844040 |
| <i>Gastrotheca dendronastes</i> KU<br>181203                           | —        | —        | —        | DQ679315 | DQ679281 | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca dummi</i> ICN 10059 +<br>MHUA A 4800                    | —        | —        | —        | DQ679316 | DQ679282 | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca ernestoi</i> MNRJ<br>57129 + MNRJ 64000                 | —        | KR138411 | —        | KR270366 | KR138424 | KR138398 | —        | —        | KR138388 | KR270381 | KR270393 |
| <i>Gastrotheca excubitor</i> KU 173171                                 | —        | —        | —        | DQ679317 | DQ679283 | —        | —        | —        | —        | —        | —        |

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| Taxon*  | C-MYC 3 | CXCR4 | H3a      | POMC     | RAG1 (1)               | RAG1 (2) | Rho      | SIAH     | SLC8A1 | SLC8A3 | Tyr      |
|---|---------|-------|----------|----------|------------------------|----------|----------|----------|--------|--------|----------|
| <i>Gastrotheca excubitor</i> MUSM<br>26280                  | —       | —     | —        | —        | —                      | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca fissipes</i> ZUFRJ 7901                      | —       | —     | —        | —        | —                      | —        | JX262904 | JX262911 | —      | —      | —        |
| <i>Gastrotheca fulvorufa</i> CTMZ<br>07467                  | —       | —     | —        | KC844977 | KC844997               | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca galeata</i> KU 181700                        | —       | —     | —        | DQ679318 | DQ679284               | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca gracilis</i> DCC 006                         | —       | —     | —        | DQ679319 | —                      | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca griswoldi</i> KU 181701                      | —       | —     | —        | DQ679320 | —                      | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca griswoldi</i> MHNSM<br>20588                 | —       | —     | —        | —        | —                      | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca guentheri</i> KU<br>173112                   | —       | —     | —        | DQ679321 | DQ679285               | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca helenae</i> KU 181070                        | —       | —     | —        | DQ679322 | DQ679286               | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca lateonota</i> QCAZ<br>45113                  | —       | —     | —        | KC844970 | —                      | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca</i> sp. 2 MNK 5286 +<br>CBG 1020             | —       | —     | DQ284069 | —        | AY844380               | —        | AY844563 | AY844789 | —      | —      | AY844039 |
| <i>Gastrotheca litonedis</i> KU 202690                      | —       | —     | —        | DQ679323 | DQ679287               | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca longipes</i> USNM<br>258905                  | —       | —     | —        | DQ679324 | DQ679288               | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca marsupiata</i> KU<br>214813 + KU 214814      | —       | —     | —        | AY819105 | DQ679289               | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca</i> sp. 3 ZFMK 66954 +<br>MNCN 43052         | —       | —     | —        | —        | —                      | —        | KR270373 | —        | —      | —      | —        |
| <i>Gastrotheca megacephala</i> JLG 90<br>+ CFBH T377        | —       | —     | —        | KC844976 | AY844381 +<br>KC844996 | —        | AY844564 | AY844790 | —      | —      | —        |
| <i>Gastrotheca microdiscus</i> CFBH T<br>1250 + CFBH T 3068 | —       | —     | —        | KC844979 | KC844999               | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca monticola</i> KU<br>212036                   | —       | —     | —        | AY819106 | DQ679290               | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca nebulanastes</i> MUSM<br>27943 + MCZ 265218  | —       | —     | —        | KC844982 | KC845001               | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca nicefori</i> KU 181071                       | —       | —     | —        | DQ679325 | DQ679291               | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca nicefori</i> MHUA A<br>5716                  | —       | —     | —        | KR270367 | —                      | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca ochoai</i> KU 173499                         | —       | —     | —        | DQ679326 | DQ679292               | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca orophylax</i> KU<br>178568                   | —       | —     | —        | DQ679327 | DQ679293               | —        | —        | —        | —      | —      | —        |
| <i>Gastrotheca ovifera</i> KU 185758                        | —       | —     | —        | —        | —                      | —        | —        | —        | —      | —      | —        |

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| Taxon*  | C-MYC 3  | CXCR4    | H3a      | POMC     | RAG1 (1)                        | RAG1 (2) | Rho      | SIAH     | SLC8A1   | SLC8A3   | Tyr      |
|---|----------|----------|----------|----------|---------------------------------|----------|----------|----------|----------|----------|----------|
| <i>Gastrotheca pachachacae</i> MUSM 28492           | —        | —        | —        | KC844983 | KC845002                        | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca peruana</i> KU 181740                | —        | —        | —        | —        | —                               | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca plumbea</i> KU 178499                | —        | —        | —        | DQ679328 | DQ679294                        | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca prasina</i> MZUSP 147060             | —        | —        | —        | —        | —                               | —        | JX262908 | JX262915 | —        | —        | —        |
| <i>Gastrotheca pseustes</i> QCAZ 42862 + TNHC 62492 | —        | —        | —        | KC844986 | —                               | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca psychrophila</i> KU 142634           | —        | —        | —        | DQ679329 | DQ679295                        | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca pulchra</i> MTR 16228                | —        | —        | —        | —        | —                               | —        | JX262907 | JX262914 | —        | —        | —        |
| <i>Gastrotheca rebecca</i> CORBIDI 08006            | —        | —        | —        | KC844987 | —                               | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca recava</i> MZUSP 147044              | —        | —        | —        | —        | —                               | —        | JX262910 | JX262919 | —        | —        | —        |
| <i>Gastrotheca riobambae</i> KU 178468              | —        | —        | —        | —        | DQ679296                        | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca riobambae</i> UIMNH 94580            | —        | —        | —        | —        | —                               | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca ruizi</i> KU 200002                  | —        | —        | —        | —        | DQ679297                        | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca</i> sp. A QCAZ 22635                 | —        | —        | —        | KC844985 | —                               | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca</i> sp. B QCAZ 21105                 | —        | —        | —        | KC844989 | —                               | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca</i> sp. C QCAZ 47299                 | —        | —        | —        | KC844984 | —                               | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca</i> sp. D QCAZ 42725                 | —        | —        | —        | KC844988 | —                               | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca</i> sp. E QCAZ 21213                 | —        | —        | —        | —        | —                               | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca stictopleura</i> MTD 45230           | —        | —        | —        | DQ679330 | DQ679298                        | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca testudinea</i> QCAZ 16444 + CBG 774  | —        | —        | —        | —        | —                               | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca trachyceps</i> KU 181189             | —        | —        | —        | DQ679331 | DQ679299                        | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca walkeri</i> Vz 89–96                 | —        | —        | —        | DQ679332 | DQ679300                        | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca weinlandii</i> KU 143105             | —        | —        | —        | DQ679333 | DQ679301                        | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca zeugocystis</i> MHNSM 18675          | —        | —        | —        | DQ679334 | DQ679302                        | —        | —        | —        | —        | —        | —        |
| <i>Haddadus binotatus</i>                           | GQ345165 | GQ345183 | DQ284142 | GQ345259 | GQ345278 + GQ345293<br>AY364221 | EF493397 | DQ283807 | GQ345309 | GQ345231 | GQ345329 | DQ282918 |
| <i>Heleophryne purcelli</i>                         | —        | AY364191 | DQ284113 | —        | —                               | —        | AY364402 | AY844791 | AY948833 | AY948892 | —        |
| <i>Hemiphractus bubalus</i> KU 143107 + KU 178588   | —        | GQ345179 | —        | DQ679335 | DQ679303                        | —        | —        | —        | GQ345226 | GQ345324 | —        |

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| Taxon*   | C-MYC 3  | CXCR4    | H3a      | POMC     | RAG1 (1)            | RAG1 (2) | Rho      | SIAH     | SLC8A1   | SLC8A3   | Tyr      |
|--|----------|----------|----------|----------|---------------------|----------|----------|----------|----------|----------|----------|
| <i>Hemiphractus fasciatus</i> MVUP 1927                            | —        | —        | —        | —        | —                   | —        | —        | —        | —        | —        | —        |
| <i>Hemiphractus fasciatus</i> sp1 CHP 6397 + EVACC 207 + EVACC 065 | —        | —        | —        | —        | —                   | —        | —        | —        | —        | —        | —        |
| <i>Hemiphractus fasciatus</i> sp2 EVACC 061 + CHP 6670             | —        | —        | —        | —        | —                   | —        | —        | —        | —        | —        | —        |
| <i>Hemiphractus helioi</i> MHNCP 9063 + MJH 3689                   | —        | KR138412 | DQ284084 | KR270368 | KR138425            | KR138399 | AY844566 | AY844792 | KR138389 | KR270382 | KR270394 |
| <i>Hemiphractus proboscideus</i> KU 217513                         | AY819266 | —        | —        | AY819107 | DQ679304            | —        | —        | —        | —        | —        | —        |
| <i>Hemiphractus scutatus</i> JMP 2150 (MNCN/ADN 46913)             | —        | KR138413 | —        | KR270369 | KR138426            | KR138400 | —        | —        | KR138390 | KR270383 | KR270395 |
| <i>Hemiphractus scutatus</i> USNM 317196                           | —        | —        | —        | DQ679336 | DQ679305            | —        | —        | —        | —        | —        | —        |
| <i>Holoaden bradei</i>   | —        | —        | —        | —        | —                   | EF493449 | —        | —        | —        | —        | EU186779 |
| <i>Holoaden luederwaldti</i>                                       | —        | —        | —        | —        | —                   | EU186747 | —        | —        | —        | —        | EU186768 |
| <i>Hydrolaetare caparu</i>   | —        | —        | —        | KC604050 | KC604031 + KC604035 | —        | KC604107 | —        | —        | —        | KC604081 |
| <i>Hyla arenicolor</i>   | AY819271 | AY364190 | —        | AY819112 | AY364220 + AY844391 | —        | AY844577 | AY844802 | EF107241 | EF107393 | AY844048 |
| <i>Hyla chinensis</i>  | —        | —        | HM998949 | DQ055789 | —                   | —        | —        | —        | HM998954 | —        | —        |
| <i>Hyla cinerea</i>  | AY819275 | DQ306493 | DQ284057 | AY819116 | AY323766            | —        | AY844597 | AY844816 | —        | —        | AY844063 |
| <i>Hylodes phyllodes</i>   | —        | —        | DQ284146 | —        | DQ503367            | —        | DQ503253 | DQ282674 | —        | —        | DQ282923 |
| <i>Hylorina sylvatica</i>  | —        | —        | —        | —        | —                   | —        | —        | —        | —        | —        | —        |
| <i>Hyloxalus chlorocraspedus</i>                                   | —        | —        | —        | —        | DQ503325            | —        | DQ503212 | DQ503074 | —        | —        | DQ503153 |
| <i>Hypodactylus brunneus</i>                                       | —        | GQ345187 | GQ345218 | GQ345264 | GQ345282 + GQ345298 | EF493422 | —        | GQ345315 | GQ345235 | GQ345333 | EF493484 |
| <i>Hypodactylus dolops</i>   | —        | —        | —        | —        | —                   | EF493414 | GQ345304 | —        | —        | —        | EF493483 |
| <i>Hypsiboas boans</i>   | AY819273 | —        | DQ284086 | AY819114 | —                   | —        | AY844588 | AY844809 | —        | —        | AY844055 |
| <i>Hypsiboas lanciformis</i>                                       | —        | —        | —        | —        | —                   | —        | AY844619 | AY844837 | —        | —        | AY844081 |
| <i>Insuetophrynus acarpicus</i>                                    | —        | —        | —        | —        | JX204088            | —        | JX204152 | JX204285 | —        | —        | —        |
| <i>Ischnocnema guentheri</i>                                       | GQ345163 | GQ345181 | —        | GQ345257 | GQ345276 + GQ345291 | EF493407 | —        | GQ345308 | GQ345229 | GQ345327 | EF493510 |
| <i>Ischnocnema juipoca</i>   | —        | —        | DQ284143 | —        | —                   | —        | DQ283809 | —        | —        | —        | DQ282920 |
| <i>Lepidobatrachus laevis</i>                                      | AY819258 | EF107461 | DQ284191 | AY819094 | EF107298            | —        | DQ283851 | DQ282707 | EF107236 | EF107386 | —        |

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| Taxon*                               | C-MYC 3  | CXCR4    | H3a      | POMC     | RAG1 (1)               | RAG1 (2) | Rho      | SIAH     | SLC8A1   | SLC8A3   | Tyr      |
|--------------------------------------|----------|----------|----------|----------|------------------------|----------|----------|----------|----------|----------|----------|
| <i>Leptodactylus melanonotus</i>     | AY337266 | AY364194 | —        | —        | AY364224               | —        | AY364405 | —        | AY948838 | AY948900 | DQ347193 |
| <i>Leptodactylus latrans</i>         | —        | DQ306492 | DQ284104 | DQ158259 | DQ158343 +<br>AY844470 | —        | AY844681 | AY844890 | —        | —        | —        |
| <i>Limnodynastes salmini</i>         | —        | AY364189 | —        | —        | AY364219               | —        | AY364400 | —        | AY523719 | AY948889 | —        |
| <i>Limnomedusa macroglossa</i>       | —        | —        | DQ284127 | —        | AY844471               | —        | AY844682 | AY844891 | —        | —        | AY844128 |
| <i>Lithodytes lineatus</i>           | —        | —        | DQ284112 | KC604060 | KC604025 +<br>AY844472 | —        | AY844683 | —        | HQ290709 | —        | AY844129 |
| <i>Litoria caerulea</i>              | AY819308 | AY948783 | —        | AY819149 | AY323767               | EF493446 | AY844685 | AY844893 | AY948821 | AY948877 | AY844131 |
| <i>Litoria infrafrenata</i>          | —        | GQ365990 | —        | —        | AY844474               | —        | AY844687 | —        | —        | —        | —        |
| <i>Lynchius nebulanastes</i>         | —        | —        | —        | AY819154 | —                      | —        | —        | —        | —        | —        | —        |
| <i>Lynchius parkeri</i>              | —        | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Macrogenioglottus alipioi</i>     | —        | —        | —        | —        | KC593355               | —        | KC593357 | KC593363 | —        | —        | KC593367 |
| <i>Mannophryne trinitatis</i>        | —        | —        | DQ284108 | JX036003 | DQ503345               | —        | DQ503236 | DQ503097 | GQ345227 | GQ345325 | —        |
| <i>Megaelosia goeldii</i>            | —        | —        | DQ284109 | —        | DQ503346               | —        | DQ283797 | —        | —        | —        | DQ282911 |
| <i>Melanophryniscus klappenbachi</i> | —        | —        | DQ284060 | —        | DQ503299               | —        | DQ283765 | AY844899 | —        | —        | —        |
| <i>Myersiohyala kanaima</i>          | —        | GQ365994 | —        | —        | AY844422               | —        | AY844617 | AY844835 | —        | —        | AY844079 |
| <i>Noblella lochites</i>             | —        | —        | —        | —        | —                      | EU186756 | —        | —        | —        | —        | EU186777 |
| <i>Noblella</i> sp. MTD 45180        | —        | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Nymphargus bejaranoi</i>          | —        | —        | DQ284066 | EU663239 | EU663522               | —        | —        | AY844777 | —        | —        | AY844029 |
| <i>Odontophrynus achalensis</i>      | —        | —        | DQ284273 | —        | —                      | —        | DQ283918 | DQ282773 | —        | —        | —        |
| <i>Oreobates cruralis</i>            | —        | —        | —        | —        | —                      | EU186743 | —        | —        | —        | —        | EU186764 |
| <i>Oreobates saxatilis</i>           | —        | —        | DQ284091 | —        | —                      | JF809910 | DQ283788 | DQ282661 | —        | —        | JF809888 |
| <i>Paratelmatobius cardosoi</i>      | —        | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Phrynopus bracki</i>              | GQ345168 | GQ345186 | GQ345217 | GQ345263 | GQ345281 +<br>GQ345297 | EF493421 | GQ345303 | GQ345314 | GQ345234 | GQ345332 | EF493507 |
| <i>Phyllodytes luteolus</i>          | —        | —        | —        | GQ366043 | AY844494               | —        | AY844708 | AY844913 | —        | —        | AY844150 |
| <i>Physalaemus cuvieri</i>           | —        | —        | —        | AY819096 | AY844499               | —        | AY844717 | AY844922 | —        | —        | —        |
| <i>Physalaemus gracilis</i>          | —        | —        | —        | —        | —                      | —        | DQ284022 | DQ282875 | —        | —        | —        |
| <i>Phrynopus auriculatus</i>         | —        | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |

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| Taxon*   | C-MYC 3  | CXCR4    | H3a      | POMC     | RAG1 (1)               | RAG1 (2) | Rho      | SIAH     | SLC8A1   | SLC8A3   | Tyr      |
|--|----------|----------|----------|----------|------------------------|----------|----------|----------|----------|----------|----------|
| <i>Phyzelaphryne miriamae</i>  | —        | —        | —        | —        | —                      | EU186753 | —        | —        | —        | —        | EU186774 |
| <i>Pleurodema brachyops</i>  | —        | —        | DQ284111 | —        | AY844503               | —        | AY844721 | AY844926 | —        | —        | —        |
| <i>Pleurodema diplolister</i>  | —        | —        | —        | KC604052 | HQ634173               | —        | JQ937153 | JQ937222 | —        | —        | KC604080 |
| <i>Pristimantis cruentus</i>   | —        | AY948792 | GQ345216 | —        | AY948935               | —        | —        | GQ345313 | AY948836 | AY948898 | —        |
| <i>Pristimantis curtipes</i>   | AY819256 | —        | —        | AY819092 | DQ679272               | EF493435 | —        | —        | —        | —        | EF493497 |
| <i>Pristimantis gaigeae</i>  | AY211290 | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Pristimantis ridens</i>   | AY211306 | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Pristimantis simonsii</i>   | AY819314 | —        | —        | AY819155 | —                      | —        | —        | —        | —        | —        | —        |
| <i>Proceratophrys avelinoi</i>   | —        | —        | DQ284065 | —        | FJ685711               | —        | DQ283769 | —        | —        | —        | DQ282903 |
| <i>Pseudis minutus</i>   | —        | GQ366028 | —        | GQ366070 | AY844505               | —        | —        | AY844929 | —        | —        | —        |
| <i>Pseudopaludicola falcipes</i>   | —        | —        | DQ284117 | KC604051 | HQ634171 +<br>AY844507 | —        | AY844728 | AY844930 | KC593352 | —        | KC520700 |
| <i>Psychrophrynella guillei</i>  | —        | —        | DQ284371 | —        | —                      | —        | —        | —        | —        | —        | DQ282995 |
| <i>Psychrophrynella wettsteini</i>   | —        | GQ345189 | GQ345219 | GQ345266 | GQ345284 +<br>GQ345300 | EU186755 | —        | GQ345316 | GQ345237 | GQ345335 | EU186776 |
| <i>Rheobates palmatus</i>  | —        | —        | —        | HQ290845 | —                      | —        | DQ503271 | —        | HQ290725 | —        | DQ503172 |
| <i>Rhinella arenarum</i>   | —        | DQ306529 | DQ284103 | DQ158271 | DQ158354 +<br>AY844370 | —        | AY844547 | AY844775 | —        | —        | —        |
| <i>Rhinoderma darwini</i>  | —        | AY364192 | DQ284320 | —        | AY364222               | —        | AY364403 | DQ282813 | AY523733 | AY948895 | —        |
| <i>Rupirana cardosoi</i>   | —        | —        | —        | KC604049 | KC604012 +<br>KC604034 | —        | KC604106 | —        | —        | —        | KC604078 |
| <i>Scinax staufferi</i>  | —        | GQ366029 | —        | GQ366071 | AY844523               | —        | AY844748 | —        | —        | —        | AY844183 |
| <i>Scythrophrys sawayae</i>  | —        | —        | DQ284149 | —        | —                      | —        | DQ283815 | —        | —        | —        | DQ282926 |
| <i>Smilisca baudinii</i>   | —        | —        | —        | DQ388720 | DQ830932               | —        | AY844749 | AY844946 | —        | —        | —        |
| <i>Sooglossus thomasseti</i>   | —        | AY364187 | DQ284425 | —        | AY323778               | —        | DQ284042 | —        | AY948828 | AY948884 | DQ347167 |
| <i>Stefania</i> aff. <i>evansi</i> ROM 44254                                     | —        | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Stefania ayangannae</i> ROM 42906   | —        | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Stefania coxi</i> ROM 39478   | —        | —        | —        | DQ679337 | DQ679306               | —        | —        | —        | —        | —        | —        |
| <i>Stefania evansi</i> AMNH A 164211<br>+ ROM 39450 + ROM 39451 +<br>IRSNB 14586 | AY819267 | KR138414 | —        | KR270370 | KR138427+<br>DQ679307  | KR138401 | AY844755 | AY844950 | KR138391 | KR270384 | AY844189 |

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| Taxon*  | C-MYC 3  | CXCR4    | H3a      | POMC     | RAG1 (1)               | RAG1 (2) | Rho      | SIAH     | SLC8A1   | SLC8A3   | Tyr      |
|---|----------|----------|----------|----------|------------------------|----------|----------|----------|----------|----------|----------|
| <i>Stefania ginesi</i> LM 1056                    | —        | GQ345178 | GQ345211 | DQ679338 | DQ679308               | —        | —        | —        | GQ345225 | GQ345323 | —        |
| <i>Stefania riae</i> VUB 3754                     | —        | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Stefania riveroi</i> IRSNB 15703               | —        | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Stefania roraimae</i> ROM 42843                | —        | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Stefania satelles</i> IRSNB 15839              | —        | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Stefania scalae</i> KU 181122 +<br>MHNLS 17152 | —        | KR138415 | —        | KR270371 | KR138428 +<br>DQ679309 | KR138402 | —        | —        | KR138392 | KR270385 | KR270397 |
| <i>Stefania schuberti</i> MNHN 2002<br>692        | —        | —        | —        | —        | AY844528               | —        | AY844756 | AY844951 | —        | —        | —        |
| <i>Stefania</i> sp. IRSNB 15853                   | —        | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Stefania woodleyi</i> IRSNB 13799              | —        | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |
| <i>Strabomantis biporcatus</i>                    | —        | GQ345188 | —        | GQ345265 | GQ345283               | EU186754 | —        | —        | GQ345236 | GQ345334 | EU186775 |
| <i>Strabomantis bufoniformis</i>                  | —        | —        | DQ284203 | —        | —                      | —        | —        | DQ282718 | —        | —        | DQ282942 |
| <i>Telmatobius truebae</i>                        | AY819260 | —        | —        | AY819097 | DQ679271               | —        | —        | —        | —        | —        | —        |
| <i>Thoropa miliaris</i>                           | —        | —        | DQ502369 | —        | FJ685702               | —        | —        | —        | —        | —        | JX298241 |
| <i>Trachycephalus typhonius</i>                   | AY819291 | GQ366030 | --       | AY819132 | EU034147               | —        | AY364396 | AY844912 | AY948824 | AY948880 | DQ347161 |
| <i>Uperoleia laevigata</i>                        | —        | EF107474 | DQ284251 | —        | EF107310               | —        | DQ283898 | DQ282758 | EF107251 | EF107410 | —        |
| <i>Yunganastes ashkapara</i>                      | —        | —        | —        | —        | —                      | JF809919 | —        | —        | —        | —        | JF809898 |
| <i>Yunganastes fraudator</i>                      | —        | —        | —        | —        | —                      | JF809916 | —        | —        | —        | —        | JF809895 |
| <i>Zachaenus parvulus</i>                         | —        | —        | —        | —        | —                      | —        | —        | —        | —        | —        | —        |

\*We selected outgroups with the objective to perform a strong test of the monophyly and relationships of Hemiphractidae. We included representatives of all currently used families of Nobleobatrachia with a denser taxon sampling within Terrarana and Hylidae because they have been historically associated with hemiphractids. Other criteria used to select terminals included:

Species diversity within a give taxon (e.g., we included more species of *Pristimantis*, with more 400 spp., than of *Adelophryne*, 9 spp.). This helps braking long branches, which often complicate tree-searches.

An attempt to maximize character coverage (*i.e.*, homologous sequences available from Genbank and phenotypic characters sampled by Mendelson *et al.* 2000). Species with more available characters were selected over those with less available characters.

An attempt to maximize phylogenetic structure according to the trees of the two most densely sampled anuran phylogenies (Frost *et al.* 2006; Pyron & Wiens 2011). For example, during exploratory analyses with fewer terminals of Leptodactylidae, members of this family were "all over the tree". We augmented the number of terminals until we recovered a monophyletic Leptodactylidae, which is a highly corroborated clade.

Constraints associated with phenotypic characters. Only a few outgroup terminals were sampled for the large majority of phenotypic characters (*Agalychnis annae*, *Hypsiboas boans*, *H. lanciformis*, and *Smilisca baudinii* from Mendelson *et al.* 2000). This meant that we could not take the luxury to exclude any of them (hence the two species of *Hypsiboas*). Also, the paucity of phenotypic character sampling created some unexpected results. The monophyly of Hylidae was not recovered because *A. annae* and *S. baudinii* broke it. Because they were the only outgroup taxa with phenotypic characters, we thought that those characters were affecting the non-monophyly of Hylidae. Thus we included some closely related terminals (other species of *Agalychnis* and *Hyla*, the sister taxon of *Smilisca*) that had as many as possible homologous sequences in GenBank. The inclusion of these taxa resulted in a monophyletic Hylidae.

**APPENDIX 2.** Specimens, voucher codes, localities, and GenBank accession numbers of DNA sequences generated in this study. Acronyms follow Frost (2014) except for CBG (Centro de Biodiversidad y Genética, Cochabamba), JMP (José M. Padial field series), IDIR (Ignacio De la Riva field series), and MNCN/ADN (tissue collection at MNCN). Not all samples were sequenced for all markers because PCR or sequencing reactions did not work for all samples and all markers despite several attempts and/or sequence variation for the same marker among samples of the same species was low (*i.e.*, genetic p-distances < 1%) and those samples were recovered as sister taxa in exploratory analyses.

| Genus                  | Species                       | Voucher                        | Locality  | tRNA<br>-Phe | 12S      | tRNA<br>-Val | 16S                                  | tRNA<br>Leu |
|------------------------|-------------------------------|--------------------------------|---|--------------|----------|--------------|--------------------------------------|-------------|
| <i>Cryptobatrachus</i> | <i>fuhrmanni</i>              | MHUA A 5160                    | Colombia: Departamento Antioquia: Municipio Gómez Plata: La Clara (1085 m)  | —            | KR559912 | KR270398     | KR270398 +<br>KR270414               | —           |
| <i>Cryptobatrachus</i> | <i>remotus</i>                | MHNLS 17664 (MNCN/ADN 59450)   | Venezuela: Estado Zulia: Municipio Jesús Enrique Losada: sierra de Perijá, cuenca alta del río Socuy, fundo El Progreso (10°43'13.30"N, 72°29'16.60"W; ± 845)       | KR559913     | KR559913 | KR270399     | KR270399+<br>KR270415                | —           |
| <i>Cryptobatrachus</i> | <i>remotus</i>                | MHNLS 18853 (MNCN/ADN 59452)   | Venezuela: Estado Zulia: Municipio Rosario de Perijá: sierra de Perijá, cerro Las Antenas, caño detrás de la casa de las antenas (10°20'37"N, 72°33'41"W; ± 1467 m) | KR559914     | KR559914 | KR270400     | KR270400 +<br>KR270416 +<br>KR138379 | KR138379    |
| <i>Flectonotus</i>     | <i>fitzgeraldi</i>            | ZSM 1610 2006 (MNCN/ADN 51094) | Trinidad and Tobago: Tobago: Gilpin Trace entrance (11°17'01"N, 60°36'25"W; 495 m)  | —            | —        | KR270401     | KR270401+<br>KR270417                | —           |
| <i>Flectonotus</i>     | <i>pygmaeus</i>               | MHNLS 17478 (MNCN/ADN 51083)   | Venezuela: Estado Aragua: Río Cata (100 m)  | —            | KR559915 | KR270402     | KR270402+<br>KR270418                | —           |
| <i>Fritziana</i>       | <i>fissilis</i>               | MNRJ 62845                     | Brazil: Estado Rio de Janeiro: Município Nova Friburgo: Baixo Caledônia   | KR559916     | KR559916 | KR270403     | KR270403 +<br>KR270419               | —           |
| <i>Fritziana</i>       | <i>fissilis</i>               | MNRJ 74620                     | Brazil: Estado Rio de Janeiro: Parnaso  | —            | —        | —            | KR270420                             | —           |
| <i>Fritziana</i>       | aff. <i>fissilis</i><br>sp. 2 | MNRJ 44622                     | Brazil: Estado Rio de Janeiro: P.E. Três Picos, Cachoeiras de Macacu  | KR559917     | KR559917 | KR270404     | KR270404 +<br>KR270421               | —           |
| <i>Fritziana</i>       | aff. <i>fissilis</i><br>sp. 2 | MNRJ 56922                     | Brazil: Estado Rio de Janeiro: Vale da Pedra Branca, Cachoeiras de Macacu   | —            | —        | —            | KR270422                             | —           |
| <i>Fritziana</i>       | <i>goeldi</i>                 | MNRJ 34921                     | Brazil: Estado Espírito Santo: Estação Biológica Santa Lúcia, Santa Teresa  | KR559918     | KR559918 | KR270405     | KR270405 +<br>KR270423               | —           |
| <i>Fritziana</i>       | sp.                           | MNRJ 44592                     | Brazil: Estado Rio de Janeiro: Município Teresópolis: Serra dos órgãos  | —            | —        | KR270406     | KR270406+<br>KR270424                | —           |
| <i>Gastrotheca</i>     | <i>albolineata</i>            | MNRJ 54401                     | Brazil: Estado Rio de Janeiro: Vale da Pedra Branca, Cachoeiras de Macacu   | —            | KR559919 | KR270407     | KR270407+<br>KR270425                | —           |
| <i>Gastrotheca</i>     | <i>dummi</i>                  | MHUA A 4800                    | Colombia: Departamento Antioquia: Municipio Belmira: Páramo Belmira (4000 m)  | —            | —        | —            | KR270426                             | —           |

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| Genus               | Species           | Voucher  | Locality  | tRNA<br>-Phe | 12S      | tRNA<br>-Val | 16S                    | tRNA<br>Leu |
|---------------------|-------------------|--|---|--------------|----------|--------------|------------------------|-------------|
| <i>Gastrotheca</i>  | <i>ernestoi</i>   | MNRJ 57129   | Brazil: Estado Rio de Janeiro: Município Nova Friburgo  | KR559920     | KR559920 | KR270408     | KR270408+<br>KR270427  | —           |
| <i>Gastrotheca</i>  | <i>nicefori</i>   | MHUA A 5716  | Colombia: Departamento Antioquia: Municipio La Estrella:<br>La Blanquita (2345 m)                                     | —            | KR559921 | KR270409     | KR270409+<br>KR138380  | KR138380    |
| <i>Gastrotheca</i>  | sp. 1             | IDIR 4073<br>(MNCN/ADN 566)  | Bolivia: Departamento Cochabamba: Aguirre (17°19'22"S,<br>65°43'01"W; 4192 m)   | —            | —        | —            | KR270428               | —           |
| <i>Gastrotheca</i>  | sp. 3             | ZFMK 66954 (MNCN/ADN<br>25033)   | Bolivia: Departamento Cochabamba: Incachaca (17°15'S,<br>65°49'W; 2300 m)   | —            | —        | —            | KR270429               | —           |
| <i>Gastrotheca</i>  | sp. 3             | MNCN 43052 (MNCN/ADN<br>2474)  | Bolivia: Departamento Cochabamba: Provincia Chapare:<br>Camino Tubos Penstock (17°12'21.6"S, 65°50'14.2"W; 2123<br>m) | —            | —        | —            | —                      | —           |
| <i>Gastrotheca</i>  | <i>testudinea</i> | CBG 774  | Bolivia: Departamento La Paz: Pílon Lajas, Boquerón (1000<br>m)   | —            | —        | —            | KR270430               | —           |
| <i>Hemiphractus</i> | <i>helioi</i>     | MHNCP 9063   | Peru: Departamento Loreto: Requena (4°59'13.24"S,<br>73°59'4.03"W, 114 m)   | KR559922     | KR559922 | KR270410     | KR270410+<br>KR270431  | —           |
| <i>Hemiphractus</i> | <i>scutatus</i>   | JMP 2150 (tissue sample,<br>specimen not collected,<br>MNCN/ADN 46913) | Colombia: Departamento Amazonas: Leticia: Km 11 carretera<br>(4°6'28.31"S, 69°57'2.37"W; 100 m)                       | KR559923     | KR559923 | KR270411     | KR270411+<br>KR270432  | —           |
| <i>Stefania</i>     | <i>evansi</i>     | IRSNB 14586 (MNCN/ADN<br>51121)  | Guyana: Potaro-Siparuni district: Muri Muri trail, Kaieteur<br>National Park (5°10'N, 59°30'W; 430 m)                 | —            | KR559924 | KR270412     | KR270412 +<br>KR270433 | —           |
| <i>Stefania</i>     | <i>scalae</i>     | MHNLS 17152 (MNCN/ADN<br>50654)  | Venezuela: Estado Bolívar: km 127 on the El Dorado-Santa<br>Helena de Uairén road (860 m)                             | —            | KR559925 | KR270413     | KR270413 +<br>KR270434 | —           |

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## APPENDIX 2. (Continued)

| Genus                  | Species                       | Voucher  | ND1          | COI          | cytb     | CXCR4    | POMC     | Rag1 (1) | Rag1(2)  | Rho      | SLC8A1   | SLC8A3   | Tyr      |
|------------------------|-------------------------------|--|--------------|--------------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
| <i>Cryptobatrachus</i> | <i>fuhrmanni</i>              | MHUA A 5160  | —            | —            | —        | —        | KR270358 | KR138418 | —        | —        | —        | —        | —        |
| <i>Cryptobatrachus</i> | <i>remotus</i>                | MHNLS 17664<br>(MNCN/ADN 59450)  | —            | —            | —        | KR138403 | KR270359 | KR138419 | KR138393 | —        | KR138381 | KR270374 | KR270386 |
| <i>Cryptobatrachus</i> | <i>remotus</i>                | MHNLS 18853<br>(MNCN/ADN 59452)  | KR13837<br>9 | —            | —        | KR138404 | KR270360 | KR138420 | KR138394 | —        | KR138382 | KR270375 | KR270387 |
| <i>Flectonotus</i>     | <i>fitzgeraldi</i>            | ZSM 1610 2006<br>(MNCN/ADN 51094)                                      | —            | —            | —        | KR138405 | KR270361 | KR138421 | KR138395 | —        | KR138383 | KR270376 | KR270388 |
| <i>Flectonotus</i>     | <i>pygmaeus</i>               | MHNLS 17478<br>(MNCN/ADN 51083)  | —            | —            | —        | —        | —        | —        | —        | —        | —        | —        | —        |
| <i>Fritziana</i>       | <i>fissilis</i>               | MNRJ 62845   | —            | —            | —        | KR138406 | —        | —        | —        | —        | KR138384 | —        | KR270389 |
| <i>Fritziana</i>       | <i>fissilis</i>               | MNRJ 74620   | —            | —            | —        | —        | —        | —        | —        | —        | —        | —        | —        |
| <i>Fritziana</i>       | aff. <i>fissilis</i><br>sp. 2 | MNRJ 44622   | —            | —            | —        | KR138407 | KR270362 | KR138422 | KR138396 | —        | KR138385 | KR270377 | KR270390 |
| <i>Fritziana</i>       | aff. <i>fissilis</i><br>sp. 2 | MNRJ 56922   | —            | —            | —        | —        | —        | —        | —        | —        | —        | —        | —        |
| <i>Fritziana</i>       | <i>goeldi</i>                 | MNRJ 34921   | —            | —            | —        | KR138408 | KR270363 | —        | —        | —        | KR138386 | KR270378 | KR270391 |
| <i>Fritziana</i>       | sp.                           | MNRJ 44592   | —            | —            | —        | KR138409 | KR270364 | —        | —        | —        | —        | KR270379 | —        |
| <i>Gastrotheca</i>     | <i>albolineata</i>            | MNRJ 54401   | —            | —            | —        | KR138410 | KR270365 | KR138423 | KR138397 | —        | KR138387 | KR270380 | KR270392 |
| <i>Gastrotheca</i>     | <i>dunni</i>                  | MHUA A 4800  | —            | —            | —        | —        | —        | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca</i>     | <i>ernestoi</i>               | MNRJ 57129   | —            | —            | —        | KR138411 | KR270366 | KR138424 | KR138398 | —        | KR138388 | KR270381 | KR270393 |
| <i>Gastrotheca</i>     | <i>nicefori</i>               | MHUA A 5716  | KR13838<br>0 | —            | —        | —        | KR270367 | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca</i>     | sp. 1                         | IDIR 4073<br>(MNCN/ADN 566)  | —            | —            | KR138416 | —        | —        | —        | —        | KR270372 | —        | —        | —        |
| <i>Gastrotheca</i>     | sp. 3                         | ZFMK 66954<br>(MNCN/ADN 25033)   | —            | —            | —        | —        | —        | —        | —        | —        | —        | —        | —        |
| <i>Gastrotheca</i>     | sp. 3                         | MNCN 43052<br>(MNCN/ADN 2474)  | —            | —            | KR138417 | —        | —        | —        | —        | KR270373 | —        | —        | —        |
| <i>Gastrotheca</i>     | <i>testudinea</i>             | CBG 774  | —            | —            | KR559927 | —        | —        | —        | —        | —        | —        | —        | —        |
| <i>Hemiphractus</i>    | <i>helioi</i>                 | MHNCP 9063   | —            | —            | —        | KR138412 | KR270368 | KR138425 | KR138399 | —        | KR138389 | KR270382 | KR270394 |
| <i>Hemiphractus</i>    | <i>scutatus</i>               | JMP 2150 (tissue sample,<br>specimen not collected,<br>MNCN/ADN 46913) | —            | KR559<br>926 | —        | KR138413 | KR270369 | KR138426 | KR138400 | —        | KR138390 | KR270383 | KR270395 |
| <i>Stefania</i>        | <i>evansi</i>                 | IRSNB 14586<br>(MNCN/ADN 51121)  | —            | —            | —        | KR138414 | KR270370 | KR138427 | KR138401 | —        | KR138391 | KR270384 | KR270396 |
| <i>Stefania</i>        | <i>scalae</i>                 | MHNLS 17152<br>(MNCN/ADN 50654)  | —            | —            | —        | KR138415 | KR270371 | KR138428 | KR138402 | —        | KR138392 | KR270385 | KR270397 |

**APPENDIX 3.** Primers used in this study. We sequenced genes SLC8A1 and SLC8A3 in two partially overlapping fragments by combining pairs F1-R1 and F2-R2 respectively. RAG1 Amp-Hemi and RAG1 R182/R270 correspond to two non-overlapping fragments of the gene RAG1. F = Forward, R = Reverse. Primers not included in the table are listed in Guayasamin *et al.* (2008).

| Marker         | Primer name | Source  | Primer sequence (5'–3')       |
|----------------|-------------|---|-------------------------------|
| CXCR4          | CXC-F1      | This work   | TCCAGAACCATGACTGATAAGTA       |
|                | CXC-R1      | This work   | CAAGGCTTCTGTGATGGAGATCC       |
| SLC8A1         | NCX-F1      | This work   | CATCTCAAGAAAAAGAGATAAC        |
|                | NCX-R1      | This work   | ACTTGATAGTTAGCCAGCTCAA        |
|                | NCX-F2      | This work   | AGGAGGCAAGAAGAGATATGGC        |
|                | NCX-R2      | This work   | ATAGTAACTGTGGYYGTTGAGG        |
| SLC8A3         | SLC-F1      | This work   | TAACRTCRCRCAAGAACGRGAAAT      |
|                | SLC-R1      | This work   | CCATCTAGAAAATGAGAATTCA        |
|                | SLC-F2      | This work   | GGTGGCRGACCGACGTCTTCTC        |
|                | SLC-R2      | This work   | AAGATGTCATCATCAATAATCC        |
| POMC           | POMC-1      | Blackburn & Duellman (2013)                             | GAATGTATYAAAGMMTGCAAGATGGWCCT |
|                | POMC-7      | Blackburn & Duellman (2013)                             | TGGCATT TTTGAAAAGAGTCAT       |
| RAG1 Amp-Hemi  | Amp-RAG-1 F | Wiens <i>et al.</i> (2007), Blackburn & Duellman (2013) | AGCTGCAGYCARTACCAYAAATGTA     |
|                | Hemi-RAG1-R | Wiens <i>et al.</i> (2007), Blackburn & Duellman (2013) | CTCTGCAGCATTTCCAATGTCAC       |
| RAG1 R182/R270 | R182        | Heinicke <i>et al.</i> (2009)                           | GCCATAACTGCTGGAGCATYAT        |
|                | R270:       | Heinicke <i>et al.</i> (2009)                           | AGYAGATGTTGCCTGGGTCTTC        |



**APPENDIX 4.** References used to code life reproductive modes of outgroup taxa.

| Taxa                                  | Reference  |
|---------------------------------------|--|
| <i>Acris crepitans</i>                | Johnson (1991)   |
| <i>Adenomera andreae</i>              | Crump (1974), Haddad & Prado (2005)                        |
| <i>Adenomera hylaedactyla</i>         | Hödl (1990), Haddad & Prado (2005)                         |
| <i>Agalychnis annae</i>               | Savage (2002)  |
| <i>Agalychnis callidryas</i>          | Warketin (1999), Savage (2002)                             |
| <i>Allobates femoralis</i>            | Weygold (1980)   |
| <i>Allophryne ruthveni</i>            | Kok & Kalamandeen (2008)                                   |
| <i>Alsodes neuquensis</i>             | Lavilla (1988)   |
| <i>Amazophrynella minuta</i>          | Duellman & Lynch (1969)                                    |
| <i>Amietophrynus brauni</i>           | Sprague & Zimkus (2011)                                    |
| <i>Atelognathus patagonicus</i>       | Martinazzo <i>et al.</i> (2011)                            |
| <i>Barycholos pulcher</i>             | Heyer (1969)   |
| <i>Barycholos ternetzi</i>            | Caramaschi & Pombal Jr. (2001)                             |
| <i>Batrachyla leptopus</i>            | Formas <i>et al.</i> (1976)                                |
| <i>Brachycephalus alipioi</i>         | Pombal Jr. & Gasparini (2006)                              |
| <i>Brachycephalus ephippium</i>       | Pombal Jr. (1999)  |
| <i>Bryophryne cophites</i>            | Lynch (1975)   |
| <i>Bufo japonicus</i>                 | Iwai & Kagaya (2005)                                       |
| <i>Calyptocephalella gayi</i>         | Diaz & Valencia (1985), Castañeda <i>et al.</i> (2006)     |
| <i>Ceratophrys cornuta</i>            | Duellman & Lizana (1994)                                   |
| <i>Ceratophrys cranwelli</i>          | Vera Candioti (2005)                                       |
| <i>Ceratophrys ornata</i>             | Natale <i>et al.</i> (2010)                                |
| <i>Chacophrys pierottii</i>           | Quinzio <i>et al.</i> (2006)                               |
| <i>Colostethus pratti</i>             | Lynch (2006)   |
| <i>Craugastor augusti</i>             | Jameson (1950)   |
| <i>Craugastor podiciferus</i>         | Schlaepfer & Figueroa-Sandy (1998)                         |
| <i>Craugastor punctariolus</i>        | Fenolio <i>et al.</i> (2010), Konstant (2007)              |
| <i>Craugastor ranoides</i>            | Sunyer <i>et al.</i> (2009)                                |
| <i>Craugastor rhodopis</i>            | Campbell (1998)  |
| <i>Crossodactylus schmidti</i>        | Faivovich (1998)   |
| <i>Cycloramphus acangatan</i>         | Dixo & Verdade (2006)                                      |
| <i>Cycloramphus boraceiensis</i>      | Haddad & Prado (2005)                                      |
| <i>Dendropsophus nanus</i>            | Lavilla (1990)   |
| <i>Diasporus diastema</i>             | Dunn (1937), Ovaska & R, (2001)                            |
| <i>Duttaphrynus melanostictus</i>     | Mogali <i>et al.</i> (2011)                                |
| <i>Edalorhina perezii</i>             | Schlüter (1990)  |
| <i>Eleutherodactylus cooki</i>        | Joglar <i>et al.</i> (1996), Burggren <i>et al.</i> (2003) |
| <i>Eleutherodactylus coqui</i>        | Townsend & Stewart (1985)                                  |
| <i>Eleutherodactylus marnockii</i>    | Jameson (1955)   |
| <i>Eleutherodactylus planirostris</i> | Goin (1947), Olson <i>et al.</i> (2012)                    |
| <i>Eleutherodactylus thorectes</i>    | Martínez <i>et al.</i> (2011)                              |
| <i>Eleutherodactylus tonyi</i>        | Stuart <i>et al.</i> (2008)                                |

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**APPENDIX 4.** (Continued)

| Taxa                                 | Reference   |
|--------------------------------------|---|
| <i>Engystomops petersi</i>           | Crump (1974)  |
| <i>Engystomops pustulosus</i>        | Montealegre-Delgado <i>et al.</i> (2013)              |
| <i>Espadarana prosoblepon</i>        | Hoffman (2010)  |
| <i>Eupsophus roseus</i>              | Formas & Pugin (1978)                                 |
| <i>Fejervarya limnocharis</i>        | Wu & Kam (2009)                                       |
| <i>Haddadus binotatus</i>            | Canedo & Rickli (2006), Hartmann <i>et al.</i> (2010) |
| <i>Holoaden luederwaldti</i>         | Martins (2010)  |
| <i>Hyla arenicolor</i>               | Zweifel (1961)  |
| <i>Hyla chinensis</i>                | Hsu <i>et al.</i> (2006)                              |
| <i>Hyla cinerea</i>                  | Roth & Jackson (1987)                                 |
| <i>Hylodes phyllodes</i>             | Weber & Caramaschi (2013)                             |
| <i>Hylorina sylvatica</i>            | Cárdenas-Rojas <i>et al.</i> (2007)                   |
| <i>Hyloxalus chlorocraspedus</i>     | Caldwell (2005)                                       |
| <i>Hypodactylus brunneus</i>         | Lynch (1975)  |
| <i>Hypsiboas boans</i>               | Duellman (1970), Lynch (2006)                         |
| <i>Hypsiboas lanciformis</i>         | Lynch & Suárez (2011)                                 |
| <i>Insuetophrynus acarpicus</i>      | Formas <i>et al.</i> (1980)                           |
| <i>Ischocnema guentheri</i>          | Lynn & Lutz (1946), Giaretta & Facure (2008)          |
| <i>Lepidobatrachus laevis</i>        | Ruibal & Thomas (1988)                                |
| <i>Leptodactylus latrans</i>         | Rodrigues (2008), Kwet <i>et al.</i> (2010)           |
| <i>Leptodactylus melanonotus</i>     | Hoffmann (2006)                                       |
| <i>Limnodynastes salmini</i>         | Davies & Watson (1994)                                |
| <i>Limnomedusa macroglossa</i>       | Kaefer <i>et al.</i> (2009)                           |
| <i>Lithodytes lineatus</i>           | Lamar & Wild (1995)                                   |
| <i>Litoria caerulea</i>              | Cabrera-Guzmán <i>et al.</i> (2013)                   |
| <i>Litoria infrafrenata</i>          | Banks <i>et al.</i> (1983)                            |
| <i>Macrogenioglottus alipioi</i>     | Lisboa <i>et al.</i> (2011)                           |
| <i>Mannophryne trinitatis</i>        | Kenny (1969), Downie <i>et al.</i> (2001)             |
| <i>Megaelosia goeldii</i>            | Nuin (2003)   |
| <i>Melanophryniscus klappenbachi</i> | Kurth <i>et al.</i> (2013), Haad <i>et al.</i> (2011) |
| <i>Myersiohyla kanaima</i>           | MacCulloch & Amy Lathrop (2005)                       |
| <i>Noblella lochites</i>             | Lynch (1976)  |
| <i>Nymphargus bejaranoi</i>          | Köhler (2000), Aguayo (2009)                          |
| <i>Odontophrynus achalensis</i>      | Haas (2003), González <i>et al.</i> (2014)            |
| <i>Oreobates cruralis</i>            | Padial <i>et al.</i> (2012)                           |
| <i>Oreobates saxatilis</i>           | Duellman (1990)                                       |
| <i>Paratelmatobius cardosoi</i>      | Pombal Jr. & Haddad (1999)                            |
| <i>Phrynopus bracki</i>              | Hedges (1990)   |
| <i>Phyllodytes luteolus</i>          | Giaretta (1996)                                       |
| <i>Physalaemus cuvieri</i>           | Bokermann (1962), Rossa-Feres <i>et al.</i> (2006)    |
| <i>Physalaemus gracilis</i>          | Langone (1989)  |
| <i>Pleurodema brachyops</i>          | Molina (2004 "2002")                                  |

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**APPENDIX 4.** (Continued)

| Taxa                               | Reference                             |
|------------------------------------|---------------------------------------|
| <i>Pleurodema diplolister</i>      | Cardoso & Arzabe (1993)               |
| <i>Pristimantis cruentus</i>       | Myers (1969)                          |
| <i>Pristimantis curtipes</i>       | Lynch (1981)                          |
| <i>Pristimantis gaigeae</i>        | Hill <i>et al.</i> (2010)             |
| <i>Pristimantis ridens</i>         | Sunyer <i>et al.</i> (2009)           |
| <i>Proceratophrys avelinoi</i>     | De Sá & Langone (2002)                |
| <i>Pseudis minutus</i>             | Melchioris <i>et al.</i> (2004)       |
| <i>Pseudopaludicola falcipes</i>   | Laufer & Barreneche (2008)            |
| <i>Psychrophrynella wettsteini</i> | Ergueta (1993), De la Riva (2007)     |
| <i>Rheobates palmatus</i>          | Dunn (1944), Anganoy-Criollo (2013)   |
| <i>Rhinella arenarum</i>           | Bionda <i>et al.</i> (2012)           |
| <i>Rhinoderma darwini</i>          | Jorquera <i>et al.</i> (1982)         |
| <i>Rupirana cardosoi</i>           | Acuña & Lugli (2009)                  |
| <i>Scinax staufferi</i>            | Savage (2002)                         |
| <i>Smilisca baudinii</i>           | Torres-Orozco <i>et al.</i> (2002)    |
| <i>Sooglossus thomasseti</i>       | Gerlach (2007)                        |
| <i>Strabomantis biporcatus</i>     | Heatwole (1962)                       |
| <i>Strabomantis bufoniformis</i>   | Castro-Herrera <i>et al.</i> (2012)   |
| <i>Telmatobius truebae</i>         | Aguilar <i>et al.</i> (2007)          |
| <i>Thoropa miliaris</i>            | Barth (1956), Giaretta & Gomes (2004) |
| <i>Trachycephalus typhonius</i>    | Savage (2002)                         |
| <i>Uperoleia laevigata</i>         | Tyler (1994)                          |
| <i>Yunganastes fraudator</i>       | De la Riva & Lynch (1997)             |
| <i>Zachaenus parvulus</i>          | Lutz (1947), Haddad & Prado (2005)    |

**APPENDIX 5.** Unambiguous transformations inferred in this study for the supraspecific taxa reported in the Systematics section. Because the relationships among *Cryptobatrachus* are ambiguous (a polytomy in our strict consensus tree) the transformations reported herein are only shared among some of the optimal trees.

|                        |                      |                      |
|------------------------|----------------------|----------------------|
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| Char. 46: 0 --> 4      | Char. 5992: 0 --> 2  | Char. 9906: 2 --> 1  |
| Char. 83: 0 --> 2      | Char. 6021: 1 --> 3  | Char. 10063: 1 --> 3 |
| Char. 519: 1 --> 4     | Char. 6180: 3 --> 1  | Char. 10136: 3 --> 1 |
| Char. 810: 0 --> 3     | Char. 6229: 3 --> 1  | Char. 10253: 0 --> 2 |
| Char. 819: 4 --> 0     | Char. 8093: 1 --> 3  | Char. 10371: 3 --> 1 |
| Char. 1249: 3 --> 1    | Char. 8499: 3 --> 2  | Char. 10424: 1 --> 0 |
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| Char. 3862: 0 --> 1    | Char. 9349: 1 --> 3  | Char. 12248: 0 --> 3 |

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#### **Cryptobatrachinae**

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Char. 17737: 1 --> 4  
Char. 17927: 1 --> 3

#### ***Cryptobatrachus***

Some trees:

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*Flectonotus*

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Char. 12114: 0 --> 3

Char. 12115: 1 --> 3  
Char. 12133: 3 --> 1  
Char. 12143: 0 --> 2  
Char. 12160: 0 --> 2  
Char. 12222: 0 --> 3  
Char. 12233: 1 --> 0  
Char. 12273: 0 --> 3  
Char. 12275: 0 --> 3  
Char. 12305: 1 --> 0  
Char. 12335: 4 --> 2  
Char. 12340: 1 --> 0  
Char. 12353: 2 --> 1  
Char. 12354: 2 --> 1  
Char. 12409: 2 --> 1  
Char. 12431: 0 --> 1  
Char. 12473: 1 --> 3  
Char. 12510: 3 --> 1  
Char. 12530: 3 --> 0  
Char. 13076: 1 --> 3  
Char. 13142: 0 --> 2  
Char. 13149: 0 --> 3  
Char. 13182: 1 --> 3  
Char. 13201: 1 --> 3  
Char. 13202: 1 --> 3  
Char. 13206: 3 --> 1  
Char. 13296: 3 --> 1  
Char. 13326: 1 --> 3  
Char. 13329: 1 --> 0  
Char. 13392: 0 --> 1  
Char. 13409: 2 --> 0  
Char. 13426: 2 --> 0  
Char. 13434: 3 --> 0  
Char. 13462: 3 --> 1  
Char. 13468: 0 --> 3  
Char. 13497: 2 --> 0  
Char. 13737: 0 --> 3  
Char. 13744: 2 --> 0  
Char. 13759: 3 --> 1  
Char. 13784: 1 --> 0  
Char. 13803: 3 --> 0  
Char. 13811: 3 --> 1  
Char. 13829: 3 --> 1  
Char. 13860: 1 --> 3  
Char. 13869: 2 --> 0  
Char. 13899: 3 --> 1  
Char. 13911: 0 --> 2  
Char. 13923: 0 --> 2  
Char. 14000: 2 --> 0  
Char. 14073: 1 --> 0  
Char. 14082: 0 --> 1  
Char. 14089: 2 --> 0  
Char. 14099: 0 --> 2  
Char. 14242: 2 --> 3  
Char. 14302: 2 --> 3  
Char. 14354: 2 --> 0  
Char. 14411: 2 --> 0  
Char. 14430: 0 --> 2

Char. 14540: 0 --> 2  
Char. 14555: 1 --> 0  
Char. 14556: 3 --> 1  
Char. 17655: 0 --> 2  
Char. 17688: 3 --> 0  
Char. 17736: 3 --> 4  
Char. 17741: 3 --> 1  
Char. 17745: 3 --> 1  
Char. 17757: 0 --> 2  
Char. 17801: 3 --> 0  
Char. 17804: 3 --> 1

#### **Hemiphractinae**

Char. 11: 0 --> 1  
Char. 19: 0 --> 1  
Char. 38: 0 --> 2  
Char. 203: 0 --> 1  
Char. 235: 0 --> 3  
Char. 359: 0 --> 1  
Char. 409: 3 --> 1  
Char. 459: 3 --> 0  
Char. 571: 0 --> 3  
Char. 681: 3 --> 1  
Char. 781: 2 --> 0  
Char. 1990: 3 --> 0  
Char. 2210: 3 --> 0  
Char. 2408: 3 --> 1  
Char. 2450: 0 --> 3  
Char. 2551: 0 --> 3  
Char. 3130: 1 --> 0  
Char. 3184: 0 --> 1  
Char. 3384: 3 --> 1  
Char. 3439: 0 --> 3  
Char. 4625: 3 --> 1  
Char. 5496: 1 --> 3  
Char. 5498: 0 --> 2  
Char. 6047: 2 --> 0  
Char. 6132: 3 --> 1  
Char. 6167: 3 --> 0  
Char. 6169: 0 --> 1  
Char. 6185: 4 --> 2  
Char. 6224: 0 --> 2  
Char. 8591: 2 --> 0  
Char. 9551: 2 --> 1  
Char. 9815: 4 --> 3  
Char. 9882: 2 --> 1  
Char. 10075: 2 --> 0  
Char. 10116: 2 --> 0  
Char. 10211: 2 --> 0  
Char. 10305: 0 --> 3  
Char. 10472: 3 --> 1  
Char. 10569: 3 --> 1  
Char. 11896: 0 --> 2  
Char. 11919: 4 --> 0  
Char. 11920: 4 --> 0  
Char. 12131: 0 --> 2  
Char. 12319: 4 --> 0

Char. 12606: 0 --> 1  
Char. 12647: 1 --> 0  
Char. 12923: 3 --> 0  
Char. 12970: 0 --> 2  
Char. 12978: 3 --> 1  
Char. 13169: 1 --> 0  
Char. 13787: 0 --> 3  
Char. 14236: 1 --> 3  
Char. 14239: 3 --> 1  
Char. 14245: 1 --> 3  
Char. 14423: 3 --> 0  
Char. 14708: 3 --> 0  
Char. 14959: 1 --> 3  
Char. 15143: 0 --> 3  
Char. 15682: 0 --> 2  
Char. 16956: 1 --> 3  
Char. 17688: 3 --> 1  
Char. 17777: 1 --> 3  
Char. 17820: 0 --> 2  
Char. 18034: 2 --> 0  
Char. 18303: 3 --> 1

*Fritziana*

Char. 8: 1 --> 0  
Char. 22: 0 --> 1  
Char. 25: 0 --> 1  
Char. 34: 1 --> 0  
Char. 45: 3 --> 2  
Char. 47: 1 --> 2  
Char. 95: 3 --> 0  
Char. 108: 3 --> 1  
Char. 238: 3 --> 1  
Char. 279: 3 --> 1  
Char. 332: 0 --> 2  
Char. 351: 0 --> 1  
Char. 414: 0 --> 3  
Char. 553: 4 --> 1  
Char. 571: 3 --> 4  
Char. 600: 0 --> 3  
Char. 626: 4 --> 3  
Char. 723: 0 --> 1  
Char. 758: 0 --> 2  
Char. 810: 3 --> 1  
Char. 815: 3 --> 0  
Char. 819: 0 --> 1  
Char. 864: 0 --> 2  
Char. 872: 3 --> 1  
Char. 940: 0 --> 1  
Char. 1033: 0 --> 1  
Char. 1068: 1 --> 3  
Char. 1088: 1 --> 2  
Char. 1112: 0 --> 3  
Char. 1193: 0 --> 3  
Char. 1209: 3 --> 1  
Char. 1258: 0 --> 1  
Char. 1508: 0 --> 1  
Char. 1547: 2 --> 0

Char. 1893: 0 --> 3  
Char. 1949: 1 --> 4  
Char. 1970: 1 --> 0  
Char. 2011: 0 --> 1  
Char. 2395: 1 --> 4  
Char. 2462: 4 --> 1  
Char. 2496: 3 --> 1  
Char. 2543: 3 --> 0  
Char. 2623: 0 --> 1  
Char. 2629: 3 --> 2  
Char. 2774: 3 --> 1  
Char. 2792: 0 --> 4  
Char. 2872: 3 --> 0  
Char. 2927: 3 --> 1  
Char. 2933: 3 --> 1  
Char. 2942: 0 --> 1  
Char. 2967: 2 --> 0  
Char. 3041: 0 --> 1  
Char. 3218: 4 --> 1  
Char. 3250: 0 --> 3  
Char. 3412: 0 --> 3  
Char. 3438: 4 --> 0  
Char. 3457: 3 --> 1  
Char. 3476: 4 --> 2  
Char. 3501: 3 --> 0  
Char. 3719: 0 --> 1  
Char. 3754: 3 --> 1  
Char. 3837: 0 --> 3  
Char. 3889: 0 --> 3  
Char. 3902: 3 --> 0  
Char. 3935: 3 --> 1  
Char. 4022: 4 --> 1  
Char. 4071: 3 --> 1  
Char. 4106: 0 --> 2  
Char. 4164: 0 --> 2  
Char. 4172: 0 --> 1  
Char. 4177: 0 --> 3  
Char. 4212: 4 --> 2  
Char. 4245: 1 --> 2  
Char. 4250: 2 --> 4  
Char. 4258: 0 --> 1  
Char. 4275: 1 --> 3  
Char. 4288: 0 --> 3  
Char. 4297: 0 --> 3  
Char. 4396: 3 --> 1  
Char. 4490: 4 --> 1  
Char. 4603: 2 --> 0  
Char. 4698: 0 --> 2  
Char. 4898: 3 --> 1  
Char. 4949: 3 --> 1  
Char. 5081: 4 --> 0  
Char. 5247: 4 --> 1  
Char. 5248: 4 --> 1  
Char. 5301: 4 --> 3  
Char. 5398: 4 --> 2  
Char. 5409: 3 --> 4  
Char. 5479: 0 --> 3

Char. 5495: 0 --> 2  
Char. 5576: 4 --> 1  
Char. 5715: 3 --> 1  
Char. 5767: 3 --> 1  
Char. 5808: 1 --> 3  
Char. 5812: 0 --> 2  
Char. 5832: 2 --> 0  
Char. 9523: 1 --> 3  
Char. 9542: 3 --> 1  
Char. 9566: 3 --> 1  
Char. 9754: 1 --> 3  
Char. 9812: 1 --> 4  
Char. 9833: 1 --> 3  
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Char. 9885: 1 --> 0  
Char. 9892: 0 --> 3  
Char. 9929: 2 --> 3  
Char. 9938: 02 --> 1  
Char. 10036: 3 --> 2  
Char. 10060: 3 --> 1  
Char. 10090: 3 --> 1  
Char. 10097: 2 --> 0  
Char. 10106: 2 --> 0  
Char. 10114: 3 --> 1  
Char. 10115: 2 --> 0  
Char. 10127: 2 --> 3  
Char. 10671: 0 --> 1  
Char. 10786: 2 --> 1  
Char. 11186: 2 --> 0  
Char. 11246: 1 --> 3  
Char. 11440: 3 --> 1  
Char. 11457: 0 --> 1  
Char. 11498: 0 --> 1  
Char. 11517: 3 --> 1  
Char. 11541: 0 --> 3  
Char. 11546: 1 --> 3  
Char. 11601: 2 --> 0  
Char. 11637: 1 --> 3  
Char. 11851: 0 --> 1  
Char. 11857: 3 --> 1  
Char. 13005: 3 --> 2  
Char. 13132: 1 --> 3  
Char. 13192: 1 --> 0  
Char. 13236: 1 --> 0  
Char. 13326: 1 --> 3  
Char. 13364: 2 --> 0  
Char. 13481: 0 --> 1  
Char. 13489: 2 --> 0  
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Char. 16559: 1 --> 0  
Char. 16634: 3 --> 1  
Char. 16662: 1 --> 2  
Char. 16727: 3 --> 2

Char. 16742: 3 --> 1  
Char. 17151: 0 --> 2  
Char. 17160: 0 --> 2  
Char. 17437: 2 --> 0  
Char. 17655: 0 --> 2  
Char. 17680: 4 --> 3  
Char. 17707: 3 --> 1  
Char. 17723: 0 --> 2  
Char. 17765: 3 --> 1  
Char. 17768: 3 --> 1  
Char. 17861: 1 --> 3  
Char. 17866: 3 --> 1  
Char. 17882: 2 --> 3  
Char. 17891: 0 --> 2  
Char. 17901: 3 --> 1  
Char. 17951: 2 --> 0  
Char. 17966: 0 --> 2  
Char. 17967: 2 --> 0  
Char. 18009: 3 --> 0  
Char. 18059: 0 --> 2  
Char. 18067: 2 --> 0  
Char. 18077: 2 --> 1  
Char. 18164: 1 --> 0  
Char. 18231: 2 --> 0  
Char. 18262: 0 --> 3  
Char. 18268: 3 --> 0  
Char. 18269: 2 --> 0  
Char. 18284: 0 --> 1

***Gastrotheca***

Char. 40: 01 --> 3  
Char. 44: 1 --> 0  
Char. 144: 0 --> 2  
Char. 344: 1 --> 3  
Char. 681: 1 --> 4  
Char. 702: 1 --> 3  
Char. 788: 1 --> 0  
Char. 804: 1 --> 3  
Char. 819: 0 --> 4  
Char. 1038: 0 --> 3  
Char. 1073: 1 --> 4  
Char. 1644: 0 --> 3  
Char. 1714: 3 --> 0  
Char. 1896: 4 --> 1  
Char. 1953: 1 --> 3  
Char. 2111: 0 --> 1  
Char. 2181: 0 --> 1  
Char. 2191: 0 --> 3  
Char. 2357: 4 --> 3  
Char. 2365: 0 --> 3  
Char. 2516: 1 --> 0  
Char. 2557: 0 --> 3  
Char. 2583: 13 --> 0  
Char. 2601: 3 --> 0  
Char. 2708: 4 --> 3  
Char. 2739: 1 --> 0  
Char. 2749: 4 --> 0  
Char. 3184: 1 --> 0

Char. 3311: 1 --> 3  
Char. 3431: 1 --> 0  
Char. 3447: 0 --> 1  
Char. 3542: 0 --> 3  
Char. 3548: 1 --> 0  
Char. 3551: 1 --> 0  
Char. 3647: 4 --> 1  
Char. 3673: 3 --> 0  
Char. 3754: 3 --> 0  
Char. 3894: 1 --> 3  
Char. 4061: 0 --> 1  
Char. 4164: 0 --> 1  
Char. 4189: 2 --> 0  
Char. 4264: 1 --> 4  
Char. 4998: 4 --> 0  
Char. 5000: 4 --> 0  
Char. 5078: 4 --> 3  
Char. 5179: 4 --> 0  
Char. 5180: 4 --> 0  
Char. 5217: 4 --> 3  
Char. 6072: 1 --> 0  
Char. 6095: 0 --> 4  
Char. 6126: 4 --> 3  
Char. 6127: 4 --> 3  
Char. 6177: 1 --> 0  
Char. 6219: 1 --> 0  
Char. 6229: 1 --> 3  
Char. 10287: 1 --> 3  
Char. 10301: 4 --> 1  
Char. 10316: 0 --> 1  
Char. 10374: 1 --> 0  
Char. 10607: 1 --> 2  
Char. 11982: 3 --> 4  
Char. 12002: 4 --> 0  
Char. 12030: 0 --> 3  
Char. 12076: 0 --> 1  
Char. 12133: 3 --> 0  
Char. 12213: 1 --> 0  
Char. 12231: 1 --> 3  
Char. 12307: 1 --> 0  
Char. 12361: 3 --> 0  
Char. 12454: 1 --> 3  
Char. 12475: 0 --> 2  
Char. 12480: 1 --> 0  
Char. 12513: 0 --> 3  
Char. 12548: 1 --> 0  
Char. 12607: 0 --> 1  
Char. 13042: 0 --> 1  
Char. 13068: 0 --> 1  
Char. 13198: 3 --> 1  
Char. 13212: 0 --> 2  
Char. 13247: 3 --> 1  
Char. 13302: 0 --> 2  
Char. 13335: 0 --> 2  
Char. 13390: 3 --> 1  
Char. 13391: 1 --> 0  
Char. 13441: 3 --> 1

Char. 13487: 3 --> 1  
Char. 13681: 0 --> 2  
Char. 13706: 0 --> 2  
Char. 13784: 1 --> 3  
Char. 13787: 3 --> 0  
Char. 13906: 3 --> 1  
Char. 14016: 3 --> 1  
Char. 14047: 0 --> 3  
Char. 14152: 3 --> 1  
Char. 14359: 3 --> 1  
Char. 14396: 3 --> 1  
Char. 14493: 3 --> 2  
Char. 14527: 3 --> 1  
Char. 14610: 3 --> 1  
Char. 14611: 1 --> 0  
Char. 14616: 0 --> 3  
Char. 14690: 0 --> 1  
Char. 14723: 3 --> 1  
Char. 14831: 3 --> 0  
Char. 14959: 3 --> 1  
Char. 17693: 3 --> 0  
Char. 17750: 1 --> 0  
Char. 17764: 0 --> 3  
Char. 17767: 3 --> 0  
Char. 18034: 0 --> 2  
Char. 18133: 1 --> 0  
Char. 18200: 1 --> 3  
Char. 18253: 1 --> 3  
Char. 18284: 0 --> 3  
Char. 18291: 3 --> 2  
Char. 18371: 2 --> 0

***G. fissipes* species group**

Char. 241: 4 --> 1  
Char. 243: 0 --> 3  
Char. 355: 0 --> 1  
Char. 372: 1 --> 0  
Char. 516: 1 --> 4  
Char. 537: 0 --> 2  
Char. 627: 0 --> 4  
Char. 650: 0 --> 3  
Char. 928: 0 --> 1  
Char. 1331: 0 --> 4  
Char. 1482: 3 --> 1  
Char. 1508: 0 --> 1  
Char. 16000: 2 --> 0  
Char. 16063: 0 --> 1  
Char. 16120: 3 --> 1  
Char. 16250: 0 --> 2  
Char. 16362: 3 --> 1  
Char. 16439: 3 --> 1

***G. longipes* species group**

Char. 15: 1 --> 0  
Char. 16: 0 --> 1  
Char. 276: 1 --> 3  
Char. 306: 0 --> 3



Char. 405: 0 --> 2  
Char. 624: 4 --> 3  
Char. 625: 4 --> 0  
Char. 757: 3 --> 0  
Char. 973: 0 --> 2  
Char. 1039: 3 --> 0  
Char. 1208: 0 --> 1  
Char. 1447: 4 --> 1  
Char. 1512: 0 --> 3  
Char. 1611: 0 --> 2  
Char. 1678: 1 --> 0  
Char. 1727: 0 --> 2  
Char. 1819: 4 --> 0  
Char. 1920: 3 --> 0  
Char. 4681: 3 --> 1  
Char. 4985: 4 --> 0  
Char. 5011: 1 --> 0  
Char. 5315: 1 --> 0  
Char. 6100: 3 --> 0  
Char. 6125: 4 --> 3  
Char. 11926: 0 --> 1  
Char. 11970: 0 --> 1  
Char. 12005: 1 --> 3  
Char. 12041: 0 --> 3  
Char. 12077: 1 --> 3  
Char. 12127: 1 --> 0  
Char. 12176: 0 --> 2  
Char. 12258: 1 --> 3  
Char. 12304: 1 --> 0  
Char. 12310: 1 --> 3  
Char. 12325: 1 --> 3  
Char. 12353: 2 --> 0  
Char. 12384: 1 --> 3  
Char. 12442: 1 --> 3  
Char. 12447: 3 --> 1  
Char. 12518: 0 --> 3  
Char. 12567: 0 --> 2  
Char. 13057: 3 --> 1  
Char. 13155: 0 --> 2  
Char. 13377: 3 --> 1  
Char. 13731: 0 --> 2  
Char. 13935: 2 --> 1  
Char. 14255: 0 --> 2  
Char. 14275: 1 --> 3  
Char. 14311: 0 --> 2  
Char. 14653: 1 --> 3  
Char. 17793: 1 --> 4  
Char. 17815: 1 --> 3

***G. marsupiata* species group**

Char. 15: 12 --> 0  
Char. 37: 12 --> 3  
Char. 80: 2 --> 0  
Char. 376: 3 --> 1  
Char. 609: 2 --> 3  
Char. 905: 4 --> 1  
Char. 925: 3 --> 4

Char. 1168: 1 --> 3  
Char. 11923: 4 --> 3  
Char. 11927: 4 --> 3  
Char. 11972: 4 --> 1  
Char. 12022: 2 --> 1  
Char. 12175: 3 --> 1  
Char. 12231: 3 --> 1  
Char. 12330: 1 --> 3  
Char. 12390: 3 --> 0  
Char. 12539: 3 --> 1  
Char. 12609: 0 --> 1  
Char. 17777: 3 --> 1

***G. microdiscus* species group**

Char. 1053: 3 --> 0  
Char. 1296: 1 --> 3  
Char. 1308: 2 --> 0  
Char. 1387: 3 --> 1  
Char. 1611: 0 --> 2  
Char. 1725: 2 --> 0  
Char. 1743: 2 --> 0  
Char. 1833: 4 --> 3  
Char. 1912: 0 --> 4  
Char. 2293: 4 --> 3  
Char. 2357: 3 --> 4  
Char. 2425: 3 --> 1  
Char. 2641: 1 --> 4  
Char. 2678: 0 --> 2  
Char. 2932: 0 --> 3  
Char. 3296: 3 --> 0  
Char. 3457: 3 --> 0  
Char. 3481: 3 --> 4  
Char. 3544: 0 --> 3  
Char. 3613: 0 --> 3  
Char. 3736: 3 --> 1  
Char. 3815: 3 --> 0  
Char. 3959: 3 --> 1  
Char. 4061: 1 --> 0  
Char. 4164: 1 --> 4  
Char. 4241: 4 --> 1  
Char. 4315: 4 --> 2  
Char. 4684: 3 --> 1  
Char. 4949: 3 --> 4  
Char. 5583: 1 --> 0  
Char. 5628: 1 --> 4  
Char. 5806: 1 --> 3  
Char. 6038: 0 --> 3  
Char. 6103: 13 --> 4  
Char. 6105: 13 --> 0  
Char. 6181: 3 --> 4  
Char. 11919: 0 --> 4  
Char. 11920: 0 --> 4  
Char. 11940: 13 --> 4  
Char. 11952: 3 --> 4  
Char. 12012: 1 --> 3  
Char. 12246: 3 --> 1  
Char. 13126: 1 --> 3

Char. 13311: 0 --> 2  
Char. 13364: 2 --> 0  
Char. 14255: 0 --> 2  
Char. 14308: 3 --> 1  
Char. 14455: 1 --> 3  
Char. 14484: 1 --> 0  
Char. 14496: 1 --> 3  
Char. 17693: 0 --> 3  
Char. 17831: 3 --> 2

***Hemiphractus***

Char. 1: 0 --> 1  
Char. 2: 0 --> 1  
Char. 9: 1 --> 2  
Char. 11: 1 --> 2  
Char. 14: 2 --> 1  
Char. 17: 1 --> 2  
Char. 19: 1 --> 2  
Char. 20: 0 --> 1  
Char. 21: 0 --> 1  
Char. 23: 0 --> 1  
Char. 24: 0 --> 1  
Char. 28: 0 --> 1  
Char. 29: 0 --> 1  
Char. 30: 0 --> 1  
Char. 36: 01 --> 2  
Char. 47: 1 --> 0  
Char. 49: 2 --> 0  
Char. 121: 3 --> 1  
Char. 126: 2 --> 0  
Char. 215: 1 --> 3  
Char. 238: 3 --> 0  
Char. 249: 2 --> 0  
Char. 329: 2 --> 0  
Char. 343: 0 --> 3  
Char. 374: 3 --> 0  
Char. 393: 3 --> 1  
Char. 480: 3 --> 1  
Char. 524: 2 --> 4  
Char. 531: 4 --> 0  
Char. 556: 3 --> 0  
Char. 686: 0 --> 1  
Char. 784: 0 --> 2  
Char. 786: 3 --> 1  
Char. 803: 3 --> 4  
Char. 851: 0 --> 4  
Char. 886: 0 --> 4  
Char. 1052: 4 --> 3  
Char. 1054: 0 --> 1  
Char. 1115: 2 --> 0  
Char. 1270: 2 --> 0  
Char. 1331: 0 --> 4  
Char. 1354: 4 --> 1  
Char. 1385: 3 --> 1  
Char. 1397: 2 --> 1  
Char. 1520: 3 --> 0  
Char. 1542: 1 --> 3

Char. 1627: 2 --> 0  
Char. 1684: 3 --> 1  
Char. 1694: 1 --> 3  
Char. 1760: 1 --> 2  
Char. 1761: 2 --> 0  
Char. 1901: 3 --> 4  
Char. 1912: 0 --> 2  
Char. 1999: 1 --> 0  
Char. 2037: 0 --> 1  
Char. 2078: 3 --> 1  
Char. 2122: 2 --> 0  
Char. 2229: 3 --> 0  
Char. 2468: 1 --> 4  
Char. 2496: 3 --> 0  
Char. 2500: 3 --> 0  
Char. 2527: 0 --> 1  
Char. 2587: 2 --> 0  
Char. 2604: 0 --> 3  
Char. 2612: 3 --> 0  
Char. 2626: 1 --> 3  
Char. 2687: 0 --> 4  
Char. 2762: 1 --> 0  
Char. 2824: 2 --> 0  
Char. 2931: 0 --> 3  
Char. 2954: 3 --> 0  
Char. 2968: 0 --> 2  
Char. 3034: 0 --> 2  
Char. 3056: 0 --> 3  
Char. 3092: 4 --> 1  
Char. 3202: 0 --> 1  
Char. 3354: 1 --> 0  
Char. 3359: 3 --> 0  
Char. 3369: 1 --> 0  
Char. 3377: 1 --> 0  
Char. 3378: 3 --> 1  
Char. 3384: 1 --> 3  
Char. 3461: 4 --> 0  
Char. 3466: 4 --> 2  
Char. 3501: 3 --> 1  
Char. 3576: 1 --> 0  
Char. 3624: 2 --> 1  
Char. 3663: 0 --> 2  
Char. 3713: 4 --> 2  
Char. 3730: 0 --> 3  
Char. 3815: 3 --> 1  
Char. 3875: 0 --> 1  
Char. 3903: 3 --> 1  
Char. 3976: 0 --> 3  
Char. 4065: 3 --> 0  
Char. 4080: 0 --> 1  
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Char. 4270: 0 --> 1  
Char. 4288: 0 --> 1  
Char. 4334: 0 --> 3  
Char. 4396: 3 --> 4  
Char. 4667: 3 --> 0  
Char. 4736: 3 --> 0

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Char. 4798: 4 --> 3  
Char. 4800: 0 --> 3  
Char. 4926: 1 --> 4  
Char. 4949: 3 --> 4  
Char. 4972: 0 --> 4  
Char. 5089: 0 --> 4  
Char. 5092: 0 --> 4  
Char. 5172: 0 --> 4  
Char. 5176: 2 --> 4  
Char. 5193: 0 --> 4  
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Char. 5242: 0 --> 4  
Char. 5330: 3 --> 4  
Char. 5355: 3 --> 1  
Char. 5451: 2 --> 0  
Char. 5466: 3 --> 1  
Char. 5482: 0 --> 1  
Char. 5545: 2 --> 4  
Char. 5583: 1 --> 0  
Char. 5628: 1 --> 0  
Char. 5651: 0 --> 4  
Char. 5671: 2 --> 4  
Char. 5685: 3 --> 0  
Char. 5692: 0 --> 3  
Char. 5718: 0 --> 1  
Char. 5802: 0 --> 1  
Char. 9560: 1 --> 3  
Char. 9615: 2 --> 0  
Char. 9632: 2 --> 0  
Char. 9742: 0 --> 2  
Char. 9752: 1 --> 3  
Char. 9767: 1 --> 2  
Char. 9770: 0 --> 2  
Char. 9815: 3 --> 4  
Char. 9838: 2 --> 1  
Char. 9851: 0 --> 3  
Char. 9887: 2 --> 0  
Char. 9927: 1 --> 3  
Char. 10075: 0 --> 2  
Char. 10128: 3 --> 0  
Char. 10155: 3 --> 2  
Char. 10695: 3 --> 1  
Char. 10810: 1 --> 3  
Char. 10858: 3 --> 2  
Char. 10999: 1 --> 3  
Char. 11005: 0 --> 2  
Char. 11062: 1 --> 3  
Char. 11066: 0 --> 1  
Char. 11210: 1 --> 3  
Char. 11370: 1 --> 3  
Char. 11424: 3 --> 0  
Char. 11505: 1 --> 2  
Char. 11559: 1 --> 3  
Char. 11594: 3 --> 1  
Char. 11640: 0 --> 2

Char. 11670: 0 --> 1  
Char. 11720: 0 --> 1  
Char. 11726: 0 --> 2  
Char. 11799: 2 --> 0  
Char. 11801: 3 --> 0  
Char. 13168: 0 --> 2  
Char. 13169: 0 --> 1  
Char. 13181: 2 --> 0  
Char. 13214: 3 --> 1  
Char. 13256: 0 --> 1  
Char. 13277: 0 --> 2  
Char. 13345: 0 --> 2  
Char. 13400: 3 --> 2  
Char. 13406: 0 --> 1  
Char. 13435: 0 --> 2  
Char. 13468: 0 --> 1  
Char. 13483: 1 --> 0  
Char. 13517: 1 --> 2  
Char. 13616: 1 --> 3  
Char. 13747: 3 --> 1  
Char. 13911: 0 --> 3  
Char. 14062: 0 --> 1  
Char. 14074: 1 --> 3  
Char. 14097: 0 --> 1  
Char. 14248: 2 --> 0  
Char. 14293: 2 --> 3  
Char. 14354: 2 --> 0  
Char. 14358: 0 --> 3  
Char. 14411: 2 --> 3  
Char. 14511: 3 --> 1  
Char. 15143: 3 --> 0  
Char. 15342: 2 --> 0  
Char. 15350: 1 --> 3  
Char. 15538: 3 --> 1  
Char. 15617: 1 --> 3  
Char. 15633: 02 --> 3  
Char. 15636: 1 --> 2  
Char. 15679: 3 --> 2  
Char. 15682: 2 --> 0  
Char. 15732: 2 --> 1  
Char. 15733: 1 --> 3  
Char. 15744: 0 --> 2  
Char. 16615: 1 --> 3  
Char. 16700: 3 --> 1  
Char. 16874: 2 --> 0  
Char. 16919: 1 --> 3  
Char. 17028: 0 --> 3  
Char. 17079: 0 --> 2  
Char. 17193: 0 --> 2  
Char. 17235: 0 --> 2  
Char. 17376: 1 --> 3  
Char. 17457: 1 --> 3  
Char. 17489: 3 --> 2  
Char. 17531: 0 --> 2  
Char. 17578: 1 --> 3  
Char. 17741: 3 --> 1  
Char. 17907: 2 --> 1

Char. 17935: 1 --> 3  
Char. 17997: 3 --> 1  
Char. 18152: 1 --> 3  
Char. 18204: 0 --> 2  
Char. 18281: 0 --> 2  
Char. 18294: 3 --> 1  
Char. 18312: 0 --> 2  
Char. 18342: 2 --> 0  
Char. 18377: 0 --> 2

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Char. 78: 3 --> 1  
Char. 213: 3 --> 1  
Char. 310: 0 --> 1  
Char. 414: 0 --> 2  
Char. 427: 3 --> 1  
Char. 595: 0 --> 2  
Char. 628: 4 --> 1  
Char. 629: 4 --> 1  
Char. 757: 3 --> 2  
Char. 765: 1 --> 3  
Char. 777: 3 --> 1  
Char. 886: 0 --> 4  
Char. 954: 3 --> 1  
Char. 1057: 4 --> 1  
Char. 1161: 0 --> 2  
Char. 1207: 0 --> 2  
Char. 1258: 0 --> 3  
Char. 1320: 1 --> 3  
Char. 1378: 0 --> 2  
Char. 1454: 4 --> 0  
Char. 1494: 4 --> 0  
Char. 1552: 3 --> 1  
Char. 1892: 4 --> 3  
Char. 1929: 0 --> 3  
Char. 4464: 4 --> 3  
Char. 4558: 3 --> 4  
Char. 4570: 4 --> 0  
Char. 4626: 1 --> 3  
Char. 4636: 2 --> 0  
Char. 4703: 1 --> 3  
Char. 4721: 2 --> 0  
Char. 4738: 0 --> 3

Char. 4858: 1 --> 3  
Char. 5125: 4 --> 1  
Char. 5126: 4 --> 1  
Char. 5129: 4 --> 1  
Char. 5130: 4 --> 1  
Char. 5154: 4 --> 2  
Char. 5156: 4 --> 2  
Char. 5172: 0 --> 2  
Char. 5303: 4 --> 0  
Char. 5426: 2 --> 0  
Char. 5457: 0 --> 1  
Char. 5466: 3 --> 1  
Char. 5678: 0 --> 2  
Char. 5829: 1 --> 0  
Char. 6038: 0 --> 3  
Char. 6061: 3 --> 0  
Char. 6095: 0 --> 2  
Char. 6112: 0 --> 3  
Char. 6129: 4 --> 1  
Char. 6140: 0 --> 3  
Char. 6148: 3 --> 1  
Char. 6160: 3 --> 0  
Char. 6179: 4 --> 0  
Char. 6222: 1 --> 0  
Char. 9675: 3 --> 1  
Char. 9814: 4 --> 2  
Char. 9875: 0 --> 3  
Char. 9892: 0 --> 2  
Char. 10109: 3 --> 1  
Char. 10731: 3 --> 2  
Char. 10758: 3 --> 0  
Char. 10828: 3 --> 1  
Char. 10852: 3 --> 0  
Char. 10988: 0 --> 2  
Char. 11080: 1 --> 3  
Char. 11496: 3 --> 1  
Char. 11532: 3 --> 1  
Char. 11616: 1 --> 3  
Char. 12045: 3 --> 1  
Char. 12049: 3 --> 0  
Char. 12114: 0 --> 3  
Char. 12130: 3 --> 1  
Char. 12139: 1 --> 2  
Char. 12214: 0 --> 2

Char. 12294: 1 --> 0  
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Char. 12370: 1 --> 0  
Char. 12378: 0 --> 3  
Char. 12416: 1 --> 0  
Char. 12450: 0 --> 2  
Char. 12639: 0 --> 2  
Char. 12666: 2 --> 0  
Char. 12767: 2 --> 3  
Char. 13198: 3 --> 0  
Char. 13211: 1 --> 3  
Char. 13293: 3 --> 1  
Char. 13376: 1 --> 2  
Char. 13382: 0 --> 2  
Char. 13392: 0 --> 2  
Char. 13400: 3 --> 1  
Char. 13401: 0 --> 1  
Char. 13402: 1 --> 3  
Char. 13439: 3 --> 0  
Char. 13441: 3 --> 1  
Char. 13453: 3 --> 1  
Char. 13681: 0 --> 2  
Char. 13808: 2 --> 0  
Char. 13856: 1 --> 3  
Char. 13893: 3 --> 0  
Char. 14147: 2 --> 0  
Char. 14152: 3 --> 1  
Char. 14176: 1 --> 3  
Char. 14411: 2 --> 3  
Char. 14473: 3 --> 2  
Char. 14563: 1 --> 3  
Char. 14650: 3 --> 0  
Char. 14820: 2 --> 0  
Char. 15011: 1 --> 3  
Char. 15065: 1 --> 3  
Char. 16576: 3 --> 0  
Char. 16865: 2 --> 0  
Char. 17355: 3 --> 0  
Char. 17516: 3 --> 2  
Char. 17581: 0 --> 2  
Char. 17844: 0 --> 1