DISSERTATION

THE EVOLUTION OF ‘EARLESSNESS’ IN THE TRUE TOAD FAMILY (BUFONIDAE)

Submitted by

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ABSTRACT

THE EVOLUTION OF 'EARLESSNESS' IN THE TRUE TOAD FAMILY (BUFONIDAE)

Anurans (frogs and toads) have a tympanic middle ear to transmit airborne sound from the environment to their inner ear sensory cells. Yet, many bufonid (true toad) species have independently evolved earlessness, the lack of a tympanic middle ear, despite the importance of acoustic communication in most toad mating systems. My thesis aims to determine why middle ear structures are so evolutionarily labile in the Bufonidae family by comparing development, sensory, and morphological data of eared and earless toads within a phylogenetic context. I show that the middle ear forms very late in the development of toads and takes many months past metamorphosis to become fully functional. Adult earless species are typically less sensitive to high frequency sound and more sensitive to low frequency vibrations compared to eared toads. I also find the skulls of eared and earless are very similar, indicating the middle ear is lost without change to other developmentally or genetically linked skull features. I conclude that alternative hearing pathways allow earless species to retain some hearing sensitivity, and discuss roles for development and behavior in shaping the evolutionary lability of ear structures.

DEDICATION

For my family, both blood related and chosen. And dogs.

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1. INTRODUCTION

Background

Convergent evolution, the independent evolution of a trait in separate lineages, is common across the tree of life (Blackburn, 1992; Knudsen and Tollsten, 1995; Fraser et al., 2004; Rosenblum, 2006; Jones and Holderied, 2007; Hofmann et al., 2008; Gleiss et al., 2011; Mcghee, 2011). Although shared selection pressures often drive the evolution of convergent traits, developmental processes also influence the variation generated by mutation and therefore the likelihood a trait evolves independently in multiple lineages. Development shapes the phenotypes that result from mutation in various ways. For example, traits do not develop independently of one another, and thus trait integration can result in pleiotropic changes in linked traits (Wright 1964, 1980; Mayr, 1976; Pigliucci 2004; Klingenberg, 2008). Also, epigenetic mechanisms produce phenotypic variation from a single genotype based on both stochastic developmental processes and environmental conditions or experiences (Arthur, 2002). Thus, the way an organism develops can bias the phenotypes that that are available for selection, making some traits more likely to evolve than others (developmental bias; Alberch 1982; Alberch and Gale 1985; Maynard Smith et al. 1985; Arthur 2004; Brakefield 2006).

Although the evolution of most convergent traits is attributed to shared selection pressures across replicate lineages, developmental biases also likely contribute to convergent phenotypes. Here I examine the joint influences of selection and developmental biases on a perplexing convergence, tympanic middle ear loss in anurans.

Study system

Anurans (frogs and toads) have a convergent trait, loss of the tympanic middle ear, which is surprisingly prevalent given the middle ear's usual ties to fitness (reviewed in Wells and Schwartz, 2007). The tympanic middle ear allows most tetrapods to better hear acoustic sound on land and has independently evolved five times in tetrapods (Clack, 1997, reviewed in Christensen-Dalsgaard and Carr, 2008, Manley, 2010; Manley and Sienknecht, 2013). Only in anurans do we find rampant loss of tympanic middle ears, despite the fact that many frogs are acoustic communicator specialists (reviewed in Wells and Schwartz 2007). Although most research has focused on acoustic communication for mate choice (reviewed in Wells and Schwartz, 2007), frogs also use acoustic communication for territoriality and defense, and perhaps acoustic cues for prey capture and predator avoidance (Wever, 1985). Given the reliance of anurans on acoustic sensitivity for behaviors relevant to survival and reproduction, tympanic middle ear loss in this group is especially perplexing

Thus far, no consistent adaptive explanation exists for the evolution of ear loss in anurans. Earless anurans occupy a wide array of habitats (Vorobyeva and Smirnov, 1987; Jaslow et al. 1988; Hetherington, 1992), often coexisting with eared species, and therefore do not experience a common set of environmental selection pressures. As such, a number of hypotheses have been proposed for how and why earlessness has evolved. Some researchers have debated whether middle ear loss has sensory costs in anurans due to conflicting hearing comparisons in a very small number of eared and earless species (Loftus-Hill, 1973; Lombard and Straughan, 1974; Jaslow and Lombard, 1996; Lindquist et al., 1998). Other researchers have hinted that developmental bias contributes to ear lability due to the late formation of the middle ear (Vorobyeva and Smirnov, 1987; Smirnov, 1991) and the common shifts in developmental timing (heterochrony) within anurans (Trueb and Alberch, 1985; Weisbecker and Mitgutsch, 2010) that preferentially affect late-forming structures (Trueb and Alberch, 1985; Weisbecker and Mitgutsch, 2010). No comparative tests of these various hypotheses exist. Ear loss in anurans provides a rare opportunity to investigate the influence of developmental bias and selection in shaping trait lability in a comparative framework.

Research Overview

Overall, this research characterizes the patterns of middle ear evolution across anurans and uses a novel comparative framework to test the validity of various hypotheses for the lability of the anuran tympanic middle ear. Chapter 1 uses multiple ancestral reconstruction approaches to characterize the evolutionary patterns of middle ear loss, as well as potential regains, throughout most existing anuran species. We find the tympanic middle ear to be incredibly labile in anurans, with a minimum of 38 total losses and two potential regains of the middle ear. Chapter 2 dives into the true toad family (Bufonidae) and explores the development of the tympanic sensory system and the functional consequences of its late formation. We find that the middle ear fully forms and becomes functional very late in toads. Chapter Three tests for sensory differences between closely related eared and earless species pairs to determine whether the middle ear is under relaxed selection due to a lack of sensory cost associated with earlessness. Earless species have high frequency hearing deficits but increased low frequency vibrational sensitivity. Finally, Chapter Four determines whether strong developmental links to other skull features bias the evolutionary lability of the middle ear, or whether the middle ear is evolving independently of other skull features. We find that middle ears are evolving independently of other skull features in the family Bufonidae and propose a role for heterochrony in middle ear lability. Together these chapters show sensory consequences of earlessness and establish evidence that trait independence and heterochrony influence the evolution of a sensory system, the tympanic middle ear.

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2. THE COMPLEX EVOLUTIONARY HISTORY OF THE TYMPANIC MIDDLE EAR IN FROGS AND TOADS (ANURA)

Summary

Most anurans possess a tympanic middle ear (TME) that transmits sound waves to the inner ear; however, numerous species lack some or all TME components. To understand the evolution of these structures, we undertook a comprehensive assessment of their occurrence across anurans and performed ancestral character state reconstructions. Our analysis indicates that the TME was completely lost at least 38 independent times in Anura. The inferred evolutionary history of the TME is exceptionally complex in true toads (Bufonidae), where it was lost in the most recent common ancestor, preceding a radiation of >150 earless species. Following that initial loss, independent regains of some or all TME structures were inferred within two minor clades and in a radiation of > 400 species. The reappearance of the TME in the latter clade was followed by at least 10 losses of the entire TME. The many losses and gains of the TME in anurans is unparalleled among tetrapods. Our results show that anurans, and especially bufonid toads, are an excellent model to study the behavioural correlates of earlessness, extratympanic sound pathways, and the genetic and developmental mechanisms that underlie the morphogenesis of TME structures.

Introduction

The function of audition in frogs and toads (Anura) is primarily the perception of airborne sounds, including those involved in social communication (Wever, 1985). Thus, hearing in anurans is thought to be a key trait for survival and reproduction. In most anurans, perception of airborne sounds is enabled by a tympanic middle ear (TME) com- posed minimally of a tympanic membrane, middle ear cavity, and middle ear bone (=columella, columella auris, stapes, plectrum) that conducts sound waves from the environment to the inner ear where they are transduced into electrical signals via hair cells (Wever, 1973; Wever, 1985; Smotherman and Narins, 2004; Mason et al., 2015).

Among other tetrapods, a TME is absent in caecilians and salamanders (Wever, 1985; Maddin and Anderson, 2012) but present in amniotes. Nevertheless, although the TME is primitively present in all extant amniotes, it is not homologous across amniote lineages, having evolved independently at least five times in turtles, lepidosaurs, archosaurs, an extinct lineage of parareptiles, and the synapsid ancestor of mammals (Clack, 1997; Christensen-Dalsgaard and Carr, 2008; Manley, 2010; Manley and Sienknecht, 2013). TME losses are extremely rare in amniotes. All mammals, turtles, and archosaurs possess a complete TME, and even the amphisbaenians, snakes, and lizards that have lost the tympanic membrane and middle ear cavity retain a columella (Manley, 1990), the sole exceptions being the pygopod lizard *Aprasia repens* (Daza and Bauer, 2015) and possibly the snakes *Atractaspis* and *Xenocalamus* (Cundall and Irish, 2008). In contrast, loss is widespread among anurans, with at least a few species of several families lacking the entire TME, a condition referred to as “earlessness” (Jaslow et al., 1988).

Earlessness is especially common in the true toad family Bufonidae, in which the TME is completely lacking in more than 200 species. Bufonidae is one of the most diversified groups of amphibians, comprising more than 580 species in 51 genera naturally distributed over numerous ecoregions of the Americas, Africa, and Eurasia15. Several authors have noted the reduction and loss of TME structures (e.g., Tihen, 1960; McDiarmid, 1971; Grandison, 1981; Lötters et al., 2011; Grant and Bolívar-G, 2014) or morphological variations in middle ear structure (e.g., Wever, 1985; Lindquist et al., 1988; Arch et al., 2011; Boistel et al., 2011) in bufonids, but the phylogenetic distribution of earlessness has never been studied either within Bufonidae or across Anura. As such, the goals of this study are to explore the sequences of gains and losses of the TME evolution across all anurans and evaluate in a phylogenetic framework the patterns of diversification of TME in Bufonidae.

Materials and Methods

Tympanic middle ear morphology and data collection

Although many variations in the structure of the anuran auditory system exist, a generalized model can be described (Wever, 1985; Smotherman and Narins, 2004; Mason et al., 2015): the lateral-most portion of this system is composed of a highly differentiated disc of thin, non-glandular skin, termed the tympanic membrane. The rim of the tympanic membrane is attached to a cartilaginous tympanic ring, the tympanic annulus. The middle ear cavity is a diverticulum of the pharynx that opens ventrally to the buccal cavity via the Eustachian tubes. The columella contacts the tympanic membrane laterally and the otic capsule medially and is divided into three portions (Wever, 1985; Gaupp, 1986): (1) the pars externa plectri or extracolumella, a cartilaginous structure that contacts the tympanic membrane and often presents a slim, flattened strip of cartilage called the ascending process or pars ascendens plectri, that extends anterodorsally to contact the crista parotica of the prootic, (2) the pars media plectri or columellar shaft, an ossified, rod-shaped portion with a dilated medial end, and (3) the pars interna plectri, a mainly cartilaginous structure that is continuous with the pars media and extends posteriorly to lie medial to the operculum. The expanded medial end of the pars media and the entire pars interna constitute the stapedial footplate, which fills the rostral portion of the oval window of the otic capsule (Wever, 1985; Vorobyeva and Smirnov, 1987). The footplate is connected to the supras- capula via the columellar muscle in some species (Wever, 1985), although the individuality of this muscle has been questioned in at least some cases (Hetherington, 1987; Mason and Narins, 2002). The otic operculum (operculum fenestrae ovalis), found only in caudates and anurans (Maddin and Anderson, 2012), is an ovoid element that is usually cartilaginous or sometimes partially calcified (Wever, 1973; Mason, 2007) that contacts the stapedial footplate and covers the caudal portion of the oval window. The operculum is present in all anurans. The opercularis muscle inserts on the operculum and originates on the suprascapular cartilage of the pectoral girdle (Wever, 1985; Vorobyeva and Smirnov, 1991). In all observed anuran species (also see Trueb, 1993), the presence/absence of TME structures follows a consistent pattern. Absence of a medial structure is accompanied by the absence of the more lateral structures, such that absence of the columella entails absence of the tympanic annulus and tympanic membrane and absence of the tympanic annulus entails absence of the tympanic membrane but not the columella. Similarly, presence of a lateral structure is accompanied by the presence of the more medial structures, such that presence of the tympanic membrane entails presence of the tympanic annulus and columella and presence of the tympanic annulus entails presence of the columella but not the tympanic membrane. Consequently, we made the following assumptions when scoring the presence/absence of the tympanic structures (Fig. 1): (1) absence of the tympanic membrane and tympanic annulus when the columella is absent; (2) absence of the tympanic membrane when the tympanic annulus is absent; (3) presence of the tympanic annulus and columella when the tympanic membrane is present; and (4) presence of the columella when the tympanic annulus is present.

In total, we scored the condition of the TME for 556 species and 51 genera of Bufonidae, representing >94% of all described species in the family. Among the sampled species, 239 were included in Pyron's (2014) phylogenetic analysis. We also scored the conditions of these structures for 1860 of the 2538 non-bufonid anuran species (representing 53 families; see[15]) included by Pyron (2014), as well as 147 non-bufonid anuran species not included in this analysis. The only frog family not sampled by Pyron (2014) is the recently described Odontobatrachidae (Barej et al., 2014). Although our outgroup sampling is not exhaustive, we included data for the vast majority of genera of all the families sampled by Pyron (2014). Details on material examined, considerations about character coding and character states scored for each transformation series, and literature sources are listed as Supplementary Material (section 2.1 of the Supplementary Information)

Ancestral state reconstructions

We employed the most recent and densely sampled phylogenetic hypothesis available for Anura, that of Pyron (2014), for ancestral state reconstruction, and we discuss bufonid species not included in Pyron's (2014) study but present in other analyses (e.g., well-supported results of Peloso et al., 2012; van Bocxlaer et al., 2010; Chandramouli et al., 2016). We focused orig- inal data collection primarily on Bufonidae and relied more extensively on literature accounts for non-bufonids, some of which were unclear or ambiguous about the occurrence of specific structures. In particular, taxonomic accounts often use imprecise terminology to describe the external morphology of the otic region (Lynch and Duellman, 1997). Consequently, we analysed the phylogenetic distribution of each of the TME structures in Bufonidae but only the columella in analyses of Anura.

To test the homology of the middle ear structures individually and explain their variation among anurans, most parsimonious ancestral state reconstructions (Fitch, 1971) on Pyron's (2014) phylogenetic hypothesis were performed using Mesquite v3.03 (Maddison and Maddison, 2015). We further explored alternative evolutionary scenarios for the complete loss of all TME struc- tures within Bufonidae with maximum likelihood ancestral reconstructions using the package APE (Paradis et al., 2004) and stochastic character mapping (Huelsenbeck et al., 2003) using phytools (Revell, 2012) in R (R Core Team, 2013). We compared Akaike Information Criterion (AIC) values for a maximum likelihood model in which transition rates were allowed to vary (ARD) throughout the tree and a maximum likelihood model in which transition rates between states were equal (ER). We used the most supported transition rate from our maximum likelihood analyses (ER) to estimate the number of gains and losses across Bufonidae using stochastic character mapping. Stochastic character mapping allowed us to explore the probability of ear transitions under various evolutionary scenarios, giving us a better understanding of the likelihood of regains throughout this family. We considered three scenarios: (1) equal transition rates, no restrictions; (2) equal transition rates and restricting the ancestor to being eared; and (3) a Dollo's model (no regains possible). We ran 10,000 simulations per scenario and counted a state change whenever nodes switched from greater than 50% support for one character state to greater than 50% support for the other character state.

Results

Tympanic middle ear evolution in Anura

The occurrence of a columella is plesiomorphic in Anura, although the sister clade of all other anurans (Ascaphidae + Leiopelmatidae) lacks this structure (see Discussion). Given that the tympanic membrane and tympanic annulus are not fossilizable structures, their occurrence in fossil material cannot be assessed, making it impossible to determine if the presence of those structures is also plesiomorphic in Anura. The TME is completely absent in at least some species of no fewer than 20 anuran families: Ascaphidae, Alsodidae, Batrachylidae, Bombinatoridae, Brachycephalidae, Brevicepitidae, Bufonidae, Calyptocephalellidae, Craugastoridae, Dicroglossidae, Hemisotidae, Leiopelmatidae, Leptodactylidae, Megophryidae, Microhylidae, Myobatrachidae, Nasikabatrachidae, Rhinophrynidae, Sooglossidae, and Telmatobiidae (section 2.1 of the Supplementary Information). Detailed description of the occurrence of the columella in anuran families other than Bufonidae are provided in section 2.1 of the Supplementary Information. Ancestral state reconstruction using Pyron's (2014) phylogenetic hypothesis shows that the complete loss of the TME, as evidenced by lack of the columella, occurred independently at least 25 times outside Bufonidae, plus two additional losses when taxa not included in Pyron's (2014) study but present in other phylogenetic analyses are considered.

Tympanic middle ear evolution in Bufonidae

Based on the phylogenetic hypothesis of Pyron (2014) and the results of both the parsimony and probabilistic ancestral state reconstructions (Fig. 2 and section 2.3 of the Supplementary Information), the tympanic membrane, tympanic annulus, and columella were lost in the most recent common ancestor of bufonids, regained subsequently, and then repeatedly re-lost again. Below we summarize the results of the ancestral reconstructions of the tympanic membrane, tympanic annulus, and columella (the numbers of regains and re-losses of TME structures in Bufonidae differs somewhat when taxa not sampled by Pyron (2014) are considered; see sections 2.1 and 2.4 of the Supplementary Information and Discussion, below).

Parsimony ancestral state reconstruction

The tympanic membrane was lost in the most recent common ancestor of Bufonidae and reappeared in the sister clade of *Nannophryne*. Subsequent independent losses occurred at least 25 times (see sections 2.3 and 2.4 of the Supplementary Information). The absence of the tympanic annulus is the inferred ancestral condition in bufonids, with two independent regains: (a) within *Atelopus* in a clade composed of *A. flavescens*, *A. franciscus*, *A. pulcher*, and *A. spumarius*, and (b) in the sister clade of *Nannophryne*. The gain of the tympanic annulus in the latter clade was followed by 10 independent losses (see sections 2.3 and 2.4 of the Supplementary Information). Finally, the phylogenetic distribution of the gains and losses of the columella is identical to that of the tympanic annulus for the taxa included in the hypothesis of Pyron (2014; see Fig. 2 and section 2.4 of the Supplementary Information). However, if bufonid species not included by Pyron (2014) are also considered, the columella sometimes occurs without a tympanic annulus (see Discussion and section 2.1 of Supplementary Information).

Stochastic mapping of complete tympanic middle ear loss under various constraints

Our stochastic character mapping estimated similar patterns of TME loss and regain within Bufonidae under various evolutionary scenarios (see section 2.3 of the Supplementary Information). When we ran an equal rates model of evolution we found results similar to the parsimony reconstructions of the tympanic annulus and columella with strong support for an ancestor lacking these structures, two regains, and 10 losses within the tree. When we assumed the ancestor had these structures and a model of equal transition rates, we found support for 12 losses and still two regains. When restricting regains from occurring (Dollo's model), we found a total of 17 losses across bufonids.

Discussion

The lack of the columella in Ascaphidae and Leiopelmatidae, which together form the sister clade of all other extant anurans (=Lalagobatrachia), has generated much discussion about the plesiomorphic condition in Anura (Stephenson, 1951; Bolt and Lombard, 1985; Green and Cannatella, 1993; Trueb, 1993). However, since most proanurans and stem anuran fossils have a columella (i.e. *Mesophryne beipiaoensis*, *Notobatrachus* spp., *Prosalirus bitis*, *Triadobatrachus massinoti*, *Yizhoubatrachus macilentus*; Rage and Rocek, 1989; Shubin and Jenkins, 1995; Gao and Chen, 2004; Gao and Wang, 2001; Báez and Nicoli, 2008), the lack of this structure in Ascaphidae + Leiopelmatidae appears to be synapomorphic. A columella could not be identified in the stem anuran *Vieraella herbstii*; however, the state of preservation of the specimen is poor (Báez and Basson, 1996), leading some authors to consider the occurrence of a columella to be unknown (e.g., Gao and Wang, 2001) and others to consider it to be absent (e.g., Green and Cannatella, 1993). Regardless, given the phylogenetic position of *Vieraella herbstii* (Báez and Basso, 1996; Gao and Wang, 2001; Gao and Chen, 2004), this controversy has nobearing on our inferences of the evolutionary history of this structure in anurans.

Although available evidence clearly indicates the plesiomorphic presence of the columella in Anura, it is unknown if the ancestral anuran also possessed a tympanic membrane and annulus. The tympanic membrane and tympanic annulus are not fossilizable structures, so their precise phylogenetic origin is unknown. As such, two scenarios are compatible with current evidence: the tympanic annulus and membrane might have been present in the most recent common ancestor of Anura and lost with the columella in Ascaphidae + Leiopelmatidae, or they might have arisen in Lalagobatrachia.

Among non-bufonid anurans, the TME was completely lost at least 27 times (see above). All these losses involve small clades scattered across the major lineages of Anura, implying several putative synapomorphies (e.g., *Atelognathus* + *Chaltenobatrachus*, *Brachycephalus*, Nasikabatrachidae + Sooglossidae, *Pseudophryne*, *Telmatobufo*) or autapomorphies (e.g., *Balebreviceps hilmani*, *Melanobatrachus indicus*, *Rhinophrynus dorsalis*).

For other anuran clades (e.g., *Alsodes*, *Microhyla*, *Nanorana*, *Scutiger*, *Telmatobius*), denser taxon sampling is necessary to obtain adequate evidence to understand the evolution of the TME (see section 2.2 of the Supplementary Information for a more exhaustive discussion about the evolution of this structure in these and other non-bufonid species). Although TME structures were lost repeatedly in Anura, TME evolution in Bufonidae is especially complex. All of the families that are closely related to Bufonidae (Pyron, 2014) (also see Frost et al., 2006; Grant et al., 2006) have a complete TME, making the absence of these structures a synapomorphy of Bufonidae. As such, the lack of a TME is plesiomorphic in the earliest diverging lineages (i.e., *Amazophrynella*, most species of *Atelopus*, *Dendrophryniscus*, *Oreophrynella*, *Osornophryne*, *Melanophryniscus*, and *Nannophryne*).

Independent of the methodological approach, available evidence indicates that the complete TME was regained within Bufonidae in *Frostius* and the sister clade of *Nannophryne*, whereas the tympanic annulus and columella were regained in a subclade of *Atelopus*. Thus, these structures are not homologous with the equivalent structures found in the TME of other anurans, although it seems likely that the underlying genetic basis for their development is homologous (i.e., deep homology (Shubin et al., 1997), see below). Subsequent losses occurred several times in different clades, indicating a complex evolutionary history of the TME in Bufonidae (see Fig. 2 and section 2.3 of the Supplementary Information).

The complex evolutionary history of the TME in Bufonidae is even more unusual when compared to other tetrapods. As noted above, although extant caecilians and salamanders do not possess a tympanic membrane or middle ear cavity, it has been hypothesized that a TME might have been present plesiomorphically and that the lateral elements might have been lost independently (Lombard and Bolt, 1979; Maddin and Anderson, 2012). Regardless, although the remaining middle ear structures underwent extensive modification, the columella was lost only once in each group, having been greatly reduced or lost in salamandrid salamanders (Wever, 1985; Rose, 2003) and lost in adult scolecomorphid caecilians (present as a cartilaginous element in fetal and juvenile *Scolecomorphus kirkii* (Müller et al., 2009).

Among amniotes, TME loss is extremely rare. There are no documented losses among turtles (e.g., Gaffney, 1979), archosaurs (e.g., Feduccia, 1975; Saunders et al., 2000; Motefeltro et al., 2016), or mammals (e.g., O'Leary et al., 2013), despite the remarkable middle ear transformations in fossorial and marine mammals (Mason, 2001; Solntseva, 2013). Among lepidosaurs, numerous lineages have lost the lateral-most components of the TME, includeing Serpentes, Amphisbaenia, Agamidae, Diploglossidae, Gymnophthalmidae, Lanthonotidae, Phrynosomatidae, and Scincidae (Smith, 1938; Manley, 1990; Saunders et al., 2000; Pellegrina et al., 2001; Greer, 2002), but the columella appears to be present in all but the pygopod lizard *Aprasia repens* (Daza and Bauer, 2015) and, possibly, the lamprophid snakes *Atractaspis* and *Xenocalamus* (Cundall and Irish, 2008).

With few exceptions, the development of TME structures in anurans follows a consistent sequence that might explain the consistenft pattern of co-occurrence of middle ear structures and provides clues about the mechanisms involved in their loss and gain. First, the medial end of the pars media plectri develops as a chondrification within the connective tissue membrane spanning the fenestra ovalis adjacent to the already formed operculum (Helff, 1928; Barry, 1956; Sedra and Michael, 1959; Hetherington, 1987; Fabrezi and Goldberg, 2009). Next, the pars interna plectri begins to chondrify and, with the incipient pars media, form the future stapedial footplate. Subsequently, a socket-like structure begins to be defined, articulating with the anterior edge of the operculum. The lateral-most portion of the stapedial footplate elongates to complete the formation of the shaft of the pars media plectri, which extends laterally towards the outside of the head. Meanwhile, the tympanic annulus and pars externa plectri develop as cartilaginous condensations associated with the posterior margin of the palatoquadrate. As the palatoquadrate swings posteriorly during metamorphosis, so too do the tympanic annulus and pars externa plectri. As the ontogenetic sequence of development of these structures progresses, they are positioned in the same medial-lateral plane. At this point, the partes media and externa plectri connect synchondrotically to each other and the tympanic annulus induces the differentiation of the tympanic membrane (Sedra and Michael, 1959; Hetherington, 1987).

The sequences of losses and gains appear to be related to the relative timing of the development of structures (heterochronies) and tissue differentiation phenomena. For example, Helff (1928) demonstrated the inductive effects of the tympanic annulus on the tegument to produce the differentiation of the tympanic membrane, which explains why the tympanic membrane never occurs in the absence of a tympanic annulus. Similarly, Hetherington (1987), Smirnov (1989), and Fabrezi and Goldberg

(2009) emphasized the relatively late development of TME structures. Hetherington (1987) and Smirnov (1989) also observed that several species undergo post-metamorphic development of previously absent or undeveloped structures (e.g., *Sclerophrys regularis*, *Pseudacris crucifer*, *Bombina orientalis).* Meanwhile, Smirnov (1991) pointed out that developmental heterochronies (progenesis, neoteny, and post-displacement) seem to play a major role in the post-metamorphic development of these structures. All these events occur in specific sequences and their disruption in particular stages could produce the observed patterns of losses in the subsequent stages of development of the TME. Therefore, research into the genetic basis for the absence of induction of lateral elements promises to be a fruitful line of investigation.

Additionally, genetic mechanisms that directly regulate the expression of these ear structures might be involved. Knowledge of the origin of the components of the vertebrate auditory system is incipient generally and for anurans particularly. However, recent studies of Xenopus laevis support a model in which the cartilaginous elements of the TME are derived from three neural crest cell streams (see Gross and Hanken, 2008): (1) the mandibular stream forms the tympanic annulus, (2) the hyoid stream gives rise to the partes media and externa plectri, and (3) the branchial stream forms the pars interna plectri. The consistent patterns of co-occurrences observed in anurans suggest that a direct role of regulatory genes and/or transcription factors might be involved in the tissular differentiation of the tympanic membrane due to inductive phenomena from the tympanic annulus. Also, it is likely that the development of the tympanic annulus and pars externa plectri (in the margins of the palatoquadrate) and the partes interna and media plectri (in the otic capsule) results from the initiation of a common developmental module, as in the morphogenesis of many other structures (Gilbert, 1996; Collin and Miglietta, 2008). Unfortunately, information on the developmental control genes that lead to the formation of elements in the amphibian middle ear is unavailable. However, some genetic pathways involved in this differentiation process have been identified in other vertebrates and could be examined in frogs (Chapman, 2011).

The lateral–medial dependency between the presence and absence of tympanic middle ear structures appears also to be related to functional constraints: a tympanic membrane without a tympanic annulus or columella would have no acoustic function, as would a tympanic annulus without a columella. In contrast, the tympanic annulus retains its acoustic function in the absence of a tympanic membrane, and the columella remains acoustically functional even in the absence of both structures, as evidenced by the middle ears of salamanders (Wever, 1985). This asymmetric functional dependency appears to have allowed these three structures to evolve sequentially rather than as a single transformation series (i.e., presence or absence of all the three structures), with losses and gains of each element occurring sequentially in a lateral–medial dependency, across the bufonid tree.

The losses, regains, and re-losses of TME structures in Bufonidae make true toads an excellent model to study the behavioural correlates of TME morphology. Previous studies have hypothesized a relationship between ear- lessness and aquatic or fossorial habitats and lack of acoustic communication or production of low-frequency calls (Hetheringotn, 1992). Additionally, based on the limited evidence presently available (see section 2.5 of the Supplementary Information), the loss of TME structures in Bufonidae appears to be coincident with the origin of a scramble competition mating system in which males in dense aggregations attempt amplexus indiscriminately and struggle for possession of females (Wells, 2007). In this mating system, acoustic territorial defence is absent and reliance on hearing for mate choice is greatly reduced or eliminated, as is the effectiveness of prezygotic isolating barriers like advertisement calls (Wells, 2007), which presumably results in the natural interspecific hybridization observed in many bufonid species (see Pereyra et al., 2016 and references therein).

Nevertheless, although most of the species of early diverging clades of Bufonidae for which the mating system is known exhibit scramble competition (see section 2.5 of the Supplementary Information), the reproductive behaviour of most species is unknown, making the character state reconstruction of this behaviour at the root node of Bufonidae ambiguous. Similarly, both within Bufonidae and across Anura, many of the groups that lack a TME employ high frequency (>1 kHz) advertisement calls during reproductive communication (*e.g., Atelopus* (Cocroft et al., 1990)*, Bombina* (Hetherington and Lindquist, 1999)*, Brachycephalus* (Condez et al., 2014)*, Melanophryniscus* (Duré et al., 2015)*, Osornophryne* (Gluesenkamp and Acosta, 2001)*, Rhinophrynus* (Sandoval et al., 2015)*, and Sechellophryne + Sooglossus* (Gerlach and Will, 2002)). Indeed, despite the absence of a TME and the occurrence of a scramble competition mating strategy, interspecific acoustic diversity is maintained in most genera (e.g., Cocroft et al., 1990; McDiarmid and Gorzula, 1989; Blair, 2013; Caldart et al.,

2013) suggesting that acoustic signals play a still unclear role in communication and/or mate choice. The maintenance of call diversity and widespread production of advertisement calls may be explained by extratympanic hearing path- ways in earless frogs. Multiple extratympanic pathways, including a lung pathway (*e.g., Atelopus* (Arch et al., 2011; Boistel et al., 2011)*, Bombina* (Hetherington and Lindquist, 1999)*, Nectophrynoides asperginis* (Arch et al., 2001))*,* an opercularis pathway (reviewed by Smotherman and Narins, 2004; Lombard and Straughan 1974; Hetherington and Lombard, 1983; Mason, 2007), and bone conduction enhanced by resonation of the oral cavity (*Sechellophryne* (Boistel et al., 2013)) have been shown effective or hypothesized so far in a few earless species. Given that in at least some anurans airborne sounds are transferred via both tympanic and extratympanic pathways (reviewed by Smotherman and Narins, 2004; Mason, 2007), anurans may experience relaxed selective pressures on the TME if TME plasticity does not greatly affect acoustic acuity. If the generality of alternative sound transfer pathways for aerial sounds is corroborated across anuran diversity, then the pre-existence of alternative pathways for airborne sound trans- mission might explain the high rate of TME loss in anurans. Nevertheless, currently proposed sound localization pathways in anurans all require middle ear coupling (Willis et al., 2013), leaving an alternative mechanism by which earless species localize audible sounds unknown.

Concluding remarks

Since the tympanic annulus and membrane first arose in combination with the plesiomorphically present columella, either prior to the origin of Anura or in Lalagobatrachia (the clade formed by all anurans except Ascaphidae and Leiopelmatidae), our analysis indicates that the TME was completely lost at least 38 times in anurans, usually in small clades within diverse families. Bufonidae is exceptional within both Anura and among all tetrapods in that the loss of all TME structures preceded a radiation of more than 150 earless species followed by independent regains and many additional losses in most derived clades. In contrast, among the approximately 26500 species of amniotes the TME was completely lost only three times and was never regained. Available evidence suggests that losses/gains of each TME structure constitute independent transformation series that occur in a lateral-medial dependency, where heterochronic events and regulation via specific genetic mechanisms are implied during development. The complex pattern of TME evolution, extensive morphological and reproductive diversity, and maintenance of bioacoustic diversity despite the loss of TME structures make Bufonidae a promising model to study extratympanic pathways of sound transmission, the physiological and behavioural conse- quences of middle ear loss, and the underlying genetic and developmental mechanisms that shaped its remarkable TME diversity.

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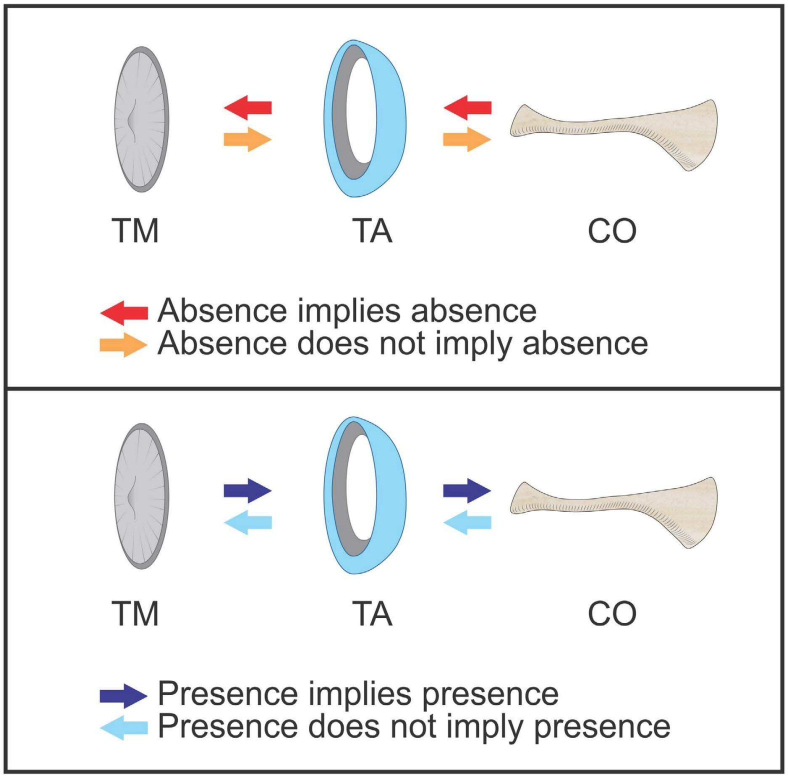

Figure 1.1 - Schematic representation of tympanic middle ear structures in anurans showing the assumptions followed herein on absence and presence of the different elements. TM, tympanic membrane; AT, tympanic annulus; CO, columella.

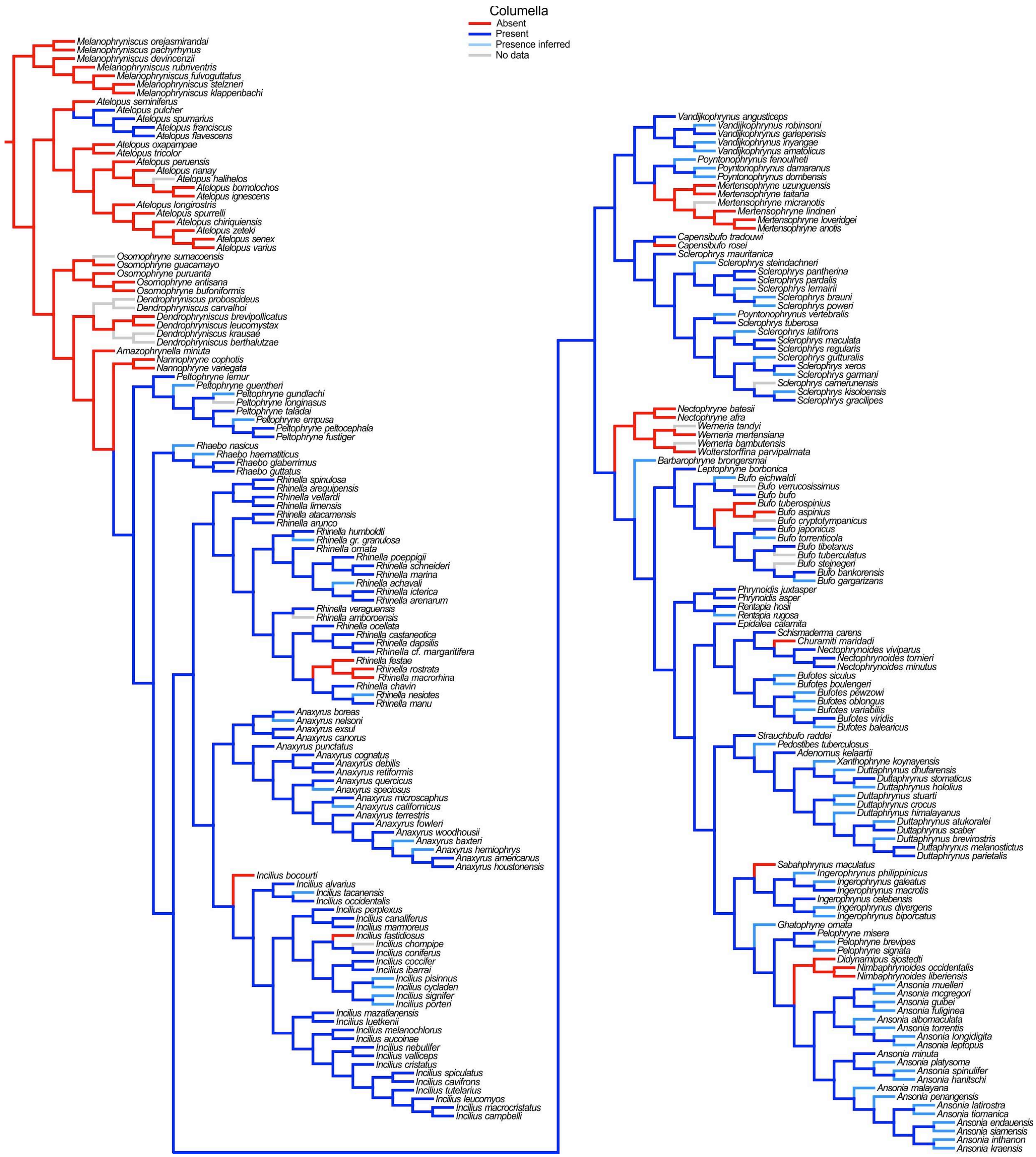

Figure 1.2 - Partial phylogenetic tree of Pyron (2014) showing ancestral state reconstructions for the columella in Bufonidae. Note that the absence of columella is synapomorphic for Bufonidae, with independent regains in a subclade of Atelopus and the common ancestor of the sister clade of Nannophryne, followed by 10 independent losses.

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3. BETTER LATE THAN NEVER: EFFECTIVE AIR-BORNE HEARING OF TOADS DELAYED DUE TO LATE MATURATION OF THE TYMPANIC MIDDLE EAR STRUCTURES

Summary

Most vertebrates have evolved a tympanic middle ear that enables effective hearing of airborne sound on land. Although inner ears develop during the tadpole stages of toads, tympanic middle ear structures are not complete until months after metamorphosis, potentially limiting the sensitivity of post-metamorphic juveniles to sounds in their environment. We tested the hearing of five species of toads to determine how delayed ear development impairs airborne auditory sensitivity. We performed auditory brainstem recordings to test the hearing of the toads and used micro-CT and histology to relate the development of ear structures to hearing ability. We find a large (14-27 dB) increase in hearing sensitivity from 900 to 2500 Hz over the course of ear development. Thickening of the tympanic annulus cartilage and full ossification of the middle ear bone are associated with increased hearing ability in the final stages of ear maturation. Thus, juvenile toads are at a hearing disadvantage, at least in the high-frequency range, throughout much of their development, because late forming ear elements are critical to middle ear function at these frequencies. We discuss the potential fitness consequences of late hearing development, although research directly addressing selective pressures on hearing sensitivity across ontogeny is lacking. Given

that most vertebrate sensory systems function very early in life, toad tympanic hearing may be a sensory development anomaly.

Introduction

Most vertebrate sensory systems function before or soon after an animal begins living autonomously (Ganchrow and Ganchrow, 1987; Noakes and Godin, 1988; Apfelbach et al., 1991; Fagiolini et al., 1994; Easter and Nicola, 1997; Northcutt, 2004). Yet, in anurans (frogs and toads), the tympanic hearing system is often not fully formed until days, weeks, months, or even a year past metamorphosing from a free-living, aquatic larval stage to a land-based, autonomous froglet (Sedra and Michael, 1959; Hetherington, 1987). Thus, the anuran hearing system is one of few sensory systems with major structural development after the animal is fully independent. Previous work has shown that tadpoles sense underwater sound well (Simmons, 2015), but that sensitivity to airborne sound increases after metamorphosis (Shofner and Feng, 1981; Boatright-Horowitz and Simmons, 1995). Behavioral consequences of this late development are possible. Species-specific calls are known to function in mate attraction, conspecific localization, territoriality, and defense in adults (Narins et al., 2006) but the fitness consequences of hearing conspecific calls or other environmental cues remains unstudied in juveniles, despite juvenile frogs showing behavioral responses to calls well before sexual maturity (Baugh and Ryan, 2010). Hearing is hypothesized to play a role in predator detection as well (Wever, 1985), though the focus of hearing research in anurans has been on its value for social communication

(Wever, 1985; Narins et al., 2006, Wells and Schwartz, 2007). This late development of the ear likely has a large impact on hearing ability throughout post-metamorphic ontogeny, but little is known about how tympanic ear function changes as individual ear structures mature and grow in size from metamorphosis to adult.

The inner ear structures, which contain the sensory hair cells that transmit sound information to the brain, are fully formed and functional during the larval stages of anuran development (Simmons and Alexander, 2014; Simmons, 2015). The medulla and midbrain both respond to underwater sound in tadpoles that lack functional tympanic ears (Simmons, 2015). In addition, the operculum, a movable cartilaginous structure found solely in amphibians in the oval window, is developed by metamorphosis (Sedra and Michael, 1959; Hetherington, 1987). The operculum is thought to be involved in low frequency sound perception (below 1kHz) in conjunction with the opercularis muscle, which attaches the suprascapular cartilage to the operculum (Lombard and Straughan, 1974; Mason, 2006). In general, middle ear structures develop in a medial-to-lateral progression during and after metamorphosis (diagrammed in Fig. 1), however, the relative timing of the other tympanic ear structures varies across species (Sedra and Michael, 1959; Hetherington, 1987; Vorobyeva and Smirnov, 1987). The anuran middle ear column, termed the columella, consists of three portions, the *pars interna*, the *pars media,* and the *pars externa* (also called the extracolumella). The more lateral middle ear structures include the tympanic membrane and a surrounding cartilaginous ring, termed the tympanic annulus. In species that require months post-metamorphosis to complete development of the tympanic middle ear structures (species of the genus *Hyla* and *Bufo*), the order of ear structure formation is quite clear. Tympanic ear development begins with the formation of cartilaginous structures comprising the columella. First, the *pars interna*, also referred to as the columella footplate, appears attached to the oval window by the climax of metamorphosis (Hetherington, 1987). The *pars interna* then grows outward, forming the *pars media* and eventually extends to become or join the *pars externa* (Hetherington, 1987). The tympanic annulus and tympanum begin to develop as the columella grows (Sedra and Michael, 1959; Hetherington, 1987). The middle ear cavity and Eustachian tube develop at the same time as the tympanic annulus and tympanum, reaching adult-like proportions before the *pars media* ossifies (*Hyla crucifer*, Hetherington, 1987). When the middle ear is fully mature, the *pars media* and a portion of the *pars interna* are ossified, while the *pars externa* remains cartilaginous (Hetherington 1987; Vorobyeva and Smirnov, 1987).

After all ear structures have formed, sound is transmitted through the tympanic hearing system in anurans similarly to the transmission of sound through comparable tympanic hearing systems across other eared tetrapods (reviewed in Christensen-Dalsgaard and Manley, 2013; Mason et al. 2015). The tympanum vibrates in response to airborne sound and transmits these vibrations to the columella. The columella footplate is in direct contact with the inner ear fluids and transmits the vibrations to the fluid, which ultimately moves hair cells, resulting in action potentials that signal to the brain (reviewed in Lewis and Narins, 1999). However, unlike the single auditory end organ found in most tetrapods, three end organs respond to sound in anurans: the sacculus, which senses very low frequencies (ca. 20-120Hz), the amphibian papilla, which senses low-mide frequencies (ca. 120-1,250Hz), and the basilar papilla, which senses higher frequencies (ca. 1,250-4,000Hz; Smotherman and Narins, 2000; Christensen-Dalsgaard and Narins, 1993).

In addition to tympanic hearing, anurans also sense airborne auditory stimuli through extratympanic hearing pathways (Wilczynski et al., 1987), which are not dependent on tympanic middle ear structures. The main extratympanic hearing pathways proposed for post-metamorphic anurans are the opercularis system and the lungs. The opercularis pathway transmits acoustic vibration to the inner ear via the operculum (Lombard and Straughan, 1974). In the lung pathway, the body wall overlying the lungs vibrates in response to sound and transmits those vibrations to the inner ear even in the absence of tympanic middle ears (Lindquist et al., 1998; Hetherington and Lindquist, 1999; Hetherington, 2001). These extratympanic hearing pathways could buffer immature anurans from potential sensory costs of late developing ear structures.

To better understand the functional consequences of delayed middle ear development in anurans, we tested the hearing of five toad species, with individuals ranging from small, juveniles at various stages of ear development to adults with completely developed ear structures. We predicted that, as in *Rana catesbeiana* (Shofner and Feng 1981; Boatwright-Horowitz and Simmons, 1995), post-metamorphic development of the middle ear structures would lead to increased sensitivity to sounds as animals grow. We further investigated which changes in tympanic middle ear structures contributed to hearing sensitivity throughout post-metamorphic development. Toad species develop their tympanic hearing system slowly in comparison to other anurans (Sedra and Michael, 1959; Hetherington, 1987), offering a unique opportunity to identify which maturational steps conferred major impacts on tympanic hearing.

Materials and methods

Animal collection

Individuals of five species (*Rhinella alata* n=9, *Rhinella leptoscelis* n=8, *Rhinella marina* n=10, *Rhinella spinulosa* n=11, *and Rhaebo haematiticus* n=12) were collected from field sites in Ecuador and Peru (Table 1). The Institutional Animal Care and Use Committee at Colorado State University approved all experiments (IACUC Protocol #12-3484A), and the Ministerio del Ambiente in Ecuador and the Servicio Nacional Forestal y de Fauna Silvestre (SERFOR) in Peru approved collection, research, and export permits (Table 1). We identified the sex in only a subset of individuals in our study, thus we did not examine patterns of sex differences among species although males and females may differ in hearing (as in Boatright-Horowitz and Simmons, 1995; Miranda and Wilczynski, 2009; Shen et al., 2011). We did not find bimodal distributions of ear structures that indicated extreme sexual dimorphism in ears is likely in this lineage.

Auditory brainstem recordings (ABRs) to test hearing throughout ear development

We characterized the hearing abilities of each species using auditory brainstem recordings to measure sensitivity of animals to tones across the range of audible frequencies. All auditory brainstem recordings were performed in Ecuador or Peru. We performed recordings in a portable wooden chamber (30” length x 15” width x 18” height) with all internal surfaces covered with acoustic foam lining. We lightly anesthetized the toads with a small topical application of 5% benzocaine and then paralyzed the toads with 0.05% succinylcholine chloride (Sigma-Aldrich, St. Louis, MO, U.S.A.) at a dosage of 7.5 µl/gram. We placed three 28-gauge stainless steel electrodes (Model F-E2, GRASS Technologies, Warwick, RI, U.S.A.) subdermally to measure electrical signal generated by the auditory nerve (the VIIIth nerve). Differential electrodes were placed over the VIIIth nerve and over the midbrain, and a third ground electrode was placed within the arm contralateral to the VIIIth nerve being measured. We linked the three electrodes to a pre-amplifier (RA4PA, Tucker-Davis Technologies, Alachua, FL, U.S.A.) connected to a mobile processor (RM2, Tucker-Davis Technologies) that relayed output and input signals from and to a laptop computer (Mini 210-2180, Hewlett Packard, Palo Alto, CA, U.S.A.). We played pure tones from a three-inch speaker (FF85K, Fostex, Tokyo, Japan) suspended within the audio chamber to minimize ground vibrations from the speaker reaching the animal. We amplified the acoustic stimuli with a digital AC/DC amplifier (DTA-1 Class T, Dayton Audio, Springboro, OH, U.S.A.) and calibrated with a ½ inch free field microphone (46AE, G.R.A.S. Sound and Vibration A/S, Skovlytoften, Denmark). We calibrated the free field microphone by using a pistonphone (Type 42AA, G.R.A.S. Sound and Vibration A/S, Skovlytoften, Denmark) to produce a 94 dB RMS re 20 μPa tone at 1 kHz. The toads lay perpendicular to and 18 inches away from the speaker on a wet paper towel. To shield electrical noise, we placed a wire mesh cage over the animal during recordings that was grounded by a connection to the pre-amplifier.

We calibrated the experimental setup using customized software (QuickABR_burst) that controlled stimulus presentation and data acquisition using the RM2 processor. We played 25 ms pure tones, ranging in frequency from 200-4000 Hz at 5 dB increments with 40 ms intervals. We tested frequencies in order from low to high frequency with amplitudes presented sequentially from high to low, unless additional high amplitude tones were necessary due to a lack of response at the starting amplitude. Response signals were averaged over 400 tone bursts. Between every two frequencies tested we measured the response to a transient generated from a half cycle 4 kHz sinusoid at 105 dB to ensure that the auditory responsiveness remained stable throughout the testing session. If transient response dropped below 25% of the original signal, we omitted all subsequent measurements from analyses. We visually determined thresholds for each frequency by finding the minimum stimulus decibel level that evoked a response signal amplitude of 0.002 mV (two times the average noise level) or greater from the auditory nerve.

Specimen fixation

After each auditory brainstem recording, we measured the snout-vent length (SVL) and tympanum diameter of each animal to the nearest 0.1 mm using a dial caliper (31-415-3, Swiss Precision Instruments Inc., Garden Grove, CA, U.S.A). We then euthanized the animals with 20% topical benzocaine before decapitation. We preserved the head of each specimen in 4% paraformaldehyde (diluted in Phosphate Buffered Saline from 16% paraformaldehyde solution; Electron Microscopy Sciences, Hatfield, PA, U.S.A.) for 24 hours and performed three 15-minute rinses in Phosphate Buffered Saline before storing cranial tissue in 70% ethanol.

Micro-CT scanning to compare ossification of bony ear structures

We used micro-computed tomography (micro-CT) to analyze the level of ossification of middle ear bones in 3-4 individuals per species spanning a range of body sizes. The Micro-CT Core Laboratory at the University of Texas Health Science Center scanned and reconstructed all samples. We secured toad skulls to the specimen stage using Parafilm (American National Can, Greenwich, CT, U.S.A.) and scanned the skulls in air in a high-resolution desktop micro-CT system (Skyscan 1173, Bruker Skyscan, Aartselaar, Belgium). Scan settings were: 60 kV, 133 µA beam intensity, a 0.7°**,** 4 frame averaging, and 1000 millisecond exposure time at each step. We used a 1.0 mm aluminum filter during scans (Kovács et al., 2009). We set pixel size to 10 µm with the exception of six very large specimens (two *R. marina*, two *R. haematiticus*, and two *R. spinulosa*) that were scanned at 30 µm. We reconstructed images using NRecon

(Bruker SkyScan, Aartselaar, Belgium) with a Feldkamp cone-beam algorithm (Feldkamp et al., 1984). We also used a polynomial correction to reduce beam-hardening effects during reconstructions (Kovács et al., 2009; Zou et al., 2011). We imported the bmp files from the reconstructions into Fiji (Schindelin et al., 2012) at a resolution of 60μm and created 3D surface models for each skull at a consistent surface threshold of 50 using the 3D viewer plugin (Schmid et al., 2010). We calculated the length of visible, ossified columella using the measure tool in Meshlab (Visual Computing Lab ISTI-CNR, 2015).

Histology and 3D reconstruction to compare development of all ear structures

We decalcified two specimens per species (total n = 10) in 10% EDTA (pH 7.4) for up to one week at room temperature and then put specimens through a graded ethanol series (30%, 50%, 70%, 90%, 95%, 100%, 100%), and embedded them in hydroxypropyl methacrylate (HPMA) plastic (Electron Microscopy Sciences, Hatfield, PA, U.S.A.). We drilled holes of 1 mm diameter into the plastic around each specimen before sectioning the tissue at 5 μm thickness using a microtome (RM1265, Leica, Wetzlar, Germany) and mounted every other section onto a Fisher Superfrost Plus Microscope Slides (Fisher Scientific, Pittsburgh, PA, U.S.A.). We then stained the tissue with Eosin and Toluidine Blue (Fisher Scientific, Pittsburgh, PA, U.S.A.) and took photographs of every third section for a final resolution of 30 μm between imaged sections. We aligned the photographed sections using the drilled holes and then 3D modeled and measured ear structures within IMOD 3D (Kremer et al., 1996).

Statistical Analyses

To determine if smaller, less developed individuals had hearing thresholds that were distinct from larger, adult individuals we performed cluster analyses. We used Ward Hierarchical Clustering analysis in R to examine which individuals fell into each of the two designated clusters based on hearing thresholds. The number of clusters (2) was designated *a priori* based on a distinct split in hearing ability observed in the audiograms. We visualized audiograms representing sensitivity of animals in each hearing cluster within each species by graphing the thresholds from the auditory brainstem recordings using the sme (Smoothing-splines Mixed-effects models) package (Berk, 2013) in R (R Core Team, 2015).

To determine the frequencies at which our two hearing clusters differed in sensitivity, we used mixed models produced in the package lme4 (Bates et al., 2014) in R. We ran a model that had hearing threshold as the response variable, a hearing cluster by frequency interaction term as the fixed effect, and species and individual as random variables. We then calculated differences in least squares means of hearing thresholds between hearing clusters at all frequencies using the package lmerTest (Kuznetsova et al., 2015) within R. The least squares means gave us an estimate of the mean hearing threshold differences between hearing clusters at all frequencies.

Results

Auditory Brainstem Recordings (ABRs)

A hierarchical cluster analysis found that hearing thresholds distinctly changed across size/development within four out of our five species. In four of the five species (*R. haematiticus, R. leptoscelis, R. marina,* and *R. spinulosa)*, small individuals (<40 mm SVL) were included in the less sensitive cluster (higher hearing thresholds) and larger individuals (>40 mm SVL) were included in the more sensitive cluster (lower hearing thresholds) with two exceptions: one 34.3 mm *R. marina* clustered with the more sensitive hearing cluster, and one 72.4 mm *R. spinulosa* clustered with the less sensitive hearing cluster (Fig. 2). All individuals of *R. alata* clustered within the more sensitive hearing cluster, regardless of body size.

Hearing clusters differed in sensitivity at only a subset of frequencies. The less sensitive hearing cluster had 14-26 dB higher thresholds of acoustic responses than more sensitive conspecifics from 900 Hz to 2.5 kHz (Fig. 3A, Table 2). Figure 3B shows within-species hearing differences between the less and more sensitive hearing clusters for *R. haematiticus, R. leptoscelis, R. marina,* and *R. spinulosa*

Differences in tympanic middle ear structure development across species and size

To characterize the development of the ear structures, we used micro-CT scanning and histology. Because of limited sample size, we present qualitative observations of species differences in the relative rate of middle ear formation. Micro-CT scans revealed high variation in the ossification of the columellae (Fig. 4A). Histological analysis showed that despite incomplete columellar ossification, all columellae had completely formed from the footplate attachment to the inner ear to the extracolumella attachment at the tympanic membrane. Likewise, the inner ear and operculum were structurally complete in all specimens examined from the less sensitive hearing cluster (n=10, Fig. 4B). However the tympanic annulus showed incomplete development in all examined *R. spinulosa, R. marina*, and *R. haematiticus* juvenile specimens. The dorsal end of the tympanic annulus remained unconnected in these individuals (Fig. 4B). Species differed in the relative rate of middle ear structure development. For example, juvenile *R. leptoscelis* have minimally ossified columellae, but complete middle ear structures. In contrast, juvenile *R. haematiticus* and *R. marina* have more ossified columellae than juvenile *R. leptoscelis*, but have incomplete tympanic annuli (Fig. 4B).

Ear structure differences between hearing clusters

We quantified the size of middle ear structures as well as the length of ossified columellae and found three structural aspects of the ear that matched auditory threshold differences. Individuals in the more sensitive hearing cluster had thicker tympanic annuli, more ossified columellae, and larger columellar volumes than less sensitive individuals (Fig. 5A-C). Individuals from both hearing clusters overlapped in tympanic membrane diameter, operculum volume, and inner ear volume (Fig. 5D-F).

Discussion

Our results support our hypothesis that protracted development of the ear confers a large hearing impairment late into juvenile development. We found a dramatic increase in hearing ability late in toad development. This increase in hearing ability was associated with two very late changes in tympanic middle ear structures: the thickening of the tympanic annulus and ossification of the columella. Our results show that in toads with late-developing middle ear structures, the tympanic hearing system does not efficiently transfer sound until it has completely formed and ossified all relevant structures.

Our results are largely consistent with previous work showing post-metamorphic development of the tympanic ear enhances sensitivity to sound, although the pattern of frequency responsiveness differs. Shofner and Feng (1981) and Boatright-Horowitz and Simmons (1995) detailed increases in overall hearing sensitivity as post-metamorphic *Rana catesbeiana* (bullfrog) froglets increased in age and size. They also described a shift in the best-sensed frequencies from higher frequencies in metamorphs (~2500 Hz) to lower frequencies in adults (~1500-1700 Hz) (Shofner and Feng, 1981; Boatright-Horowitz and Simmons, 1995) that do not match our results. Our juvenile toadlets were most sensitive to low frequencies (<900 Hz). This low-frequency sensitivity remained relatively constant from juvenile to adult stages in our recordings as adults became more sensitive to frequencies between 900 and 2500 Hz. These different patterns in toads and bullfrogs likely reflect lineage differences in the developmental rate of ear structures as well differences in adult tympanic ear function.

The novelty of our study was the ability to tease apart the formation and development of individual tympanic middle ear structures in five separate species ranging in body size, allowing us to draw strong conclusions about which ear development milestones most affected hearing ability. Previous studies on changes in post-metamorphic hearing in *Rana* did not characterize changes in the development of the tympanic hearing structures except for tympanic membrane size (Shofner and Feng, 1981; Boatright-Horowitz and Simmons, 1995). Compared to *Rana,* the toad species we examined have protracted development of the tympanic auditory system (Hetherington, 1987), which allowed us to disentangle the effects of individual structures. Individuals with thickened tympanic annuli and highly ossified columellae have much better hearing abilities than juveniles at earlier stages of tympanic ear development. Thus, we conclude that the thickening of the tympanic annulus and ossification of the columella are critical for tympanic ear functionality.

Although hearing above 1 kHz was greatly affected by development of the middle ear structures, low frequency (<900 Hz) hearing does not rely on the tympanic hearing pathway. Previous studies have found that frequencies below 1 kHz are mainly sensed via extratympanic pathways (Wilczynski et al. 1987; Lombard and Straughan, 1974; Fox, 1995; reviewed in Christensen-Dalsgaard, 2005), and our results support this conclusion, given the lack of hearing differences among individuals with complete and incomplete tympanic hearing pathways. The opercularis pathway and the body wall overlying the lungs have both been shown to transmit sound frequencies below 1kHz to the inner ear (Lindquist et al., 1998; Hetherington and Lindquist, 1999; Hetherington, 2001). Both the opercularis complex as well as the lungs and Eustachian tube were formed in all of our specimens and could be important for this similarity in low frequency hearing between our juvenile and adult animals.

The late development of mid-high hearing sensitivity for acoustic communication may have fitness consequences, although natural history information is lacking to estimate costs and benefits of hearing conspecific calls, predator cues, or prey sounds. All four species that displayed immature middle ear structures had poor hearing sensitivity in the 0.9-2.5 kHz range, which contains the dominant frequencies of many toad species' calls (Castellano et al., 2000; B. Gregory Pauly, *Phylogenetic Systematics, Historical Biogeography, and the Evolution of Vocalizations in Nearctic Toads (Bufo)*, PhD thesis, University of Texas at Austin, 2008; Guerra et al., 2011). Unfortunately, the importance of acoustic sensitivity for social communication in juvenile anurans remains unstudied, and we completely lack information about how auditory sensitivity impacts predator avoidance and prey capture, limiting our understanding of the performance and fitness consequences of late developing hearing sensitivity.

This study provides an example of an unusually late-forming sensory system. The completion of the middle ear structures in bufonids drastically improves airborne hearing capabilities at frequencies that are vital to conspecific communication in many toad species. Ability of the tympanic hearing system to function in toads depends on columellar ossification as well as tympanic annulus volume, two very late-forming and understudied structures in the tympanic hearing system of anurans. We posit that relaxed selection on hearing sensitivity until sexual maturity may allow for the late development of these hearing structures in toads; however, more natural history studies are needed to determine the fitness consequences to juvenile anurans of reduced sensitivity above 1 kHz due to impaired detection and localization of prey, predators, and conspecifics.

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Table 2.1 – Collection country, sites, and permit numbers for animals in the study.

Species	Country	Specific Region	Permit #
Rhaebo haematiticus	Ecuador	Mindo Forest Reserve and Rio Guajalito Reserve in Pastaza	Permit: 001-13 IC-FAU-DNB/MA
Rhinella alata	Ecuador	Rio Rutuno, Pastaza	Permit: 001-13 IC-FAU-DNB/MA
Rhinella leptoscelis	Peru	Yanachaga buffer zone of Chemillén National Park in the basins of San Alberto (CDS/CNEH-Perú) Llamaquizú, San Luis, and San Daniel	Permit: 0071-2015-SERFOR-DGFFS/DGEFFS
Rhinella marina	Ecuador	Canelos, Pastaza and in Mindo Forest Reserve and Maquipucuna Biological Reserve in Pastaza	Permit: 001-13 IC-FAU-DNB/MA
Rhinella spinulosa	Peru	K'iripampa Acopia in Acomayo, Cusco	Permit: 0071-2014-MINAGRI-DGFFS/DGEFFS

Table 2.2 – Estimated least squares means differences in hearing thresholds between the more and less sensitive hearing clusters.

Frequency (Hz)	**Hearing threshold differences between hearing clusters dB (±SE)**
200 Hz	-1(±3)
300 Hz	3 (±3)
400 Hz	-2 (±3)
500 Hz	1 (±3)
700 Hz	-4 (±3)
900 Hz	**-14 (±3)*** **
1100 Hz	**-22 (±3)*** **
1300 Hz	**-27 (±3)*** **
1500 Hz	**-26 (±3)*** **
1750 Hz	**-20 (±3) *** **
2000 Hz	**-15 (±3)*** **
2250 Hz	**-16 (±3)*** **
2500 Hz	**-14 (±3)*** **
3000 Hz	-4 (±3)
35000 Hz	-2 (±3)
4000 Hz	1 (±3)

Estimated differences and standard error rounded to the nearest dB are given for each frequency with significant differences between hearing stages bolded and indicated with asterisks (p<.05=*, p<.01=**, p<.001=***). A negative estimated difference indicates that the more sensitive hearing cluster had a lower hearing threshold (better hearing ability) at that frequency while a positive estimated difference indicates the more sensitive hearing stage had a higher hearing threshold (worse hearing ability) at that frequency.

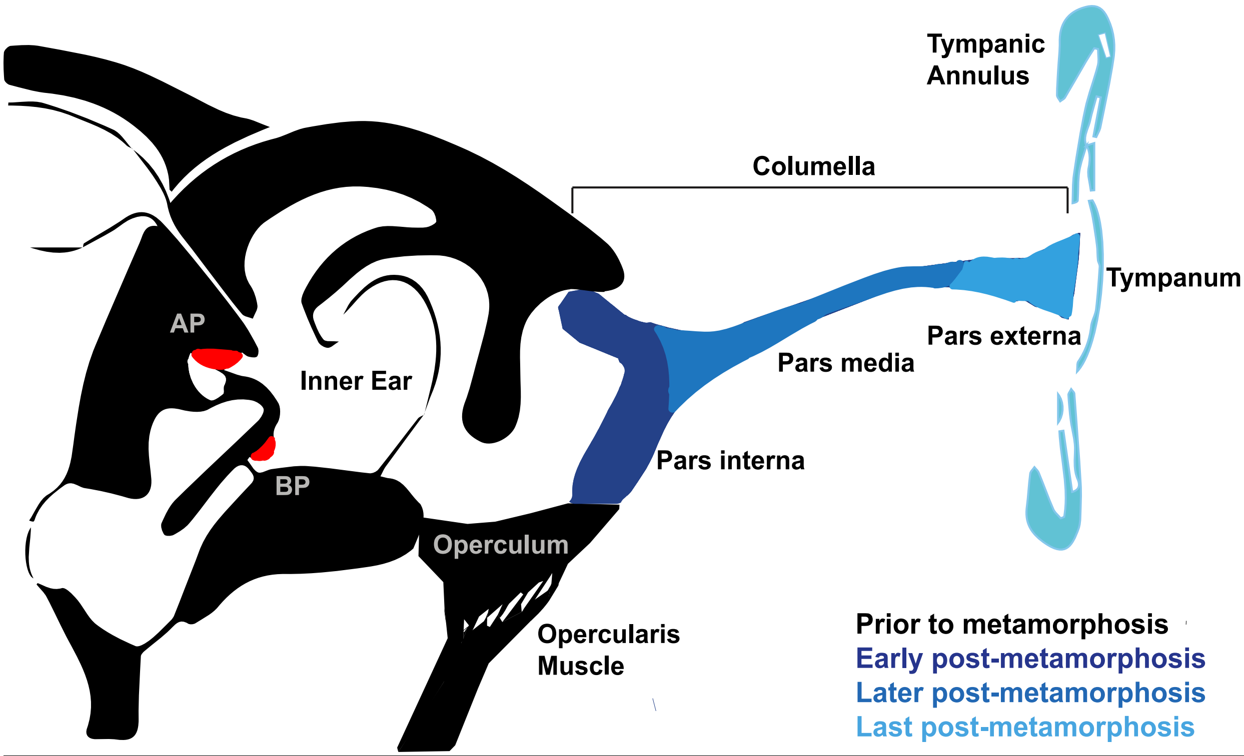

Figure 2.1 – Developmental progression of tympanic middle ear structures in anurans. Horizontal section of adult *Rana pipiens*, modified from Wever (1985) to depict the medial-to-lateral development of middle ear structures after metamorphosis. Black structures indicate muscles and bones that surround the inner ear cavity and form prior to metamorphosis. The amphibian papilla (AP) and basilar papilla (BP), depicted in red, house the sensory hair cells. The saccule is not visible in this section plane. We color code middle ear structures according to the relative time at which the structure initially appears in previous studies of anuran development (Sedra and Michael, 1959; Hetherington, 1987; Vorobyeva and Smirnov, 1987), as absolute timing differs in each lineage. Middle ear structures that form early are colored in darker shades of blue, with later forming middle ear structures depicted in lighter shades of blue.

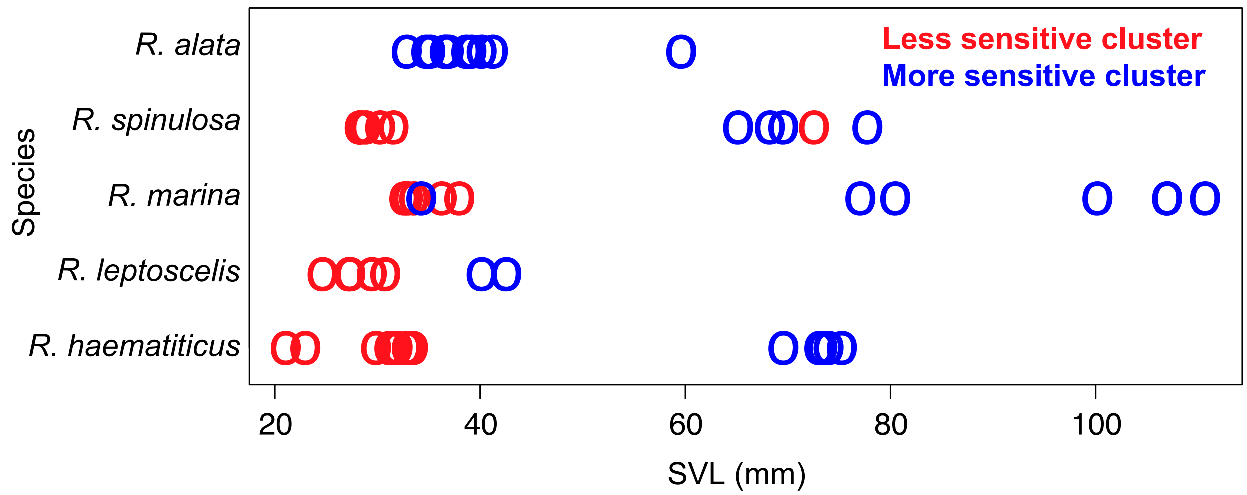

Figure 2.2 – How species and size predict which individuals are assigned to the less (red) or more (blue) sensitive hearing clusters. Each circle represents an individual used in the hearing cluster analysis, with species on the y axis and body size (snout-vent length; SVL) in millimeters on the x axis.

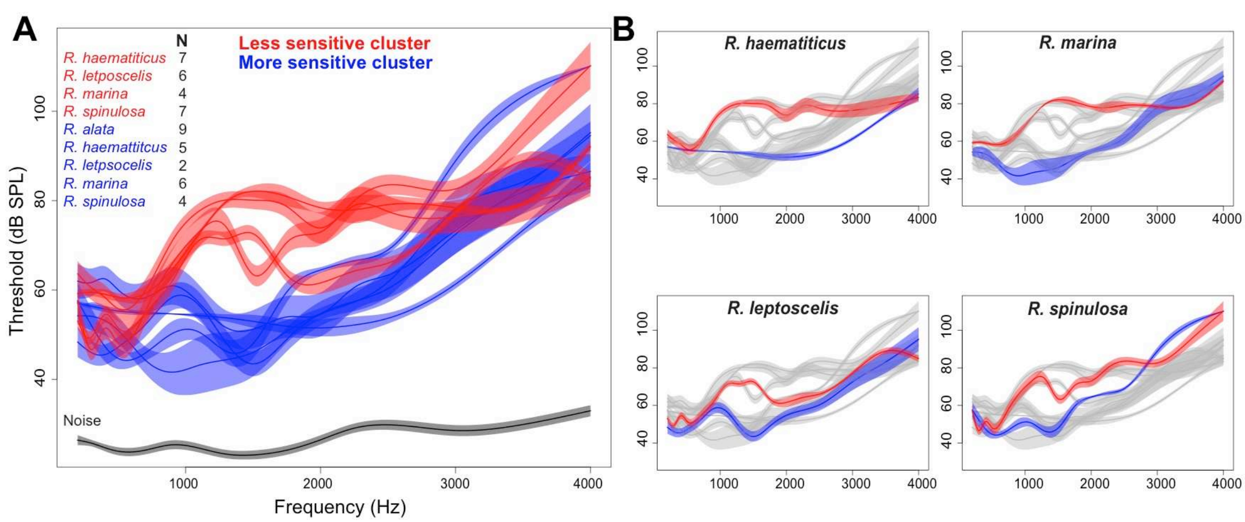

Figure 2.3 – Hearing differences between the more and less sensitive hearing stages. A – Audiograms of less sensitive (red) and more sensitive (blue) hearing clusters, separate lines within each stage represent different species. Within-chamber noise level shown in black. **B –** Audiograms of less sensitive (red) and more sensitive (blue) hearing stages within *R. haematiticus, R. leptoscelis, R. marina,* and *R. spinulosa*. Each panel displays a species' audiogram separated by hearing stage. The separate hearing stage audiograms of the other three species are displayed in grey in each panel.

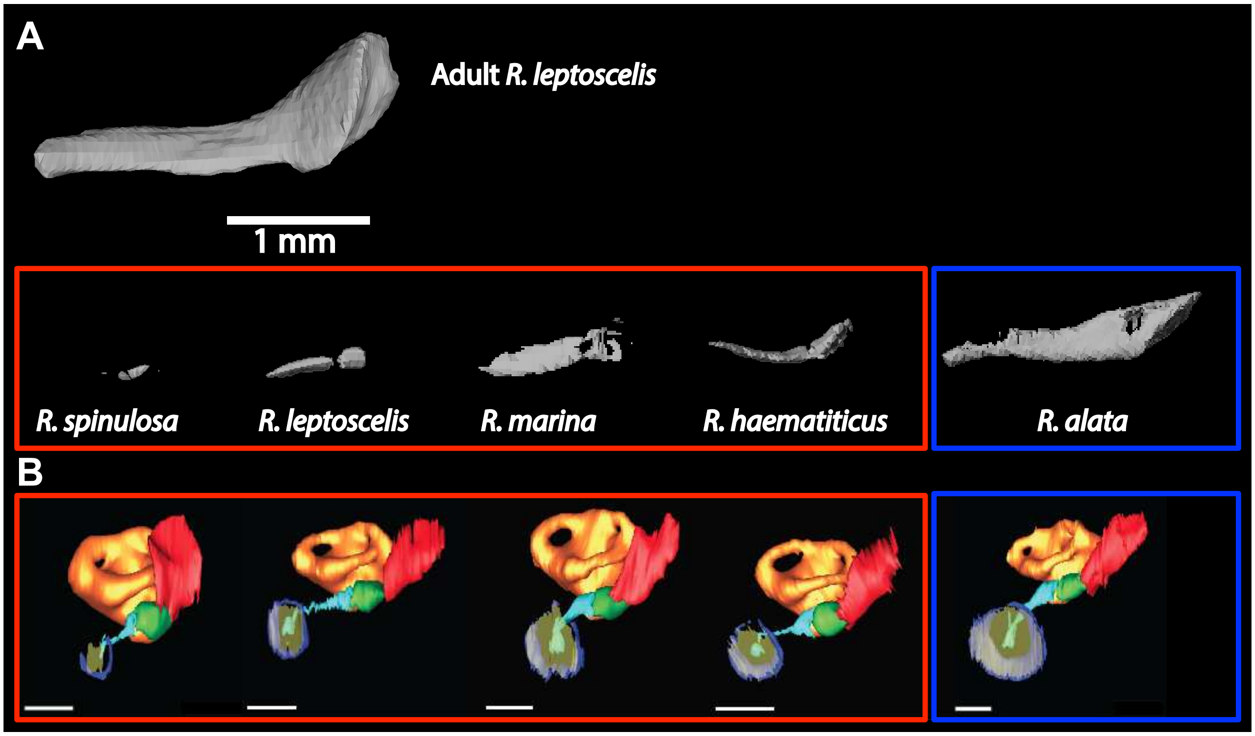

Figure 2.4 – Micro-CT and histology 3D reconstructions showing variation in development of tympanic middle ear structures across species and hearing cluster. Hearing cluster assignment for each individual is indicated by the boxes (the less sensitive hearing cluster = red and the more sensitive hearing cluster = blue). **A**- Micro-CT of one adult *R. leptoscelis* columella (SVL = 42.4 mm) and an exemplar columella from similarly sized individuals of each species. All columellae are scaled to the 1 mm scale bar shown. Despite being similar in size (SVL of *R. spinulosa* = 28.7 mm, *R. leptoscelis* = 30.6 mm, *R. marina* = 32.7 mm, *R. haematiticus* = 29.9 mm, *R. alata* = 32.7 mm) different species show extreme variation in amount of columellar ossification. **B** - 3D reconstructions of ear structures show variation in completion of the tympanic annuli (dark blue) and tympanic membranes (yellow) in similarly sized individuals of different species. All specimens examined had complete columellae (light blue), opercula (green), inner ears (orange), and opercularis muscles (red). Individuals are different between panel A and panel B, but species align vertically.

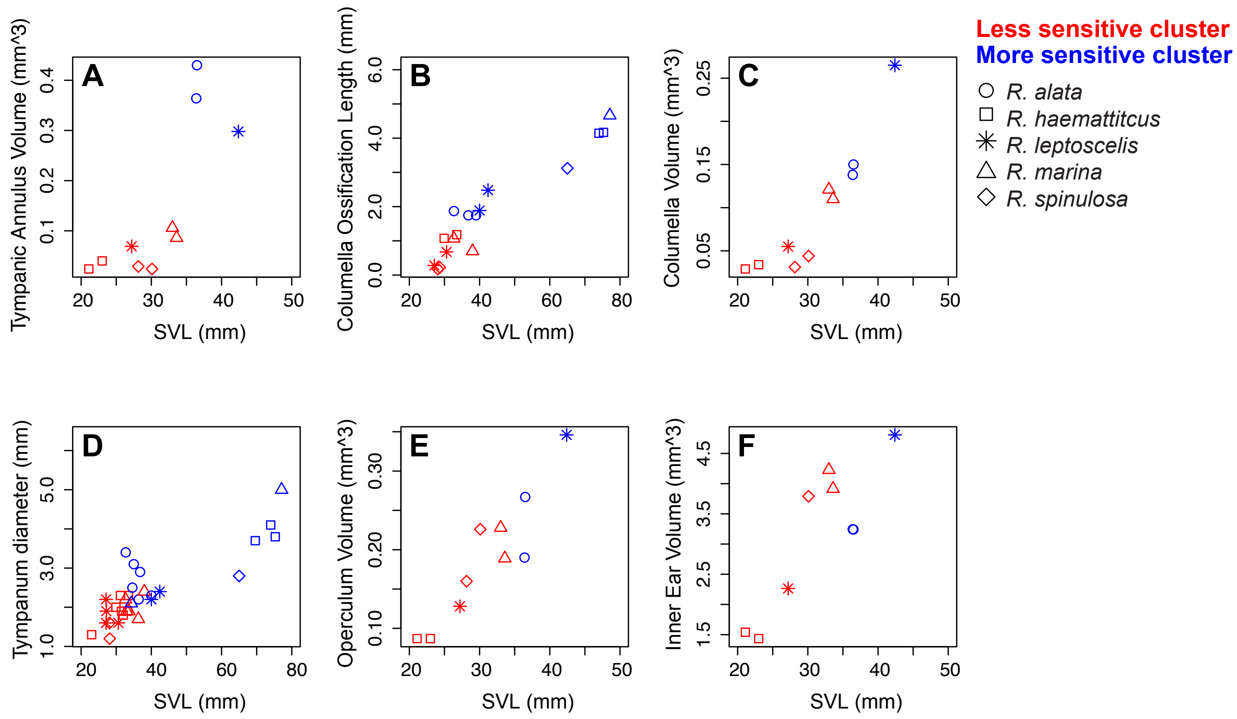

Figure 2.5 – Differences in the sizes of hearing structures between the more and less sensitive hearing clusters. Species are indicated by symbol type while hearing cluster is indicated by color (the less sensitive hearing cluster = red and the more sensitive hearing cluster = blue). **A** - Volume of an individual's tympanic annulus plotted by their snout-vent length (SVL). **B** - Length of the ossified portion of an individual's columella plotted by their SVL. **C** - Volume of an individual's columella (ossified and cartilaginous portions) plotted by their SVL. **D** - Diameter of an individual's tympanic membrane plotted by their SVL. **E** - Volume of an individual's operculum plotted by their SVL. **F** - Volume of an individual's inner ear plotted by their SVL.

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4. WHO NEEDS AN EAR? 'EARLESS' TOADS STILL HEAR LOW FREQUENCIES AND THEY FEEL THEM EVEN BETTER

Summary

Although sensory losses or reductions are largely attributed to relaxed environmental selection and/or pleiotropy, evidence for either of these hypotheses is lacking for tympanic middle ear loss frogs and toads. The tympanic middle ear functions in most tetrapods for hearing airborne sound. Yet earlessness, lacking a tympanic middle ear, has evolved many times across anurans despite use of auditory cues for fitness-related traits. Here we determine whether alternative sensory pathways have facilitated the lability of the tympanic middle ear in anurans. We used auditory brainstem recordings to compare hearing and vibrational sensitivity between ten species (six eared, four earless) within the true toad family (Bufonidae). We also compared extratympanic hearing ability across body sizes and compared operculum morphology between eared and earless species. We found that middle ear absence has costs for high frequency hearing that could affect the ability of earless species to detect conspecific calls. However, the loss of high-frequency hearing ability may be tolerated or even outweighed if low frequency hearing or vibrations can be effectively used for communication and predator or prey detection. In contrast to our predictions, larger anurans had more sensitive extratympanic hearing, which raises questions about how extratympanic pathways are functioning in earless species. Based on our findings, we

propose a number of evolutionary scenarios that may relax selection on the tympanic middle ear.

Introduction

The loss of sensory traits has intrigued evolutionary biologists since Darwin first pondered eye loss in cavefish in *Origin of Species* (1857) because the strong, positive impacts sensory systems typically have on fitness makes their loss unexpected. In most studied systems, sensory loss or reduction has an adaptive explanation involving changes in the sensory environment that relax selection on that sensory system (Jefferey et al., 2005; Lehmann et al., 2007) and/or selection for another trait that inhibits development of the sensory structure(s) (Norris and Lowe, 1951; Wright, 1964; Berman and Regal, 1967; Nijhout and Emlen, 1998; Yamamoto et al., 2009; Manley, 2010). However, many species of frogs and toads have lost tympanic middle ears, a condition termed earlessness, without a consistent adaptive explanation. Tympanic middle ear loss is unlikely due to changes in the acoustic environment (Vorobyeva and Smirnov, 1987; Jaslow et al., 1988; Hetherington, 1992a) or changes in genetically or developmentally linked structures (Chapter 4), but may instead result from the presence of alternative sensory pathways that either substitute for or preserve hearing sensitivity.

The tympanic middle ear functions in hearing airborne sound. Ancestral tetrapods were unable to hear most airborne sound when they transitioned onto land because sound waves in air are 99.99% reflected by the animal's dense body tissues (Mallo, 2001). The tympanic middle ear resolves this issue by transducing airborne sound waves to fluid vibrations sensed by hair cells in the inner ear (reviewed in Manley, 2010). Similar tympanic hearing systems have evolved independently in the major tetrapod lineages: amphibians, lizards, turtles, mammals, and archosaurs (Clack, 1997, Christensen-Dalsgaard and Carr, 2008, Manley, 2010; Manley and Sienknecht, 2013), signifying the tympanic middle ear's importance for hearing on land.

In eared anurans, the middle ear is morphologically and functionally similar to the middle ear of other tetrapods, but has a few key distinctions (Wever, 1985; reviewed in Lewis and Narins 1999). Airborne sound first vibrates a thin membrane on the side of the animal's head, the tympanic membrane, which is surrounded by a cartilaginous ring, the tympanic annulus. The oscillation of the tympanic membrane then causes the mostly bony middle ear column, the columella (= stapes), to move in a piston-like fashion. One end of the columella is connected to the tympanic membrane via a cartilaginous extension, the extracolumella, and the other end of the columella, the columellar footplate, sits in the oval window of the inner ear. The columella's movement transfers the motion of the tympanic membrane to the inner ear fluids, where it can be sensed by hair cells within the inner ear. The anuran middle ear also consists of a middle ear cavity that connects to the buccal cavity via the Eustachian tube. This connection between the two middle ears, through the buccal cavity, allows anurans to determine sound directionality (Willis et al., 2013). Earless species lack all middle ear structures while retaining the inner ear (Wever, 1985; Jaslow et al., 1988).

Despite the clear benefits of tympanic hearing and fossil evidence that the middle ear evolved in the ancestor to all extant anurans (Rage and Rocek, 1989, Shubin and

Jenkins, 1995, Gao and Wang, 2001, Gao and Chen, 2004, Gao and Wang, 2001; Baez and Nicoli, 2008), earlessness has evolved at least 38 times within the order Anura (Chapter 1). These convergent losses of the middle ear are puzzling given that anurans are well known for using acoustic communication for mating, defense, and territoriality (reviewed in Wells and Schwartz 2007). Furthermore, earless species occupy diverse habitats, making it unlikely that earless species share environmental selection pressures that relax selection on the tympanic middle ear (Vorobyeva and Smirnov, 1987; Jaslow et al. 1988; Hetherington, 1992a). Additionally, earless anurans have few associated changes in other skull features besides smaller average skull size (Chapter 4), rejecting the hypothesis that earlessness is a pleiotropic side effect of changes in other developmentally or genetically linked skull structures. However, use of alternative sensory pathways, specifically alternative hearing pathways or substrate vibration sensors, remains a viable explanation for the lability of the middle ear in anurans.

Extratympanic hearing pathways (Lombard and Straughan, 1974; Hetherington and Lombard, 1983; Ehret, 1994; Lindquist et al., 1998; Hetherington and Lindquist, 1999) and low frequency vibration sensitivity (Koyama et al., 1982; Narins and Lewis, 1984; Christensen-Dalsgaard and Jørgensen, 1988; Christensen-Dalsgaard and Narins, 1993) are both known to be effective in anurans and could alter typical patterns of selection on tympanic ears. These alternative sensory pathways could preserve airborne hearing sensitivity or provide equivalent or superior sensory information that could be used for conspecific communication and predator and prey detection in earless anurans. Three non-mutually exclusive hypotheses exist. First, extratympanic hearing pathways (pathways which do not require a tympanic middle ear) could compensate for lack of a middle ear and relax selection on the tympanic middle ear. Second, smaller body size, in concert with extratympanic hearing pathways, could relax selection on tympanic middle ears if extratympanic pathways are more effective in smaller anurans. Third, vibrational sensitivity could be enhanced in earless species and relax selection on or have antagonistic pleiotropic effects on the tympanic middle ear. All three hypotheses fall under the umbrella hypothesis that alternative sensory pathways allow for or even select for tympanic middle ear loss in anurans. We discuss evidence for each of these hypotheses in turn.

Extratympanic pathways could relax selection on tympanic hearing by counteracting hearing costs due to earlessness. Multiple extratympanic pathways have been proposed (Wilczynski et al., 1987; Narins et al. 1988), and some have been shown effective in a few eared and earless anurans (Lombard and Straughan 1974; Hetherington & Lombard 1982; Narins et al., 1988; Ehret, 1990, 1994; Lindquist et al., 1998; Hetherington and Lindquist, 1999). However, the exact pathways and their effectiveness in all anurans remain unknown. The effectiveness of these pathways in relation to tympanic hearing remains likewise unclear given that comparisons of anurans with and without functional tympanic ears yield inconsistent results. Experimentally removing the tympanum of two eared frog species, *Hyla regilla* and *Hyla versicolor*, decreased hearing sensitivity by 25 dB above 1 kHz (Lombard and Straughan, 1974). Yet, closely related eared and earless species from the genus *Atelopus* differ in sensitivity by only 8-13 dB between 2000 and 2500 Hz (Lindquist et al., 1998), and similarly sized *Hyla regilla* (eared) and *Atelopus chiriquiensis* (earless species) differ by only 5dB in sensitivity (Jaslow and Lombard, 1996). However, these studies only tested the hearing of one or two earless species, making it hard to generalize their results or tease out confounding factors known to affect hearing ability, such as body size. Thus, existing evidence is insufficient to estimate how well extratympanic pathways buffer earless anurans from decreased hearing sensitivity due to lack of a tympanic middle ear.

Extratympanic pathways may not be equally efficient across anurans of different body sizes, and extratympanic pathways might only relax selection on tympanic hearing in smaller anurans (Hetherington, 1992a). Two lines of indirect evidence support this hypothesis. One, earless species are smaller on average than eared species (Hetherington, 1992a; Jaslow et al., 1988; Chapter 4). Two, multiple body surfaces involved in proposed extratympanic pathways (shoulder girdle and body lung wall) are more responsive to sound than the tympanum across a large range of frequencies (up to 2500 Hz) in small but not large anurans (Hetherington, 1992b). It could be that the relative effectiveness of tympanic hearing and extratympanic pathways changes with body size and therefore the tympanic middle ear provides a large hearing advantage over extratympanic pathways only at larger body sizes. How efficiency of extratympanic hearing varies with body size has not been robustly tested.

Finally, alternative sensory modalities, such as very low frequency substrate vibration, may relax selection on the tympanic middle ear or may even be selected for at the expense of the tympanic middle ear. Hearing is a response to sound vibrations, but low frequency sound vibrations can also travel through dense media, such as the ground, plants, etc., and be sensed through substrate vibrations. Anurans are known to have excellent vibrational sensitivity (Koyama et al., 1982; Narins and Lewis, 1984; Christensen-Dalsgaard and Jørgensen, 1988; Christensen-Dalsgaard and Narins, 1993), and some evidence suggests earless species may have enhanced sensitivity to very low frequencies and use substrate vibrations for communication. Both eared and earless anurans have a unique cartilaginous disc, the operculum, in the oval window of the inner ear. The operculum is implicated in transferring vibrational stimuli from an attached muscle (the opercularis muscle) to hair cells within the inner ear (Kingsbury and reed, 1909; Hetherington, 1985; Hetherington, 1988). Furthermore, the operculum is proportionally larger in smaller anurans (Hetherington, 1992a), which could give small, earless species enhanced sensitivity to vibrations through this pathway. Using this pathway, earless species that call when very close or in direct contact with conspecifics (Cocroft et al., 1990; Gluesenkamp and Acosta, 2001) could be communicating via substrate vibrations. However, no one has compared vibrational sensitivity or the size of the operculum between eared and earless species to determine whether vibrational sensitivity could relax selection on ears or select for ear loss.

To determine whether alternative sensory pathways could have facilitated the lability of the tympanic middle ear in anurans, we compared hearing, vibrational sensitivity, and operculum morphology between ten species (six eared, four earless) within the true toad family (Bufonidae). Although other anuran families exhibit ear loss, Bufonidae has the highest prevalence of ear transitions within a single family (Chapter

1), making it a powerful system for comparing closely related eared and earless species that have independently evolved middle ear modifications. The ten species of toads used in this study encompass three independent ear loss events as well as a range of body sizes. This chapter tests three main hypotheses. First, we test whether earless toads retain or regain hearing sensitivity via extratympanic pathways by comparing the hearing sensitivities of eared and earless species. We then relate the hearing ability of a subset of the focal species to their mating call frequencies to assess the impact of any hearing differences on conspecific communication. Secondly, we test the hypothesis that smaller body size relaxes selection on the tympanic middle ear by assessing whether the relative effectiveness of tympanic hearing compared to extratympanic pathways increases with body size. Third, we test whether earless species have enhanced sensitivity in another sensory modality, substrate vibrations, by comparing the sensitivity of eared and earless species to vibrational stimuli. We also determine whether any morphological differences between the opercula of eared and earless species predict differences in vibrational sensitivity. Comparing independent transitions in ear structures informs us about drivers of middle ear lability, and analyzing species differences defines both mechanisms by which middle ear structures alter hearing and provides novel information that reshapes our view of extratympanic hearing pathways and how they operate in anurans.

Methods

Animal Collection

Ten species of toads (*Rhaebo haematiticus* n= 14, *Rhamphophryne festae* n= 4, *Rhinella alata* n= 10, *Rhinella arborescandens*, n= 9, *Rhinella leptoscelis* n= 10, *Rhinella marina* n= 10, *Rhinella spinulosa* n= 11, *Rhinella tacana* n= 5, *Rhinella yunga* n= 13, *Osornorphryne guacamayo* n= 9) were collected from field sites in Ecuador and Peru (Table 1). The Institutional Animal Care and Use Committee at Colorado State University approved all experiments (IACUC Protocol #12-3484A), and the Ministerio del Ambiente in Ecuador and the Servicio Nacional Forestal y de Fauna Silvestre in Peru approved collection, research, and export permits (Table 1).

Auditory Brainstem Recordings (ABRs) to test hearing and vibrational sensitivity

We tested the hearing and vibrational sensitivities of each species using auditory brainstem recordings to measure sensitivity of animals to tones across a range of frequencies. The hearing set-up was similar to the ABR set-up described in Chapter Two. But the animals tested in this study only partially overlap with those tested in Chapter Two. All auditory brainstem recordings were performed in Ecuador or Peru. We performed recordings in a portable wooden chamber (30” length x 15” width x 18” height) in which all internal surfaces were covered with acoustic foam lining. We lightly anesthetized the toads with a small topical application of 5% benzocaine and then paralyzed the toads with 0.05% succinylcholine chloride (Sigma-Aldrich, St. Louis, MO, U.S.A.) at a dosage of 7.5 µl/gram. We placed three 28-gauge stainless steel electrodes

(Model F-E2, GRASS Technologies, Warwick, RI, U.S.A.) subdermally to measure electrical signals generated by the auditory nerve (the VIIIth nerve). Differential electrodes were placed over the VIIIth nerve and over the midbrain, and a third ground electrode was placed within the arm contralateral to the VIIIth nerve being measured. To shield electrical noise, we placed a wire mesh cage over the animal during recordings that was grounded by a connection to the pre-amplifier.

We tested sensitivity to airborne sound exactly as described in Chapter Two. The toads lay perpendicular to and 18 inches away from the three-inch speaker (FF85K, Fostex, Tokyo, Japan) on a wet paper towel. We amplified the acoustic stimuli with a digital AC/DC amplifier (DTA-1 Class T, Dayton Audio, Springboro, OH, U.S.A.) and calibrated with a ½ inch free field microphone (46AE, G.R.A.S. Sound and Vibration A/S, Skovlytoften, Denmark). We calibrated the free field microphone with a pistonphone (Type 42AA, G.R.A.S. Sound and Vibration A/S, Skovlytoften, Denmark), which produced a 94 dB RMS re 20 µPa tone at 1 kHz. We used customized software (QuickABR_burst) that controlled calibrated stimulus presentation and data acquisition using the RM2 processor. We played 25 ms pure tones, ranging in frequency from 200-4000 Hz at 5 dB increments with 40 ms intervals. We tested frequencies in order from low to high frequency. Response signals were averaged over 400 tone bursts.

To test sensitivity to vibrational stimuli, we placed the toads on a small plastic platform connected to a mini-shaker (Type 4810, Brüel & Kjær Sound & Vibration Measurement A/S, Nærum, Denmark) within the audio chamber. We calibrated the mini-shaker with a Triaxial charge accelerometer (Type 4527-C, Brüel & Kjær Sound &

Vibration Measurement A/S, Nærum, Denmark) using customized software (QuickABR_burst) that controlled stimulus presentation and data acquisition using the RM2 processor. We stimulated the platform with 25 ms pure tones, ranging in frequency from 200-900 Hz at 5 dB increments with 40 ms intervals. We tested frequencies in order from low to high frequency. Response signals were averaged over 400 tone bursts.

During both the auditory and vibrational ABRs, we measured the response to a transient signal between every two frequencies tested. For the auditory tests, the transient was generated from a half cycle 4 kHz sinusoid at 105 dB, and for vibrational tests we used a half cycle 2 kHz sinusoid at 90 dB. We verified that the individual's responsiveness to this signal remained stable throughout the testing session for comparable measurements of hearing sensitivity. If transient responses dropped below 25% of the original signal, we omitted all subsequent measurements from analyses (reducing datasets for nine of the 69 total individuals in the hearing study and six of the total 76 individuals in the vibrational study). We visually determined thresholds for each frequency by finding the minimum stimulus decibel level that evoked a response signal amplitude of 0.002 mV (two times the average noise level) or greater from the auditory nerve.

Specimen preservation

After each auditory brainstem recording, we measured the snout-vent length (SVL) and tympanum diameter of each animal to the nearest 0.1 mm using a dial caliper

(31-415-3, Swiss Precision Instruments Inc., Garden Grove, CA, U.S.A). We then euthanized the animals with 20% topical benzocaine before decapitation. We preserved the head of each specimen in 4% paraformaldehyde (diluted in Phosphate Buffered Saline from 16% paraformaldehyde solution; Electron Microscopy Sciences, Hatfield, PA, U.S.A.) for 24 hours and performed three 15-minute rinses in Phosphate Buffered Saline before storing cranial tissue in 70% ethanol.

Histology & 3D modeling

We decalcified two specimens per species (with the exception of *R. haematiticus*, which had three samples, total n = 21) in 10% EDTA (pH 7.4) for up to one week at room temperature and then put specimens through a graded ethanol series (30%, 50%, 70%, 90%, 95%, 100%, 100%), and embedded them in hydroxypropyl methacrylate (HPMA) plastic (Electron Microscopy Sciences, Hatfield, PA, U.S.A.). We drilled holes of 1 mm diameter into the plastic around each specimen before sectioning the tissue at 5 µm thickness using a microtome (RM1265, Leica, Wetzlar, Germany) and mounted every other section onto Fisher Superfrost Plus Microscope Slides (Fisher Scientific, Pittsburgh, PA, U.S.A.). We then stained the tissue with Eosin and Toluidine Blue (Fisher Scientific, Pittsburgh, PA, U.S.A.).

To measure opercular volumes, we took photographs of every third section for a final resolution of 30 µm between imaged sections. We aligned the photographed sections using the drilled holes and then 3D modeled and measured the volume of the opercula with IMOD 3D (Kremer et al., 1996).

Call collection & analysis

The calls of two earless species, *R. yunga* (n=1) and *R. arborescandens* (n=1), and two eared species, *R. leptoscelis* (n=1) and *R. tacana* (n=1), were recorded and examined in this study. All calls were analyzed using the package seewave (Berk, 2013) in R (R Core Team, 2015). The call files were visualized with spectrograms and then trimmed to the time frame of the call. We eliminated background noise at frequencies above and below the call using a single bandpass frequency filter. From these trimmed call files we calculated the median dominant frequency for each species.

Statistical analyses

Hearing and vibration sensitivity differences between eared and earless species

To visually compare hearing thresholds in response to airborne sound between eared and earless species, we graphed the hearing threshold of each species using the package sme (Smoothing-splines Mixed-effects models) package (Berk, 2013) in R (R Core Team, 2015). To quantitatively determine the overall effect of ear presence/absence on hearing thresholds we used linear mixed-effects models in the package lme4 (Bates et al., 2014). We ran a model with hearing threshold as the dependent variable, a frequency by ear (presence/absence) interaction as a fixed term, and species and individual as nested random effects (Table 2, Model 1). We then calculated the overall effect of ear (presence/absence) on hearing sensitivity thresholds as well as the variation in how ear (presence/absence) affected hearing sensitivity thresholds by frequency using Type III tests of fixed effects. Finally, to examine differences in hearing between eared and earless species at each frequency, we calculated least squares means of the hearing thresholds for eared and earless species at each frequency and estimated Tukey's honestly significant differences using the package lsmeans (Russell, 2016). Since our goal was to determine overall species differences in hearing sensitivity, we did not examine patterns of sex differences among species despite the possibility that males and females may differ in hearing (as in Boatright-Horowitz and Simmons, 1995; Miranda and Wilczynski, 2009; Shen et al., 2011).

Since both click response and hearing thresholds varied among species we wanted to confirm that hearing differences between eared and earless species could not be accounted for by overall ABR signal strength. Therefore, we checked that ears still had a significant effect when controlling for click response level by adding click response level as an additional fixed effect to our hearing threshold model and checking the Type III fixed effects (Table 2, Model 2). We found that the effect of ear (presence/absence) was still significant ($F_{1, 12} = 10.5$, $p = 0.007$) as well as the interaction between ear (presence/absence) and frequency ($F_{15, 829.3} = 10.8$, $p < 0.001$), consistent with our results from Model 1. We do not discuss this model in the main text or interpret lsmeans differences using this model since click response is confounded with overall hearing ability.

To determine whether extratympanic and tympanic hearing ability varied among eared and earless species, we ran two mixed-effects models (Table 2, Models 3 and 4). In one model, hearing thresholds for eared species were the independent variable, frequency and species were fixed terms, and individual was a random variable (Table 2, Model 3). The other model (Table 2, Model 4) was the same except that hearing thresholds for earless species were used for the independent variable. We checked the Type III fixed effects for species in both models.

We used similar mixed-effects models to compare vibrational sensitivity between eared and earless species. We ran a model with vibration threshold as the dependent variable, a frequency by ear (presence/absence) interaction as a fixed term, and species and individual as random effects (Table 2, Model 4). We then calculated the effect of ear presence/absence as well as the ear by frequency interaction term on vibrational sensitivity thresholds using Type III tests of fixed effects. Lastly, to examine differences in hearing between eared and earless species at each frequency, we calculated least-squares means of vibration thresholds for eared and earless species at each frequency and estimated Tukey's honestly significant differences using the package lsmeans (Russell, 2016). We also checked that ear (presence/absence) still had a significant effect on vibrational sensitivity when controlling for click level response by adding it as a fixed effect to our model (Table 2, Model 5). We found that the interaction of ear (presence/absence) and frequency was still significant ($F_{5, 361.3} = 3.7$, $p = 0.003$), consistent with our results from Model 4, but do not discuss these results in the main text or interpret lsmeans differences using this model since click response is confounded with overall vibrational sensitivity. We lastly examined species differences in vibration thresholds using separate mixed-effects models for eared and earless species (Table 2, Models 7 and 8). In one model, vibration thresholds for eared species were the independent variable, frequency and species, and individual was a random variable (Table 2, Model 7). The other model (Table 2, Model 8) was the same except that vibration thresholds for earless species were used for the independent variable. We checked the Type III fixed effects for species in both models.

Relationship between size and extratympanic hearing sensitivity

To investigate whether presence of a tympanic middle ear increases hearing sensitivity at smaller body sizes as much as at larger body sizes, we ran a mixed-effects model using the package lme4 (Bates et al., 2014) within R (R Core Team, 2015). We ran a model with hearing thresholds of all individuals as the dependent variable, a frequency by ear (presence/absence) by SVL interaction term as the predictor variable, and species and individuals as random effects (Table 2, Model 9). We then estimated least squares means of hearing thresholds for small (SVL = 25 mm) and large (SVL = 50 mm) earless species and compared them to estimated least squares means of hearing thresholds of eared species at the same body sizes using Tukey's honest significant differences in the package lsmeans (Russell, 2016) within R (R Core Team, 2015). These body sizes (25 and 50 mm) were within the range limits of eared and earless individuals within our study. If tympanic hearing were less important at smaller body sizes, we would expect the relative increase in hearing sensitivity provided by a tympanic middle ear to decrease with body size.

To test whether smaller anurans have better extratympanic hearing compared to larger earless anurans, we compared extratympanic hearing in small and large individuals both across earless species and within a single earless species. First, we used the hearing thresholds of all earless individuals (Table 2, Model 9) to estimate the least squared means of hearing threshold at a small body size (SVL = 25 mm) and a larger body size (SVL = 50 mm). We compared these thresholds estimated for earless species at different body sizes with Tukey's honest significant differences. Next we used a second model (Table 2, Model 10) to test whether extratympanic hearing sensitivity was elevated at smaller body sizes within a single species. We analyzed data from the focal earless species with the largest range of body sizes, *R. yunga*. We ran a mixed effects model with the hearing thresholds of *R. yunga* as the dependent variable, a frequency by body size interaction term as the fixed term, and individual as a random effect. We then estimated the least squared means of hearing threshold for *R. yunga* individuals with small body size (SVL = 25 mm) and a body size twice as large (SVL = 50 mm) to compare differences in hearing sensitivity between small and large *R. yunga* individuals using Tukey's honest significant differences.

To check that size effects were not completely driven by changes in ABR signal strength, we checked that SVL still had a significant effect in the same direction when controlling for click level response by adding it as a fixed effect to each of the two models (Table 2, Models 11 and 12). For model 11, we found that SVL still significantly affected hearing thresholds overall ($F_{1, 58.1} = 11.9$, $p = 0.001$) and that the effect of SVL varied by frequency ($F_{15, 819.1} = 15.1$, $p < 0.001$), consistent with our results from Model 9, which did not control for click. For Model 12 we found that the effect of SVL varied by frequency ($F_{15, 195.8} = 6.7$, $p < 0.001$), but that SVL had no overall directional effect on hearing thresholds ($F_{1, 15.3} = 1.0$, $p = 0.326$), consistent with our results from Model 10, which did not control for click. We again did not discuss this result in the main text or interpret lsmeans differences using this model since click response is confounded with overall hearing ability.

Differences in operculum size between eared and earless species

We used ANCOVA analyses in R (R Core Team, 2015) to compare the proportional size of the operculum between eared and earless species. We used the volume of each individual's operculum divided by SVL as the dependent variable and ear status (presence/absence) as a fixed effect.

Results

Hearing sensitivity of eared and earless species

Overall, ear presence/absence had a significant effect on hearing ($F_{1,10.1}=14.1$, $p = 0.004$; Table 2, Model 1), as did the interaction of ear presence/absence and frequency ($F_{15, 859.6}=12.3$, $p < 0.001$; Table 2, Model 1). Below 900 Hz, eared and earless species had no difference in hearing, but above 900 kHz, earless species were 8-24 dB less sensitive than eared species (Table 3; Fig. 1A). Hearing varied among both eared and earless species (eared species: $F_{5, 29.1} = 6.2$, $p < 0.001$, Table 2, Model 3; earless species: $F_{3, 38.2} = 26.2$, $p < 0.001$, Table 2, Model 4; Fig. 1B).

Hearing data in relation to species' call frequencies

The median dominant frequency of each species' call varied greatly within eared and earless species from our study (Fig. 2A-D). While one earless species, *R. yunga* (Fig. 2A), had very sensitive hearing at its call frequencies, another earless species, *R. arborescandens* (Fig. 2B), had poor hearing sensitivity at its call frequencies. Within eared species, *R. leptoscelis* had very sensitive hearing thresholds at its call dominant frequency (Fig. 2C), while *R. tacana* had a very high frequency call and was not as sensitive at these frequencies (Fig. 2D).

The effect of size on extratympanic hearing

We found differences between smaller and larger toads in the hearing advantage provided by the tympanic middle ear (Fig. 4A-B). At 25 mm SVL, eared species had more sensitive hearing than earless species at all frequencies above 900 Hz (Fig. 4A), while at 900 Hz and below, eared and earless species had equivalent hearing. At 50 mm SVL, eared species had more sensitive hearing than earless species at all frequencies above 2000 Hz (Fig. 4A), while at 2000 Hz and below, eared and earless species had equivalent hearing.

When comparing hearing thresholds among earless species between 25 mm and 50 mm individuals, we find 25 mm earless toads have less sensitive hearing than 50 mm earless toads from 700 Hz to 2000 Hz. Hearing is equivalent at all other frequencies with the exception of 300 Hz, at which 25 mm earless toads are more sensitive than 50 mm toads. Within individuals of a single earless species, *Rhinella yunga*, we found a similar pattern of decreased hearing sensitivity at smaller sizes. 50 mm *R. yunga* individuals were more sensitive than 25 mm *R. yunga* from 900 to 1750 Hz (Fig. 4B). At all other frequencies hearing in *R. yunga* was equivalent between 25 and 50 mm individuals with the exception of 3000 Hz, at which 25 mm individuals were more sensitive than 50 mm individuals.

Vibrational sensitivity and opercular volume of eared and earless species

Ear presence/absence had no overall effect on vibrational sensitivity ($F_{1, 10.4} = 3.4$ $p = 0.094$; Table 2, Model 5), however, ear presence/absence altered vibrational thresholds differently depending on frequency ($F_{5, 358.4} = 3.7$, $p = 0.003$; Table 2, Model 5). Earless species were 6 dB more sensitive at 200 Hz and 5 dB more sensitive at 300 Hz compared to eared species (Table 4; Fig. 5A). Vibration sensitivities did not differ among eared species ($F_{5, 40.1} = 0.7$, p = 0 0.651, Table 2, Model 7) but did differ among earless species ($F_{3, 36} = 3.0$, $p = 0.044$, Table 2, Model 8; Fig. 5B).

We observed no qualitative differences in the opercula between eared and earless species (Fig. 6A, B). In addition, opercular size proportional to body size did not differ between eared and earless species ($F_{1, 18} = 0.5$, $p = 0.480$; Fig. 6C).

Discussion

Overall, we found some support that alternative sensory pathways contribute to the lability of the tympanic middle ear in toads. Although earless species bore an overall hearing deficit at high frequencies (above 900 Hz), earless species showed surprising variation in hearing ability above 900 Hz that we predict affects sensitivity to conspecific mating calls. In addition, extratympanic hearing ability was not more effective in smaller earless toads compared to larger earless toads in our study. In fact, tympanic middle ears benefitted hearing sensitivity more in smaller toads than in larger animals. Perhaps most surprisingly, earless species were more sensitive to ground vibration compared to eared species at very low frequencies (200 and 300 Hz) despite the lack of morphological differences in their opercula. Below we will discuss the implications of these results for proposed extratympanic hearing pathways, the association of small body size and earlessness, social communication, and the use of vibration as an alternative sensory modality by earless species.

Hearing and vibrational sensitivity differ between eared and earless species

The hearing deficits earless species occur at higher frequencies are not as dramatic as might be expected from the reduction in sensitivity in gekkonid lizards lacking middle ears (up to 62 dB, Wever, 1963). Earless species could thus still make use of high frequency hearing at close ranges, consistent with the moderate effects of middle ears in *Hyla* and *Atelopus* (Lombard and Straughan, 1974; Jaslow and Lombard, 1996; Lindquist et al., 1998). However, none of these extratympanic pathways propose a way for earless anurans to sense sound directionality, although evidence exists that earless anurans orient to conspecific calls (Lindquist and Hetherington, 1996). The hearing advantage of eared bufonids compared to eared species in our study (10 – 26 dB above 900 Hz) was comparable to the magnitude of extratympanic hearing measured using experimental manipulations in two hylid species (25 dB above 1 k Hz, Lombard and Straughan, 1974). Our results thus do not provide evidence that middle ears are especially labile in bufonids because extratympanic hearing in this family is exceptional for anurans.

Earless species suffer no reduction in hearing sensitivity at low frequencies (below 900Hz), consistent with the ideas that tympanic hearing is mainly important above 1 kHz and that extratympanic pathways play a larger role in hearing below 1 kHz (Lombard and Straughan, 1974). The two most studied and discussed extratympanic pathways are the opercularis pathway and the lung pathway, which could both contribute to the lack of hearing difference between eared and earless species below 900 Hz, as both are most effective at frequencies below ca. 1 kHz (Lombard and Straughan, 1974; Hetherington and Lombard, 1983; Ehret, 1994; Lindquist et al., 1998; Hetherington and Lindquist, 1999). The opercularis pathway involves the transfer of vibrations from the opercularis muscle to the operculum to ultimately stimulate hair cells in the inner ear (reviewed in Hetherington, 1992a). Some researchers hypothesize a function of the opercularis pathway in detecting low-frequency airborne sound (Lombard and Straughan, 1974; Hetherington and Lombard, 1983), although other researchers propose it stabilizes the columellar footplate during breathing or vocalization (Mason and Narins, 2002). The lung-based hearing pathway brings sound to the inner ear through vibrations of the body wall overlying the lungs in both eared and earless anurans (Narins et al., 1988; Ehret, 1990, 1994; Lindquist et al., 1998; Hetherington and Lindquist, 1999). A third extratympanic pathway, bone conduction enhanced by resonance of the mouth cavity (Boistel et al., 2013), has been proposed but lacks experimental data to validate its effectiveness. The exact extratympanic pathway(s) responsible for airborne hearing remains unclear in our focal species and other earless anurans, pending experimental manipulations that isolate contributions of each proposed pathway.

We reject the hypothesis that smaller body sizes that typify earless toads relax selection on tympanic hearing by decreasing the relative effectiveness of the tympanic hearing pathway compared to the extratympanic hearing pathway(s). At smaller body sizes (25 mm SVL), earless species showed a hearing deficit compared to eared species at all frequencies above 900 Hz, while at larger body sizes (50 mm SVL) hearing sensitivity is equivalent between eared and earless species up to 2000 Hz. Thus, larger, not smaller, body size would relax selection on tympanic hearing.

Airborne hearing is only one of the sensory modalities that may be used by toads for conspecific communication, and/or predator and prey detection. Toads are extremely sensitive to vibration, and we demonstrated that earless species are even more sensitive than eared species at low frequencies (200 - 300 Hz). Our results do not distinguish whether the increased vibrational sensitivity precedes ear loss, the loss of an ear is responsible for this increase in vibrational sensitivity, or whether increased vibrational sensitivity is an evolved compensation for lack of tympanic hearing in earless species. However, the overlap in eared and earless species' vibrational sensitivity indicates that being very sensitive to vibration does not require loss of the tympanic middle ear. Additionally, we find no differences in opercular size between eared and earless species, leaving us with no indication that earless species have opercular modifications that would result in increased sensitivity to vibration. In general, toads, like other frogs (Koyama et al., 1982; Narins and Lewis, 1984; Christensen-Dalsgaard and Jørgensen, 1988; Christensen-Dalsgaard and Narins, 1993) and salamanders (Ross and Smith, 1978, 1980, 1982), are equally or more sensitive to substrate vibrations that most other vertebrates (Hartline, 1971; Wever and Vernon, 1960; Heffner et al., 2001; Brittan-Powell et al., 2010; Christensen et al., 2012), indicating substrate vibrations may be an important sensory modality in all anurans and could relax selection on communication via airborne sound.

Hearing differences among earless species raise questions about mechanisms

The variation in hearing among earless species begs the question: Why are some earless species much more sensitive than others? Any of the extratympanic pathways discussed above could allow earless species to sense airborne sound, however, we lack morphological explanations for species differences in the efficiency of extratympanic pathways. Thus, the biomechanical mechanisms resulting in the variety of hearing abilities seen in this study remain uncertain.

Body size might be responsible for some of the variation in extratympanic hearing sensitivity, both across earless species as well as within *R. yunga*. Our statistical models indicated that larger earless individuals have more sensitive extratympanic hearing than smaller earless individuals at mid-range frequencies (~700 – 2000 Hz). Fox (1995) suggested that larger extratympanic surfaces, such as the body lung wall or suprascapula, could increase hearing ability in the low-mid range frequencies. It could be that the pathways bringing airborne sound to the inner ear in earless species are more efficient when these, or other, extratympanic surfaces are larger. Given that the lung pathway is the only pathway that has been shown effective above 1 kHz (Lindquist et al., 1998; Hetherington and Lindquist, 1999), where large variation in sensitivity among earless species occurs, we propose lung resonance as the most likely candidate for explaining the variation among earless species. However, body size differences do not explain all the variation we see among earless species, and how size affects the efficiency of each extratympanic pathway remains unknown.

Communication strategies may relax selection on tympanic hearing

We find evidence for two non-mutually exclusive scenarios that could relax selection on tympanic hearing. The positive relationships between body size and both call dominant frequency (Blair, 1955a,b; Ryan, 1988) and extratympanic hearing ability support the first scenario: Large anurans typically call at low frequencies and also have excellent extratympanic hearing that is equivalent to tympanic hearing at those frequencies (below 2000 Hz). This first strategy is exemplified by *R. yunga*, which has a larger body size, a low frequency call, and excellent extratympanic hearing at its call dominant frequency. A second scenario is that substrate vibrations facilitate communication in earless species. We lack natural history information in toads about the use of substrate vibrations for conspecific communication or for the detection of prey and predators. We propose that substrate vibrations could be particularly important for species that do not hear their call frequencies well, such as *O. guacamayo,* which has only been observed calling when in close proximity or when in contact with conspecifics (Gluesenkamp and Acosta, 2001). Similarly, R*. arborescandens* calls when close to conspecifics perched on ferns and other plants that would be excellent vibrational conduits (personal observations). More natural history studies are needed to decipher whether either of these sensory scenarios are relaxing selection on the tympanic ear in anurans.

Concluding remarks

Our results suggest that earlessness is a physiological mixed bag for toads. Middle ear absence has high frequency hearing costs that could affect the ability of earless species to detect conspecifc calls. However, the loss of high frequency hearing ability may be tolerated or even outweighed if low frequency hearing or vibrations can be effectively used for communication and predator or prey detection. Our results raise questions about which extratympanic pathways are effective in earless species and why some earless species are much more sensitive to airborne sound than others. Given the diversity of call frequencies and hearing and vibrational sensitivities within earless toads, different selection pressures may be influencing each middle ear transition within Bufonidae. Earless species may use low frequency communication and/or rely on substrate vibrations for conspecific communication, predator and/or prey detection. These and other behavioral strategies could relax selection on the tympanic middle ear. More natural history studies are needed to test whether extratympanic hearing and vibrational sensitivity function in conspecific communication as well as predator and prey detection. Alternative sensory pathways, acoustic environment, body size, and signaling behavior may jointly create unique selection regimes within different earless clades that relax selection on the tympanic middle ear, resulting in widespread convergent loss of what is a vital sensory structure to most land-living tetrapods.

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Table 3.1 – Collection country, sites, and permit numbers for animals in the study.

Species	Country	Region	Permit #
Osornophryne guacaymayo	Ecuador	Sumaco, Ecuador	Permit: 001-13 IC-FAU-DNB/MA
Rhaebo haematiticus	Ecuador	Mindo Forest Reserve and Rio Guajalito Reserve in Pastaza	Permit: 001-13 IC-FAU-DNB/MA
Rhamphophryne festae	Ecuador	Rio Rutuno, Pastaza	Permit: 001-13 IC-FAU-DNB/MA
Rhinella alata	Ecuador	Rio Rutuno, Pastaza	Permit: 001-13 IC-FAU-DNB/MA
Rhinella arborescandens	Peru	Rodríguez de Mendoza	Permit: 0071-2014-MINAGRI-DGFFS/DGEFFS
Rhinella leptoscelis	Peru	Yanachaga buffer zone of Chemillén National Park in the basins of San Alberto (CDS/CNEH-Perú) Llamaquizú, San Luis, and San Daniel	Permit: 0071-2015-SERFOR-DGFFS/DGEFFS
Rhinella marina	Ecuador	Canelos, Pastaza and in Mindo Forest Reserve and Maquipucuna Biological Reserve in Pastaza	Permit: 001-13 IC-FAU-DNB/MA
Rhinella spinulosa	Peru	K'iripampa Acopia in Acomayo, Cusco	Permit: 0071-2014-MINAGRI-DGFFS/DGEFFS
Rhinella tacana	Peru	Quispicanchi	Permit: 0071-2014-MINAGRI-DGFFS/DGEFFS
Rhinella yunga	Peru	Yanachaga buffer zone of Chemillén National Park in the basins of San Alberto (CDS/CNEH-Perú) Llamaquizú, San Luis, and San Daniel	Permit: 0071-2014-MINAGRI-DGFFS/DGEFFS; Permit: 0071-2015-SERFOR-DGFFS/DGEFFS

Table 3.2 – Mixed models used in the likelihood ratio testing.

Model #	Model (y~ fixed effects + (1|random effects)
1	hearing thresholds ~ frequency*ear(Y/N) + (1|species/individual)
2	hearing thresholds ~ frequency*ear(Y/N) + click + (1|species/individual)
3	eared hearing thresholds ~ frequency + species + (1|individual)
4	earless hearing thresholds ~ frequency + species + (1|individual)
5	vibration thresholds ~ frequency*ear(Y/N) + (1|species/individual)
6	vibration thresholds ~ frequency*ear(Y/N) + click + (1|species/individual)
7	eared vibration thresholds ~ frequency + species + (1|individual)
8	earless vibration thresholds ~ frequency + species + (1|individual)
9	hearing thresholds ~ frequency*ear(Y/N)*SVL + (1|species/individual)
10	*R. yunga* hearing thresholds ~ frequency*SVL + (1|individual)
11	hearing thresholds ~ frequency*ear(Y/N)*SVL + click + (1|species/individual)
12	*R. yunga* hearing thresholds ~ frequency*SVL + click + (1|individual)

Table 3.3 – Estimated least squares means differences between hearing thresholds of eared and earless species in response to airborne sound and the relationship between size and hearing threshold in earless species. Estimated least squares means differences and standard error rounded to the nearest dB are given for each frequency with Tukey's honest significant differences between hearing stages bolded and indicated with asterisks (p<.05=*, p<.01=**, p<.001=***). A negative estimated difference indicates that the eared species had a lower threshold (were more sensitive) at that frequency while a positive estimated difference indicates that eared species had a higher hearing threshold (were less sensitive) at that frequency.

Frequency (Hz)	**Airborne sound sensitivity differences between eared and earless species dB (±SE)**
200 Hz	-2 (±5)
300 Hz	0 (±5)
400 Hz	-6 (±5)
500 Hz	-6 (±5)
700 Hz	-7 (±5)
900 Hz	**-10 (±5)***
1100 Hz	**-13 (±5)***
1300 Hz	**-17 (±5)****
1500 Hz	**-18 (±5)*****
1750 Hz	**-19 (±5)*****
2000 Hz	**-22 (±5)*****
2250 Hz	**-26 (±5)******
2500 Hz	**-25 (±5)*****
3000 Hz	**-18 (±5)*****
35000 Hz	**-19 (±5)*****
4000 Hz	**-15 (±5)****

Table 3.4 – Estimated least squares means differences between hearing thresholds of eared and earless species in response to vibration stimuli. Estimated least squares means differences and standard error rounded to the nearest dB are given for each frequency with Tukey's honest significant differences between hearing stages bolded and indicated with asterisks (p<.05=*, p<.01=**, p<.001=***). A negative estimated difference indicates that the eared species had a lower threshold (were more sensitive) at that frequency while a positive estimated difference indicates that eared species had a higher hearing threshold (were less sensitive) at that frequency.

Frequency (Hz)	Vibration sensitivity differences between eared and earless species dB (±SE)
200 Hz	**6 (±2)***
300 Hz	**5 (±2)***
400 Hz	4 (±2)
500 Hz	3 (±2)
700 Hz	1 (±2)
900 Hz	-2 (±2)

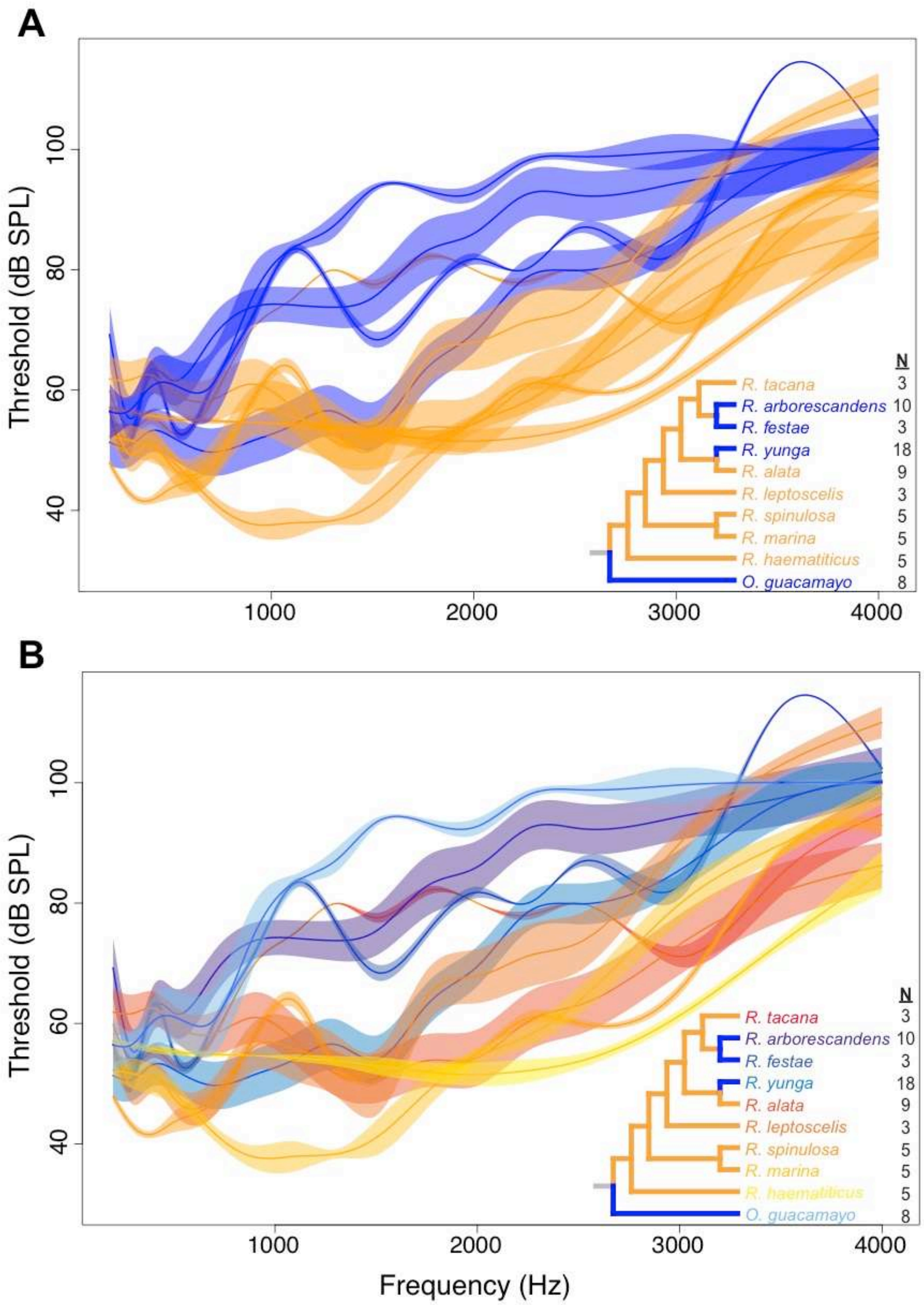

Fig. 3.1 – Hearing sensitivity differences between eared and earless species.
A – Eared (orange) and earless (blue) species' hearing thresholds are plotted by frequency. The average hearing thresholds are plotted for each species (bold lines) with the standard errors indicated by ribbon width. **B –** The hearing thresholds of individual species are plotted by frequency. Each eared species is represented by a unique shade of orange and each earless species is represented by a unique shade of blue.

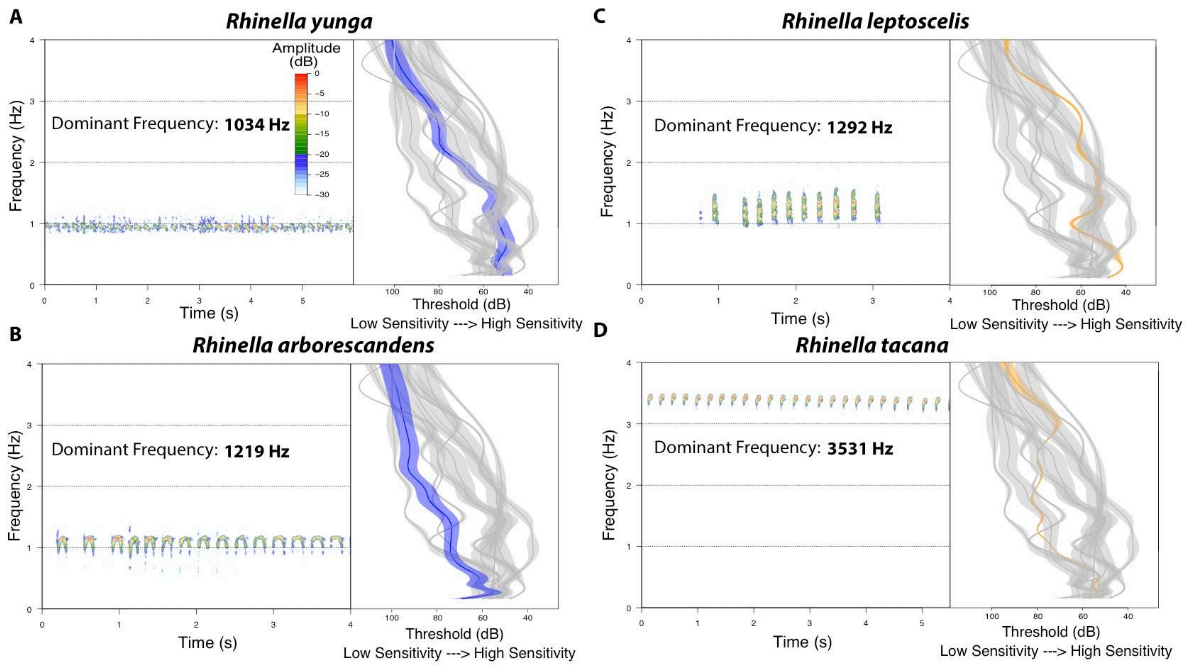

Fig. 3.2 – Call frequencies and hearing sensitivities of eared and earless species. Spectrograms (left graphs in each panel) represent the energy in each frequency bin over time. Energy fluctuations across time (x-axis) are coded by color (inset scale) within frequency bands (y-axis). Hearing thresholds at each frequency (x-axis) for each species are plotted on the right graph in each panel, with frequencies aligned to the spectrogram (y-axis). The hearing threshold of the species highlighted is blue (if earless) or orange (if eared) and the frequencies of all other species are in light grey.

A – On the left is a spectrogram of *Rhinella yunga's* call with median dominant frequency given. On the right is the hearing sensitivity of *R. yunga* for comparison with call frequencies. **B –** On the left is a spectrogram of *Rhinella arborescandens'* call with median dominant frequency given. On the right is the hearing sensitivity of *R. arborescandens* for comparison with call frequencies. **C –** On the left is a spectrogram of *Rhinella leptoscelis'* call with median dominant frequency given. On the right is the hearing sensitivity of *R. leptoscelis* for comparison with call frequencies. **D –** On the left is a spectrogram of *Rhinella tacana's* call with median dominant frequency given. On the right is the hearing sensitivity of *R. tacana* for comparison with call frequencies.

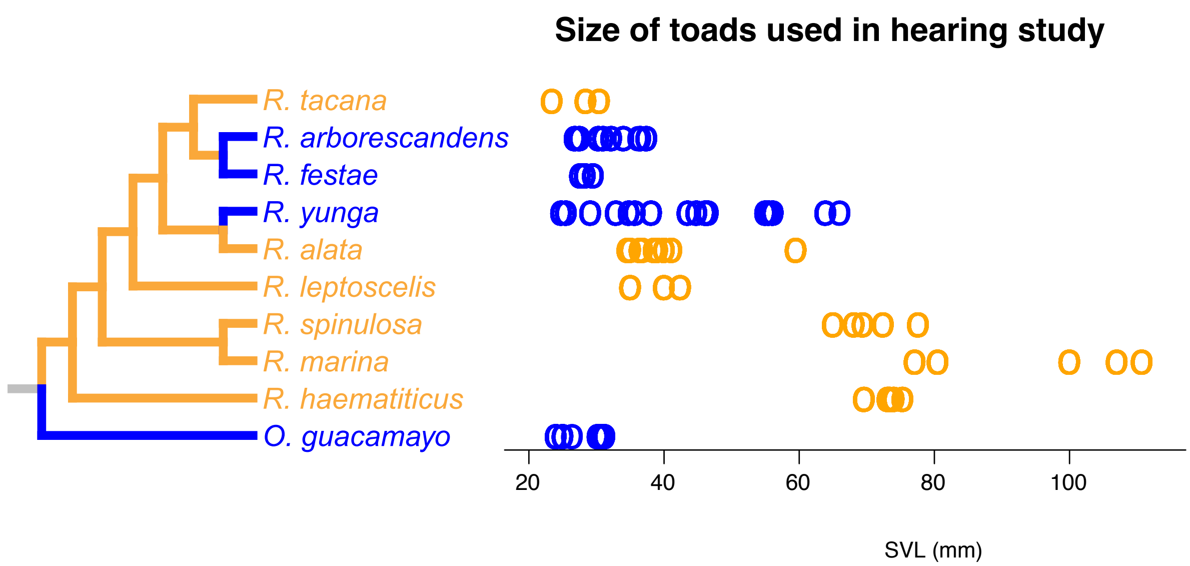

Fig. 3.3 – Sizes of eared and earless individuals used in the hearing study. Circles represent the snout-vent length (SVL) of each individual (x axis) for each species (y axis). Eared species are drawn in orange and earless species in blue.

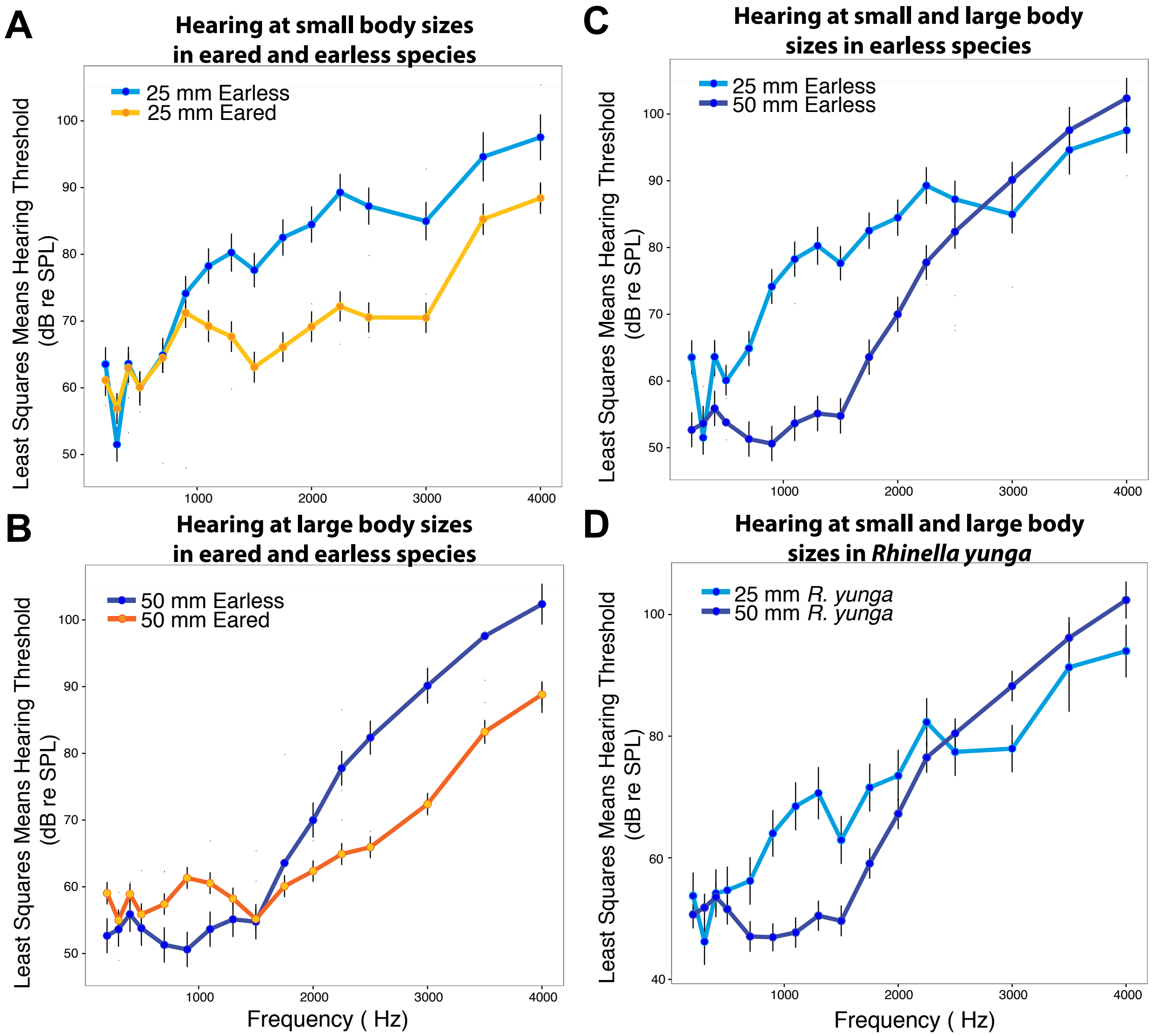

Fig. 3.4 – Differences in extratympanic hearing between small and large individuals.

A – Estimated least squares means of hearing thresholds for small (25 mm) eared (light orange) and earless (light blue) species are plotted by frequency. **B –** Estimated least squares means of hearing thresholds for larger (50 mm) eared (dark orange) and earless (dark blue) species are plotted by frequency. **C –** Estimated least squares means of hearing thresholds for small (25 mm, light blue) and larger (50 mm, dark blue) earless species are plotted by frequency. **D –** Estimated least squares means of hearing thresholds for small (25 mm, light blue) and larger (50 mm, dark blue) *Rhinella yunga* are plotted by frequency.

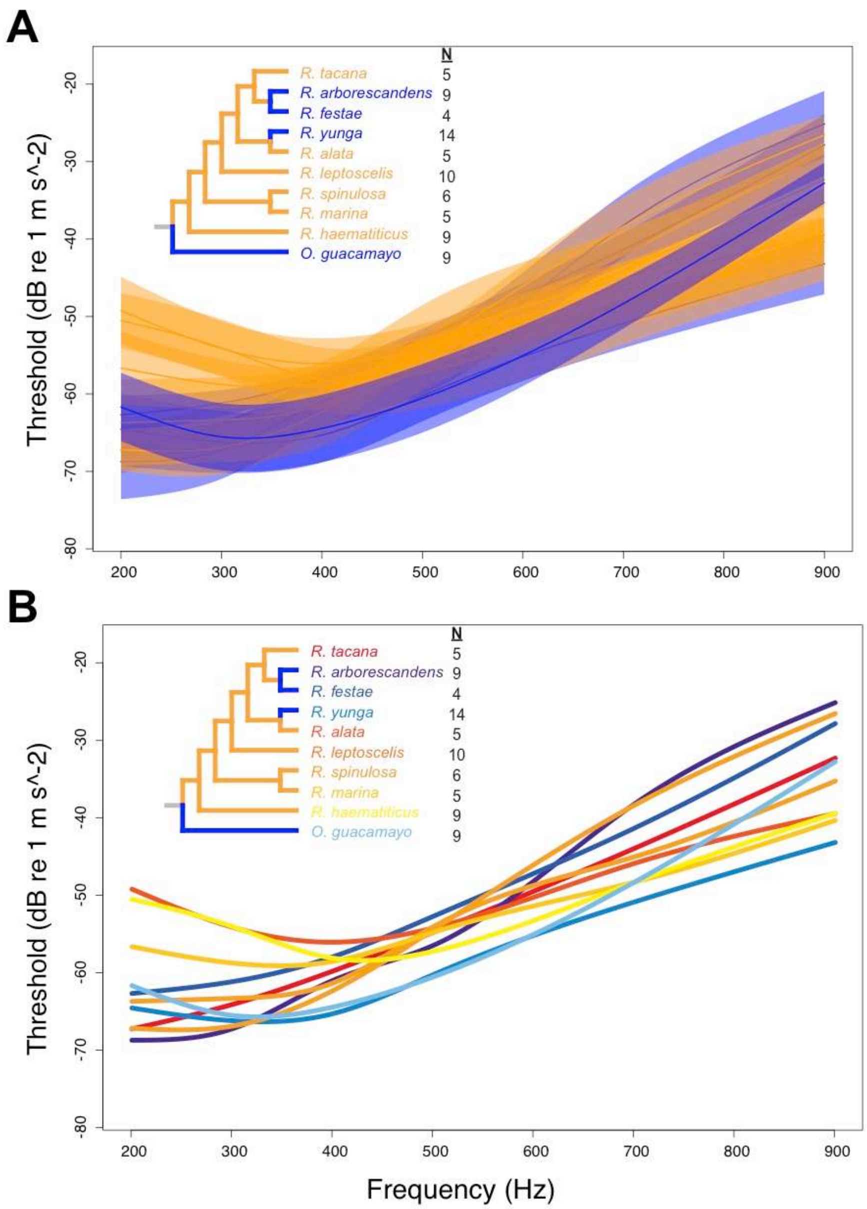

Fig. 3.5 – Vibration sensitivity differences between eared and earless species.
A – Eared (orange) and earless (blue) species' vibration thresholds are plotted by frequency. The average vibration thresholds are plotted (bold lines) with the standard errors indicated by ribbon width. **B –** The vibration thresholds of individual species are plotted by frequency. Each eared species is represented by a unique shade of orange and each earless species is represented by a unique shade of blue. Standard errors are not shown to better display average species differences.

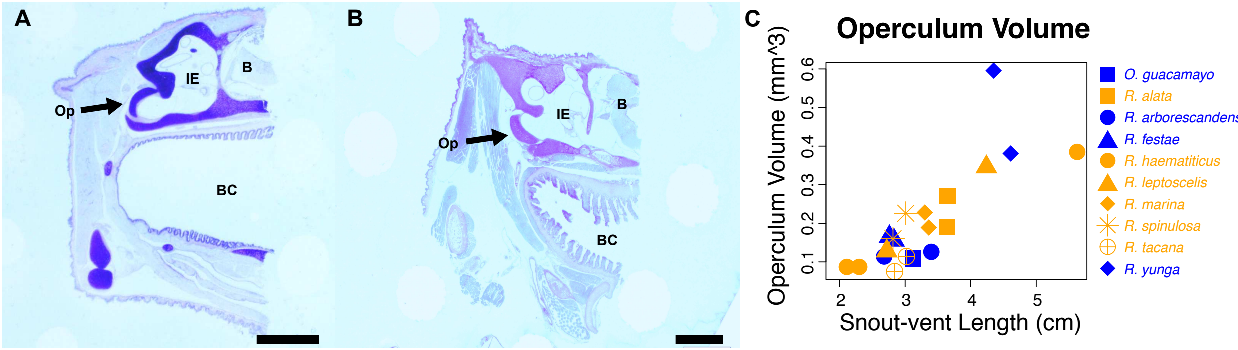

Fig. 3.6 – Opercula of eared and earless species.

A – A 5 *μ*m frontal section through the inner ear that displays the operculum of an eared species, *Rhinella alata*. **B –** A 5 *μ*m frontal section through the inner ear that displays the operculum of an eareless species, *Rhamphophryne festae*. **C –** Opercular volumes (y-axis) of eared (orange) and earless (blue) species plotted as a function of snout-vent length (x-axis). Each species has a unique symbol displayed in the legend. Symbols indicate average volumes from 1-3 specimens per species. B = brain, BC = buccal cavity, IE = inner ear, Op = operculum.

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5. HOW DEVELOPMENTAL BIAS MAY INFLUENCE MIDDLE EAR LABILITY IN TRUE TOADS (FAMILY BUFONIDAE)

Summary

Traits that have evolved independently in many species (convergent traits) may emerge from shared selection pressures across independent lineages; however, developmental bias can also affect the lability of a structure. Here we use convergent loss and regain of the tympanic middle ear, a highly labile trait within toads that currently lacks adaptive explanation, to investigate mechanisms by which developmental biases shape ear evolvability in anurans. We compare the skulls of 55 species (39 eared, 16 earless), spanning at least five hypothesized independent middle ear transitions, within the family Bufonidae. We test whether distinct changes in shape, overall ossification, or size characterize earless lineages, and whether earless skulls lack other late-forming skull bones. We find little evidence for pleiotropic shifts in other skull features associated with lack of a middle ear in bufonids. The smaller skull sizes and minor shape shifts in earless species do not provide clear evidence that either pleiotropic trade-offs between skull structures or underdevelopment of the skull has driven ear loss in bufonids. We propose that the pervasiveness of ear transitions in anurans may reflect either heterochrony via post-displacement or other developmental biases that enable mutations to alter middle ear development without detrimental effects on other traits. The apparent independence of middle ear development could be a key contributor to middle ear lability in anurans.

Introduction

Traits do not evolve independently of one another due to genetic and/or developmental links (Wright 1964, 1980; Mayr, 1976). Selection for trait integration can result in developmental processes that coordinate functionally linked traits, or alternatively pleiotropy might constrain evolution due to fitness tradeoffs (Pigliucci 2004; Klingenberg, 2008). Few studies examine how developmental processes bias the evolution of traits in nature (Beldade et al, 2002; Arthur, 2002; Kavanagh et al., 2013). Traits that have evolved independently in many species (convergent traits) with no known positive impacts on fitness may provide unique insights into the influence of developmental bias on evolution because their lability cannot be explained by selection pressures that vary across environments. Here we use convergent loss and regain of the tympanic middle ear, a highly labile trait within toads that currently lacks adaptive explanation, to investigate mechanisms by which developmental biases shape ear evolvability in anurans.

Most tetrapods have a tympanic middle ear, which functions to transmit airborne sound from the environment to the inner ear sensory hair cells (reviewed in Manley, 2010). Most anurans have middle ear structures that function similarly to those found in other tetrapods (Lewis and Narins, 1999). The anuran middle ear consists of a tympanic membrane that is surrounded by a cartilaginous ring, the tympanic annulus. The tympanic membrane oscillates in response to airborne sound waves and those oscillations are transferred to the inner ear fluids via the mostly bony middle ear column, the columella (sometimes referred to as stapes). The columella is connected to the tympanum on one end, while the other end sits within the oval window of the inner ear. The middle ear also contains a middle ear cavity that is connected to the buccal cavity by a Eustachian tube (Wever, 1985; reviewed in Mason, 2007). In species that have lost their tympanic middle ear, a condition termed earlessness, the inner ear remains but all middle ear structures are missing (Wever, 1985; Jaslow et al., 1988), eliminating this mode of transferring sound from the environment to the inner ear.

Middle ear loss in anurans is perplexing because frogs and toads are well known for their use of acoustic communication in finding mates, territoriality, and defense (reviewed in Wells and Schwartz, 2007). Yet, at least 38 independent losses of middle ear structures have occurred across anurans (Chapter 1) without evidence of shared environmental selection pressures across ear transitions (Jaslow et al., 1988). The middle ear may be developmentally integrated with other skull features, such that its loss is the result of or results in changes in other developmentally linked skull structures with fitness impacts. Alternatively, the middle ear may be labile due to its independence from the rest of the skull. These hypotheses are explained in turn in the following paragraphs.

Developmental integration with other skull features could lead to middle ear loss when shifts in skull shape or specific skull features occur. The genes patterning middle ear structures pattern many other skull features in vertebrates (Chapman, 2011). In anurans, middle ear structures arise from three separate neural crest streams (Cerny et al., 2004; Gross and Hanken, 2008; Chapman, 2011), linking development of the ear to the formation of most other skull structures. Thus, middle ear transitions could result from or result in pleiotropic changes in other skull features. However, within anurans, little work has tested whether the middle ear is lost in concert with other changes in the skull that may have adaptive value.

Middle ear transitions could also result from changes in developmental timing (heterochrony) that affect many late-forming skull structures. The middle ear bone is one of the last bones to form and ossify in the skull during and after metamorphosis in many species (Sedra and Michael, 1959; Hetheringotn 1987, Gaudin, 1978; Weisbecker and Mitgutsch, 2010; Hanken and Hall, 1984; Wiens, 1989; Kerney, 2007), and middle ear loss could be a pleiotropic consequence of skull underdevelopment. Ear loss could be the consequence of neoteny (a slowing of development rate) or progenesis (an acceleration of sexual maturity), two forms of heterochrony (Gould, 1977; McNamara, 1986) that would result in premature arrest of skull development. Existing support for this skull underdevelopment hypothesis includes the lack of other late-forming skull bones in some earless species (Smirnov, 1991; Yeh, 2002) and reduced ossification in a few earless species (Pramuk, 2006). In addition, smaller skull size is associated both with earlessness (Hetherington, 1992a; Yeh, 2002) as well as with neoteny and progenesis (Hanken and Wake, 1993). Therefore, the columella may simply be one of many late-forming bones lost as a pleiotropic effect of heterochrony. However, no one has compared eared and earless skulls to determine whether earless skulls show signs of underdevelopment.

Another mode by which developmental processes can influence trait lability is trait modularity, that is, the lack of high developmental integration with other traits. Traits that have large mutational target sizes or undergo strong selection pressures may be more evolutionarily labile if they can change without negative pleiotropic consequences for other traits. Evidence for this hypothesis can be found in several features of tetrapod skulls. The tetrapod skull has consistently lost bones over evolutionary time (Williston's law; Gregory, 1935), preferentially losing bones that are more loosely connected to others (Esteve-Altava et al., 2014). In anurans, the middle ear is loosely connected (physically) to other skull features and is known to vary in developmental timing (Gaudin, 1978; Hanken and Hall, 1984; Wiens, 1989; Kerney, 2007), indicating potential developmental lability. In some species the columella is the last bone to ossify (Kerney, 2007), suggesting that a third form of heterochrony, post-displacement (later formation of a structure; Gould, 1977; McNamara, 1986), could result in middle ear loss in concert with either neoteny or progrenesis. Moreover, extremely late columellar development makes its precursors unlikely to induce the development of other traits, limiting opportunities for pleiotropy. Lack of developmental links to other skull features in concert with large mutational target size, heterochrony, or strong selection pressures, could explain the lability of middle ear evolution.

To address whether the middle ear is associated with pleiotropic changes in developmentally linked skull features, or whether it is evolving largely independently of the rest of the skull, we compared skull morphology of 55 species (39 eared, 16 earless) within the family Bufonidae. The family Bufonidae has the largest number of ear loss events, and also has potential regains of the ear structures (Chapter 1), making it ideal for comparing closely related eared and earless species. Our sampling captured at least five hypothesized independent middle ear transitions, allowing us to distinguish changes in the skull associated with earlessness from changes due to shared phylogenetic history. Specifically, we tested (1) whether earless toad skulls shared changes in overall skull shape or specific features that were distinct from eared skulls and (2) whether earless toad species had lower levels of overall skull ossification, smaller overall skull size, or lack of other late-forming skull bones, consistent with the hypothesis of heterochrony via neoteny or progenesis. Evidence supporting either of these pleiotropic hypotheses would illuminate potential fitness trade-offs as well as developmental mechanisms of earlessness that bias evolution towards middle ear loss. In contrast, a lack of support for these two hypotheses would demonstrate that the middle ear is able to evolve independently of other skull features, allowing it to be lost by active or passive processes without large pleiotropic consequence to other skull features. Testing these hypotheses will illuminate how developmental processes could bias the evolvability of the middle ear in anurans.

Materials and methods

Specimen collection and fixation

We examined 102 total specimens from 55 species (39 eared, 16 earless) in this study. For most species, two specimens were available, however, a few species were represented by only one specimen and a single species had three specimens. We obtained 49 species (89 specimens) from the Smithsonian National Museum of Natural History (Supplementary Information 5.1). We collected an additional six species (13 specimens) from various field sites in Ecuador and Peru (Supplementary Information 5.2). The Institutional Animal Care and Use Committee approved all collections methods (IACUC Protocol #12-3484A) and the Ministerio del Ambiente in Ecuador and the Servicio Nacional Forestal y de Fauna Silvestre in Peru approved collection, research, and export permits. Field caught animals were euthanized with 20% topical benzocaine and then decapitated. We preserved the head of each specimen in 4% paraformaldehyde diluted in Phosphate Buffered Saline from 16% paraformaldehyde solution (Electron Microscopy Sciences, Hatfield, PA, U.S.A.) for 24 hours and performed three 15-minute rinses in Phosphate Buffered Saline before storing cranial tissue in 70% ethanol. We measured the snout-vent length (SVL) and head width of all animals (field-caught and museum-loaned) to the nearest 0.1 mm using a dial caliper (31-415-3, Swiss Precision Instruments Inc., Garden Grove, CA, U.S.A).

Micro-CT scanning

We used micro-computed tomography (micro-CT) to analyze differences in skull shape, size, ossification level, as well as the presence/absence of specific bones. The Micro-CT Core Laboratory at the UT Health Science Center scanned and reconstructed all samples. We secured toad skulls to the specimen stage using Parafilm (American National Can, Greenwich, CT, U.S.A.) and scanned the skulls in air in a high-resolution desktop micro-CT system (Skyscan 1173, Bruker Skyscan, Aartselaar, Belgium). Scan settings were: 60 kV, 133 µA beam intensity, a 0.7°, 4 frame averaging, and a 1000 millisecond exposure time at each step. We used a 1 mm aluminum filter during scans

(Kovács et al., 2009). We set the pixel size to 10 µm for most skulls under 25 mm head width and 30 µm for most skulls with a head width greater than 25 mm. We reconstructed the images with NRecon (Bruker SkyScan, Aartselaar, Belgium) with a Feldkamp cone-beam algorithm (Feldkamp et al., 1984). We used a polynomial correction to reduce beam-hardening effects during reconstructions (Kovács et al., 2009; Zou et al., 2011). We imported the bmp files from the reconstructions into Fiji (Schindelin et al., 2012) at a resolution of 60 µm and created two 3D surface models for each skull using the 3D viewer plugin (Schmid et al., 2010).

Landmark placement & bone presence/absence survey

For the geometric morphometrics analysis of overall skull shape, we created 3D surface models of the skulls within the 3D viewer plugin (Schmid et al., 2010) of Fiji (Schindelin et al., 2012) and selected thresholds manually for each skull to best depict all skull features. We then imported these 3D surface models into Landmark (Wiley et al., 2005) and placed 57 3D landmarks on specific cranial elements that were reliably found in each skull, defined the borders of many bones, and characterized overall skull shape (Fig. 1).

To determine whether eared and earless species were missing any other bones consistently, we examined the 3D surface models used in the landmark placement in Meshlab (Visual Computing Lab ISTI-CNR, 2015). We paid special attention to the neopalatines, quadratojugal, prevomers, septomaxillae, and sphemethmoid (Fig. 2A) because presence/absence of these bones varies between anuran species (Yeh, 2002) and they are some of the last to form in the anuran skull (Gaudin, 1978; Weisbecker and Mitgutsch, 2010).

Ossification analysis

To compare the ossification level of all available species, we created 3D surface models at a consistent threshold (40) using the 3D Viewer plugin (Schmid et al., 2010) in Fiji (Schindelin et al., 2012). Only museum specimens were used in this analysis because samples collected by the authors were preserved via paraformaldehyde while museum specimens were preserved with formalin. These differences in preservation method could affect the mineralization levels of the fixed tissues registered by the scanner. Thus, a total of 89 specimens and 49 species (32 earless, 14 eared) were used in the ossification analysis. Using these standardized skull surface models, we compared nine bone junctures on the skull that varied as to whether two bones were fused or un-fused across individuals and also checked for presence of dermal ossification, ossification of the operculum, and co-ossification of the skull and epidermis (Fig. 2B). Each skull was given a score from 0 to 12 of overall ossification with 12 being the highest level of ossification. We averaged individuals from the same species to get a single ossification score for each species.

To determine differences between eared and earless species in ossification level while controlling for non-independence due to phylogenetic relatedness, we performed phylogenetic generalized least squares analysis (PGLS) using the packages phytools (Revell, 2012), geiger (Harmon et al., 2008), and nlme (Pinheiro et al., 2016) in R (R

Core Team, 2015). First we trimmed the most recent phylogeny of Amphibia (Pyron, 2014) to contain only the species used in this study using the ape (Paradis et al., 2004) and geiger (Harmon et al., 2008) packages in R (R Core Team, 2015). Then we determined the amount of non-independence in skull shape and size due to phylogenetic relatedness, by estimating phylogenetic signal of skull ossification level with Blomberg's K in picante (Kembel et al., 2010) within R (R Core Team, 2015). Finally, we ran our PGLS model with ossification level as the dependent variable and ear presence/absence as the predictor variable.

Skull shape and size analyses

To initially align all of the skulls and landmark data generated from placing the 57 landmarks on each of our skulls, we used the program MorphoJ (Klingenberg, 2011). We imported our landmark data into MorphoJ and performed a Procustes fit to the landmark data, which superimposes the landmarks from each skull onto one another so that they can be appropriately compared. We then averaged skull size (centroid size) and the shape data by species. To determine the amount of non-independence in skull shape and size due to phylogenetic relatedness, we estimated phylogenetic signal in skull shape and size with the multivariate permutation test implemented in MorphoJ (Tree length, Klingenberg and Gidaszewski 2010) using the most recent phylogenetic tree of amphibians (Pyron 2014) trimmed to our species.

To determine differences between eared and earless species in skull size, we performed phylogenetic generalized least squares analyses (PGLS) in R (R Core Team, 2015). We again trimmed the most recent phylogeny of amphibians (Pyron, 2014) to only the species used in this analysis, and then used skull log centroid size as the dependent variable and ear presence/absence as the predictor variable.

To analyze the differences in skull shape between eared and earless species, we used a phylogenetic analysis of variance for shape data (Procrustes ANCOVA) in the package geomorph (Adams and Otarola-Castillo, 2013) within R (R Core Team, 2015). We used a Procrustes ANOVA instead of a PGLS, because unlike the skull size analysis above, our shape analysis required many dependent variables to be analyzed in a single model. We used the Procrustes data from MorphoJ (before controlling for size) as the dependent variable, ear presence/absence as the predictor variable, and controlled for the effects of skull size on skull shape by adding skull size as a covariate to the model. The same phylogeny of amphibians used above (Pyron, 2014) was trimmed to the species used in this analysis. Using this analysis, we were able to test for differences in skull shape between eared and earless species while controlling for both the effects of phylogeny and size in a single model.

To visualize how eared and earless skulls differed in shape, we created multiple figures in MorphoJ. First we generated a covariance matrix from our Procrustes shape data and performed a Principal Component Analysis to visualize how eared and earless species compared in overall shape without controlling for size. We next performed a regression of the shape data by size and used the residuals from this analysis to perform a second Principal Component Analysis of shape differences between eared and earless species. Using the residuals from the shape and size data regression allowed us to visualize differences in shape that were not due to differences in skull size. Finally, we performed a canonical variance analysis on the size-corrected shape data within MorphoJ, a procedure for selecting and visualizing axes that maximize the differences between eared and earless species that were not due to skull size.

Results

Overall differences in skull shape between eared and earless species

We detected significant phylogenetic signal for skull shape (Tree length = 0.439, $P < 0.001$), which varied greatly across the phylogeny (Fig. 3A). Eared and earless skulls differed in shape when accounting for both phylogeny and size ($F_{54,52}$= 5.1376, p = 0.003; Fig. 3B). Our canonical variance analysis revealed the maximal differences between the average eared and earless skull to be minor when controlling for size (Fig. 4A-C). Earless skulls were slightly longer (Fig. 4A, B), slightly thinner (Fig. 4A, C), slightly shallower (Fig. 4B, C), and were less likely to have large supraorbital crests (indicated by the placement of the landmark with the asterisk, Fig. 4B).

Differences in skull size, ossification, and other missing bones

Eared and earless species varied in skull size and ossification (Fig. 5). We detected significant phylogenetic signal for both log skull centroid size and ossification level (skull size: Tree length = 4.9, p < 0.001; ossification: K= 0.4, p = 0.003). Log skull centroid size was larger in eared than in earless species when accounting for phylogeny ($t_{55,53}$ = 3.619454, p < 0.001). However, skull sizes of eared and earless species overlapped. Seven eared species (*Amietophrynus gracilipes*, *Atelopus flavescens, A. franciscus*, *A. pulcher*, *A. spumarius*, *Duttaphrynus scaber*, *Rhinella castaneotica*) had skulls less than or equal to the largest earless skull. Eared and earless species did not differ in ossification level when accounting for phylogeny ($t_{49,47}$= 0.807751, p = 0.4233; full dataset in Supplementary Information 5.3).

In addition, other late forming bones (neopalatines, quadratojugal, prevomers, septomaxillae, and sphenethmoid) were not consistently missing in earless species. Only one earless species, *Nectophryne batesii*, was missing additional skull bones, the neopalatines, and three other earless species, *Werneria mertensiana*, *Melanophryniscus stelzneri*, and *Dendrophryniscus brevipollicatus*, had reduced palatoquadrates (structures displayed in Fig. 2; full dataset Supplementary Information 5.4).

Discussion

Our results support the conclusion that middle ear transitions occurred largely independently of the evolution of other skull features. Earlessness was associated with smaller average skull size, but only minor shape differences distinguish earless from eared skulls. Additionally, we found no evidence of reduced skull ossification or general bone loss in earless species. Overall, eared and earless skulls were remarkably similar, indicating that middle ear lability does not depend on large pleiotropic effects of other cranial features. Below we discuss our interpretation of the shape changes found, why heterochrony remains a viable hypothesis for earlessness, and existing hypotheses for explaining the smaller size of earless skulls.

Eared and earless species differed consistently in skull shape when accounting for both size and phylogenetic relationships. However, these changes are minor, with earless skulls only slightly longer, thinner, shallower, and having less pronounced supraorbital crests. Additionally, Figure 2B shows considerable variation in earless skull shape, indicating that not all earless species share a uniform skull shape. Moreover, the shape differences in adult skulls between eared and earless species have no likely fitness consequences, as might be inferred for features such as changes in jaw length (Emerson, 1985). Studies linking tadpole and adult skull morphology are too limited to determine whether these minor changes in adult skull features might reflect differences in tadpole skulls that could have performance and fitness consequences. We therefore lack evidence that these minor shape differences between eared and earless skulls confer fitness advantages that could offset hearing costs of earlessness (Chapter 3).

Other than smaller average skull sizes, earless species also lacked expected indicators of skull underdevelopment, as predicted if neoteny (a slowing of development rate) or progenesis (an acceleration of sexual maturity) prematurely arrested skull development. Our ossification analysis and survey of presence/absence of other bones reject the hypothesis that the skulls of earless species are highly underdeveloped as adults. The lack of correlation between earlessness and our ossification data complements other studies on other anuran families that do not find a relationship between ossification level and bone loss (Trueb and Alberch, 1985). Thus, premature arresting of skull development is not a likely cause of ear loss, although other paedomorphic shifts in developmental timing might still drive ear loss.

If ear development was delayed beyond all other skull structures (post-displacement), the middle ear could be lost via heterochrony without large effects on other skull features. Smirnov (1991) proposed post-displacement as a mechanism for incomplete differentiation of the tympanum in *Bufo bufo* (Smirnov, 1991). Additionally, in *Bufo boreas*, the columella is the second to last bone to begin formation (Gaudin, 1978). The sequence of skull bone formation varies across anurans (Gaudin, 1978; Hanken and Hall, 1984; Wiens, 1989; Kerney, 2007), with the columella forming last in some species (Kerney, 2007). Thus, heterochrony (as post-displacement) remains a viable mechanism for the evolution of earlessness. Comparing development timing, the rate of cranial structure formation, and ossification among eared and earless species will provide critical insight into how the ear is lost while other structures are retained.

Furthermore, the smaller skull size of earless toads may not be an indicator of neoteny or progenesis but instead may relate to size-based sensory differences. Smaller anurans may have more effective extratympanic hearing pathways (alternative means to transfer sound energy from air to the inner ear not requiring tympanic middle ears) (Hetherington 1992b). The body wall overlying the lung can effectively transfer sound to the inner ear in some species (Ehret, 1990, 1994; Hetherington and Lindquist, 1999) and is more responsive to a greater range of frequencies in smaller anurans compared to larger species (Hetherington, 1992b). Additionally, experiments that compared auditory brainstem recordings of smaller anuran species found surprisingly small differences in hearing between eared and earless species (Loftus-Hill, 1973; Jaslow and Lombard, 1996; Lindquist et al., 1998). However, our analyses in Chapter 3 do not support the hypothesis that smaller anurans have better extratympanic hearing than larger animals. Thus, selection on tympanic hearing in smaller individuals is unlikely relaxed due to smaller body size mitigating the hearing consequences of ear loss.

In conclusion, our paper finds little evidence for pleiotropic shifts in other skull features associated with lack of a middle ear in bufonids. The smaller skull sizes and minor shape shifts in earless species do not provide clear evidence that pleiotropic trade-offs between skull structures or underdevelopment of the skull has driven ear loss in bufonids. The shape differences appear too minor to change skull functionality or impose clear fitness trade-offs, and instead suggest that middle ear structures evolve relatively independently from the rest of the skull. As shown in Chapter 3, extratympanic hearing or vibrational sensitivity may relax selection on tympanic hearing. We propose that the pervasiveness of ear transitions in anurans may reflect either heterochrony via post-displacement or other developmental biases that enable numerous mutations to alter middle ear development without detrimental effects on other traits. Why this seemingly important sensory system is commonly lost in anurans remains a perplexing evolutionary puzzle; however, the apparent independence of middle ear development could be a key contributor to middle ear lability in anurans. Middle ear evolution in anurans is a unique study system for investigating the effects of developmental bias on the evolution and its role in convergence.

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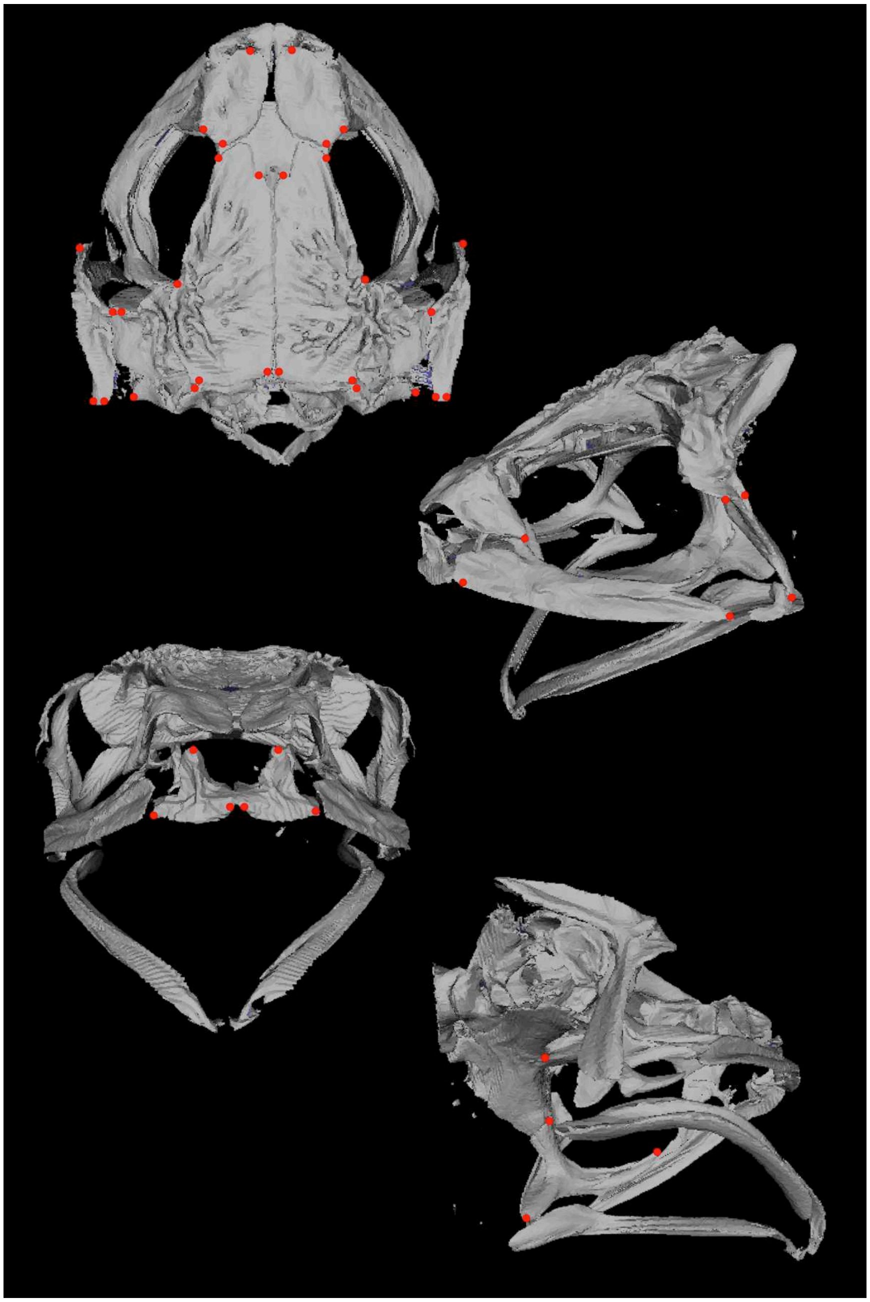

Figure 4.1 – Landmark placement for size and shape analyses. The placements of all 57 landmarks are indicated with red dots on the skull.

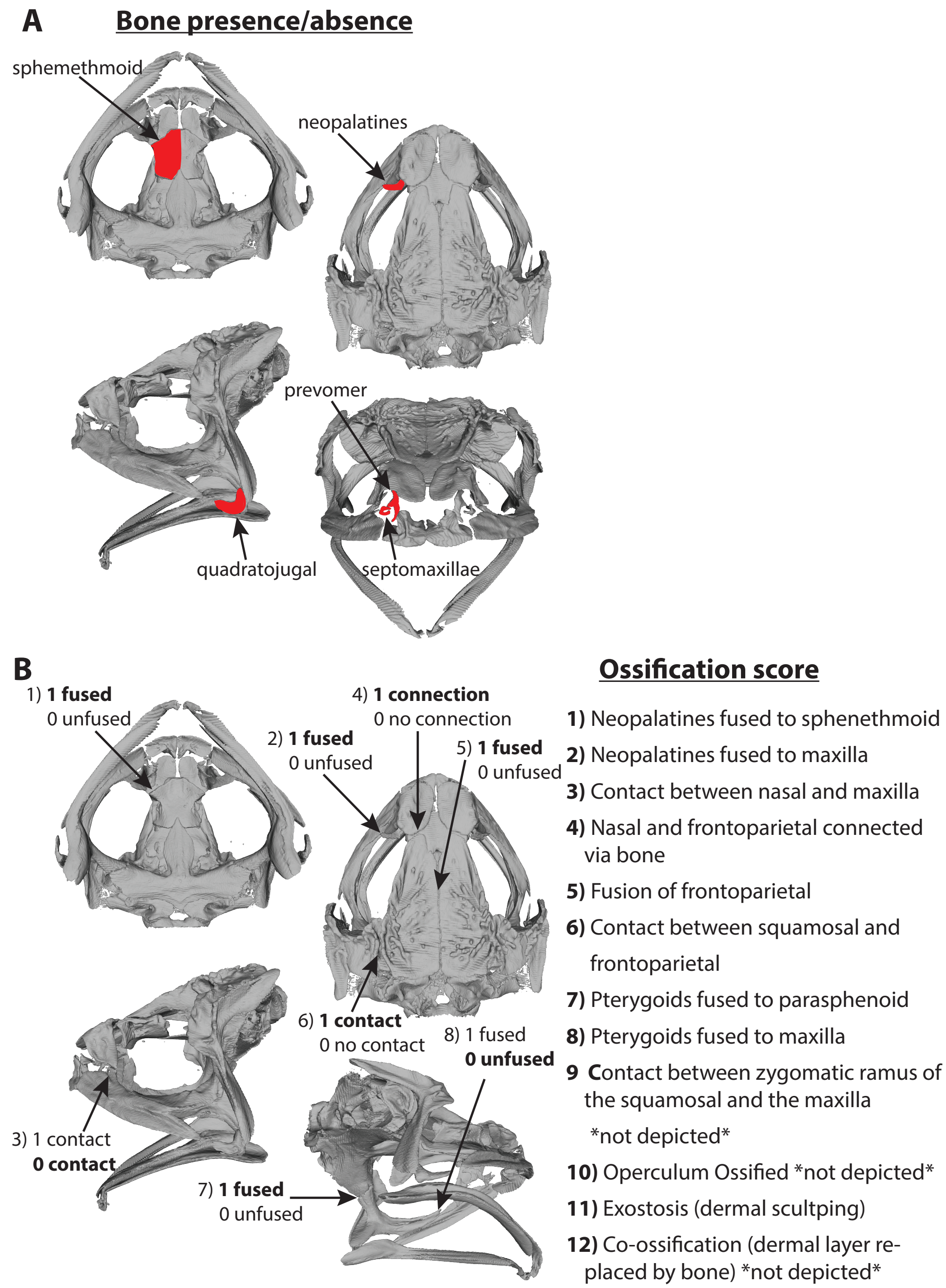

Figure 4.2 – Bones used in absence/presence analysis and skull features used in ossification analysis. A – The five late-forming bones scored in our bone presence/absence analysis are highlighted in red and labeled. **B –** The 12 skull features that were used for the ossification analysis are listed and numbered, with the nine visible features labeled on the skull. The ossification score for the depicted skull is bolded.

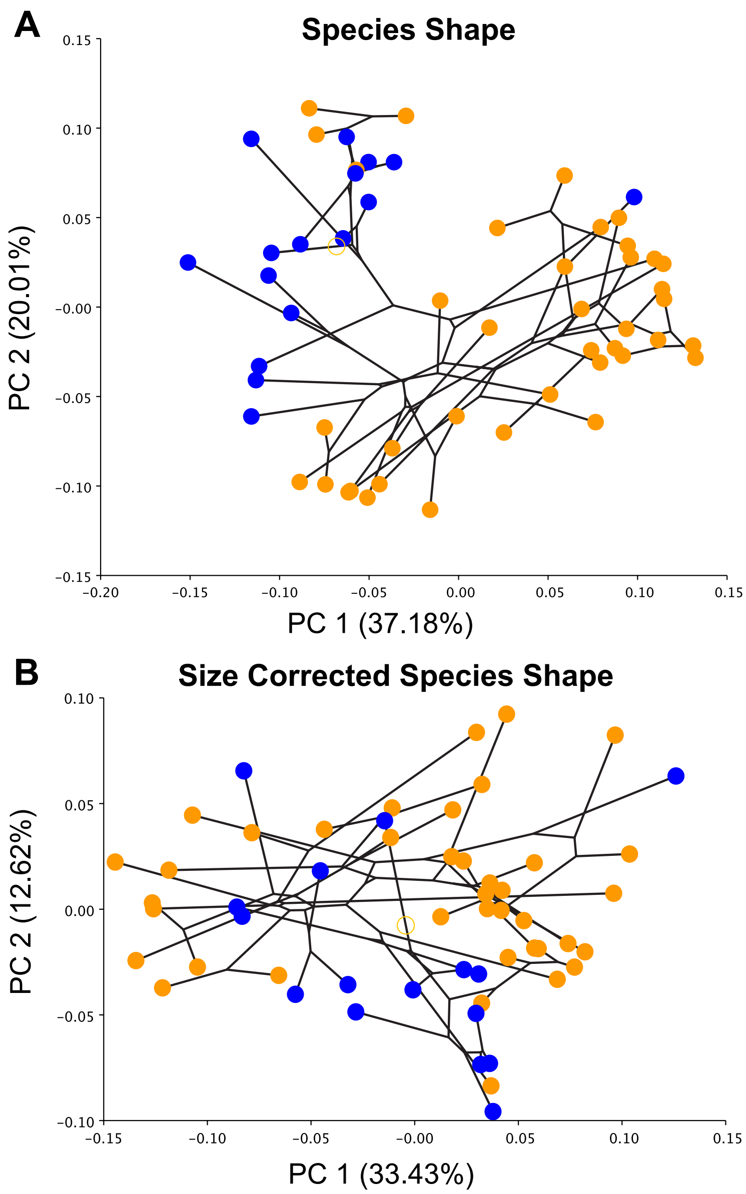

Figure 4.3 – Skull shape differences between eared (orange) and earless (blue) species before and after adjusting for overall skull size. A – Each point represents a species' skull shape from the principal component analysis of skull shape with no adjustment for overall skull size. **B –** Each point represents a species' skull shape after controlling for overall skull size from the principal component analysis on the residuals of the regression of skull shape by size. The proportion of the variance explained by each principal component is given by the percentage along the axis. Phylogenetic relationships and estimated ancestor relationships are indicated with black lines. The root, ancestral shape is indicated with the gold, unfilled circle.

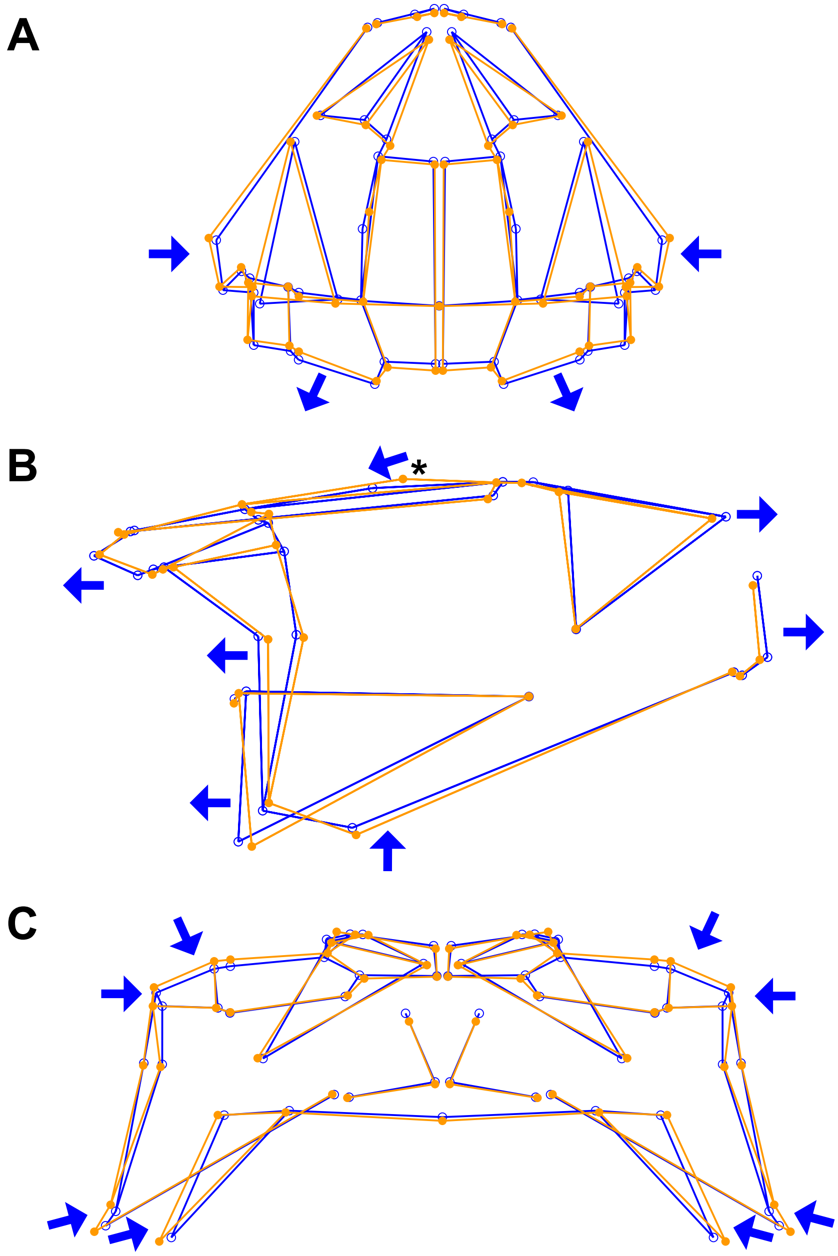

Figure 4.4 – Canonical Variance Analysis results showing shape differences between eared (orange) and earless (blue) skulls after controlling for body size. The average canonical variance score for eared and earless species is depicted by the wireframe graph. Landmarks are represented by the dots, and the blue arrows indicate the direction of skull shape differences of earless species compared to eared species. The landmark with the asterisk indicates the size of the supraorbital crests, with rostral locations signifying larger crests.

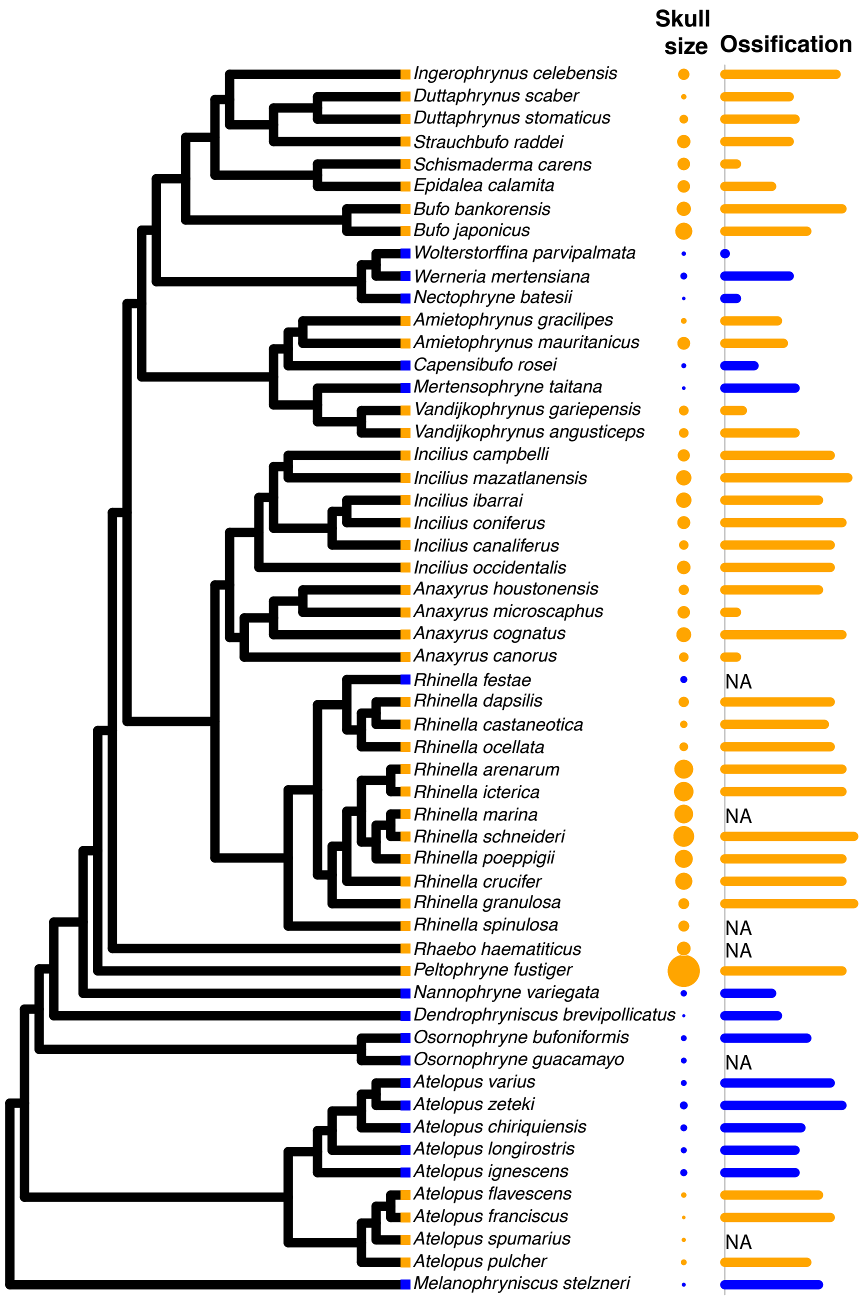

Figure 4.5 – Differences between eared (orange) and earless (blue) species in ossification level and skull size. Skull centroid size is represented by the size of the blobs next to each species name, with larger blob indicating larger skull centroid size. Overall skull ossification scores are represented by the length of the segments next to each species name, with longer lengths representing more ossified skulls.

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6. CONCLUSIONS & SYNTHESIS

Middle ear evolution in anurans is a unique trait loss due to its lack of adaptive explanation and the possible fitness costs of reduced hearing sensitivity. The tympanic middle ear has been lost minimally 38 times in anurans, with at least 10 losses and likely two regains inferred within the family Bufonidae alone. Extratympanic pathways buffer earless anurans from low frequency hearing costs as both juveniles and adults through unknown pathways. However, at high frequencies (above 900 Hz), earless species have reduced hearing sensitivity that likely impacts conspecific communication. Yet, earless species have slight increases in vibrational sensitivity that may relax selection on or compensate for hearing costs. How these sensory differences affect conspecific communication seems to vary across earless species and will be strongly influences by signaling behavior, indicating that selective pressures on the middle ear may likewise vary across species. Additionally, the middle ear forms late in the development of bufonids and the rate of the middle ear development varies across bufonids. We find little evidence of pleiotropic effects on other skull features when the middle ear is lost. We therefore suggest heterochrony (specifically post-displacement in concert with progenesis or neoteny) as a potential mechanism of ear loss that avoids pleiotropic consequences for the rest of the skull and explains the incredibly late formation of the middle ear in bufonids. Overall, these results demonstrate that earlessness is likely the result of developmental bias towards loss of late forming structures. Although earlessness in anurans has puzzled biologists for decades and a few, our work has made unprecedented leaps in testing various hypotheses for earlessness in a comparative framework.

Our comparative analysis also illuminates current gaps in our understating of hearing in anurans. We demonstrate large variation in both extratympanic hearing and vibrational sensitivity. The mechanisms that generate this variation in hearing and vibrational sensitivity remain unresolved. Currently proposed pathways of extratympanic hearing give no clear hypotheses for how this variation in earless species hearing is created. However, the positive relationship between extratympanic hearing and body size in our species implicate size of extratympanic body surfaces as important in generating some of the variation in extratympanic hearing sensitivity. More comparative experimental studies manipulating potential extratympanic pathways are necessary to determine how extratympanic hearing in anurans is functioning.

Finally, ear loss and regain also provides an exemplary opportunity to communicate the importance of developmental bias in the evolution of traits. Trait loss is a particularly hard concept for teachers and students of evolution to understand and explain (Ha and Nehm, 2014), and this is partially due to an inadequate understanding of processes such as developmental bias. Ear transitions highlight how the development of an organism strongly affects evolutionary trajectories, and may be an example of developmental bias giving rise to convergent loss of a sensory system without strong selective pressures

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SUPPLEMENTARY INFORMATION 2.1

Specimens examined and details about character coding

Considerations about character coding

We scored the presence and absence of the tympanic membrane, tympanic annulus, and columella for Bufonidae and other families of Anura based on dissections, MicroCT images, osteological preparations, and bibliographic information. The morphology of the tympanic membrane and tympanic annulus were studied with the aid of a stereomicroscope. When differentiation of structures in the tympanic region was not evident externally, we performed dissections to ascertain the condition of the tympanic annulus. To study the condition of the columella, specimens were cleared and double-stained for bone and cartilage (Wassersug, 1976). MicroCT scans were performed in air with a desktop Skyscan 1173 (Bruker Skyscan, Aartselaar, Belgium) system at a scanning resolution of 10 µm. The images were reconstructed with NRecon (Bruker SkyScan, Aartselaar, Belgium) with a Feldkamp cone-beam algorithm (Feldkamp *et al.* 1984).

Lynch and Duellman (1997) reviewed some of the confusions and misinterpretations surrounding the conditions of the tympanic membrane and tympanic annulus in many taxonomic studies, and we followed their considerations when scoring the character states of both structures: the definition of a ―tympanum‖ does not necessarily imply the presence of a tympanic membrane but can also refer only to a tympanic annulus. Thus, we only scored the tympanic membrane as present when we observed it ourselves or when published accounts explicitly describe it as a differentiated region of the skin or clearly depict it in the figures provided in publications. Regarding the condition of the columella, we scored it as present even if there are only rudiments of this structure in the adult forms. This latter situation is exceptional and was only reported for a few species of anurans (e.g., *Bombina* and *Telmatobius*).

Specimens examined

Collection abbreviations are as follow: AMNH (American Museum of Natural History, New York, United States); CBF (Colección Boliviana de Fauna, La Paz, Bolivia); CENAI (Centro Nacional de Investigaciones Iológicas, Buenos Aires, Argentina); CFBH (Collection Célio F.B. Haddad, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil); DB (Diego Baldo field series); ICN (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá , Colombia); KU (University of Kansas Natural History Museum, Lawrence, United States); LGE (Instituto de Biología Subtropical, Universidad Nacional de Misiones, Posadas, Misiones, Argentina); MACN (Museo Argentino de Ciencias Naturales -Bernardino Rivadavia‖, Buenos Aires, Argentina); MCP (Museu de Ciências e Tecnologia da PUCRS, Porto Alegre, Brazil.); MLP (Museo La Plata, La Plata, Argentina); MNCN (Museo Nacional de Ciencias Naturales, Madrid, Spain); MNRJ (Museu Nacional do Rio de Janeiro, Universidade Federal de Rio de Janeiro, Rio de Janeiro, Brazil); MZUSP (Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil); MNK (Museo de Historia Natural Noel Kempff, Santa Cruz de la Sierra, Bolivia); TG (Taran Grant field series); TNHC (Texas Memorial Museum, Austin, Texas, USA); UMMZ (University of Michigan Museum of Zoology, Ann Arbor, Michigan, United States); USNM (National Museum of Natural History, Washington, D.C., United States); ZUEC (Museu de História Natural, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil).

BUFONIDAE

Amazophrynella minuta.—**Colombia**: Amazonas: Leticia (ICN 50301).

Anaxyrus canorus.—**United States**: California: Tioga Pass Mono-Tuolumne county border (USNM 311300); Tuolumne Yosemite National Park, Aspen Valley (USNM 311297).

Anaxyrus cognatus.—**United States**: New Mexico: Luna: Columbus (USNM 320094, 320103).

Anaxyrus houstonensis.—**United States**: Texas: Harris Fairbanks (USNM 542211); near Houston airport (USNM 542212).

Anaxyrus microscaphus.—**United States**: New Mexico: Grant: San Lorenzo (USNM 320140); near New Mexico Hwy 35, Mimbres River Drainage (USNM 320144).

Ansonia muelleri.—**Philippines**: Mindanao Island: Agusan Del Norte: Cabadbaran (USNM 305567, 305569).

Atelopus chiriquiensis.—**Costa Rica**: Limon: Pico Blanco (= Cerro Kamuk) (USNM 30643-4).

Atelopus cruciger.—**Venezuela**: Aragure (ICN 14387).

Atelopus flavescens.—**French Guiana**: Cayenne, 82 km S of, 3 km W of Kaw (USNM

331415, 331417).

Atelopus franciscus.—**French Guiana**: Cayenne: Crique Gregoire, Inini (USNM 192815).

Atelopus ignescens.—**Ecuador**: Imbabura: near Odovalo (= Otavalo) (USNM 236903-4).

Atelopus longirostris.—**Ecuador**: Pichincha: Llambo (USNM 193825); Tandayapa (USNM 193835).

Atelopus pulcher.—**Peru**: Amazonas: La Poza (USNM 569373); Shiringa (USNM 569381).

Atelopus varius.—**Colombia**: Chocó: Río Sucio (ICN 31489). **Costa Rica**: San Jose Desamparados, near, along Rio Jorco (USNM 279113, 279119).

Atelopus zeteki.—**Panama**: Coclé: El Valle, Cerro Gaital (USNM 129893, 129896).

Bufo bankorensis.—**Taiwan**: Kaohsiung Hsien: Kosempo (= Chiasien) (USNM 66082–3).

Bufo japonicus.—**Japan**: Honshu Island: Nagano: Karuizawa (USNM 51997–8).

Capensibufo rosei.—**South Africa**: Western Cape: Cape Town, Table Mountain (USNM 159110, 159113).

Dendrophryniscus leucomystax.—**Brazil**: São Paulo: Ilha Comprida (CFBH 19007).

Didynamipus sjostedti.—**Cameroon**: Southwest: Nguti, near, Banyang-Mbo Forest (USNM 505739).

Duttaphrynus scaber.—**Sri Lanka**: North Eastern Mannar: Marichchukkadi (USNM 254716, 254718).

Duttaphrynus stomaticus.—**Nepal**: Narayani: Chitwan Sauraha, vicinity of Smithsonian Institution Camp, Royal Chitwan National Park (USNM 266829, 266836).

Epidalea calamita.—**Spain**: Madrid (MACN 36530). **Germany**: Bavaria: Nuremberg (USNM 579882, 579890).

Frostius pernambucensis.—**Brazil**: Bahia (LGE 7566).

Incilius campbelli.—**Belize**: Toledo: Maya Mountain Forest Reserve, Snake Creek (USNM 498198, 498200).

Incilius canaliferus.—**Mexico**: Chiapas: La Esperanza (USNM 116005, 116019).

Incilius coniferus.—**Panama**: Bocas del Toro: Isla Cristobal Bocatorito camp (USNM 348058–9).

Incilius ibarrai.—**Honduras**: Ocotepeque: El Volcan (USNM 523715, 523723).

Incilius mazatlanensis.—**Mexico**: Sonora: Bahia Kino (USNM 214074, 214077).

Incilius occidentalis.—**Mexico**: Puebla: Tecamachalco (USNM 116539, 116541).

Ingerophrynus celebensis.—**Indonesia**: Celebes: Sulawesi Tengah: Toli Toli (USNM 52986); Bada Toeare (USNM 61189).

Leptophryne borbonica.—**Malaysia**: Selangor: Templer's Park (CENAI 7616).

Melanophryniscus atroluteus.—**Brazil**: Rio Grande do Sul: São Borja (MCP 12667).

Melanophryniscus cambaraensis.—**Brazil**: Rio Grande do Sul: (MCN 13473).

Melanophryniscus cupreuscapularis.—**Argentina**: Corrientes: Capital, Paraje Perichón (DB 1759, 1761).

Melanophryniscus devincenzii.—**Argentina**: Misiones: Candelaria, Ñu Pyahú (DB 753).

Melanophryniscus dorsalis.—**Brazil**: Rio Grande do Sul: Torres (MCP 235, 244).

Melanophryniscus estebani.—**Argentina**: San Luis: Carolina (MACN 35405).

Melanophryniscus fulvoguttatus.—**Brazil**: Mato Grosso Do Sul: Maracaju (USNM 107712, 107722).

Melanophryniscus klappenbachi.—**Argentina**: Chaco: Resistencia (MACN 38532).

Melanophryniscus macrogranulosus.—**Brazil**: Rio Grande do Sul: Maquiné, Barra do Ouro (MCP 8104).

Melanophryniscus montevidensis.—**Uruguay**: Maldonado: Laguna Garzón (DB 4120).

Melanophryniscus pachyrhynus.—**Uruguay**: Maldonado: Sierra de Ánimas (DB 3988).

Melanophryniscus setiba.—**Brazil**: Espírito Santo: Parque Estadual Paulo Cesar Vinha (CFBH 15735, 15745).

Melanophryniscus simplex.—**Brazil**: Santa Catarina: Campos Novos (MCP 9472–3).

Melanophryniscus spectabilis.—**Brazil**: Santa Catarina: (MLP 1808).

Melanophryniscus vilavelhensis.—**Brazil**: Parana: Parque Estadual de Vila Velha (DZUP 208).

Mertensophryne taitana.—**Malawi**: Rumphi (USNM 153417).

Nannophryne variegata.—**Argentina**: Santa Cruz: Lago del Desierto (MACN 41452). **Chile**: Magallanes: Mayne Harbor (USNM 15124).

Nectophryne batesii.—**Cameroon**: Littoral: Nguengue (USNM 571097, 571100).

Nectophrynoides tornieri.—**Tanzania**: Magrotto Mts. (CENAI 7674); Tanga: Muheza (USNM 226759).

Osornophryne bufoniformis.—**Ecuador**: Sucumbíos: Santa Bárbara (USNM 193537, 193540).

Osornophryne guacamayo.—**Colombia**: Putumayo: Santiago (ICN 47811).

Osornophryne talipes.—**Colombia**: Nariño (ICN 12256).

Peltophryne empusa.—**Cuba**: Isla de Pinos: near Santa Fe (MACN 39144).

Peltophryne fustiger.—**Cuba**: Pinar del Río: La Mulata (USNM 51864).

Peltophryne peltocephala.—**Cuba**: Camagüey: Camagüey (CENAI 8343).

Rentapia hosii.—**Malaysia**: Pahang: Ulu Tahan, Kuala Teku (CENAI 7716).

Rhaebo andinophrynoides.—**Colombia**: Nariño: Barbacoas (ICN 53535).

Rhaebo glaberrimus.—**Colombia**: Meta: Restrepo (ICN 36350).

Rhaebo guttatus.—**Colombia**: Vaupés: Mitú, Villa Fátima (ICN 34808).

Rhaebo haematiticus.—**Colombia**: Caldas: Samaná (ICN 3472, 43493).

Rhinella achalensis.—**Argentina**: Córdoba: Pampa de Achala (MACN 24953).

Rhinella arenarum.—**Argentina**: Salta: Santa Victoria, Lipeo (MACN 39220). **Uruguay**: Montevideo (USNM 70620, 70622).

Rhinella castaneotica.—**Brazil**: Para: Itaituba (USNM 518807, 518809).

Rhinella dapsilis.—**Ecuador**: Pastaza: Río Rutuno, tributary of Río Bobonaza (USNM 196951). **Brazil**: Amazonas: Borba, Río Madeira (USNM 201814).

Rhinella dorbignyi.—**Argentina**: Buenos Aires: Dolores (MACN 43695).

Rhinella fernandezae.—**Argentina**: Entre Rios: Chajarí (LGE 8716).

Rhinella icterica.—**Brazil**: Sâo Paulo, Quarter Parque Jabaquara (USNM 100954, 100957).

Rhinella major.—**Argentina**: Chaco: 9 de Julio: Las Breñas (LGE 8719).

Rhinella merianae.—**Guyana**: East Berbice: Dubulay Ranch (USNM 566017–8).

Rhinella ocellata.—**Brazil**: Goias: Río Araguaia USNM 130177); Mato Grosso: Utuariti, Río

Papagaio (USNM 200548); Minas Gerais: Januaria (USNM 121334).

Rhinella ornata.—**Brazil**: Rio de Janeiro (USNM 70613–4).

Rhinella poeppigii.—**Peru**: San Martín (USNM 346829–30).

Rhinella schneideri.—**Bolivia**: Santa Cruz (USNM 281765). **Paraguay**: Boquerón: Filadelfia (USNM 340561).

Rhinella spinulosa.—**Argentina**: Mendoza: Uspallata (MACN 17574, 17567).

Schismaderma carens.—**Malawi**: Rumphi (USNM 153377, 153380). **South Africa**: Natal: Durban (CENAI 5984).

Sclerophrys capensis.—**South Africa**: Western Cape: Cape Town (CENAI 6851).

Sclerophrys gracilipes.—**Congo**: Likouala: Impongui (USNM 576239, 576391).

Sclerophrys mauritanica.—**Morocco**: Tetouan: Larache, 20 km SE of (USNM 346809, 346811).

Sclerophrys tuberosa.—**Cameroon**: Littoral: Ekomtolo (USNM 571083); Southwest: Nfainchang, near, Mt. Entali (USNM 324327).

Strauchbufo raddei.—**China**: Manchuria: Hei Sui (USNM 53371–2).

Vandijkophrynus angusticeps.—**South Africa**: Cape Of Good Hope: Kommetjie, near Cape Town (USNM 165087, 165089); Western Cape: Durbanville, near Cape Town (CENAI 6466).

Vandijkophrynus gariepensis.—**Lesotho**: Butha-Buthe (USNM 239871, 239873).

Werneria mertensiana.—**Cameroon**: Littoral: Nguengue (USNM 571101, 571105).

Wolterstorffina parvipalmata.—**Cameroon**: Littoral: Nguengue (USNM 571108–9).

OUTGROUPS

Adelphobates castaneoticus.—**Brazil**: Pará: near Cachoeira Juruá, Río Xingú (AMNH 133451–5).

Adelphobates galactonotus.—**Brazil**: Pará: Cachoeira do Limão, Río Tapajós (AMNH 128232–3).

Allobates femoralis.—**Colombia**: Putumayo*:* 10 km (airline) S Mocoa (AMNH 85258, 85260).

Allobates insperatus.—**Ecuador**: Napo: Santa Cecilia (KU 109310, 149671).

Allobates juanii.—**Colombia**: Meta: Acacias, Portachuelo (ICN 5097).

Allobates kingsburyi.—**Ecuador**: Pastaza: Abitagua Napo-Pastaza (UMMZ 217617).

Allobates talamancae.—**Costa Rica**: Puntarenas: Osa Peninsula, Corcovado National Park (UMMZ 193379).

Allobates undulatus.—**Venezuela**: Amazonas: Cerro Yutajé (AMNH 159141–2).

Alsodes gargola.—**Argentina**: Neuquén: Aluminé (MACN 37845)

Ameerega bassleri.—**Peru**: San Martín: Pachiza, Río Huallaga (AMNH 43402).

Ameerega bilinguis.—**Colombia**: Putumayo: 10 km (airline) S Mocoa, (AMNH 85215, 85219).

Ameerega hahneli.—**Peru**: Loreto: 5 rd km NE Previsto, near Boquerón del Padre Abad, upper Río Aguaytía (AMNH 118421).

Ameerega petersi.—**Peru**: Huánuco: Monte Alegre, Río Pachitea (AMNH 43016).

Ameerega picta.—**Bolivia**: Beni: Prov. Ballivian: Lago del Gringo, 10 km N of Puerto Salinas, 1 km from Beni River (UMMZ 184099).

Ameerega silverstonei.—**Peru**: Huánuco: 30 km NE Tingo María, Cordillera Azul (AMNH 91847– 9).

Ameerega trivittata.—**Suriname**: Brokopondo: Brownsberg Nature Park, near Mazaroni Top (AMNH 118431).

Andinobates claudiae.—**Panama**: Bocas del Toro: Isla Colón, near La Gruta (AMNH 103514).

Andinobates fulguritus.—**Panama**: Panamá: km 12.8 on El Llano-Cartí Rd, 290 m (AMNH 89448).

Anomaloglossus beebei.—**Guyana**: near Kaieteur Falls (AMNH 18683).

Aplastodiscus perviridis.—**Argentina**: Misiones: Guaraní (MACN 37040).

Arcovomer passarelii.—**Brazil**: Espírito Santo: Linhares (CFBH 2181).

Aromobates nocturnus.—**Venezuela**: Trujillo: about 2 km (airline) ESE Agua de Obispos (AMNH 129940, 130014).

Atelognathus patagonicus.—**Argentina**: Neuquén: Laguna Blanca (CENAI 1070).

Batrachyla leptopus.—**Argentina**: Chubut: Desemboque (MACN 41291).

Ceratophrys cranwelli.—**Argentina**: Santa Fe: Vera (MACN 42340).

Colostethus panamensis.—**Panama**: Veraguas: 6.12 km N Santa Fe N of Altopiedra and Agricultural School in montane area called Buenos Aires (UMMZ 167459).

Colostethus pratti.—**Panama**: Darién: Río Jaque, 1.5 km above Río Imamadó (AMNH 118364,118371).

Crossodactylus schmidtii.—**Argentina**: Misiones: Cainguás: Parque Provincial Salto Encantado (LGE 164), San Vicente (MACN 35122).

Chacophrys pierottii.—**Argentina**: Chaco: General Güemes, 10 km S Misión Nueva Pompeya (LGE 7716).

Chiasmocleis avilapiresae.—**Brazil**: Mato Grosso: Aripuanã (MNRJ 44231, 44283).

Chiasmocleis capixaba.—**Brazil**: Bahia: Nova Viçosa (MNRJ 18924, 19155).

Chiasmocleis carvalhoi.—**Brazil**: Rio de Janeiro: Magé (MNRJ 55166).

Chiasmocleis leucosticta.—**Brazil**: São Paulo: Ribeirão Branco (MNRJ 17901).

Chiasmocleis schubarti.—**Brazil**: Linhares: Espírito Santo (MNRJ 22961). *Ctenophryne aequatorialis*.—**Ecuador**: Azuay (MNRJ 59150).

Ctenophryne aterrima.—**Costa Rica**: Cartago (MNRJ 59144).

Ctenophryne geayi.—**Brazil***:* Mato Grosso: Aripuanã (MNRJ 44208).

Cycloramphus boraceiensis.—**Brazil**: Rio de Janeiro: Paraty (CFBH 17308).

Dasypops schirchi.—**Brazil**: Espírito Santo: Linhares (MNRJ 22684).

Dendrobates auratus.—**Costa Rica**: Puntarenas: 8 km ENE Palmar Norte (AMNH 118524). **Panama**: Panama: Isla Tobago (AMNH 118528).

Dendrobates tinctorius.—**Brazil**: Amapá: Serra do Navio (KU 93147).

Dendrobates truncatus.—**Colombia**: Tolima: Shore of Río Gualí, 1–2 km above Mariquita (AMNH 118401, 118403).

Dendropsophus minutus.—**Argentina**: Salta: Isla de Cañas (MACN 1302).

Elachistocleis bicolor.—**Argentina**: Formosa: Bermejo, Ing. Enrique H. Faure (MACN 37324).

Dermatonotus muelleri.—**Brazil**: Bahia: Itajibá (MNRJ 19299).

Dyscophus guineti.—pet trade (MNRJ 59154).

Epipedobates boulengeri.—**Colombia**: Cauca: Isla Gorgona (USNM 145253).

Epipedobates espinosai.—**Ecuador**: Pichincha: Río Baba, 5–10 km SSW Santo Domingo de los Colorados (AMNH 118411, 118417).

Elachistocleis bicolor.—**Brazil**: Paraná: Bituruna (MNRJ 6932).

Espadarana prosoblepon.—**Colombia**: Antioquia: Urrao: Parque Natural Nacional Las Orquideas, Quebrada Honda (ICN 19657).

Eupsophus roseus.—**Argentina**: Neuquén: Huiliches: Lago Curruhue (MACN 37981).

Gastrophryne carolinensis.—**United States**: Florida (MZUSP 5753).

Gastrotheca christiani.—**Argentina**: Jujuy: Ledesma, Valle Grande (CENAI 3209).

Gastrotheca riobambae.—**Ecuador**: Imbabura: Cotacachi (MACN 34025).

Geocrinia victoriana.—**Australia**: Victoria: 96 km NW Melbourne (KU 186877).

Haddadus binotatus.—**Brazil**: São Paulo: Serra de Paranapiacaba (MACN 17042).

Hamptophryne boliviana.—**Brazil**: Acre: Marechal Thaumaturgo (MNRJ 28922).

Hylorina sylvatica.—**Chile**: Llanquihué: Chamiza (CENAI 1870).

Hyloxalus awa.—**Ecuador**: Pichincha: 8 km SE Santo Domingo de los Colorados, Hacienda Delta (UMMZ 217614).

Hyloxalus bocagei.—**Ecuador**: Pastaza: Hills N of Mera (UMMZ 182465).

Hyloxalus elachyhistus.—**Ecuador**: Loja (KU 120543).

Hyloxalus pulchellus.—**Ecuador**: Napo: Río Azuela, Quito-Lago Agrio Road, eastern base Volcán Reventador (AMNH 89538).

Hyloxalus sauli.—**Ecuador**: Napo: Río Nachiyacu S of Venecia (UMMZ 182477).

Hyloxalus subpunctatus.—**Colombia**: Cundinamarca: Bogotá, near Monserrate (UMMZ 221158–9).

Hyloxalus sylvaticus.—**Peru**: SW slope Abra de Porculla (KU 164093).

Hyloxalus vertebralis.—**Ecuador**: Cañar: Cuenca (KU 120633–4).

Hypopachus variolosus.—**San Salvador**: El Salvador (MZUSP 77593).

Hypsiboas picturatus.—**Colombia**: Antioquia: Dabeiba (ICN 9279, 9275).

Hypsiboas pulchellus.—**Argentina**: Corrientes: Estancia Celina (LGE 2757, 2759).

Kaloula pulchra.—pet trade (MNRJ 51715).

Lepidobatrachus laevis.—**Argentina**: Formosa: Bermejo: Laguna Yema (MACN 39062).

Leptodactylus bufonius.—**Argentina**: Chaco: General Güemes: Wichi (LGE 12152).

Leptodactylus chaquensis.—**Argentina**: Chaco: General Güemes: near to Misión Nueva Pompeya (LGE 12002).

Leptodactylus latinasus.—**Argentina**: Chaco: 25 km NE Fuerte Esperanza (LGE 10524).

Leptodactylus latrans.—**Argentina**: Corrientes: Capital: Paraje Perichón (LGE 11278).

Leptodactylus mystacinus.—**Argentina**: Misiones: Guaraní: San Vicente (MACN 43782).

Leptodactylus podicipinus.—**Argentina**: Chaco: Antequera (LGE 10523).

Leptodactylus syphax.—**Brazil**: Goiás: Minaçu, Usina Hidrelétrica Serra da Mesa (LGE 10626–7).

Physalaemus ephippifer.—**Brazil**: Pará Santa Bárbara: Reserva Privada Gunma (LGE

2659).

Pseudopaludicola boliviana.—**Argentina**: Corrientes: General Paz: Itá Ibaté (LGE 3026).

Pseudopaludicola saltica.—**Brazil**: Goiás: Sitio D´Abadia (LGE 3066).

Limnomedusa macroglossa.—**Argentina**: Misiones: Colonia Delicia (LGE 10520).

Lysapsus limellum.—**Argentina**: Corrientes: San Miguel, 10 km N Loreto (MACN 39478).

Mannophryne collaris.—**Venezuela**: Mérida (UMMZ 217615).

Mannoprhyne herminae.—**Venezuela**: Aragua: Río Ocumare (UMMZ 210143–4).

Mannophryne trinitatis.—**Trinidad and Tobago**: Northern Range, 8 km (airline) N Arima (AMNH 118384, 118389).

Minyobates steyermarki.—**Venezuela**: Amazonas: SW sector Cerro Yapacana, 900 m (AMNH 118579).

Mixophyes fasciolatus.—**Australia**: Queensland: Bellthorpe State Forest (KU 179957).

Myersiella microps.—**Brazil**: Rio de Janeiro: Rio de Janeiro (MNRJ 27545).

Odontophrynus achalensis.—**Argentina**: Córdoba: Pampa de Achala (CENAI 2972)

Odontophrynus americanus.—**Argentina**: Misiones: Posadas (LGE 9094–5).

Oophaga arborea.—**Panama**: Chiriquí: continental divide above upper Quebrada de Arena (AMNH 116761).

Oophaga granulifera.—**Costa Rica**: 4.5 km W Rincón de Osa (KU 110223).

Oophaga histrionica.—**Colombia**: Chocó: Risaralda: 7 km (airline) SE Santa Cecilia, upper Río San Juan (AMNH 118458, 118461–2).

Oophaga lehmanni.—**Colombia**: Valle del Cauca: 13 km W Dagua, Río Anchicayá drainage (AMNH 88231, 118442).

Oophaga pumilio.—**Panama**: Bocas del Toro: East end Isla Escudo de Veraguas, (AMNH 118510).

Oophaga speciosa.—**Panama**: Chiriquí: Continental divide above upper Quebrada de Arena (AMNH 118447, 118454).

Oophaga sylvatica.—**Ecuador**: Pichincha: About 10 mi S of Santo Domingo de los Colorados, in banana plantation (AMNH 88225–6).

Oophaga vicentei.—**Panama**: Coclé: East shoulder Cerro Caracol (AMNH 114587).

Paratelmatobius poecilogaster.—**Brazil**: São Paulo: São Luis do Paraitinga (CFBH9877).

Phrynomantis microps.—pet trade (MNRJ 51711).

Phyllobates aurotaenia.—**Colombia**: Chocó: Vicinity of Playa de Oro, upper Río San Juan (AMNH 161108).

Phyllobates bicolor.—**Colombia**: Risaralda: about 7 km (airline) SE Santa Cecilia (AMNH 98256).

Phyllobates lugubris.—**Panama**: Bocas del Toro: ca. 5 km W Almirante (AMNH 118554, 118557).

Phyllobates terribilis.—**Colombia**: Cauca: Quebrada Guanguí, about .5 km above junction with Río Patia, in upper Río Saija drainage, 100–200 m, (AMNH 86319).

Phyllobates vittatus.—**Costa Rica**: Puntarenas: 8 km ENE Palmar Norte, 90 m, (AMNH 118542–5).

Phyllodytes luteolus.—**Brazil**: Bahia: Nova Viçosa (MNRJ 23275).

Phyllomedusa azurea.—**Argentina**: Chaco: Road between Resistencia and Sáenz Peña (CENAI 7772).

Phyllomedusa sauvagii.—**Argentina:** Formosa: Ramón Lista (MACN 38145)

Phyllomedusa tetraploidea.—**Argentina**: Misiones: General Manuel Belgrano, near to Leiten (LGE 2293).

Physalaemus albonotatus.—**Argentina**: Formosa: Tatané (LGE 10513, 10516).

Physalaemus biligonigerus.—**Argentina**: Santiago del Estero: Totora Pampa (LGE 10527).

Physalaemus cuvieri.—**Argentina**: Misiones: Villa Lanús (LGE 10512).

Physalaemus nattereri.—**Paraguay**: Amambay: Estancia Pirá Potrero, near Río Aquidabán (LGE 10518).

Pleurodema kriegi.—**Argentina**: Córdoba: Pampa de Achala (CENAI 5170).

Pleurodema marmoratum.—**Argentina**: Jujuy: El Quemado (LGE 6193).

Pleurodema tucumanum.—**Argentina**: Santiago del Estero: Totora Pampa (LGE 10636–7, 10514).

Pristimantis duellmani.—**Ecuador**: Carchi: 14 km SE Maldonado (KU 179268).

Pristimantis gentryi.—**Ecuador**: Cotopaxi: Pilalo, ca. 9 km (airline) E of Latacunga (USNM 239768).

Pristimantis juanchoi.—**Colombia**: Valle Del Cauca: Santiago De Cali (ICN 35063).

Pristimantis palmeri.—**Colombia**: Valle Del Cauca: Carretera El Cairo (ICN 29348).

Pristimantis thymalopsoides.—**Ecuador**: Cotopaxi: Pilaló (KU 177878).

Pristimantis surdus.—**Ecuador**: Pichincha: 7 km W Aloag, N slope Cerro Corazon (KU 109077).

Proceratophrys avelinoi.—**Argentina**: Misiones: Guaraní: San Vicente (MACN 36854).

Proceratophrys boiei.—**Brazil**: Santa Catarina: Florianopolis: Praia dos Naufragados (LGE 10564).

Pseudis minuta.—**Argentina**: Entre Ríos: Islas del Ibicuy (MACN 40425).

Pseudopaludicola falcipes.—**Argentina**: Corrientes: Perugorría (LGE 2969, 3105).

Pseudopaludicola mystacalis.—**Argentina**: Corrientes: Caá Catí (LGE 2842).

Ranitomeya imitator.—**Peru**: San Martín: Km 33, Carretera Tarapoto-Yurimagaus, Valle del Río Cainarache, 500–650 m (KU 209412–3).

Ranitomeya reticulata.—**Peru**: Loreto: 3 km airline SSW Mishana, on Río Nanay, 150 m (AMNH 103676, 103680–1).

Ranitomeya ventrimaculata.—**Peru**: Loreto: 3 km NE Pebas on Río Amazonas, 100 m (AMNH 103603–4).

Rheobates palmatus.—**Colombia**: Cundinamarca: Anolaima (AMNH 13472).

Rhinoderma darwinii.—**Chile**: Valdivia: Mehuín (CENAI 5491).

Scaphiophryne marmorata.—Pet trade (MNRJ 59152).

Scarthyla goinorum.—**Brazil**: Acre: Cruzeiro do Sul (TG 2774).

Silverstoneia flotator.—**Panama**: Coclé: Barro Colorado Island (KU 77678).

Silverstoneia nubicola.—**Panama**: Chiriquí: Río Frijoles (UMMZ 145585).

Scinax acuminatus.—**Argentina**: Chaco: Antequera (LGE 10534).

Scinax fuscovarius.—**Argentina**: Salta: Isla de Cañas (MCN 1301).

Scinax catharinae.—**Brazil** (MZUSP 55892).

Scinax cruentommus.—**Ecuador:** Sucumbios: Santa Cecilia (KU 111928).

Scinax garbei.—**Peru**: Loreto (AMNH 86792).

Scinax nebulosus.—**Bolivia** (MNK 886).

Scinax perpusillus.—**Brazil:** Rio de Janeiro: Recreio das Bandeirantes (THNC 37203).

Scinax ruber.—**Bolivia** (MNK 1640).

Scinax squalirostris.—**Argentina:** Santa Fe: Vera: Ea. Las Gamas (MACN 36970).

Sphaenorhynchus lacteus.—**Brazil**: Acre: Cruzeiro do Sul, Humaitá do Moa (ZUEC 5429).

Stereocyclops histrio.—**Brazil**: Bahia: Una (MZUSP 138155).

Stereocyclops incrassatus.—**Brazil***:* Espírito Santo: Linhares (MNRJ 22810).

Stereocyclops parkeri.—**Brazil**: Rio de Janeiro: Macaé (MNRJ 43987, 47478).

Strabomantis necerus.—**Colombia**: Valle Del Cauca: Restrepo: Vereda Campo Alegre (ICN 13229).

Synapturanus mirandaribeiroi.—**Brazil**: Amazonas: Oriximiná (MNRJ 52832).

Telmatobius culeus.—**Bolivia**: La Paz: Manco Kapac, Isla Tariquí, Lago Titicaca (CBF 4050, 4057).

Telmatobius hintoni.—**Bolivia**: Cochabamba: Cochabamba (MNCN 17361–2).

Telmatobius marmoratus.—**Bolivia**: La Paz: Charazani (CBF 3622). Huatajata, Lago Titicaca (CBF 2167).

Telmatobius niger.—**Ecuador**: Cañar: ca 8 km NW Biblián (KU 131795).

Telmatobius sibiricus.—**Bolivia**: Cochabamba: Río Chua Khocha, Sierra de la Siberia,

P. N. Carrasco-Ichilo (MNCN 17364).

Telmatobius simonsi.—**Bolivia**: Chuquisaca: El Palmar (CBF 3081–2); Santa Cruz: 15 km from Mairana (MNCN 17366).

Telmatobius truebae.—**Peru**: Amazonas: E slope Abra Chanchillo, 44 km ENE Balsas (KU 212464); Pomacochas (=Florida) (KU 212477–80).

Telmatobius verrucosus.—**Bolivia**: La Paz: Zongo, Laguna Viscachani (CBF 2765); Apolobamba (CBF 5372).

Telmatobius yuracare.—**Bolivia**: Cochabamba: La Siberia (MNCN 16645); Río Apaza (MNCN 16646).

Thoropa taophora. – **Brazil:** Sao Paulo: Ubatuba (CFBH12734).

Vitreorana uranoscopa. - **Argentina:** Misiones: Parque Provincial Esmeralda (LGE 10521).

Xenohyla truncata.- **Brazil:** Rio de Janeiro: Marie: Restinga de Marica (MNRJ 33276).

Table 2.1.1—Character states scored for each transformation series. 0: absent, 1: present, ?: unknown character state, inf: character state inferred following the lateral–medial dependency between the presence and absence of tympanic middle ear structures, †states codified from late larval stages (> Gosner Stage 42), *adults only have rudiments of columella.

Bufonidae included in Pyron (2014)			
Species	**Tympanic membrane**	**Tympanic annulus**	**Columella**
Adenomus kelaartii	0	1	1
Amazophrynella minuta	0	0	0
Anaxyrus americanus	1	1	1
Anaxyrus baxteri	1	1	1inf
Anaxyrus boreas	1	1	1
Anaxyrus californicus	1	1	1inf
Anaxyrus canorus	1	1	1
Anaxyrus cognatus	1	1	1
Anaxyrus debilis	1	1	1
Anaxyrus exsul	0	1	1
Anaxyrus fowleri	1	1	1
Anaxyrus hemiophrys	1	1	1inf
Anaxyrus houstonensis	1	1	1
Anaxyrus microscaphus	1	1	1
Anaxyrus nelsoni	1	1	1inf
Anaxyrus punctatus	1	1	1
Anaxyrus quercicus	1	1	1
Anaxyrus retiformis	?	1	1inf
Anaxyrus speciosus	1	1	1inf
Anaxyrus terrestris	1	1	1
Anaxyrus woodhousii	1	1	1
Ansonia albomaculata	0	1	1inf
Ansonia endauensis	1	1	1inf
Ansonia fuliginea	1	1	1inf
Ansonia guibei	1	1	1inf
Ansonia hanitschi	1	1	1inf
Ansonia inthanon	1	1	1inf
Ansonia kraensis	1	1	1inf
Ansonia latirostra	1	1	1inf
Ansonia leptopus	1	1	1inf

Ansonia longidigita	1	1	1inf
Ansonia malayana	1	1	1inf
Ansonia mcgregori	0	1	1inf
Ansonia minuta	1	1	1
Ansonia muelleri	0	1	1
Ansonia penangensis	1	1	1inf
Ansonia platysoma	1	1	1inf
Ansonia siamensis	0	1	1inf
Ansonia spinulifer	1	1	1inf
Atelopus bomolochos	0	0	0
Atelopus chiriquiensis	0	0	0
Atelopus flavescens	0	1	1
Atelopus franciscus	0	0&1	1
Atelopus halihelos	0	?	?
Atelopus ignescens	0	0	0
Atelopus longirostris	0	0	0
Atelopus nanay	0	0	0
Atelopus oxapampae	0	0	0
Atelopus peruensis	0	0	0
Atelopus pulcher	0	1	1
Atelopus seminiferus	0	0	0
Atelopus senex	0	0	0
Atelopus spumarius	0	1	1
Atelopus spurrelli	0	0	0
Atelopus tricolor	0	0inf	0
Atelopus varius	0	0	0
Atelopus zeteki	0	0	0
Barbarophryne brongersmai	1	1	1inf
Bufo aspinius	0	0inf	0
Bufo bankorensis	1	1	1
Bufo bufo	0&1	1	1
Bufo cryptotympanicus	0	?	?
Bufo eichwaldi	1	1	1inf
Bufo gargarizans	1	1	1inf
Bufo japonicus	1	1	1
Bufo stejnegeri	0	1	1inf
Bufo torrenticola	0	1	1inf
Bufo tuberculatus	1	1	1inf

Bufo tuberospinius	0	0inf	0
Bufo verrucosissimus	1	1	1inf
Bufotes balearicus	?	1	1inf
Bufotes oblongus	1	1	1inf
Bufotes pewzowi	1	1	1inf
Bufotes siculus	1	1	1inf
Bufotes variabilis	1	1	1inf
Bufotes viridis	1	1	1
Capensibufo rosei	0	0	0
Capensibufo tradouwi	1	1	1
Churamiti maridadi	0	0	0
Dendrophryniscus berthalutzae	0	?	?
Dendrophryniscus brevipollicatus	0	0	0
Dendrophryniscus carvalhoi	0	?	?
Dendrophryniscus krausae	0	?	?
Dendrophryniscus leucomystax	0	0	0
Dendrophryniscus proboscideus	0	0	?
Didynamipus sjostedti	0	0	0
Duttaphrynus atukoralei	?	1	1inf
Duttaphrynus brevirostris	?	1	1inf
Duttaphrynus crocus	1	1	1inf
Duttaphrynus himalayanus	0	1	1inf
Duttaphrynus hololius	1	1	1inf
Duttaphrynus melanostictus	1	1	1
Duttaphrynus parietalis	1	1	1
Duttaphrynus scaber	1	1	1
Duttaphrynus stomaticus	1	1	1
Duttaphrynus stuarti	1	1	1inf
Epidalea calamita	0	1	1
Ghatophryne ornata	1	1	1inf
Incilius alvarius	1	1	1
Incilius aucoinae	1	1	1
Incilius bocourti	0	0inf	0
Incilius campbelli	1	1	1
Incilius canaliferus	1	1	1
Incilius cavifrons	1	1	1
Incilius chompipe	0	?	?
Incilius coccifer	1	1	1

Incilius coniferus	1	1	1
Incilius cristatus	0	1	1
Incilius cycladen	1	1inf	1inf
Incilius fastidiosus	0	0	0
Incilius ibarrai	1	1	1
Incilius leucomyos	1	1	1
Incilius luetkenii	1	1	1
Incilius macrocristatus	1	1	1
Incilius marmoreus	1	1	1
Incilius mazatlanensis	1	1	1
Incilius melanochlorus	1	1	1
Incilius nebulifer	?	?	1
Incilius occidentalis	0	1	1
Incilius perplexus	1	1	1
Incilius pisinnus	1	1	1inf
Incilius porteri	1	1inf	1inf
Incilius signifer	1	1	1inf
Incilius spiculatus	1	1	1
Incilius tacanensis	1	1inf	1inf
Incilius tutelarius	1	1	1
Incilius valliceps	1	1	1
Ingerophrynus biporcatus	1	1	1inf
Ingerophrynus celebensis	1	1	1
Ingerophrynus divergens	1	1	1inf
Ingerophrynus galeatus	1	1	1inf
Ingerophrynus macrotis	1	1	1
Ingerophrynus philippinicus	1	1	1inf
Leptophryne borbonica	0	1	1
Melanophryniscus devincenzii	0	0	0
Melanophryniscus fulvoguttatus	0	0	0
Melanophryniscus klappenbachi	0	0	0
Melanophryniscus pachyrhynus	0	0	0
Melanophryniscus rubriventris	0	0	0
Melanophryniscus stelzneri	0	0	0
Mertensophryne anotis	0	0	0
Mertensophryne lindneri	0	0	0
Mertensophryne loveridgei	0	0inf	0
Mertensophryne micranotis	0	?	?

Mertensophryne taitana	0	0	0
Mertensophryne uzunguensis	0	0	0
Nannophryne cophotis	0	0inf	0
Nannophryne variegata	0	0	0
Nectophryne afra	0	0	0
Nectophryne batesii	0	0inf	0
Nectophrynoides minutus	1	1	1
Nectophrynoides tornieri	1	1	1
Nectophrynoides viviparus	1	1	1
Nimbaphrynoides occidentalis	0	0	0
Osornophryne antisana	0	0	0
Osornophryne bufoniformis	0	0	0
Osornophryne guacamayo	0	0	0
Osornophryne puruanta	0	0inf	0
Osornophryne sumacoensis	0	?	?
Pedostibes tuberculosus	1	1	1inf
Pelophryne brevipes	1	1	1inf
Pelophryne misera	1	1	1
Pelophryne signata	1	1	1inf
Peltophryne empusa	1	1	1inf
Peltophryne fustiger	1	1	1
Peltophryne guentheri	1	1	1inf
Peltophryne gundlachi	1	1	1inf
Peltophryne lemur	1	1	1
Peltophryne longinasus	0	?	?
Peltophryne peltocephala	1	1	1
Peltophryne taladai	1	1	1
Phrynoidis asper	1	1	1
Phrynoidis juxtasper	1	1	1
Poyntonophrynus damaranus	0	1	1inf
Poyntonophrynus dombensis	1	1	1inf
Poyntonophrynus fenoulheti	1	1	1inf
Poyntonophrynus vertebralis	1	1	1inf
Rentapia hosii	1	1	1
Rentapia rugosa	1	1	1inf
Rhaebo ecuadorensis	0	1inf	1inf
Rhaebo glaberrimus	1	1	1
Rhaebo guttatus	1	1	1

Rhaebo nasicus	0	1	1inf
Rhinella achavali	1	1	1inf
Rhinella amboroensis	0	?	?
Rhinella arenarum	1	1	1
Rhinella arequipensis	1	1	1
Rhinella arunco	1	1	1
Rhinella atacamensis	1	1	1
Rhinella castaneotica	0	1	1
Rhinella chavin	1	1	1
Rhinella dapsilis	1	1	1
Rhinella festae	0	0	0
Rhinella granulosa	1	1	1inf
Rhinella humboldti	1	1	1
Rhinella icterica	1	1	1
Rhinella limensis	1	1	1
Rhinella macrorhina	0	0	0
Rhinella manu	1	1	1
Rhinella margaritifera	1	1	1
Rhinella marina	1	1	1
Rhinella nesiotes	1	1	1inf
Rhinella ocellata	1	1	1
Rhinella ornata	1	1	1
Rhinella poeppigii	1	1	1
Rhinella rostrata	0	0	0
Rhinella schneideri	1	1	1
Rhinella spinulosa	1	1	1
Rhinella vellardi	?	1	1
Rhinella veraguensis	0	?	1
Sabahphrynus maculatus	0	0	0
Schismaderma carens	1	1	1
Sclerophrys brauni	1	1	1inf
Sclerophrys garmani	1	1	1inf
Sclerophrys gracilipes	1	1	1
Sclerophrys gutturalis	1	1	1inf
Sclerophrys kisoloensis	1	1	1inf
Sclerophrys latifrons	1	1	1inf
Sclerophrys lemairii	1	1	1inf
Sclerophrys maculata	1	1	1

Sclerophrys mauritanica	1	1	1
Sclerophrys pantherina	1	1	1
Sclerophrys pardalis	1	1	1
Sclerophrys poweri	1	1	1inf
Sclerophrys regularis	1	1	1
Sclerophrys steindachneri	1	1	1inf
Sclerophrys tuberosa	1	1	1
Sclerophrys xeros	1	1	1
Strauchbufo raddei	1	1	1
Vandijkophrynus amatolicus	1	1	1inf
Vandijkophrynus angusticeps	1	1	1
Vandijkophrynus gariepensis	1	1	1
Vandijkophrynus inyangae	1	1	1inf
Vandijkophrynus robinsoni	0	1	1inf
Werneria bambutensis	0	?	?
Werneria mertensiana	0	0inf	0
Werneria tandyi	0	?	?
Wolterstorffina parvipalmata	0	0inf	0
Xanthophryne koynayensis	1	1	1inf

Bufonidae not included in Pyron (2014)			
Species	**Tympanic membrane**	**Tympanic annulus**	**Columella**
Adenomus kandianus	0	1	1
Altiphrynoides malcolmi	0	0	0
Altiphrynoides osgoodi	0	0	0
Amazophrynella amazonicola	0	?	?
Amazophrynella bokermanni	0	?	?
Amazophrynella javierbustamantei	0	?	?
Amazophrynella manaos	0	?	?
Amazophrynella matses	0	?	?
Amazophrynella vote	0	?	?
Anaxyrus compactilis	1	1	1inf
Anaxyrus kelloggi	?	1	1inf
Anaxyrus mexicanus	1	1	1inf

Ansonia echinata	0	1	1inf
Ansonia glandulosa	1	1	1inf
Ansonia jeetsukumarani	1	1	1inf
Ansonia latidisca	1	1	1
Ansonia latiffi	1	1	1inf
Ansonia lumut	1	1	1inf
Ansonia thinthinae	1	1	1inf
Ansonia vidua	1	1	1inf
Atelopus angelito	0	0	0
Atelopus ardila	0	0	0
Atelopus arthuri	0	0	0
Atelopus balios	0	0	0
Atelopus barbotini	0	?	1
Atelopus boulengeri	0	0	0
Atelopus carbonerensis	0	0	0
Atelopus carrikeri	0	0	0
Atelopus certus	0	0	0
Atelopus chirripoensis	0	0	?
Atelopus chrysocorallus	0	?	?
Atelopus coynei	0	0	0
Atelopus cruciger	0	0	0
Atelopus dimorphus	0	0	0
Atelopus ebenoides	0	0	0
Atelopus elegans	0	0	0
Atelopus epikeisthos	0	?	?
Atelopus eusebianus	0	0	0
Atelopus eusebiodiazi	0	0	?
Atelopus exiguus	0	0	0
Atelopus farci	0	0	0
Atelopus gigas	0	0	0
Atelopus glyphus	0	0	0
Atelopus guanujo	0	0	0
Atelopus guitarraensis	0	0	0
Atelopus hoogmoedi	0	?	1
Atelopus laetissimus	0	0	0
Atelopus limosus	0	0	?
Atelopus loettersi	0	0	0
Atelopus longibrachius	0	0	0

Atelopus lozanoi	0	0	0
Atelopus lynchi	0	0	0
Atelopus mandingues	0	0	0
Atelopus marinkellei	0	?	?
Atelopus mindoensis	0	0	0
Atelopus mittermeieri	0	0	?
Atelopus monohernandezii	0	0	0
Atelopus mucubajiensis	0	0	0
Atelopus muisca	0	0inf	0
Atelopus nahumae	0	0	0
Atelopus nepiozomus	0	?	?
Atelopus nicefori	0	0	0
Atelopus nocturnus	0	0	0
Atelopus onorei	0	0	?
Atelopus orcesi	0	0	0
Atelopus oxyrhynchus	0	0	0
Atelopus pachydermus	0	0	0
Atelopus palmatus	0	?	?
Atelopus pastuso	0	0	0
Atelopus patazensis	0	0	?
Atelopus pedimarmoratus	0	1	1inf
Atelopus petersi	0	0	0
Atelopus petriruizi	0	0	0
Atelopus pictiventris	0	?	?
Atelopus planispina	0	0	0
Atelopus podocarpus	0	0	0
Atelopus pyrodactylus	0	?	?
Atelopus reticulatus	0	?	?
Atelopus sanjosei	0	0	0
Atelopus sernai	0	0	0
Atelopus simulatus	0	0	0
Atelopus siranus	0	1	1inf
Atelopus sonsonensis	0	0	0
Atelopus sorianoi	0	0	0
Atelopus tamaense	0	?	?
Atelopus subornatus	0	0	0
Atelopus vogli	0	0	0
Atelopus walkeri	0	0	0

Blythophryne beryet	1	1	1
Bufo ailaoanus	0	?	?
Bufo pageoti	0	1	?
Bufoides meghalayana	0	?	?
Bufotes latastii	1	1	1inf
Bufotes luristanicus	1	1	1inf
Bufotes pseudoraddei	?	1	1inf
Bufotes surdus	0	?	?
Bufotes turanensis	1	1	1inf
Bufotes zugmayeri	1	1	1inf
Dendrophryniscus oreites	0	?	?
Dendrophryniscus organensis	0	?	?
Dendrophryniscus skuki	0	?	?
Dendrophryniscus stawiarskyi	0	?	?
Duttaphrynus beddomii	0	1	1inf
Duttaphrynus chandai	0	1	1inf
Duttaphrynus kiphirensis	1	1	1inf
Duttaphrynus kotagamai	1	1	1inf
Duttaphrynus mamitensis	1	1	1inf
Duttaphrynus manipurensis	1	1	1inf
Duttaphrynus microtympanum	?	1	1inf
Duttaphrynus mizoramensis	1	1	1inf
Duttaphrynus nagalandensis	1	1	1inf
Duttaphrynus noellerti	1	1	1inf
Duttaphrynus olivaceus	1	1inf	1inf
Duttaphrynus sumatranus	1	1	1inf
Duttaphrynus totol	1	1	1inf
Duttaphrynus valhallae	1	1	1inf
Duttaphrynus wokhaensis	1	1	1inf
Frostius erythrophthalmus	1	1inf	1inf
Frostius pernambucensis	1	1	1
Ghatophryne rubigina	1	1inf	1inf
Incilius aurarius	1	1	1inf
Incilius epioticus	0	0	0
Incilius guanacaste	0	?	?
Incilius holdridgei	0	0	0
Incilius intermedius	?	1	1inf
Incilius karenlipsae	1	1	1inf

Incilius majordomus	0	0	0
Incilius mccoyi	0	1	?
Incilius periglenes	0	0	0
Incilius peripatetes	0	0	0
Ingerophrynus claviger	1	1	1inf
Ingerophrynus gollum	1	1inf	1inf
Ingerophrynus kumquat	1	1inf	1inf
Ingerophrynus parvus	1	1	1inf
Ingerophrynus quadriporcatus	1	1	1inf
Laurentophryne parkeri	0	0	0
Leptophryne cruentata	0	1	1inf
Melanophryniscus admirabilis	0	?	?
Melanophryniscus alipioi	0	?	?
Melanophryniscus atroluteus	0	0	0
Melanophryniscus biancae	0	?	?
Melanophryniscus cambaraensis	0	?	?
Melanophryniscus cupreuscapularis	0	?	?
Melanophryniscus dorsalis	0	?	?
Melanophryniscus estebani	0	?	?
Melanophryniscus krauczuki	0	0	0
Melanophryniscus langonei	0	?	?
Melanophryniscus macrogranulosus	0	0	0
Melanophryniscus milanoi	0	?	?
Melanophryniscus montevidensis	0	0	0
Melanophryniscus moreirae	0	0	0
Melanophryniscus paraguayensis	0	?	?
Melanophryniscus peritus	0	?	?
Melanophryniscus sanmartini	0	?	?
Melanophryniscus setiba	0	0	0
Melanophryniscus simplex	0	?	?
Melanophryniscus spectabilis	0	?	?
Melanophryniscus tumifrons	0	0	0
Melanophryniscus vilavelhensis	0	?	?
Melanophryniscus xanthostomus	0	?	?
Mertensophryne howelli	0	0inf	0
Mertensophryne lonnbergi	0	0	0
Mertensophryne melanopleura	0	0	?
Mertensophryne mocquardi	0	?	?

Mertensophryne nairobiensis	0	?	?
Mertensophryne nyikae	0	?	?
Mertensophryne schmidti	0	0	0
Mertensophryne usambarae	0	0inf	0
Metaphryniscus sosai	0	0	?
Nannophryne apolobambica	0	0	?
Nannophryne corynetes	0	0	0
Nectophrynoides asperginis	0	?	1
Nectophrynoides cryptus	0&1	0	0
Nectophrynoides frontierei	0	0	0
Nectophrynoides laevis	0	?	?
Nectophrynoides laticeps	0	1	1inf
Nectophrynoides paulae	1	1	1inf
Nectophrynoides poyntoni	1	1	1
Nectophrynoides pseudotornieri	0	?	?
Nectophrynoides vestergaardi	1	1	1
Nectophrynoides wendyae	0	?	?
Oreophrynella cryptica	0	?	?
Oreophrynella dendronastes	0	?	?
Oreophrynella huberi	0	?	?
Oreophrynella nigra	0	?	?
Oreophrynella quelchii	0	0	0
Oreophrynella seegobini	0	?	?
Oreophrynella vasquezi	0	?	?
Oreophrynella weiassipuensis	0	?	?
Osornophryne angel	0	?	?
Osornophryne cofanorum	0	?	?
Osornophryne occidentalis	0	0	?
Osornophryne percrassa	0	0	0
Osornophryne simpsoni	0	0	0
Osornophryne talipes	0	?	?
Parapelophryne scalpta	0	1	1
Pedostibes kempi	0	?	?
Pelophryne albotaeniata	1	1	1
Pelophryne api	1	1	1inf
Pelophryne guentheri	1	1	1inf
Pelophryne lighti	1	1	1inf
Pelophryne linanitensis	1	1	1inf

Pelophryne murudensis	1	1	1inf
Pelophryne rhopophilia	1	1	1inf
Pelophryne saravacensis	0	1	1inf
Peltophryne cataulaciceps	0	1	1inf
Peltophryne florentinoi	1	1	1inf
Peltophryne fluviatica	?	1	1inf
Peltophryne fracta	?	1	1inf
Poyntonophrynus beiranus	0	1	1inf
Poyntonophrynus grandisonae	1	1	1
Poyntonophrynus hoeschi	0	1	1inf
Poyntonophrynus kavangensis	1	1	1inf
Poyntonophrynus lughensis	1	1inf	1inf
Poyntonophrynus parkeri	?	1	1inf
Pseudobufo subasper	1	1	1
Pedostibes everetti	1	1	1inf
Rhaebo andinophrynoides	1	1	1inf
Rhaebo atelopoides	1	1	1
Rhaebo blombergi	1	1	1
Rhaebo caeruleostictus	0	1	1
Rhaebo colomai	0	1	1
Rhaebo haematiticus	1	1	1
Rhaebo hypomelas	1	1	1inf
Rhaebo lynchi	1	1inf	1inf
Rhaebo olallai	0	1	1
Rhinella abei	1	1	1inf
Rhinella achalensis	1	1	1
Rhinella acrolopha	0	0	0
Rhinella acutirostris	1	1	1inf
Rhinella alata	1	1	1inf
Rhinella amabilis	1	1	1
Rhinella arborescandens	0	0	0
Rhinella azarai	1	1	1inf
Rhinella bergi	1	1	1inf
Rhinella bernardoi	1	1	1inf
Rhinella casconi	1	1	1inf
Rhinella centralis	1	1	1inf
Rhinella ceratophrys	1	1	1inf
Rhinella cerradensis	1	1	1inf

Rhinella chrysophora	0	1	1
Rhinella cristinae	0	0	0
Rhinella crucifer	1	1	1
Rhinella diptycha	?	1	1inf
Rhinella dorbignyi	0&1	1	1inf
Rhinella fernandezae	0&1	1	1
Rhinella fissipes	0	?	?
Rhinella gallardoi	1	1	1inf
Rhinella gildae	1	1	1inf
Rhinella gnustae	1	1	1inf
Rhinella henseli	1	1	1inf
Rhinella hoogmoedi	1	1	1inf
Rhinella inca	1	1	?
Rhinella inopina	1	1	1inf
Rhinella iserni	0	0	0
Rhinella jimi	1	1	1inf
Rhinella justinianoi	0	?	?
Rhinella leptoscelis	1	1	1inf
Rhinella lescurei	1	1	1inf
Rhinella lindae	0&1	0&1	1
Rhinella magnussoni	1	1	1inf
Rhinella major	1	1	1
Rhinella martyi	1	1	1inf
Rhinella merianae	1	1	1inf
Rhinella mirandaribeiroi	1	1	1
Rhinella multiverrucosa	1	1	1
Rhinella nattereri	1	1	1inf
Rhinella nicefori	0	0	0
Rhinella paraguas	0	0	1
Rhinella paraguayensis	0	1	1inf
Rhinella proboscidea	1	1	1
Rhinella pygmaea	1	1	1
Rhinella quechua	0	?	?
Rhinella roqueana	1	1inf	1inf
Rhinella rubescens	1	1	1
Rhinella rubropunctata	1	1	1
Rhinella ruizi	0	0	0
Rhinella rumbolli	1	1	1inf

Rhinella scitula	1	1	1inf
Rhinella sclerocephala	1	1	1inf
Rhinella sebbeni	1	1	1inf
Rhinella stanlaii	1	1	1
Rhinella sternosignata	1	1	1
Rhinella tacana	1	1	1inf
Rhinella tenrec	0	0	0
Rhinella truebae	1	1inf	1inf
Rhinella veredas	1	1	1inf
Rhinella yanachaga	1	1	1
Rhinella yunga	0	?	?
Sclerophrys arabica	1	1	1inf
Sclerophrys asmarae	1	1	1inf
Sclerophrys blanfordii	?	1	1inf
Sclerophrys buchneri	1	1	1inf
Sclerophrys capensis	1	1	1inf
Sclerophrys channingi	1	1	1inf
Sclerophrys chudeaui	0	1	1inf
Sclerophrys cristiglans	1	1	1inf
Sclerophrys danielae	1	1	1inf
Sclerophrys dodsoni	1	1	1inf
Sclerophrys fuliginata	1	1	1inf
Sclerophrys funerea	?	?	1
Sclerophrys kassasii	1	1	1inf
Sclerophrys kerinyagae	1	1	1inf
Sclerophrys pentoni	?	1	1inf
Sclerophrys perreti	1	1	1inf
Sclerophrys reesi	1	1	1inf
Sclerophrys superciliaris	1	1	1inf
Sclerophrys taiensis	1	1	1inf
Sclerophrys urunguensis	1	1	1inf
Sclerophrys vittata	1	1	1inf
Truebella skoptes	0	0	0
Truebella tothastes	0	0	0
Werneria iboundji	0	?	?
Werneria preussi	0	0	0
Werneria submontana	0	?	?
Wolterstorffina mirei	0	0	0

Xanthophryne tigerina	0	1	1inf

Anura included in Pyron (2014)				
Family	**Species**	**Tympanic membrane**	**Tympanic annulus**	**Columella**
Allophrynidae	*Allophryne ruthveni*	1	1	1
Alsodidae	*Alsodes barrioi*	0	0	0
	Alsodes coppingeri	0	0	0
	Alsodes gargola	0	0	0
	Alsodes nodosus	0	1	1
	Alsodes pehuenche	0inf	0inf	0
	Alsodes tumultuosus	0	0	0
	Alsodes valdiviensis	0	0	0
	Alsodes vanzolinii	0inf	0inf	0
	Eupsophus calcaratus	?	?	1
	Eupsophus contulmoensis	1	1inf	1inf
	Eupsophus emiliopugini	?	1	1inf
	Eupsophus roseus	1	1	1
	Eupsophus septentrionalis	1	1inf	1
	Eupsophus vertebralis	1	1	1
	Limnomedusa macroglossa	0	1	1
Alytidae	*Alytes cisternasii*	?	1	1inf
	Alytes obstetricans	1	1	1
	Discoglossus montalentii	?	1	1inf
	Discoglossus pictus	0	?	1
	Discoglossus sardus	?	1	1
	Discoglossus scovazzi	?	1	1inf
Aromobatidae	*Allobates brunneus*	1	1	1inf
	Allobates femoralis	?	1	1
	Allobates granti	?	1	1inf
	Allobates insperatus	?	1	1
	Allobates juanii	?	1	1
	Allobates kingsburyi	?	1	1
	Allobates talamancae	0	1	1
	Allobates undulatus	?	1	1
	Anomaloglossus baebatrachus	1	1	1inf
	Anomaloglossus beebei	?	1	1inf
	Anomaloglossus kaiei	0	1	?
	Aromobates nocturnus	?	1	1
	Mannophryne collaris	?	1	1
	Mannophryne herminae	1	1	1
	Mannophryne trinitatis	?	1	1

	Rheobates palmatus	?	1	1inf
Arthroleptidae	*Arthroleptis adolfifriederici*	?	?	1
	Arthroleptis affinis	1	1	1inf
	Arthroleptis poecilonotus	?	1	1
	Arthroleptis stenodactylus	0&1	1	1
Arthroleptidae (cont.)	*Arthroleptis taeniatus*	1	1	1
	Arthroleptis reichi	?	?	1
	Arthroleptis schubotzi	?	?	1
	Arthroleptis tanneri	1	1	1inf
	Arthroleptis variabilis	0	1	1
	Arthroleptis wahlbergii	?	1	1inf
	Arthroleptis xenodactyloides	1	1	1
	Astylosternus batesii	0	1	1inf
	Astylosternus diadematus	1	1	1
	Cardioglossa gracilis	1	1	1
	Cardioglossa leucomystax	1	1	1inf
	Cardioglossa manengouba	0	1	1inf
	Cardioglossa oreas	0	1	1inf
	Leptodactylodon bicolor	0	?	?
	Leptopelis argenteus	?	1	1inf
	Leptopelis bocagii	0	1	1
	Leptopelis calcaratus	?	1	1
	Leptopelis kivuensis	1	1	1inf
	Leptopelis millsoni	?	1	1
	Leptopelis vermiculatus	1	1	1
	Nyctibates corrugatus	0	1	1
	Scotobleps gabonicus	1	1	1
	Trichobatrachus robustus	0	1	1
Ascaphidae	*Ascaphus truei*	0	0	0
Batrachylidae	*Atelognathus patagonicus*	0inf	0inf	0
	Atelognathus salai	0inf	0inf	0
	Batrachyla leptopus	1	1	1
	Batrachyla taeniata	?	?	1
	Hylorina sylvatica	1	1	1
Bombinatoridae	*Barbourula busuangensis*	0	?	1
	Bombina bombina	0	0	0
	Bombina maxima	?	?	1*
	Bombina orientalis	0	0	1*

	Bombina pachypus	?	?	1*
	Bombina variegata	0	0	1*
Brachycephalidae	*Brachycephalus alipioi*	0	0	?
	Brachycephalus brunneus	0	0	0
	Brachycephalus didactylus	0	0	0
	Brachycephalus ephippium	0	0	0
	Brachycephalus ferruginus	0	0	0
	Brachycephalus hermogenesi	0	0	0
	Brachycephalus izeckshoni	0	0	0
	Brachycephalus nodoterga	0	0	0
	Brachycephalus pernix	0	0	0
	Brachycephalus pitanga	0	0	?
Brachycephalidae (cont.)	*Brachycephalus pombali*	0	0	0
	Brachycephalus vertebralis	0	0	0
	Ischnocnema bolbodactyla	1	1	1inf
	Ischnocnema erythromera	1	1	1inf
	Ischnocnema guentheri	1	1	1
	Ischnocnema hoehnei	1	1	1inf
	Ischnocnema holti	0	1	1inf
	Ischnocnema izecksohni	1	1	1inf
	Ischnocnema juipoca	1	1	1inf
	Ischnocnema lactea	1	1	1inf
	Ischnocnema nasuta	1	1	1
	Ischnocnema octavioi	1	1	1
	Ischnocnema oea	1	1	1inf
	Ischnocnema parva	1	1	1
	Ischnocnema sambaqui	1	1	1inf
	Ischnocnema spanios	0	?	?
	Ischnocnema venancioi	1	1	1
	Ischnocnema verrucosa	1	1	1inf
Brevicipitidae	*Balebreviceps hillmani*	0	0	0
	Breviceps fuscus	0	?	1
	Breviceps mossambicus	0	1	1
	Callulina kreffti	1	1	1
	Probreviceps loveridgei	0	1	1

	Probreviceps macrodactylus	0	1	1
	Probreviceps rungwensis	0	1	1
	Probreviceps uluguruensis	0	1	1
	Spelaeophryne methneri	?	1	1
Calyptocephalellidae	*Calyptocephalella gayi*	1	1	1
	Telmatobufo bullocki	0	0	0
	Telmatobufo venustus	0	0	0
Centrolenidae	*Celsiella revocata*	?	1	1inf
	Celsiella vozmedianoi	?	1	1inf
	Centrolene altitudinale	1	1	1inf
	Centrolene bacatum	1	1	1inf
	Centrolene ballux	?	1	1inf
	Centrolene buckleyi	0	1	1inf
	Centrolene condor	0	1	1inf
	Centrolene daidaleum	1	1	1inf
	Centrolene geckoideum	1	1	1inf
	Centrolene heloderma	?	1	1inf
	Centrolene peristictum	1	1	1inf
	Centrolene pipilatum	1	1	1inf
	Centrolene venezuelense	?	1	1inf
	Cochranella euknemos	1	1	1
	Cochranella litoralis	?	1	1inf
Centrolenidae (cont.)	*Cochranella nola*	?	1	1inf
	Espadarana andina	1	1	1inf
	Espadarana callistomma	1	1	1
	Espadarana prosoblepon	1	1	1inf
	Hyalinobatrachium aureoguttatum	1	1	1
	Hyalinobatrachium bergeri	0	1	1inf
	Hyalinobatrachium colymbiphyllum	0	1	1
	Hyalinobatrachium eccentricum	?	1	1inf
	Hyalinobatrachium fleischmanni	0&1	1	1
	Hyalinobatrachium iaspidiense	0	1	1inf
	Hyalinobatrachium ibama	?	1	1inf
	Hyalinobatrachium ignioculis	?	1	1inf

	Hyalinobatrachium mondolfii	0	1	1inf
	Hyalinobatrachium munozorum	0	1	1inf
	Hyalinobatrachium orocostale	0	1	1inf
	Hyalinobatrachium talamancae	0	1	1inf
	Hyalinobatrachium taylori	1	1	1inf
	Ikakogi tayrona	0	1	1
	Nymphargus bejaranoi	1	1	1inf
	Nymphargus cochranae	1	1	1inf
	Nymphargus grandisonae	?	1	1inf
	Nymphargus griffithsi	?	1	1inf
	Nymphargus megacheirus	?	1	1inf
	Nymphargus posadae	0	1	1inf
	Nymphargus siren	1	1	1inf
	Nymphargus wileyi	1	1	1inf
	Rulyrana adiazeta	?	1	1inf
	Rulyrana flavopunctata	?	1	1inf
	Sachatamia albomaculata	1	1	1inf
	Sachatamia ilex	0	1	1inf
	Teratohyla midas	1	1	1inf
	Teratohyla pulverata	1	1	1inf
	Vitreorana antisthenesi	1	1	1inf
	Vitreorana gorzulae	0	1	1inf
	Vitreorana ritae	1	1	1inf
	Vitreorana uranoscopa	1	1	1
Ceratobatrachidae	*Alcalus baluensis*	?	1	1inf
	Cornufer guentheri	?	1	1
	Cornufer guppyi	?	1	1
	Cornufer papuensis	1	1	1inf
Ceratobatrachidae (cont.)	*Cornufer vertebralis*	0	1	1
	Platymantis corrugatus	1	1	1
	Platymantis dorsalis	?	1	1
	Platymantis hazelae	?	1	1
Ceratophryidae	*Ceratophrys cornuta*	0	1	1inf
	Ceratophrys ornata	1	1	1
	Chacophrys pierottii	1	1	1
	Lepidobatrachus laevis	1	1	1

Conrauidae	*Conraua crassipes*	0	1	1
	Conraua goliath	?	1	1
Craugastoridae	*Barycholos pulcher*	1	1	1
	Bryophryne cophites	0	0	0
	Ceuthomantis smaragdinus	1	1	1
	Craugastor alfredi	1	1	1inf
	Craugastor andi	1	1	1inf
	Craugastor angelicus	1	1	1inf
	Craugastor augusti	1	1	1
	Craugastor bocourti	1	1	1inf
	Craugastor bransfordii	1	1	1inf
	Craugastor crassidigitus	1	1	1inf
	Craugastor cuaquero	1	1	1inf
	Craugastor daryi	1	1	1inf
	Craugastor emcelae	1	1	1inf
	Craugastor fitzingeri	1	1	1
	Craugastor fleischmanni	1	1	1inf
	Craugastor laticeps	1	1	1inf
	Craugastor lineatus	1	1	1inf
	Craugastor loki	1	1	1inf
	Craugastor longirostris	1	1	1
	Craugastor megacephalus	1	1	1inf
	Craugastor melanostictus	1	1	1inf
	Craugastor mexicanus	1	1	1inf
	Craugastor montanus	1	1	1inf
	Craugastor obesus	1	1	1inf
	Craugastor podiciferus	1	1	1
	Craugastor punctariolus	1	1	1inf
	Craugastor pygmaeus	1	1	1inf
	Craugastor raniformis	1	1	1inf
	Craugastor ranoides	1	1	1inf
	Craugastor rhodopis	1	1	1
	Craugastor rugulosus	1	1	1inf
	Craugastor rupinius	1	1	1inf
	Craugastor sandersoni	1	1	1inf
	Craugastor spatulatus	1	1	1inf
	Craugastor stuarti	1	1	1inf
Craugastoridae (cont.)	*Craugastor tabasarae*	1	1	1inf
	Craugastor talamancae	1	1	1inf
	Craugastor	1	1	1inf

	tarahumaraensis			
	Craugastor uno	1	1	1inf
	Euparkerella brasiliensis	0	0	0
	Haddadus binotatus	1	1	1
	Holoaden bradei	0	0	0
	Holoaden luederwaldti	0	0	?
	Hypodactylus brunneus	1	1	1inf
	Hypodactylus dolops	1	1	1
	Hypodactylus elassodiscus	1	1	1inf
	Hypodactylus peraccai	1	1	1inf
	Lynchius flavomaculatus	1	1	1
	Lynchius nebulanastes	1	1	1
	Lynchius parkeri	0	1	1inf
	Lynchius simmonsi	1	1	1inf
	Noblella heyeri	1	1inf	1
	Noblella lochites	1	1	1inf
	Noblella myrmecoides	1	1	1
	Noblella peruviana	1	1	1
	Oreobates barituensis	1	1	1inf
	Oreobates choristolemma	1	1	1inf
	Oreobates cruralis	1	1	1inf
	Oreobates discoidalis	1	1	1
	Oreobates granulosus	1	1	1inf
	Oreobates heterodactylus	1	1	1inf
	Oreobates ibischi	1	1	1inf
	Oreobates lehri	1	1	1inf
	Oreobates madidi	1	1	1inf
	Oreobates pereger	1	1	1inf
	Oreobates quixensis	1	1	1
	Oreobates sanctaecrucis	1	1	1inf
	Oreobates sanderi	1	1	1inf
	Oreobates saxatilis	1	1	1inf
	Phrynopus barthlenae	0	0	?
	Phrynopus bracki	0	0	?
	Phrynopus bufoides	0	0	?
	Phrynopus horstpauli	0	0	?
	Phrynopus juninensis	0	0	0
	Phrynopus kauneorum	0	0	?
	Phrynopus pesantesi	0	0	?
	Phrynopus tautzorum	0	0	?
	Pristimantis acatallelus	0	1	1inf

	Pristimantis acerus	1	1	1inf
	Pristimantis achatinus	1	1	1
Craugastoridae (cont.)	*Pristimantis actites*	1	1	1inf
	Pristimantis acuminatus	0	1	1inf
	Pristimantis altae	1	1	1inf
	Pristimantis altamazonicus	0	1	1
	Pristimantis angustilineatus	1	1	1inf
	Pristimantis aniptopalmatus	?	1	1inf
	Pristimantis appendiculatus	1	1	1inf
	Pristimantis ardalonychus	0	1	1inf
	Pristimantis bipunctatus	?	1	1inf
	Pristimantis bogotensis	1	1	1
	Pristimantis brevifrons	1	1	1inf
	Pristimantis bromeliaceus	1	1	1inf
	Pristimantis buccinator	1	1	1inf
	Pristimantis buckleyi	1	1	1inf
	Pristimantis cajamarcensis	1	1	1inf
	Pristimantis calcaratus	1	1	1inf
	Pristimantis calcarulatus	1	1	1inf
	Pristimantis caprifer	1	1	1inf
	Pristimantis caryophyllaceus	?	?	1
	Pristimantis celator	?	1	1inf
	Pristimantis cerasinus	1	1inf	1
	Pristimantis ceuthospilus	1	1	1inf
	Pristimantis chalceus	0	1	1
	Pristimantis chiastonotus	1	1	1inf
	Pristimantis chloronotus	1	1	1
	Pristimantis citriogaster	1	1	1inf
	Pristimantis colomai	1	1	1inf
	Pristimantis condor	1	1	1inf
	Pristimantis conspicillatus	1	1	1
	Pristimantis cremnobates	1	1	1inf
	Pristimantis crenunguis	1	1	1inf
	Pristimantis croceoinguinis	0	1	1

	Pristimantis crucifer	1	1	1inf
	Pristimantis cruentus	0	1	1
	Pristimantis cryophilius	1	1	1inf
	Pristimantis curtipes	0	1	1
	Pristimantis danae	1	1	1inf
	Pristimantis devillei	1	1	1
	Pristimantis diadematus	1	1	1inf
	Pristimantis dissimulatus	1	1	1inf
	Pristimantis duellmani	0	0	0
	Pristimantis eriphus	1	1	1inf
	Pristimantis erythropleura	0	1	1inf
	Pristimantis euphronides	1	1	1inf
	Pristimantis fenestratus	1	1	1inf
Craugastoridae (cont.)	*Pristimantis frater*	1	1	1
	Pristimantis gaigei	1	1	1
	Pristimantis galdi	1	1	1
	Pristimantis gentry	0	1	1inf
	Pristimantis glandulosus	1	1	1inf
	Pristimantis gutturalis	1	1	1inf
	Pristimantis hectus	1	1	1inf
	Pristimantis imitatrix	0	0	?
	Pristimantis inguinalis	?	1	1inf
	Pristimantis inusitatus	1	1	1inf
	Pristimantis juanchoi	1	1	1inf
	Pristimantis jubatus	1	1	1inf
	Pristimantis kelephus	1	1	1inf
	Pristimantis koehleri	1	1	1inf
	Pristimantis labiosus	1	1	1inf
	Pristimantis lanthanites	1	1	1inf
	Pristimantis latidiscus	1	1	1inf
	Pristimantis leoni	0	1	1inf
	Pristimantis librarius	?	1	1inf
	Pristimantis lirellus	0	0	?
	Pristimantis llojsintuta	1	1	1inf
	Pristimantis luteolateralis	1	1	1inf
	Pristimantis lymani	1	1	1inf
	Pristimantis malkini	1	1	1inf
	Pristimantis marmoratus	1	1	1inf
	Pristimantis martiae	0	1	1inf
	Pristimantis	0	1	1inf

	melanogaster			
	Pristimantis miyatai	0	1	1inf
	Pristimantis moro	0	?	?
	Pristimantis museosus	1	1	1inf
	Pristimantis myops	1	1	1inf
	Pristimantis nervicus	1	1	1inf
	Pristimantis nyctophylax	?	1	1inf
	Pristimantis ockendeni	1	1	1inf
	Pristimantis ocreatus	0	1	1inf
	Pristimantis orcesi	1	1	1inf
	Pristimantis orestes	1	1	1inf
	Pristimantis paisa	0	1	1inf
	Pristimantis palmeri	1	1	1
	Pristimantis pardalis	1	1	1inf
	Pristimantis parvillus	1	1	1inf
	Pristimantis peruvianus	1	1	1inf
	Pristimantis petrobardus	1	1	1inf
	Pristimantis phoxocephalus	1	1	1inf
	Pristimantis pirrensis	1	1	1inf
Craugastoridae (cont.)	*Pristimantis platydactylus*	1	1	1inf
	Pristimantis prolatus	1	1	1inf
	Pristimantis ptochus	?	1	1inf
	Pristimantis pulvinatus	1	1	1inf
	Pristimantis pycnodermis	1	1	1inf
	Pristimantis pyrrhomerus	1	1	1inf
	Pristimantis quantus	1	1	1inf
	Pristimantis quaquaversus	0	0	?
	Pristimantis quinquagesimus	1	1	1inf
	Pristimantis ramagii	1	1	1inf
	Pristimantis reichlei	1	1	1inf
	Pristimantis rhabdocnemus	0	0	?
	Pristimantis rhabdolaemus	1	1	1inf
	Pristimantis rhodoplichus	1	1	1inf
	Pristimantis ridens	1	1	1
	Pristimantis riveti	1	1	1inf
	Pristimantis rozei	1	1	1inf
	Pristimantis sagittulus	1	1	1inf

	Pristimantis samaipatae	1	1	1inf
	Pristimantis savagei	1	1	1inf
	Pristimantis schultei	1	1	1inf
	Pristimantis shrevei	1	1	1inf
	Pristimantis simonbolivari	1	1	1inf
	Pristimantis simonsii	0	0	0
	Pristimantis skydmainos	1	1	1inf
	Pristimantis spinosus	1	1	1inf
	Pristimantis stictogaster	1	1	1inf
	Pristimantis subsigillatus	1	1	1inf
	Pristimantis suetus	1	1	1inf
	Pristimantis supernatis	1	1	1inf
	Pristimantis surdus	0	0	0
	Pristimantis taeniatus	1	1	1inf
	Pristimantis terraebolivaris	1	1	1inf
	Pristimantis thectopternus	1	1	1inf
	Pristimantis thymalopsoides	1	1	1inf
	Pristimantis thymelensis	0	1	1inf
	Pristimantis toftae	1	1	1inf
	Pristimantis truebae	0	1	1inf
	Pristimantis unistrigatus	1	1	1
	Pristimantis urichi	1	1	1inf
	Pristimantis ventrimarmoratus	0	1	1inf
	Pristimantis verecundus	1	1	1inf
	Pristimantis versicolor	1	1	1inf
	Pristimantis vertebralis	1	1	1inf
	Pristimantis viejas	1	1	1inf
Craugastoridae (cont.)	*Pristimantis walkeri*	1	1	1inf
	Pristimantis wiensi	?	1	1inf
	Pristimantis wnigrum	1	1	1
	Pristimantis zophus	1	1	1inf
	Psychrophrynella iatamasi	0	?	?
	Psychrophrynella wettsteini	1	1inf	1
	Strabomantis anomalus	1	1	1inf
	Strabomantis biporcatus	1	1	1inf
	Strabomantis bufoniformis	1	1	1

	Strabomantis necerus	1	1	1
	Strabomantis sulcatus	1	1	1
	Yunganastes ashkapara	1	1	1inf
	Yunganastes bisignatus	1	1	1inf
	Yunganastes fraudator	1	1	1inf
	Yunganastes mercedesae	1	1	1inf
	Yunganastes pluvicanorus	1	1	1inf
Cycloramphidae	*Cycloramphus boraceiensis*	0	?	?
	Cycloramphus eleutherodactylus	0	1	1
	Thoropa miliaris	?	1	1
	Thoropa taophora	1	1	1inf
	Zachaenus parvulus	0	1	1
Dendrobatidae	*Adelphobates castaneoticus*	?	1	1
	Adelphobates galactonotus	?	1	1
	Ameerega bassleri	?	1	1
	Ameerega bilinguis	1	1	1
	Ameerega hahneli	?	1	1
	Ameerega macero	?	1	1inf
	Ameerega parvula	?	1	1inf
	Ameerega petersi	?	1	1
	Ameerega picta	?	1	1
	Ameerega silverstonei	?	1	1
	Ameerega simulans	1	1	1
	Ameerega trivittata	?	1	1
	Andinobates claudiae	?	1	1
	Andinobates fulguritus	?	1	1
	Colostethus fugax	?	1	1inf
	Colostethus inguinalis	1	1	1
	Colostethus latinasus	?	1	1inf
	Colostethus panamensis	?	1	1
	Colostethus pratti	?	1	1
	Dendrobates auratus	1	1	1
	Dendrobates tinctorius	?	1	1
	Dendrobates truncatus	?	1	1
	Epipedobates anthonyi	?	?	1
Dendrobatidae (cont.)	*Epipedobates boulengeri*	?	1	1
	Epipedobates espinosai	?	1	1
	Excidobates captivus	?	1	1inf

	Excidobates mysteriosus	?	1	1inf
	Hyloxalus awa	?	1	1
	Hyloxalus bocagei	1	1	1
	Hyloxalus chlorocraspedus	?	1	1inf
	Hyloxalus elachyhistus	?	1	1
	Hyloxalus nexipus	?	1	1inf
	Hyloxalus pulchellus	?	1	1
	Hyloxalus sauli	?	1	1
	Hyloxalus subpunctatus	1	1	1
	Hyloxalus sylvaticus	?	1	1
	Hyloxalus vertebralis	?	1	1
	Minyobates steyermarki	?	1	1
	Oophaga arborea	?	1	1
	Oophaga granulifera	?	1	1
	Oophaga histrionica	?	1	1
	Oophaga lehmanni	?	1	1
	Oophaga pumilio	0	1	1
	Oophaga speciosa	?	1	1
	Oophaga sylvatica	?	1	1
	Oophaga vicentei	?	1	1
	Phyllobates aurotaenia	?	1	1
	Phyllobates bicolor	?	1	1
	Phyllobates lugubris	?	1	1
	Phyllobates terribilis	?	1	1
	Phyllobates vittatus	?	1	1
	Ranitomeya amazonica	?	1	1int
	Ranitomeya imitator	?	1	1
	Ranitomeya reticulata	?	1	1
	Ranitomeya ventrimaculata	1	1	1
	Silverstoneia flotator	?	1	1
	Silverstoneia nubicola	?	1	1
Dicroglossidae	*Euphlyctis cyanophlyctis*	0	1	1
	Euphlyctis hexadactylus	?	1	1inf
	Fejervarya cancrivora	1	1	1inf
	Fejervarya caperata	0	1	1inf
	Fejervarya granosa	0	1	1inf
	Fejervarya kudremukhensis	0	1	1inf
	Fejervarya iskandari	?	1	1inf
	Fejervarya limnocharis	?	1	1inf

	Fejervarya mudduraja	0	1	1inf
	Fejervarya rufescens	?	1	1inf
	Fejervarya sahyadris	?	1	1
Dicroglossidae (cont.)	*Hoplobatrachus occipitalis*	1	1	1
	Hoplobatrachus rugulosus	?	1	1inf
	Hoplobatrachus tigerinus	1	1	1
	Ingerana tenasserimensis	?	1	1inf
	Limnonectes asperatus	?	1	1inf
	Limnonectes blythii	0	1	1
	Limnonectes dabanus	?	1	1inf
	Limnonectes doriae	?	1	1inf
	Limnonectes finchi	1	1	1inf
	Limnonectes hascheanus	1	1	1inf
	Limnonectes ibanorum	?	1	1inf
	Limnonectes kuhlii	0	1	1
	Limnonectes laticeps	0	1	1inf
	Limnonectes leporinus	1	1	1inf
	Limnonectes leytensis	1	1	1inf
	Limnonectes macrodon	?	1	1inf
	Limnonectes magnus	?	1	1inf
	Limnonectes malesianus	1	1	1inf
	Limnonectes microdiscus	?	1	1inf
	Limnonectes microtympanum	?	1	1inf
	Limnonectes modestus	?	1	1inf
	Limnonectes palavanensis	1	1	1inf
	Limnonectes paramacrodon	1	1	1inf
	Limnonectes plicatellus	1	1	1inf
	Limnonectes woodworthi	?	1	1inf
	Nannophrys ceylonensis	1	1	1
	Nannophrys marmorata	?	?	1
	Nanorana aenea	?	1	1inf
	Nanorana arnoldi	?	1	1inf
	Nanorana liebigii	0	1	1
	Nanorana parkeri	0	0	0
	Nanorana pleski	0	1	1
	Nanorana quadranus	?	1	1inf
	Nanorana ventripunctata	0	0inf	0
	Nanorana yunnanensis	0	1	1inf

	Occidozyga baluensis	?	1	1inf
	Occidozyga laevis	0&1	1	1
	Occidozyga lima	0	?	1
	Quasipaa delacouri	?	1	1inf
	Quasipaa shini	0	1	1inf
	Quasipaa spinosa	?	?	1
	Sphaerotheca breviceps	?	1	1inf
	Sphaerotheca dobsonii	?	1	1inf
Eleutherodactylidae	*Adelophryne adiastola*	1	1	1inf
	Adelophryne baturitensis	1	1	1inf
Eleutherodactylidae (cont.)	*Adelophryne gutturosa*	1	1	1inf
	Adelophryne maranguapensis	1	1	1inf
	Adelophryne pachydactyla	1	1	1inf
	Adelophryne patamona	1	1	1inf
	Diasporus diastema	1	1	1
	Diasporus hylaeformis	1	1	1inf
	Diasporus vocator	1	1	1inf
	Eleutherodactylus abbotti	1	1	1
	Eleutherodactylus acmonis	1	1	1inf
	Eleutherodactylus adelus	1	1	1inf
	Eleutherodactylus albipes	1	1	1inf
	Eleutherodactylus alcoae	1	1	1inf
	Eleutherodactylus alticola	1	1	1inf
	Eleutherodactylus amadeus	1	1	1inf
	Eleutherodactylus amplinympha	1	1	1inf
	Eleutherodactylus andrewsi	1	1	1inf
	Eleutherodactylus antillensis	1	1	1
	Eleutherodactylus apostates	1	1	1inf
	Eleutherodactylus armstrongi	1	1	1
	Eleutherodactylus atkinsi	1	1	1
	Eleutherodactylus audanti	1	1	1
	Eleutherodactylus auriculatoides	1	1	1

	Eleutherodactylus auriculatus	1	1	1inf
	Eleutherodactylus bakeri	1	1	1inf
	Eleutherodactylus barlagnei	1	1	1
	Eleutherodactylus bartonsmithi	1	1	1inf
	Eleutherodactylus blairhedgesi	1	1	1inf
	Eleutherodactylus bothroboans	1	1	1inf
	Eleutherodactylus bresslerae	1	1	1inf
	Eleutherodactylus brevirostris	1	1	1inf
	Eleutherodactylus brittoni	1	1	1inf
	Eleutherodactylus caribe	1	1	1inf
	Eleutherodactylus casparii	1	1	1inf
	Eleutherodactylus cavernicola	1	1	1inf
	Eleutherodactylus chlorophenax	1	1	1inf
	Eleutherodactylus cochranae	1	1	1
	Eleutherodactylus cooki	1	1	1inf
	Eleutherodactylus coqui	1	1	1
	Eleutherodactylus corona	1	1	1inf
	Eleutherodactylus counouspeus	1	1	1inf
	Eleutherodactylus cubanus	1	1	1inf
	Eleutherodactylus cundalli	1	1	1
Eleutherodactylidae (cont.)	*Eleutherodactylus cuneatus*	1	1	1inf
	Eleutherodactylus darlingtoni	1	1	1inf
	Eleutherodactylus dimidiatus	1	1	1inf
	Eleutherodactylus dolomedes	1	1	1inf
	Eleutherodactylus eileenae	1	1	1inf
	Eleutherodactylus emiliae	1	1	1inf
	Eleutherodactylus	1	1	1

	eneidae			
	Eleutherodactylus etheridgei	1	1	1inf
	Eleutherodactylus eunaster	1	1	1inf
	Eleutherodactylus flavescens	1	1	1inf
	Eleutherodactylus fowleri	1	1	1inf
	Eleutherodactylus furcyensis	1	1	1
	Eleutherodactylus fuscus	1	1	1inf
	Eleutherodactylus glamyrus	1	1	1inf
	Eleutherodactylus glandulifer	1	1	1inf
	Eleutherodactylus glanduliferoides	1	1	1inf
	Eleutherodactylus glaphycompus	1	1	1inf
	Eleutherodactylus glaucoreius	1	1	1inf
	Eleutherodactylus goini	1	1	1inf
	Eleutherodactylus gossei	1	1	1
	Eleutherodactylus grabhami	1	1	1inf
	Eleutherodactylus grahami	1	1	1inf
	Eleutherodactylus greyi	1	1	1inf
	Eleutherodactylus griphus	1	1	1inf
	Eleutherodactylus gryllus	1	1	1inf
	Eleutherodactylus guanahacabibes	1	1	1inf
	Eleutherodactylus guantanamera	1	1	1inf
	Eleutherodactylus gundlachi	1	1	1inf
	Eleutherodactylus haitianus	1	1	1
	Eleutherodactylus hedricki	1	1	1inf
	Eleutherodactylus heminota	1	1	1
	Eleutherodactylus hypostenor	1	1	1inf
	Eleutherodactylus iberia	1	1	1inf
	Eleutherodactylus	1	1	1

	inoptatus			
	Eleutherodactylus intermedius	1	1	1inf
	Eleutherodactylus ionthus	1	1	1inf
	Eleutherodactylus jamaicensis	1	1	1inf
	Eleutherodactylus jaumei	1	1	1inf
	Eleutherodactylus johnstonei	1	1	1inf
	Eleutherodactylus jugans	1	1	1
	Eleutherodactylus junori	1	1	1inf
	Eleutherodactylus klinikowskii	1	1	1inf
Eleutherodactylidae (cont.)	*Eleutherodactylus lamprotes*	1	1	1inf
	Eleutherodactylus leberi	1	1	1inf
	Eleutherodactylus lentus	1	1	1
	Eleutherodactylus leoncei	1	1	1inf
	Eleutherodactylus limbatus	1	1	1
	Eleutherodactylus locustus	1	1	1
	Eleutherodactylus luteolus	1	1	1inf
	Eleutherodactylus maestrensis	1	1	1inf
	Eleutherodactylus mariposa	1	1	1inf
	Eleutherodactylus marnockii	1	1	1
	Eleutherodactylus martinicensis	1	1	1
	Eleutherodactylus melacara	1	1	1inf
	Eleutherodactylus minutus	1	1	1
	Eleutherodactylus monensis	1	1	1inf
	Eleutherodactylus nitidus	1	1	1
	Eleutherodactylus nortoni	1	1	1inf
	Eleutherodactylus nubicola	1	1	1
	Eleutherodactylus orcutti	1	1	1
	Eleutherodactylus orientalis	1	1	1inf

	Eleutherodactylus oxyrhyncus	1	1	1inf
	Eleutherodactylus pantoni	1	1	1
	Eleutherodactylus parabates	1	1	1inf
	Eleutherodactylus parapelates	1	1	1inf
	Eleutherodactylus patriciae	1	1	1
	Eleutherodactylus paulsoni	1	1	1inf
	Eleutherodactylus pentasyringos	1	1	1inf
	Eleutherodactylus pezopetrus	1	1	1inf
	Eleutherodactylus pictissimus	1	1	1
	Eleutherodactylus pinarensis	1	1	1inf
	Eleutherodactylus pinchoni	1	1	1inf
	Eleutherodactylus pipilans	1	1	1
	Eleutherodactylus pituinus	1	1	1inf
	Eleutherodactylus planirostris	1	1	1
	Eleutherodactylus poolei	1	1	1inf
	Eleutherodactylus portoricensis	1	1	1
	Eleutherodactylus principalis	1	1	1inf
	Eleutherodactylus probalaeus	1	1	1inf
	Eleutherodactylus rhodesi	1	1	1inf
	Eleutherodactylus richmondi	1	1	1
	Eleutherodactylus ricordii	1	1	1
	Eleutherodactylus riparius	1	1	1inf
	Eleutherodactylus rivularis	1	1	1inf
	Eleutherodactylus rogersi	1	1	1inf
Eleutherodactylidae	*Eleutherodactylus ronaldi*	1	1	1inf

(cont.)	*Eleutherodactylus rufifemoralis*	1	1	1inf
	Eleutherodactylus ruthae	1	1	1
	Eleutherodactylus schmidti	1	1	1inf
	Eleutherodactylus schwartzi	1	1	1inf
	Eleutherodactylus sciagraphus	1	1	1inf
	Eleutherodactylus simulans	1	1	1inf
	Eleutherodactylus sisyphodemus	1	1	1inf
	Eleutherodactylus sommeri	1	1	1inf
	Eleutherodactylus symingtoni	1	1	1inf
	Eleutherodactylus thomasi	1	1	1inf
	Eleutherodactylus thorectes	1	1	1inf
	Eleutherodactylus toa	1	1	1inf
	Eleutherodactylus tonyi	1	1	1inf
	Eleutherodactylus turquinensis	1	1	1inf
	Eleutherodactylus unicolor	1	1	1inf
	Eleutherodactylus varians	1	1	1inf
	Eleutherodactylus varleyi	1	1	1
	Eleutherodactylus ventrilineatus	1	1	1inf
	Eleutherodactylus weinlandi	1	1	1
	Eleutherodactylus wetmorei	1	1	1inf
	Eleutherodactylus wightmanae	1	1	1
	Eleutherodactylus zeus	1	1	1inf
	Eleutherodactylus zugi	1	1	1
	Phyzelaphryne miriamae	1	1	1inf
Heleophrynidae	*Hadromophryne natalensis*	0	?	1
	Heleophryne purcelli	0	1	1
Hemiphractidae	*Flectonotus fitzgeraldi*	?	1	1inf
	Flectonotus pygmaeus	?	1	1inf
	Gastrotheca	?	1	1inf

	argenteovirens			
	Gastrotheca atympana	0	0	1
	Gastrotheca aureomaculata	1	1	1inf
	Gastrotheca christiani	1	1	1
	Gastrotheca chrysosticta	1	1	1inf
	Gastrotheca cornuta	1	1	1inf
	Gastrotheca dendronastes	?	1	1
	Gastrotheca dunni	?	1	1
	Gastrotheca excubitor	1	1	1inf
	Gastrotheca fissipes	1	1	1inf
	Gastrotheca galeata	?	1	1
	Gastrotheca gracilis	1	1	1inf
	Gastrotheca griswoldi	?	1	1
	Gastrotheca guentheri	?	1	1
Hemiphractidae (cont.)	*Gastrotheca helenae*	0	1	1
	Gastrotheca litonedis	?	1	1
	Gastrotheca longipes	?	1	1
	Gastrotheca marsupiata	?	1	1
	Gastrotheca monticola	?	1	1
	Gastrotheca nicefori	1	1	1
	Gastrotheca ochoai	?	1	1
	Gastrotheca orophylax	?	1	1
	Gastrotheca peruana	?	1	1
	Gastrotheca plumbea	?	1	1inf
	Gastrotheca pseustes	?	1	1
	Gastrotheca psychrophila	?	1	1
	Gastrotheca riobambae	1	1	1inf
	Gastrotheca ruizi	?	1	1
	Gastrotheca stictopleura	?	1	1
	Gastrotheca trachyceps	?	1	1
	Gastrotheca weinlandii	?	1	1
	Gastrotheca zeugocystis	?	1	1
	Gastrotheca walkeri	0	1	1
	Hemiphractus bubalus	?	1	1
	Hemiphractus helioi	?	1	1
	Hemiphractus proboscideus	?	1	1
	Hemiphractus scutatus	?	1	1
	Stefania evansi	1	1	1
	Stefania ginesi	1	1	1

	Stefania scalae	?	1	1
	Stefania schuberti	1	1	1
Hemisotidae	*Hemisus marmoratus*	0	0	0
Hylidae	*Acris crepitans*	?	1	1
	Acris gryllus	?	1	1inf
	Agalychnis annae	?	1	1inf
	Agalychnis aspera	?	1	1inf
	Agalychnis callidryas	1	1	1
	Agalychnis dacnicolor	1	1	1
	Agalychnis granulosa	?	1	1
	Agalychnis hulli	0	1	1inf
	Agalychnis lemur	?	1	1
	Agalychnis litodryas	?	1	1inf
	Agalychnis moreletii	?	1	1
	Agalychnis saltator	?	1	1inf
	Agalychnis spurrelli	?	1	1
	Anotheca spinosa	1	1	1inf
	Aparasphenodon brunoi	?	?	1
	Aplastodiscus albofrenatus	1	1	1inf
	Aplastodiscus albosignatus	1	1	1inf
Hylidae (cont.)	*Aplastodiscus arildae*	?	1	1inf
	Aplastodiscus cavicola	?	1	1inf
	Aplastodiscus eugenioi	?	1	1inf
	Aplastodiscus leucopygius	?	1	1inf
	Aplastodiscus perviridis	1	1	1
	Aplastodiscus weygoldti	?	1	1inf
	Argenteohyla siemersi	1	1	1
	Bokermannohyla astartea	1	1	1inf
	Bokermannohyla circumdata	1	1	1inf
	Bokermannohyla hylax	1	1	1inf
	Bokermannohyla martinsi	?	1	1inf
	Bromeliohyla bromeliacia	?	1	1
	Charadrahyla nephila	?	1	1inf
	Charadrahyla taeniopus	?	1	1inf
	Corythomantis greeningi	?	?	1
	Cruziohyla calcarifer	1	1	1inf
	Dendropsophus anceps	1	1	1inf

	Dendropsophus berthalutzae	1	1	1inf
	Dendropsophus bifurcus	1	1	1inf
	Dendropsophus bipunctatus	1	1	1inf
	Dendropsophus branneri	1	1	1inf
	Dendropsophus brevifrons	?	1	1inf
	Dendropsophus ebraccatus	1	1inf	1
	Dendropsophus elegans	?	1	1inf
	Dendropsophus gaucheri	?	1	1inf
	Dendropsophus juliani	?	1	1inf
	Dendropsophus koechlini	?	1	1inf
	Dendropsophus labialis	?	1	1inf
	Dendropsophus marmoratus	1	1	1inf
	Dendropsophus melanargyreus	?	1	1inf
	Dendropsophus microcephalus	1	1	1
	Dendropsophus minutus	1	1	1
	Dendropsophus miyatai	?	1	1inf
	Dendropsophus nanus	1	1	1inf
	Dendropsophus parviceps	?	1	1inf
	Dendropsophus pelidna	1	1	1inf
	Dendropsophus rhodopeplus	?	1	1inf
	Dendropsophus robertmertensi	?	1	1inf
	Dendropsophus rubicundulus	?	1	1inf
	Dendropsophus sarayacuensis	?	1	1inf
	Dendropsophus sartoti	?	1	1inf
	Dendropsophus schubarti	0&1	1	1inf
	Dendropsophus seniculus	1	1	1inf
	Dendropsophus timbeba	0	1	1inf
	Dendropsophus triangulum	?	1	1inf
Hylidae (cont.)	*Dendropsophus tritaeniatus*	?	1	1inf
	Diaglena spatulata	?	1	1
	Duellmanohyla rufioculis	?	1	1inf
	Duellmanohyla soralia	1	1	1inf

	Ecnomiohyla miliaria	1	1	1inf
	Ecnomiohyla miotympanum	?	1	1
	Exerodonta abdivita	?	1	1inf
	Exerodonta chimalaà	?	1	1inf
	Exerodonta melanomma	?	?	1
	Exerodonta perkinsi	?	1	1inf
	Exerodonta smaragdina	?	1	1inf
	Exerodonta sumichrasti	?	1	1
	Exerodonta xera	?	1	1inf
	Hyla annectans	?	1	1inf
	Hyla andersonii	1	1	1inf
	Hyla arborea	?	1	1
	Hyla arenicolor	?	?	1
	Hyla avivoca	1	1	1inf
	Hyla chinensis	?	1	1
	Hyla chrysoscelis	1	1	1inf
	Hyla cinerea	1	1	1
	Hyla euphorbiacea	?	1	1inf
	Hyla eximia	?	?	1
	Hyla femoralis	1	1	1inf
	Hyla gratiosa	1	1	1inf
	Hyla meridionalis	1	1	1inf
	Hyla plicata	?	1	1inf
	Hyla squirella	1	1	1inf
	Hyla versicolor	1	1inf	1
	Hyla walkeri	1	1	1inf
	Hyla wrightorum	1	1	1inf
	Hyloscirtus alytolylax	?	1	1inf
	Hyloscirtus armatus	?	1	1inf
	Hyloscirtus colymba	?	1	1
	Hyloscirtus larinopygion	1	1	1inf
	Hyloscirtus lindae	?	1	1
	Hyloscirtus pacha	?	?	1
	Hyloscirtus palmeri	0	1	1inf
	Hyloscirtus pantostictus	1	1	1
	Hyloscirtus phyllognathus	?	1	1inf
	Hyloscirtus psarolaimus	1	1	1
	Hyloscirtus ptychodactylus	1	1	1
	Hyloscirtus simmonsi	?	1	1inf

	Hyloscirtus staufferorum	1	1	1
	Hyloscirtus tapichalaca	?	1	1
Hylidae (cont.)	*Hyloscirtus tigrinus*	1	1	1inf
	Hypsiboas albomarginatus	1	1	1
	Hypsiboas albopunctatus	?	1	1inf
	Hypsiboas andinus	?	1	1inf
	Hypsiboas balzani	?	1	1inf
	Hypsiboas bischoffi	1	1	1inf
	Hypsiboas boans	1	1	1inf
	Hypsiboas caingua	1	1	1inf
	Hypsiboas calcaratus	?	1	1inf
	Hypsiboas cinerascens	0	1	1inf
	Hypsiboas cordobae	?	1	1inf
	Hypsiboas crepitans	?	1	1inf
	Hypsiboas dentei	?	1	1inf
	Hypsiboas ericae	?	1	1inf
	Hypsiboas faber	1	1	1inf
	Hypsiboas fasciatus	?	1	1inf
	Hypsiboas geographicus	1	1	1inf
	Hypsiboas guentheri	?	1	1inf
	Hypsiboas heilprini	?	?	1
	Hypsiboas joaquini	0	1	1inf
	Hypsiboas lanciformis	1	1	1inf
	Hypsiboas latistriatus	?	1	1inf
	Hypsiboas leptolineatus	?	1	1inf
	Hypsiboas lundii	?	1	1inf
	Hypsiboas marginatus	0	1	1inf
	Hypsiboas marianitae	?	1	1inf
	Hypsiboas melanopleura	?	1	1inf
	Hypsiboas microderma	?	1	1inf
	Hypsiboas multifasciatus	?	1	1inf
	Hypsiboas nympha	?	1	1inf
	Hypsiboas ornatissimus	1	1	1inf
	Hypsiboas pardalis	?	1	1inf
	Hypsiboas pellucens	?	1	1inf
	Hypsiboas picturatus	1	1	1inf
	Hypsiboas polytaenius	1	1	1inf
	Hypsiboas prasinus	?	1	1inf
	Hypsiboas pulchellus	1	1	1inf
	Hypsiboas punctatus	1	1	1inf
	Hypsiboas raniceps	1	1	1inf

	Hypsiboas riojanus	1	1	1inf
	Hypsiboas roraima	?	1	1inf
	Hypsiboas rosenbergi	1	1	1
	Hypsiboas rufitelus	?	?	1
	Hypsiboas semiguttatus	?	1	1inf
	Hypsiboas semilineatus	1	1	1inf
Hylidae (cont.)	*Hypsiboas sibleszi*	?	1	1inf
	Isthmohyla pseudopuma	1	1	1inf
	Isthmohyla rivularis	0	1	1inf
	Isthmohyla tica	?	1	1
	Itapothyla langsdorfii	1	1	1inf
	Litoria adelaidensis	1	1	1inf
	Litoria alboguttata	1	1	1inf
	Litoria amboinensis	1	1	1inf
	Litoria andiirrmalin	1	1	1inf
	Litoria angiana	?	?	1
	Litoria arfakiana	?	1	1inf
	Litoria aurea	1	1	1inf
	Litoria australis	1	1	1
	Litoria barringtonensis	1	1	1inf
	Litoria bicolor	1	1	1inf
	Litoria booroolongensis	1	1	1inf
	Litoria brevipes	1	1	1
	Litoria burrowsi	1	1	1inf
	Litoria caerulea	1	1	1
	Litoria cavernicola	1	1	1inf
	Litoria chloris	?	1	1inf
	Litoria citropa	1	1	1inf
	Litoria congenita	1	1	1inf
	Litoria coplandi	1	1	1inf
	Litoria cryptotis	?	1	1inf
	Litoria cultripes	1	1	1
	Litoria cyclorhyncha	1	1	1inf
	Litoria dahlii	1	1	1
	Litoria darlingtoni	1	1	1inf
	Litoria daviesae	?	1	1inf
	Litoria dayi	0	1	1inf
	Litoria dentata	1	1	1inf
	Litoria electrica	1	1	1inf
	Litoria eucnemis	1	1	1inf
	Litoria ewingii	1	1	1

	Litoria fallax	1	1	1inf
	Litoria freycineti	1	1	1inf
	Litoria genimaculata	1	1	1inf
	Litoria gilleni	1	1	1inf
	Litoria gracilenta	?	1	1inf
	Litoria havina	1	1	1inf
	Litoria impura	1	1	1inf
	Litoria inermis	?	1	1inf
	Litoria jervisiensis	1	1	1inf
	Litoria jungguy	1	1	1inf
Hylidae (cont.)	*Litoria kumae*	1	1	1inf
	Litoria latopalmata	?	?	1
	Litoria lesueurii	1	1	1
	Litoria longipes	1	1	1inf
	Litoria longirostris	1	1	1inf
	Litoria maculosa	1	1	1inf
	Litoria maini	1	1	1inf
	Litoria manya	?	1	1inf
	Litoria meiriana	1	1	1inf
	Litoria microbelos	1	1	1inf
	Litoria micromembrana	?	?	1
	Litoria modica	?	?	1
	Litoria moorei	1	1	1
	Litoria nannotis	0	?	?
	Litoria nasuta	1	1	1inf
	Litoria nigrofrenata	1	1	1inf
	Litoria novaehollandiae	1	1	1inf
	Litoria nudidigita	?	1	1inf
	Litoria nyakalensis	0	1	1inf
	Litoria pallida	?	1	1inf
	Litoria paraewingi	1	1	1inf
	Litoria pearsoniana	1	1	1inf
	Litoria peronii	1	1	1inf
	Litoria personata	1	1	1inf
	Litoria phyllochroa	0	1	1
	Litoria platycephala	1	1	1
	Litoria pronimia	1	1	1inf
	Litoria raniformis	1	1	1inf
	Litoria revelata	1	1	1inf
	Litoria rheocola	?	1	1inf
	Litoria rothi	1	1	1inf

	Litoria rubella	1	1	1inf
	Litoria splendida	1	1	1inf
	Litoria subglandulosa	0	1	1inf
	Litoria tornieri	1	1	1inf
	Litoria tyleri	1	1	1inf
	Litoria vagitus	1	1	1inf
	Litoria verreauxii	1	1	1
	Litoria verrucosa	1	1	1inf
	Litoria watjulumensis	1	1	1inf
	Litoria wilcoxii	1	1	1inf
	Litoria xanthomera	1	1	1inf
	Lysapsus limellum	1	1	1inf
	Megastomatohyla mixe	0	1	1inf
	Myersiohyla imparquesi	1	1	1inf
Hylidae (cont.)	*Myersiohyla kanaima*	?	1	1inf
	Nyctimantis rugiceps	?	1	1inf
	Nyctimystes brevipalmatus	1	1	1inf
	Nyctimystes foricula	?	?	1
	Nyctimystes infrafrenatus	1	1	1
	Nyctimystes kubori	?	?	1
	Nyctimystes narinosus	?	?	1
	Nyctimystes papua	?	?	1
	Nyctimystes pulcher	?	1	1
	Nyctymistes zweifeli	?	?	1
	Osteocephalus alboguttatus	?	1	1inf
	Osteocephalus buckleyi	1	1	1inf
	Osteocephalus cabrerai	1	1	1inf
	Osteocephalus deridens	1	1	1inf
	Osteocephalus fuscifascies	1	1	1inf
	Osteocephalus leprieurii	1	1	1
	Osteocephalus mutabor	1	1	1inf
	Osteocephalus planiceps	1	1	1inf
	Osteocephalus oophagus	1	1	1inf
	Osteocephalus taurinus	?	?	1
	Osteocephalus verruciger	1	1	1inf
	Osteocephalus yasuni	1	1	1inf
	Osteopilus brunneus	?	1	1inf
	Osteopilus crucialis	?	1	1inf
	Osteopilus dominicensis	?	1	1inf

	Osteopilus marianae	?	1	1inf
	Osteopilus pulchrilineatus	?	1	1inf
	Osteopilus septentrionalis	1	1	1
	Osteopilus vastus	?	1	1inf
	Osteopilus wilderi	?	?	1
	Phasmahyla cochranae	?	1	1inf
	Phasmahyla cruzi	?	1	1inf
	Phasmahyla exilis	?	1	1inf
	Phasmahyla guttata	?	?	1
	Phasmahyla jandaia	?	1	1inf
	Phrynomedusa marginata	?	1	1inf
	Phyllodytes auratus	?	1	1inf
	Phyllodytes luteolus	?	?	1
	Phyllomedusa atelopoides	?	1	1
	Phyllomedusa ayeaye	?	1	1inf
	Phyllomedusa azurea	1	1	1
	Phyllomedusa bahiana	?	1	1inf
	Phyllomedusa baltea	?	1	1inf
	Phyllomedusa bicolor	0	1	1
	Phyllomedusa boliviana	?	1	1inf
Hylidae (cont.)	*Phyllomedusa burmeisteri*	?	1	1inf
	Phyllomedusa camba	0	1	1inf
	Phyllomedusa centralis	?	1	1inf
	Phyllomedusa duellmani	?	1	1inf
	Phyllomedusa hypochondrialis	?	1	1inf
	Phyllomedusa iheringii	?	1	1inf
	Phyllomedusa megacephala	?	1	1inf
	Phyllomedusa neildi	?	1	1inf
	Phyllomedusa nordestina	?	1	1inf
	Phyllomedusa oreades	?	1	1inf
	Phyllomedusa palliata	1	1	1inf
	Phyllomedusa perinesos	?	1	1inf
	Phyllomedusa rohdei	?	1	1inf
	Phyllomedusa sauvagii	1	1	1
	Phyllomedusa tarsius	1	1	1inf
	Phyllomedusa tetraploidea	?	1	1inf

	Phyllomedusa tomopterna	0	1	1inf
	Phyllomedusa trinitatis	?	1	1inf
	Phyllomedusa vaillanti	?	1	1inf
	Plectrohyla ameibothalame	?	1	1inf
	Plectrohyla arborescandens	?	1	1inf
	Plectrohyla bistincta	?	1	1inf
	Plectrohyla calthula	?	1	1inf
	Plectrohyla chrysopleura	?	1	1inf
	Plectrohyla cyclada	?	1	1inf
	Plectrohyla glandulosa	?	1	1inf
	Plectrohyla guatemalensis	?	1	1inf
	Plectrohyla mutadai	?	1	1inf
	Plectrohyla pentheter	?	1	1inf
	Plectrohyla siopela	?	1	1
	Pseudacris brachypona	1	1	1inf
	Pseudacris brimleyi	1	1	1inf
	Pseudacris cadaverina	1	1	1inf
	Pseudacris clarkii	?	?	1
	Pseudacris crucifer	1	1	1inf
	Pseudacris feriarum	1	1	1inf
	Pseudacris fouquetti	1	1	1inf
	Pseudacris illinoensis	1	1	1inf
	Pseudacris kalmi	1	1	1inf
	Pseudacris maculata	1	1	1inf
	Pseudacris nigrita	?	1	1inf
	Pseudacris ocularis	?	1	1
	Pseudacris ornata	?	1	1
	Pseudacris regilla	?	1	1
	Pseudacris streckeri	1	1inf	1
Hylidae (cont.)	*Pseudacris triseriata*	?	1	1inf
	Pseudis bolbodactyla	?	1	1inf
	Pseudis cardosoi	?	1	1inf
	Pseudis fusca	?	1	1inf
	Pseudis minuta	1	1	1
	Pseudis paradoxa	1	1	1
	Pseudis tocantins	?	1	1inf
	Ptychohyla dendrophasma	?	1	1inf
	Ptychohyla euthysanota	?	1	1inf

	Ptychohyla hypomykter	?	1	1inf
	Ptychohyla leonhardschultzei	?	1	1inf
	Ptychohyla spinipollex	?	1	1
	Ptychohyla zophodes	?	1	1inf
	Scarthyla goinorum	1	1	1
	Scinax acuminatus	1	1	1inf
	Scinax berthae	1	1	1inf
	Scinax boesemani	1	1	1inf
	Scinax boulengeri	1	1inf	1
	Scinax catharinae	?	1	1
	Scinax crospedospilus	?	1	1
	Scinax cruentommus	?	1	1
	Scinax elaeochrous	?	1	1
	Scinax faivovichi	1	1	1inf
	Scinax fuscovarius	1	1	1inf
	Scinax garbei	1	1	1
	Scinax nasicus	?	1	1inf
	Scinax nebulosus	?	1	1
	Scinax perpusillus	1	1	1
	Scinax rostratus	?	1	1
	Scinax ruber	?	1	1
	Scinax squalirostris	?	1	1
	Scinax staufferi	?	1	1inf
	Scinax uruguayus	1	1	1inf
	Smilisca baudinii	1	1	1inf
	Smilisca cyanosticta	?	1	1inf
	Smilisca fodiens	?	1	1
	Smilisca phaeota	1	1	1
	Smilisca puma	?	1	1inf
	Smilisca sila	?	1	1inf
	Smilisca sordida	?	1	1
	Sphaenorhynchus lacteus	1	1	1
	Tepuhyla talbergae	1	1	1inf
	Tepuihyla aecii	?	1	1inf
	Tepuihyla edelcae	?	1	1inf
	Tepuihyla exophthalma	1	1	1
Hylidae (cont.)	*Tepuihyla rodriguezi*	?	1	1inf
	Tlalocohyla godmani	?	1	1inf
	Tlalocohyla loquax	1	1	1
	Tlalocohyla picta	?	1	1inf
	Tlalocohyla smithtii	?	1	1inf

	Trachycephalus hadroceps	1	1	1inf
	Trachycephalus jordani	?	?	1
	Trachycephalus mesophaeus	1	1	1inf
	Trachycephalus nigromaculatus	?	?	1
	Trachycephalus resinifictrix	1	1	1inf
	Trachycephalus typhonius	1	1	1
	Triprion petasatus	?	1	1
	Xenohyla truncata	1	1	1
Hylodidae	*Crossodactylus schmidti*	1	1	1
	Hylodes ornatus	?	1	1inf
	Megaelosia goeldii	?	?	1
Hyperoliidae	*Acanthixalus spinosus*	0	1	1inf
	Afrixalus dorsalis	?	1	1inf
	Afrixalus fornasini	0	1	1
	Afrixalus laevis	?	?	1
	Alexteroon obstetricans	?	1	1inf
	Cryptothylax greshoffi	?	1	1
	Heterixalus alboguttatus	?	1	1inf
	Heterixalus betsileo	0	?	1
	Heterixalus boettgeri	0	1	1inf
	Heterixalus carbonei	?	1	1inf
	Heterixalus madagascariensis	0	1	1
	Heterixalus punctatus	?	1	1inf
	Heterixalus tricolor	?	1	1inf
	Hyperolius benguellensis	0	?	1
	Hyperolius castaneus	?	1	1
	Hyperolius chlorosteus	?	1	1inf
	Hyperolius concolor	?	1	1inf
	Hyperolius guttulatus	?	1	1inf
	Hyperolius nasutus	0	1	1
	Hyperolius ocellatus	?	1	1
	Hyperolius phantasticus	?	1	1
	Hyperolius puncticulatus	?	1	1inf
	Hyperolius pusillus	0	?	1
	Hyperolius tuberilinguis	0	1	1inf
	Hyperolius viridiflavus	1	1	1
	Kassina maculata	0	1	1inf

	Kassina senegalensis	0	1	1
	Morerella cyanophthalma	1	1	1
Hyperoliidae (cont.)	*Opisthotylax immaculatus*	0	?	1
	Phlyctimantis leonardi	?	1	1inf
	Phlyctimantis verrucosus	0	1	1
	Semnodactylus wealii	0	1	1inf
	Tachycnemis seychellensis	?	1	1inf
Leiopelmatidae	*Leiopelma archeyi*	0inf	0inf	0
	Leiopelma hochstetteri	0	0	0
Leptodactylidae	*Adenomera andreae*	1	1	1inf
	Adenomera heyeri	1	1	1
	Adenomera hylaedactyla	1	1	1
	Edalorhina perezi	1	1	1
	Engystomops coloradum	1	1inf	1inf
	Engystomops guayaco	1	1inf	1inf
	Engystomops montubio	1	1inf	1inf
	Engystomops petersi	1	1	1
	Engystomops pustulatus	1	1	1
	Engystomops pustulosus	1	?	1
	Engystomops randi	1	1inf	1inf
	Leptodactylus albilabris	1	1	1
	Leptodactylus bolivianus	1	1	1
	Leptodactylus bufonius	1	1	1
	Leptodactylus chaquensis	1	1	1
	Leptodactylus diedrus	1	1	1inf
	Leptodactylus discodactylus	1	1	1inf
	Leptodactylus didymus	1	1	1inf
	Leptodactylus elenae	1	1	1inf
	Leptodactylus fallax	1	1	1inf
	Leptodactylus fuscus	1	1	1
	Leptodactylus gracilis	1	1	1
	Leptodactylus griseigularis	1	1	1inf
	Leptodactylus knudseni	1	1	1inf
	Leptodactylus labyrinthicus	1	1	1inf
	Leptodactylus latrans	1	1	1
	Leptodactylus leptodactyloides	1	1	1inf

	Leptodactylus longirostris	1	1	1inf
	Leptodactylus melanonotus	1	1	1
	Leptodactylus myersi	1	1	1inf
	Leptodactylus mystaceus	1	1	1
	Leptodactylus mystacinus	1	1	1
	Leptodactylus notoaktites	1	1	1inf
	Leptodactylus pentadactylus	1	1	1
	Leptodactylus plaumanni	1	1	1inf
	Leptodactylus podicipinus	1	1	1
	Leptodactylus rhodonotus	1	1	1inf
	Leptodactylus rhodomystax	1	1	1inf
Leptodactylidae (cont.)	*Leptodactylus riveroi*	1	1	1inf
	Leptodactylus silvanimbus	1	1	1inf
	Leptodactylus spixi	1	1	1inf
	Leptodactylus stenodema	1	1	1inf
	Leptodactylus syphax	1	1	1
	Leptodactylus validus	1	1	1inf
	Leptodactylus vastus	1	1	1inf
	Leptodactylus wagneri	1	1	1
	Lithodytes lineatus	1	1	1
	Paratelmatobius cardosoi	?	?	1
	Paratelmatobius poecilogaster	?	?	1
	Physalaemus albonotatus	1	1	1
	Physalaemus biligonigerus	0	?	1
	Physalaemus centralis	1	1	1
	Physalaemus cuvieri	0&1	1	1
	Physalaemus gracilis	1	1	1
	Physalaemus nattereri	0	1	1
	Physalaemus signifer	?	?	1
	Pleurodema brachyops	1	1	1
	Pleurodema cinereum	1	1	1
	Pleurodema diplolister	?	1	1
	Pleurodema kriegi	?	1	1
	Pleurodema marmoratum	?	?	1

	Pleurodema tucumanum	?	1	1
	Pseudopaludicola falcipes	0	0	1
	Pseudopaludicola mystacalis	0	0	1
	Scythrophrys sawayae	0	?	1
Limnodynastidae	*Adelotus brevis*	0	?	1
	Heleioporus australiacus	1	1	1
	Lechriodus fletcheri	0	1	1
	Lechriodus melanopyga	1	1	1inf
	Limnodynastes depressus	0	1	1inf
	Limnodynastes dorsalis	0	?	1
	Limnodynastes dumerilii	0&1	1	1inf
	Limnodynastes fletcheri	0	?	1
	Limnodynastes lignarius	1	1	1inf
	Limnodynastes peronii	0	1	1
	Limnodynastes salmini	0	1	1
	Limnodynastes tasmaniensis	0	?	1
	Neobatrachus pelobatoides	?	1	?
	Neobatrachus pictus	0	?	1
	Neobatrachus sudelli	0	?	1
	Notaden bennettii	0	?	1
	Philoria sphagnicolus	0	?	1
	Platyplectrum ornatum	0	1	1
Mantellidae	*Aglyptodactylus madagascariensis*	1	1	1inf
	Blommersia blommersae	0	1	1inf
	Blommersia domerguei	0	1	1inf
	Blommersia grandisonae	0	1	1inf
	Blommersia madinika	0	1	1inf
	Blommersia sarotra	0	1	1inf
	Boehmantis microtympanum	0	1	1inf
	Boophis ankaratra	0	1	1inf
	Boophis axelmeyeri	0	1	1inf
	Boophis bottae	0	1	1inf
	Boophis englaenderi	0	1	1inf
	Boophis goudotii	1	1	1
	Boophis idae	0	1	1inf
	Boophis madagascariensis	?	1	1inf
	Boophis mandraka	0	1	1inf

	Boophis marojezensis	0	1	1inf
	Boophis pauliani	0	1	1inf
	Boophis phyrrus	0	1	1inf
	Boophis picturatus	0	1	1inf
	Boophis rufioculis	0	1	1inf
	Boophis sambirano	?	1	1inf
	Boophis sibilans	0	1	1inf
	Boophis tephraeomystax	1	1	1inf
	Boophis viridis	0	1	1inf
	Boophis vittatus	0	1	1inf
	Boophis williamsi	0	1	1inf
	Gephyromantis asper	1	1	1inf
	Gephyromantis azurrae	1	1	1inf
	Gephyromantis blanci	?	1	1inf
	Gephyromantis boulengeri	1	1	1inf
	Gephyromantis cornutus	1	1	1inf
	Gephyromantis corvus	1	1	1inf
	Gephyromantis eiselti	1	1	1inf
	Gephyromantis granulatus	?	1	1inf
	Gephyromantis horridus	0	1	1inf
	Gephyromantis klemmeri	1	1	1inf
	Gephyromantis luecocephalus	1	1	1inf
	Gephyromantis leucomaculatus	1	1	1inf
	Gephyromantis luteus	0	1	1inf
	Gephyromantis malagasius	0	1	1inf
	Gephyromantis plicifer	1	1	1inf
	Gephyromantis pseudoasper	1	1	1inf
	Gephyromantis redimitus	1	1	1inf
Mantellidae (cont.)	*Gephyromantis rivicola*	1	1	1inf
	Gephyromantis salegy	1	1	1inf
	Gephyromantis sculpturatus	1	1	1inf
	Gephyromantis striatus	0	1	1inf
	Gephyromantis ventrimaculatus	1	1	1inf
	Gephyromantis zavona	1	1	1inf
	Guibemantis albolineatus	0	1	1inf
	Guibemantis punctatus	0	1	1inf

	Guibemantis liber	0	1	1inf
	Guibemantis pulcher	?	1	1inf
	Guibemantis punctatus	0	1	1inf
	Guibemantis tornieri	1	1	1inf
	Laliostoma labrosum	1	1	1inf
	Mantella aurantiaca	0	1	1
	Mantella baroni	0	1	1inf
	Mantella bernhardi	0	1	1inf
	Mantella betsileo	?	1	1inf
	Mantella crocea	?	1	1inf
	Mantella ebenaui	?	1	1inf
	Mantella expectata	0	1	1inf
	Mantella laevigata	?	1	1inf
	Mantella madagascariensis	?	1	1inf
	Mantella nigricans	?	1	1inf
	Mantidactylus aerumnalis	1	1	1inf
	Mantidactylus ambreensis	1	1	1inf
	Mantidactylus argenteus	1	1	1inf
	Mantidactylus betsileanus	1	1	1inf
	Mantidactylus biporus	1	1	1inf
	Mantidactylus charlotteae	1	1	1inf
	Mantidactylus curtus	1	1	1inf
	Mantidactylus femoralis	0&1	1	1
	Mantidactylus lugubris	?	1	1inf
	Mantidactylus majori	1	1	1inf
	Mantidactylus mocquardi	1	1	1inf
	Mantidactylus opiparis	1	1	1inf
	Mantidactylus ulcerosus	1	1	1inf
	Spinomantis aglavei	?	1	1inf
	Spinomantis guibei	?	1	1inf
	Tsingymantis antitra	1	1	1inf
Megophryidae	*Brachytarsophrys feae*	0	?	?
	Leptobrachium banae	?	1	1inf
	Leptobrachium chapaense	1	1	1inf
	Leptobrachium echinatum	0	1	1inf
	Leptobrachium hasseltii	1	1	1
Megophryidae	*Leptobrachium*	1	1	1inf

(cont.)	*hendricksoni*			
	Leptobrachium mouhoti	?	1	1inf
	Leptobrachium montanum	1	1	1inf
	Leptobrachium nigrops	1	1	1inf
	Leptobrachium pullum	1	1	1inf
	Leptobrachium smithi	1	1	1inf
	Leptolalax arayai	1	1	1inf
	Leptolalax bourreti	0	1	1inf
	Leptolalax oshanensis	?	1	1inf
	Leptolalax pelodytoides	0	1	1inf
	Leptolalax pictus	1	1	1inf
	Leptolalax pluvialis	1	1	1inf
	Leptolalax ventripunctatus	1	1	1inf
	Megophrys baluensis	?	1	1inf
	Megophrys longipes	?	1	1inf
	Megophrys major	?	1	1inf
	Megophrys minor	?	1	1inf
	Megophrys nasuta	0	1	1
	Megophrys parva	?	1	1inf
	Megophrys shapingensis	?	1	1inf
	Megophrys spinata	?	1	1inf
	Ophryophryne han si	?	1	1inf
	Ophryophryne microstoma	?	1	1inf
	Oreolalax chuanbeiensis	0	1	1
	Oreolalax jiandongensis	0	?	?
	Oreolalax liangbeiensis	0	1	1
	Oreolalax lichuanensis	0	1	1
	Oreolalax major	0	1	1
	Oreolalax multipunctatus	0	1	1
	Oreolalax nanjiangensis	0	1	1
	Oreolalax omeimontis	0	1	1
	Oreolalax pingii	0	1	1
	Oreolalax popei	0	1	1
	Oreolalax rhodostigmatus	1	1	1
	Oreolalax rugosus	0	0	0
	Oreolalax schmidti	0	1	1
	Oreolalax xiangchengensis	0	?	?
	Scutiger boulengeri	?	?	1

	Scutiger chintingensis	0inf	0inf	0
	Scutiger mammatus	0	1	1
	Scutiger muliensis	0inf	0inf	0
	Scutiger tuberculatus	0inf	0inf	0
Micrixalidae	*Micrixalus fuscus*	?	1	1
	Micrixalus kottigeharensis	?	1	1inf
	Micrixalus saxicola	?	1	1
Microhylidae	*Anodonthyla boulengerii*	0	1	1
	Anodonthyla montana	1	1	1
	Anodonthyla moramora	0	1	1inf
	Anodonthyla rouxae	0	1	1inf
	Apantophryne pansa	?	1	1
	Asterophrys turpicola	1	1	1inf
	Austrochaperina palmipes	0	1	1
	Barygenys flavigularis	0	1	1inf
	Calluela guttulata	0	1	1
	Calluela minuta	?	1	1
	Calluela yunnanensis	0	1	1
	Callulops robustus	0	1	1
	Chaperina fusca	0	1	1
	Chiasmocleis albopunctata	?	1	1
	Chiasmocleis hudsoni	0	1	1inf
	Choerophryne rostellifer	?	1	1
	Cophixalus ornatus	?	?	1
	Cophyla berara	?	1	1
	Cophyla phyllodactyla	0	1	1
	Copiula derongo	0	1	1inf
	Copiula guttata	?	?	1
	Ctenophryne aequatorialis	?	?	1
	Ctenophryne geayi	0	1	1
	Dasypops schirchi	0	1	1
	Dermatonotus muelleri	0	?	1
	Dyscophus antongilii	0	1	1
	Dyscophus guineti	0	1	1
	Dyscophus insularis	0	1	1
	Elachistocleis bicolor	0	1	1
	Gastrophryne carolinensis	0	1	1
	Gastrophryne elegans	?	1	1

	Genyophryne thomsoni	?	1	1
	Glyphoglossus molossus	1	1	1
	Hamptophryne boliviana	0	1	1
	Hoplophryne rogersi	0	0	0
	Hoplophryne uluguruensis	0	0	0
	Hylophorbus picoides	0	1	1inf
	Hylophorbus rufescens	0	1	1
	Hypopachus variolosus	0	1	1
	Kalophrynus baluensis	?	1	1
	Kalophrynus interlineatus	?	1	1
	Kalophrynus intermedius	?	1	1inf
	Kalophrynus pleurostigma	0	1	1
	Kaloula borealis	?	1	1
	Kaloula conjuncta	?	1	1
Microhylidae (cont.)	*Kaloula mediolineata*	?	1	1
	Kaloula picta	?	1	1
	Kaloula pulchra	1	1	1
	Liophryne rhododactyla	?	1	1
	Liophryne schlaginhaufeni	?	1	1
	Mantophryne lateralis	0	1	1inf
	Melanobatrachus indicus	0	0	0
	Metamagnusia slateri	?	1	1inf
	Metaphrynella pollicaris	?	1	1
	Metaphrynella sundana	?	1	1
	Microhyla achatina	?	1	1
	Microhyla annectens	0	1	1
	Microhyla berdmorei	0	1	1
	Microhyla borneensis	0	1	1
	Microhyla butleri	0	0&1	0&1
	Microhyla heymonsi	0inf	0&1	0&1
	Microhyla okinavensis	0	1	1
	Microhyla ornata	?	1	1
	Microhyla palmipes	0	1	1
	Microhyla pulchra	0	1	1
	Microhyla superciliaris	0	1	1
	Micryletta inornata	?	1	1
	Oreophryne monticola	?	1	1
	Oreophryne sibilans	0	1	1inf

	Oreophryne unicolor	0	1	1inf
	Otophryne pyburni	1	1	1inf
	Oxydactyla crassa	?	?	1
	Paradoxophyla palmata	0	1	1inf
	Phrynella pulchra	?	1	1
	Phrynomantis bifasciatus	0	1	1
	Phrynomantis microps	0	1	1
	Platypelis grandis	?	1	1
	Platypelis milloti	0	1	1inf
	Platypelis pollicaris	0	1	1
	Platypelis tuberifera	?	1	1
	Plethodonthyla bipunctata	?	1	1inf
	Plethodonthyla guentheri	?	1	1inf
	Plethodonthyla inguinalis	0	1	1
	Plethodonthyla mihanika	0	1	1inf
	Plethodonthyla notosticta	0	1	1
	Plethodonthyla ocellata	0	1	1
	Plethodonthyla tuberata	?	1	1
	Pseudocallulops eurydactylus	1	1	1inf
	Ramanella montana	?	1	1
	Ramanella obscura	?	1	1
Microhylidae (cont.)	*Ramanella variegata*	?	1	1
	Rhombophryne alluaudi	0	1	1inf
	Rhombophryne coronata	0	1	1inf
	Rhombophryne coudreaui	0	1	1inf
	Rhombophryne grandis	?	1	1inf
	Rhombophryne helenae	?	1	1inf
	Rhombophryne psologlossa	?	1	1
	Rhombophryne serratopalpebrosa	0	1	1
	Rhombophryne testudo	0	1	1
	Rhombophryne tetradactyla	1	1	1inf
	Rhombophryne tridactyla	0	1	1inf
	Scaphiophryne calcarata	0	1	1
	Scaphiophryne marmorata	0	1	1
	Scaphiophryne menabensis	0	1	1inf
	Sphenophryne cornuta	?	1	1

	Synapturanus mirandaribeiroi	0	1	1
	Uperodon systoma	0	?	1
	Xenorhina bouwensi	?	1	1
	Xenorhina obesa	0	1	1inf
	Xenorhina oxycephala	?	1	1inf
Myobatrachidae	*Assa darlingtoni*	0	1	1
	Crinia deserticola	?	?	1
	Crinia parinsignifera	?	?	1
	Crinia riparia	?	?	0
	Crinia signifera	0	?	1
	Crinia tinnula	?	?	1
	Geocrinia victoriana	0	1	1
	Metacrinia nichollsi	?	?	1
	Mixophyes carbinensis	1	1	1inf
	Mixophyes coggeri	1	1	1inf
	Mixophyes fasciolatus	1	1	1
	Mixophyes schevilli	1	1	1
	Myobatrachus gouldii	?	?	1
	Pseudophryne bibronii	0	0	0
	Pseudophryne coriacea	0	0	0
	Rheobatrachus silus	0	?	1
	Spicospina flammocaerulea	1	1	1
	Taudactylus acutirostris	0	?	1
	Uperoleia aspera	0	?	1
	Uperoleia borealis	?	?	1
	Uperoleia crassa	?	?	1
	Uperoleia fusca	?	?	1
	Uperoleia glandulosa	?	?	1
	Uperoleia inundata	?	?	1
Myobatrachidae (cont.)	*Uperoleia laevigata*	0	?	1
	Uperoleia lithomoda	?	?	1
	Uperoleia littlejohni	?	?	1
	Uperoleia micromeles	?	?	1
	Uperoleia minima	?	?	1
	Uperoleia mjobergii	?	?	1
	Uperoleia rugosa	0	?	1
	Uperoleia russelli	0	?	1
	Uperoleia talpa	?	?	1
	Uperoleia trachyderma	?	?	1
	Uperoleia tyleri	?	?	1

Nasikabatrachidae	*Nasikabatrachus sahyadrensis*	0	?	0†
Nyctibatrachidae	*Nyctibatrachus beddomii*	?	1	1inf
	Nyctibatrachus deccanensis	0	?	?
	Nyctibatrachus kempholeyensis	?	1	1inf
	Nyctibatrachus major	0	?	?
	Nyctibatrachus minimus	?	1	1inf
	Nyctibatrachus minor	?	1	1inf
	Nyctibatrachus sylvaticus	?	1	1
Odontophrynidae	*Macrogenioglottus alipioi*	0	1	1
	Odontophrynus achalensis	0	1	1
	Odontophrynus americanus	0	1	1
	Odontophrynus carvalhoi	0	1	1
	Odontophrynus cultripes	0	1	1
	Proceratophrys appendiculata	0	1	1
	Proceratophrys avelinoi	0	1	1
	Proceratophrys boiei	0	1	1
	Proceratophrys concavitympanum	?	1	1inf
	Proceratophrys cristiceps	0	1	1
	Proceratophrys laticeps	?	?	1
	Proceratophrys melanopogon	?	?	1
Pelodytidae	*Pelobates cultripes*	?	?	1
	Pelobates fuscus	0	?	1
	Pelobates syriacus	?	?	1
	Pelobates varaldii	?	?	1
	Pelodytes caucasicus	?	?	1
	Pelodytes ibericus	?	?	1
	Pelodytes punctatus	?	?	1
Petropedetidae	*Arthroleptides martiensseni*	1	1	1
	Arthroleptides yakusini	1	1	1inf
	Aubria subsigillata	1	1	1
	Petropedetes cameronensis	1	1	1
	Petropedetes newtoni	1	1	1
	Petropedetes parkeri	1	1	1
Phrynobatrachidae	*Phrynobatrachus acridoides*	1	1	1

	Phrynobatrachus africanus	0	1	1
	Phrynobatrachus calcaratus	0	?	?
	Phrynobatrachus cricogaster	0	1	1
	Phrynobatrachus dispar	?	1	1inf
	Phrynobatrachus krefftii	0	1	1
	Phrynobatrachus natalensis	0	1	1
	Phrynobatrachus sandersoni	0	1	1
Pipidae	*Hymenochyrus boettgeri*	?	1	1
	Pipa carvalhoi	?	?	1
	Pipa parva	?	1	1
	Pipa pipa	0	1	1
	Xenopus borealis	0	1	1
	Xenopus epitropicalis	?	1	1
	Xenopus fraseri	?	1	1
	Xenopus laevis	0	1	1
	Xenopus muelleri	?	1	1
	Xenopus tropicalis	1	1	1
Ptychadenidae	*Hildebrandtia ornata*	1	1	1
	Ptychadena aequiplicata	?	1	1inf
	Ptychadena anchietae	1	1	1
	Ptychadena mascareniensis	1	1	1
	Ptychadena oxyrhynchus	1	1	1inf
	Ptychadena porosissima	1	1	1inf
	Ptychadena taenioscelis	1	1	1inf
Pyxicephalidae	*Amietia angolensis*	1	1	1
	Amietia fuscigula	1	1	1
	Anhydrophryne rattrayi	1	1	1
	Arthroleptella landdrosia	0	1	1
	Cacosternum boettgeri	0	1	1
	Cacosternum capense	0	1	1
	Cacosternum nanum	0	1	1
	Microbatrachella capensis	0	1	1
	Natalobatrachus bonebergi	1	1	1
	Poyntonia paludicola	0	1	1
	Pyxicephalus adspersus	1	1	1
	Pyxicephalus edulis	1	1	1

	Strongylopus fasciatus	1	1	1inf
	Strongylopus grayii	1	1	1
	Tomopterna delalandii	0	1	1inf
	Tomopterna marmorata	0	1	1
	Tomopterna natalensis	0	1	1inf
	Tomopterna tandyi	0	1	1
	Tomopterna tuberculosa	1	1	1inf
Ranidae	*Abavorana luctuosa*	1	1	1inf
	Amnirana albolabris	1	1	1
	Amnirana galamensis	1	1	1
	Amolops chunganensis	?	1	1inf
	Amolops daorum	1	1	1inf
	Amolops granulosus	?	1	1inf
	Amolops hainanensis	?	1	1inf
	Amolops hongkongensis	?	1	1inf
	Amolops jinjiangensis	?	1	1inf
	Amolops larutensis	?	1	1inf
	Amolops loloensis	?	1	1inf
	Amolops mantzorum	?	1	1inf
	Amolops ricketti	0	1	1
	Amolops spinapectoralis	1	1	1inf
	Amolops viridimaculatus	0	1	1inf
	Babina adenopleura	?	1	1inf
	Babina okinavana	?	1	1inf
	Babina pleuraden	?	1	1inf
	Chalcorana chalconota	1	1	1inf
	Chalcorana eschatia	?	1	1inf
	Chalcorana megalonesa	?	1	1inf
	Chalcorana parvaccola	?	1	1inf
	Chalcorana raniceps	?	1	1inf
	Clinotarsus alticola	?	1	1inf
	Clinotarsus curtipes	?	1	1inf
	Glandirana rugosa	?	1	1inf
	Glandirana tientaiensis	1	1	1inf
	Huia cavitympanum	1	1	1inf
	Huia masonii	?	1	1inf
	Hydrophylax gracilis	1	1	1
	Hydrophylax malabaricus	1	1	1inf
	Hylarana erythrea	1	1	1inf
	Hylarana macrodactyla	?	1	1inf
	Hylarana taipehensis	1	1	1

	Indosylvirana aurantiaca	1	1	1inf
	Indosylvirana milleti	?	1	1inf
	Lithobates areolatus	1	1	1inf
	Lithobates berlandieri	?	1	1inf
	Lithobates blairi	1	1	1inf
	Lithobates bwana	1	1	1inf
	Lithobates capito	?	1	1inf
	Lithobates catesbeianus	1	1	1
	Lithobates chiricahuensis	1	1	1inf
	Lithobates clamitans	1	1	1
	Lithobates fisheri	?	1	1inf
Ranidae (cont.)	*Lithobates forreri*	1	1	1inf
	Lithobates grylio	1	1	1inf
	Lithobates heckscheri	1	1	1inf
	Lithobates juliani	1	1	1inf
	Lithobates macroglossa	?	1	1inf
	Lithobates maculatus	?	1	1inf
	Lithobates montezumae	?	1	1inf
	Lithobates okaloosae	1	1	1inf
	Lithobates onca	1	1	1inf
	Lithobates palmipes	1	1	1inf
	Lithobates palustris	1	1	1inf
	Lithobates pipiens	1	1	1
	Lithobates septentrionalis	1	1	1inf
	Lithobates sevosus	1	1	1inf
	Lithobates sierramadrensis	?	1	1inf
	Lithobates sphenocephalus	1	1	1inf
	Lithobates sylvaticus	?	1	1inf
	Lithobates tarahumarae	?	1	1inf
	Lithobates taylori	1	1	1inf
	Lithobates vaillanti	1	1	1inf
	Lithobates vibicarius	1	1	1inf
	Lithobates virgatipes	1	1	1
	Lithobates warszewitschii	1	1	1
	Lithobates yavapaiensis	1	1	1inf
	Meristogenys jerboa	?	1	1inf
	Meristogenys kinabaluensis	1	1	1inf
	Meristogenys	1	1	1inf

	phaeomerus			
	Meristogenys poecilus	?	1	1inf
	Meristogenys whiteheadi	?	1	1inf
	Odorrana andersonii	?	1	1inf
	Odorrana bacboensis	1	1	1inf
	Odorrana chloronota	1	1	1
	Odorrana grahami	?	1	1inf
	Odorrana hosii	?	1	1inf
	Odorrana ishikawae	?	1	1inf
	Odorrana jingdongensis	?	1	1inf
	Odorrana junlianensis	?	1	1inf
	Odorrona khalam	1	1	1inf
	Odorrona livida	1	1	1inf
	Odorrona margaretae	1	1	1inf
	Odorrana morafkai	?	1	1inf
	Odorrana narina	?	1	1inf
	Odorrana tiannanensis	1	1	1inf
	Odorrana tormota	1	1	1
	Odorrana schmackeri	1	1	1inf
Ranidae (cont.)	*Odorrana swinhoana*	1	1	1inf
	Papurana arfaki	?	1	1inf
	Papurana daemeli	1	1	1inf
	Pelophylax cerigensis	1	1	1inf
	Pelophylax cretensis	1	1	1inf
	Pelophylax epeiroticus	?	1	1inf
	Pelophylax esculentus	1	1	1
	Pelophylax fukienensis	1	1	1inf
	Pelophylax nigromaculatus	1	1	1inf
	Pelophylax plancyi	1	1	1
	Pelophylax ridibundus	1	1	1
	Pelophylax saharicus	1	1	1inf
	Pulchrana baramica	?	1	1inf
	Pulchrana glandulosa	?	1	1inf
	Pulchrana signata	?	1	1inf
	Rana arvalis	1	1	1inf
	Rana aurora	1	1	1inf
	Rana boylii	?	1	1inf
	Rana cascadae	1	1	1inf
	Rana chaochiaoensis	?	1	1inf
	Rana chensinensis	?	1	1inf
	Rana dalmatina	?	1	1inf

	Rana hanluica	?	1	1inf
	Rana iberica	?	1	1inf
	Rana japonica	?	1	1inf
	Rana johnsi	?	1	1inf
	Rana latastei	?	1	1inf
	Rana longicrus	1	1	1inf
	Rana luteiventris	1	1	1inf
	Rana macrocnemis	?	1	1inf
	Rana muscosa	?	1	1inf
	Rana pirica	1	1	1inf
	Rana pretiosa	?	1	1inf
	Rana sauteri	1	1	1inf
	Rana shuchinae	?	1	1inf
	Rana tagoi	?	1	1inf
	Rana temporaria	?	1	1inf
	Sanguina sanguinea	1	1	1inf
	Staurois latopalmatus	?	1	1inf
	Staurois natator	1	1	1
	Staurois tuberilinguis	?	1	1inf
	Sylvirana guentheri	1	1	1inf
	Sylvirana maosonensis	?	1	1inf
	Sylvirana nigrovittata	?	1	1inf
Ranixalidae	*Indirana beddomi*	?	1	1inf
	Indirana brachytarsus	?	1	1inf
	Indirana diplosticta	?	1	1inf
	Indirana semipalmata	?	1	1
Rhacophoridae	*Buergeria buergeri*	?	1	1inf
	Buergeria japonica	1	1	1inf
	Buergeria robusta	1	1	1inf
	Chiromantis doriae	?	1	1inf
	Chiromantis petersii	?	1	1
	Chiromantis rufescens	?	1	1
	Chiromantis vittatus	?	1	
	Chiromantis xerampelina	0	1	1
	Feihyla kajau	?	1	1inf
	Feihyla palpebralis	?	1	1inf
	Ghatixalus variabilis	?	1	1
	Gracixalus gracilipes	?	1	1inf
	Gracixalus supercornutus	?	1	1inf
	Kurixalus appendiculatus	?	1	1inf
	Kurixalus banaensis	?	1	1inf

	Kurixalus eiffingeri	1	1	1inf
	Kurixalus idiooticus	1	1	1inf
	Kurixalus odontotarsus	?	1	1inf
	Liuixalus romeri	1	1	1inf
	Nyctixalus pictus	1	1	1inf
	Philautus acutirostris	0	?	?
	Philautus acutus	0	?	?
	Philautus aurantius	?	1	1inf
	Philautus aurifasciatus	?	1	1inf
	Philautus bunitus	1	1	1inf
	Philautus hosii	?	1	1inf
	Philautus petersi	0	1	1inf
	Philautus surdus	0	1	1
	Philautus umbra	?	1	1inf
	Polypedates colletti	?	1	1inf
	Polypedates leucomystax	?	1	1
	Polypedates macrotis	?	1	1inf
	Polypedates maculatus	1	1	1
	Polypedates otilophus	?	1	1
	Pseudophilautus alto	?	1	1inf
	Pseudophilautus amboli	1	1	1inf
	Pseudophilautus cavirostris	?	1	1inf
	Pseudophilautus decoris	1	1	1inf
	Psudophilautus femoralis	?	1	1inf
	Pseudophilautus folicola	?	1	1inf
	Pseudophilautus hoffmanni	1	1	1inf
Rhacophoridae (cont.)	*Pseudophilautus jayarami*	0	1	1inf
	Pseudophilautus kani	1	1	1inf
	Pseudophilautus leucorhinus	?	1	1inf
	Pseudophilautus lunatus	?	1	1inf
	Pseudophilautus microtympanum	?	1	1inf
	Pseudophilautus mooreorum	0	?	?
	Pseudophilautus ocularis	?	1	1inf
	Pseudophilautus papillosus	?	1	1inf
	Pseudophilautus pleurotaenia	?	1	1inf
	Pseudophilautus	?	1	1inf

	popularis			
	Pseudophilautus reticulatus	?	1	1inf
	Pseudophilautus sarasinorum	?	1	1inf
	Pseudophilautus schmarda	?	1	1inf
	Pseudophilautus tanu	1	1	1inf
	Pseudophilautus zorro	?	1	1inf
	Raorchestes anili	?	1	1inf
	Raorchestes beddomii	?	1	1inf
	Raorchestes charius	?	1	1inf
	Raorchestes chlorosoma	?	1	1inf
	Raorchestes chotta	0	?	?
	Raorchestes chromasynchysi	?	1	1inf
	Raorchestes coonoorensis	?	1	1inf
	Raorchestes dubois	?	1	1inf
	Raorchestes glandulosus	0	1	1
	Raorchestes graminirupes	?	1	1inf
	Raorchestes griet	?	1	1inf
	Raorchestes luteolus	?	1	1inf
	Raorchestes marki	?	1	1inf
	Raorchestes munnarensis	?	1	1inf
	Raorchestes nerostagona	?	1	1inf
	Raorchestes ponmudi	?	1	1inf
	Raorchestes sushili	?	1	1inf
	Raorchestes tinniens	?	1	1inf
	Raorchestes tuberohumerus	?	1	1inf
	Rhacophorus annamensis	?	1	1inf
	Rhacophorus angulirostris	1	1	1inf
	Rhacophorus calcaneus	?	1	1inf
	Rhacophorus chenfui	0	1	1inf
	Rhacophorus dennysi	?	1	1
	Rhacophorus dugritei	0	1	1inf
	Rhacophorus dulitensis	?	1	1inf
	Rhacophorus fasciatus	?	1	1inf
	Rhacophorus gauni	?	1	1inf
	Rhacophorus harrisoni	1	1	1inf
Rhacophoridae	*Rhacophorus maximus*	?	1	1inf

(cont.)	*Rhacophorus minimus*	1	1	1inf
	Rhacophorus nigropalmatus	1	1	1
	Rhacophorus omeimontis	1	1	1inf
	Rhacophorus orlovi	1	1	1inf
	Rhacophorus pardalis	1	1	1inf
	Rhacophorus reindwartii	1	1	1inf
	Rhacophorus rhodopus	0	1	1inf
	Rhacophorus rufipes	1	1	1inf
	Rhacophorus schlegelii	?	1	1
	Taruga eques	?	1	1
	Taruga fastigo	?	1	1inf
	Taruga longinasus	?	1	1inf
	Theloderma asperum	1	1	1inf
	Theloderma corticale	?	1	1inf
	Theloderma moloch	?	1	1inf
	Theloderma stellatum	?	1	1inf
Rhinodermatidae	*Insuetophrynus acarpicus*	1	1	1
	Rhinoderma darwinii	1	1	1
Rhinophrynidae	*Rhinophrynus dorsalis*	0	0	0
Scaphiopodidae	*Scaphiopus couchii*	0	1	1
	Scaphiopus holbrookii	1	1	1
	Scaphiopus hurteri	1	1	1
	Spea bombifrons	0	1	1
	Spea hammondi	0	1	1
	Spea intermontana	?	1	1
	Spea multiplicata	?	?	1
Sooglossidae	*Sechellophryne gardineri*	0	0	0
	Sooglosus sechellensis	0	0	0
	Sooglosus thomasseti	0	0	0
Telmatobiidae	*Telmatobius bolivianus*	0	0	1
	Telmatobius culeus	0	0&1	1
	Telmatobius gigas	0	?	?
	Telmatobius hintoni	0	0&1	1
	Telmatobius huayra	0	0	0
	Telmatobius marmoratus	0	0	0&1*
	Telmatobius niger	0	0&1	0&1
	Telmatobius sibiricus	0	1	1
	Telmatobius simonsi	0	1	1
	Telmatobius truebae	0	1	1
	Telmatobius vellardi	0	0	1
	Telmatobius verrucosus	0	1	1

	Telmatobius vilamensis	0	0	0
	Telmatobius yuracare	0	0	1*
	Telmatobius zapahuirensis	0	1	1inf
Anura not included in Pyron (2014)				
Family	**Species**	**Tympanic membrane**	**Tympanic annulus**	**Columella**
Alsodidae	*Eupsophus altor*	?	?	1
Arthroleptidae	*Letodactylodon ventrimarmoratus*	0	1	1
	Leptopelis mossambicus	1	1	1
	Cardioglossa escalaerae	1	1	1
Batrachylidae	*Atelognathus nitoi*	0inf	0inf	0
	Atelognathus praebasalticus	0inf	0inf	0
	Atelognathus reverberii	inf 0	inf 0	0
	Atelognathus solitarius	0inf	0inf	0
	Chaltenobatrachus grandisonae	0	0	0
Brachycephalidae	*Ischnocnema nigriventris*	?	?	1
Callyptocephalellidae	*Telmatobufo australis*	0	0	0
Ceratobatrachidae	*Alcalus mariae*	?	1	1
	Cornufer bufoniformis	0	1	1
Ceratophryidae	*Ceratophrys aurita*	1	1	1
	Ceratophrys calcarata	1	1	1
	Ceratophrys cranwelli	1	1	1
Craugastoridae	*Bryophryne abramalagae*	0	0	?
	Bryophryne bakersfield	0	0	?
	Bryophryne bustamantei	0	0	?
	Bryophryne flammiventris	1	1	1inf
	Bryophryne gymnotis	1	1	1inf
	Bryophryne hanssaueri	0	0	?
	Bryophryne nubilosus	0	0	?
	Bryophryne zonalis	0	0	?
	Euparkerella cochranae	0inf	0inf	0
	Euparkerella cryptica	0inf	0inf	0
	Euparkerella robusta	0inf	0inf	0
	Euparkerella tridactyla	0inf	0inf	0
	Hypodactylus nigrovittatus	?	?	1
Cycloramphidae	*Cycloramphus asper*	0	1	1

	Cycloramphus dubius	?	?	1
	Cycloramphus granulosus	?	1	1
	Cycloramphus ohausi	0	1	1
	Cycloramphus stejnegeri	0	1	1
	Thoropa lutzi	?	?	1
	Thoropa petropolitana	?	?	1
Eleutherodactylidae	*Eleutherodactylus albolabris*	?	?	1
	Eleutherodactylus grandis	?	?	1
	Eleutherodactylus guttilatus	?	?	1
	Eleutherodactylus karlschmidti	?	?	1
	Eleutherodactylus leprus	?	?	1
Eleutherodactylidae (cont.)	*Eleutherodactylus pallidus*	?	?	1
	Eleutherodactylus rubrimaculatus	?	?	1
	Phrynopus montium	0inf	0inf	0
	Pristimantis festae	?	?	1
	Pristimantis ornatissimus	?	?	1
	Pristimantis variabilis	?	?	1
Hemiphractidae	*Cryptobatrachus conditus*	?	?	1
	Cryptobatrachus fuhrmanni	?	1	1
	Fritziana fissilis	?	1	1
	Fritziana goeldii	?	1	1
	Fritziana ohausi	?	1	1
	Fritziana ulei	?	1	1
Hylidae	*Duellmanohyla uranochroa*	?	1	1
	Hyla hallowellii	?	1	1
	Hyloscirtus bogotensis	1	1	1inf
Hylodidae	*Crossodactylus dispar*	1	1	1
	Crossodactylus grandis	?	1	1
	Crossodactylus gaudichaudii	?	1	1
	Hylodes asper	?	?	1
	Hylodes dactylocinus	1	1	1inf
	Hylodes glaber	?	?	1
	Hylodes lateristrigatus	?	?	1
	Hylodes magalhaesi	?	1	1
	Hylodes nasus	?	1	1

	Hylodes perplicatus	?	1	1inf
	Hylodes phyllodes	1	1	1inf
Hyperoliidae	*Callixalus pictus*	?	1	1
	Hyperolius horstockii	0	?	?
	Kassinula wittei	?	1	1
Leptodactylidae	*Crossodactylodes bokermanni*	0	0inf	0
	Crossodactylodes izecksohni	0	0inf	0
	Crossodactylodes pintoi	0	0inf	0
	Crossodactylodes septentrionalis	0	inf	0
	Hydrolaetare schmidti	1	1	1
	Leptodactylus latinasus	1	1	1
	Leptodactylus macrosternum	?	?	1
	Leptodactylus poecilochilus	?	1	1
	Leptodactylus pustulatus	?	?	1
	Paratelmatobius lutzii	0	0inf	0
	Paratelmatobius mantiqueira	?	1	1inf
	Paratelmatobius yepiranga	1	1	1inf
	Physalaemus ephippifer	1	1	1
	Physalaemus maculiventris	?	?	1
0				
Leptodactylidae (cont.)	*Physalaemus nanus*	?	?	1
	Pseudopaludicola boliviana	0	0	1
	Pseudopaludicola saltica	0	0	1
	Pseudopaludicola pusilla	?	?	1
	Rupirana cardosoi	?	?	1
Limnodynastidae	*Heleioporus albopunctatus*	?	?	1
	Heleioporus eyrei	?	?	1
	Notaden nichollsi	0	1	1
	Philoria frosti	?	?	1
Mantellidae	*Boophis rhodoscelis*	?	?	1
	Tsingymantis antitra	1	1	1inf
Megophryidae	*Leptobrachella mjobergi*	1	1	1inf
Microhylidae	*Adelastes hylonomus*	?	1	1
	Arcovomer passarelii	0	0	0

	Callulops glandulosus	1	1	1inf
	Chiasmocleis avilapiresae	0	1	1
	Chiasmocleis capixaba	0	1	1
	Chiasmocleis carvalhoi	0	1	1
	Chiasmocleis leucosticta	0	1	1
	Chiasmocleis schubarti	0	1	1
	Cophixalus saxatilis	?	?	1
	Ctenophryne aterrima	0	1	1
	Myersiella microps	0	1	1
	Otophryne pyburni	?	?	1
	Otophryne steyermarki	1	1	1inf
	Oxydactyla coggeri	?	?	1
	Stereocyclops histrio	0	1	1
	Stereocyclops incrassatus	0	1	1
	Stereocyclops parkeri	0	1	1
	Uperodon mormorata	?	1	1
Myobatrachidae	*Arenophryne rotunda*	0inf	0inf	0
	Crinia bilingua	?	?	1
	Crinia georgiana	?	1	1
	Crinia glauerti	?	?	1
	Crinia insignifera	?	?	1
	Crinia tasmaniensis	?	?	1
	Crinia subinsignifera	?	?	1
	Pseudophryne australis	0inf	0inf	0
	Pseudophryne corroboree	0inf	0inf	0
	Pseudophryne dendyi	0inf	0inf	0
	Pseudophryne douglasi	0inf	0inf	0
	Pseudophryne guentheri	0inf	0inf	0
	Pseudophryne major	0inf	0inf	0
	Pseudophryne occidentalis	0inf	0inf	0
	Pseudophryne semimarmorata	0	0	0
	Taudactylus diurnus	0	1	1
Odontobatrachidae	*Odontobatrachus natator*	0	1	1
Phrynobatrachidae	*Phrynobatrachus plicatus*	1	1	1
Pyxicephalidae	*Anhydrophryne hewitti*	1	1	1
	Arthroleptella lightfooti	1	1	1
	Ericabatrachus baleensis	?	1	1
	Nothophryne broadleyi	0	1	1
Ranidae	*Hydrophylax gracilis*	1	1	1inf
	Indosylvirana temporalis	1	1	1inf

	Indosylvirana flavescens	?	1	1
Ranixalidae	*Indirana temporalis*	?	1	1inf
Rhacophoridae	*Pseudophilautus silus*	1	1inf	1
	Theloderma pictum	?	?	1
Telmatobiidae	*Telmatobius brachydactylus*	?	?	1
	Telmatobius laticeps	?	?	1
	Telmatobius macrostomus	?	?	1
Incertae sedis (Brachycephaloidea)	*Atopophrynus syntomopus*	0inf	0inf	0
	Geobatrachus walkeri	0	1	1

Table 2.1.2—Sources for each character scored by species. Abbreviations: BLB, Boris L. Blotto; DB, Diego Baldo; JJOS, Jhon Jairo OspinSarria; JF, Julián Faivovich; KAV, Katyuscia Araujo-Vieira; MOP, Martín O. Pereyra; MT, Mariane Targino; MCW, Molly C. Womack; JSB, J. Sebastián Barrionuevo; TG, Taran Grant.

Bufonidae included in Pyron (2014)			
Species	**Tympanic membrane**	**Tympanic annulus**	**Columella**
Adenomus kelaartii	Günther, 1858; Boulenger, 1882, 1890; Manamendra-Arachchi & Pethiyagoda, 1998	Günther, 1858; Boulenger, 1882, 1890; Manamendra-Arachchi & Pethiyagoda, 1998; Meegaskumbura *et al.*, 2015	Meegaskumbura *et al.*, 2015
Amazophrynella minuta	MOP pers. obs.; Melin, 1941; McDiarmid, 1971	McDiarmid, 1971	McDiarmid, 1971
Anaxyrus americanus	Cope, 1889; Wright & Wright, 1949	Wright & Wright, 1949; Pramuk, 2006	Mendelson, 1997c, Pramuk, 2006
Anaxyrus baxteri	Smith *et al.*, 1998	Smith *et al.*, 1998	----
Anaxyrus boreas	Boulenger, 1882; Cope, 1889; Wright & Wright, 1949	Wright & Wright, 1949; Pramuk, 2006	Gaudin, 1978; Pramuk, 2006; Mendelson *et al.*, 2011
Anaxyrus californicus	Wright & Wright, 1949	Camp, 1915; Wright & Wright, 1949	----
Anaxyrus canorus	Wright & Wright, 1949	Camp, 1916; Wright & Wright, 1949	MCW pers. obs.
Anaxyrus cognatus	Cope, 1889; Wright & Wright, 1949	Wright & Wright, 1949; Pramuk, 2006	MCW pers. obs.
Anaxyrus debilis	Girard, 1854; Boulenger, 1882; Cope, 1889; Wright & Wright, 1949	Wright & Wright, 1949; Pramuk, 2006	Baldauf, 1959

Anaxyrus exsul	Wright & Wright, 1949	Wright & Wright, 1949	----
Anaxyrus fowleri	Cope, 1889; Wright & Wright, 1949	Wright & Wright, 1949; Pramuk, 2006	----
Anaxyrus hemiophrys	Cope, 1889	Cope, 1887; Wright & Wright, 1949	----
Anaxyrus houstonensis	Sanders, 1953	Sanders, 1953	MCW pers. obs.; Sanders, 1953
Anaxyrus microscaphus	Cope, 1867	Cope, 1867	MCW pers. obs.; Baldauf, 1959
Anaxyrus nelsoni	Wright & Wright, 1949	Wright & Wright, 1949	----
Anaxyrus punctatus	Cope, 1889; Wright & Wright, 1949	Cope, 1889; Wright & Wright, 1949	Baldauf, 1959; Pramuk, 2006
Anaxyrus quercicus	Cope, 1889; Wright & Wright, 1949	Pramuk, 2006	Baldauf, 1959; Pramuk, 2006
Anaxyrus retiformis	----	Barrera & Rodríguez, 2004	----
Anaxyrus speciosus	Girard, 1854	Girard, 1854	----
Anaxyrus terrestris	Cope, 1889; Wright & Wright, 1949	Pramuk, 2006	Baldauf, 1959; Pramuk, 2006
Anaxyrus woodhousii	Cope, 1867; Girard, 1854; Wright & Wright, 1949; Baldauf, 1955	Baldauf, 1955; Wright & Wright, 1949; Pramuk, 2006	Baldauf, 1955; Pramuk, 2006
Ansonia albomaculata	Inger, 1960, 1966	Inger, 1960	----
Ansonia endauensis	Grismer, 2006	Grismer, 2006	----
Ansonia fuliginea	van Kampen, 1923; Inger, 1966	van Kampen, 1923	----
Ansonia guibei	Inger, 1966	Inger, 1966	----
Ansonia hanitschi	Inger, 1960, 1966 Grismer, 2006	Inger, 1960; Grismer, 2006	----
Ansonia inthanon	Matsui *et al.*, 1998	Matsui *et al.*, 1998	----
Ansonia kraensis	Matsui *et al.*, 1998; Grismer, 2006	Matsui *et al.*, 1998; Grismer, 2006	----
Ansonia latirostra	Grismer, 2006	Grismer, 2006	----

Ansonia leptopus	Boulenger, 1882; van Kampen, 1923; Inger, 1960, 1966; Grismer, 2006	van Kampen, 1923; Inger, 1960; Grismer, 2006	----
Ansonia longidigita	Inger, 1960, 1966; Grismer, 2006	Inger, 1960; Grismer, 2006	----
Ansonia malayana	Inger, 1960, 1966; Grismer, 2006	Inger, 1960; Grismer, 2006	----
Ansonia mcgregori	Inger, 1960; Grismer, 2006	Inger, 1960; Grismer, 2006	----
Ansonia minuta	Inger, 1960, 1966; Grismer, 2006	Inger, 1960; Grismer, 2006	Tihen, 1960
Ansonia muelleri	Inger, 1960; Grismer, 2006	Inger, 1960; Grismer, 2006	MCW pers. obs.; Tihen, 1960
Ansonia penangensis	Boulenger, 1882; van Kampen, 1923; Inger, 1960, 1966; Taylor, 1962; Quah *et al.*, 2011; Grismer, 2006	Boulenger, 1882; van Kampen, 1923; Inger, 1960, 1966; Taylor, 1962; Quah *et al.*, 2011; Grismer, 2006	----
Ansonia platysoma	Inger, 1960, 1966	Inger, 1960	----
Ansonia siamensis	Matsui *et al.*, 1998; Grismer, 2006	Grismer, 2006	----
Ansonia spinulifer	van Kampen, 1923	van Kampen, 1923	----
Atelopus bomolochos	Peters, 1973; Coloma, 1997	Coloma, 1997	Coloma, 1997; Lötters *et al.*, 2011
Atelopus chiriquiensis	Jaslow & Lombard, 1996; McDiarmid, 1971	Jaslow & Lombard, 1996; McDiarmid, 1971	MCW pers. obs.; McDiarmid, 1971; Jaslow & Lombard, 1996; Lindquist & Hetherington, 1996
Atelopus flavescens	McDiarmid, 1971; Lescure & Marty, 2000	McDiarmid, 1971, 1973; Coloma, 1997	MCW pers. obs.; McDiarmid, 1971, 1973; Coloma, 1997

Atelopus franciscus	Lescure & Marty, 2000; Boistel *et al.*, 2011	Coloma, 1997 present; Boistel *et al.*, 2011 absent	MCW pers. obs.; Coloma, 1997; Boistel *et al.*, 2011
Atelopus halihelos	Peters, 1973	----	----
Atelopus ignescens	McDiarmid, 1971; Peters, 1973; Coloma *et al.*, 2000	McDiarmid, 1971; Coloma *et al.*, 2000	MCW pers. obs.; McDiarmid, 1971; Coloma *et al.*, 2000
Atelopus longirostris	Cochran & Goin, 1970	McDiarmid, 1971	MCW pers. obs.; McDiarmid, 1971
Atelopus nanay	Coloma, 2002	Coloma, 2002	Coloma, 2002
Atelopus oxapampae	Lehr *et al.*, 2008	Lehr *et al.*, 2008	Lötters *et al.*, 2011
Atelopus peruensis	Gray & Cannatella, 1985	Gray & Cannatella, 1985	Gray & Cannatella, 1985; Lötters *et al.*, 2011
Atelopus pulcher	Peters, 1973; Lötters *et al.*, 2002b	de la Riva *et al.*, 2011	MCW pers. obs.; de la Riva *et al.*, 2011; Lötters *et al.*, 2011
Atelopus seminiferus	Boulenger, 1882	Lötters *et al.*, 2011	Lötters *et al.*, 2011
Atelopus senex	McDiarmid, 1971	McDiarmid, 1971	McDiarmid, 1971
Atelopus spumarius	Cochran & Goin, 1970; McDiarmid, 1971	McDiarmid, 1971; Coloma, 1997	McDiarmid, 1971; Lindquist & Hetherington, 1996; Coloma, 1997
Atelopus spurrelli	McDiarmid, 1971	McDiarmid, 1971	McDiarmid, 1971
Atelopus tricolor	Lötters & de la Riva, 1998	----	Lötters *et al.*, 2011
Atelopus varius	Parker, 1881; Lötters *et al.*, 1998; Nussbaum & Wu, 2007	MOP pers. obs.; Parker, 1881; Nussbaum & Wu, 2007	MOP & MCW pers. obs.; Parker, 1881; Laurent, 1942; McDiarmid, 1971; Nussbaum & Wu, 2007
Atelopus zeteki	McDiarmid, 1971	McDiarmid, 1971	MCW pers. obs.; McDiarmid, 1971
Barbarophryne brongersmai	Hoogmoed, 1972	Hoogmoed, 1972	----
Bufo aspinius	Yang *et al.*, 1996	----	Yang *et al.*, 1996

Bufo bankorensis	Nussbaum & Wu, 2007	----	MCW pers. obs.; Nussbaum & Wu, 2007
Bufo bufo	Boulenger, 1882, 1897	Boulenger, 1897; Ecke, 1934	Boulenger, 1897; Ecke, 1934; Vorobieva & Smirnov, 1987
Bufo cryptotympanicus	Kou, 1984	----	----
Bufo eichwaldi	Litvinchuck *et al.*, 2008	Litvinchuck *et al.*, 2008	----
Bufo gargarizans	Liu, 1950	Liu, 1950	----
Bufo japonicus	Matsui, 1984	Yamazaki *et al.*, 2008	MCW pers. obs.;
Bufo stejnegeri	Matsui, 1980	Matsui, 1980	----
Bufo torrenticola	Matsui, 1976	Yamazaki *et al.*, 2008	----
Bufo tuberculatus	Milto & Barabanov, 2011	Milto & Barabanov, 2011	----
Bufo tuberospinius	Yang *et al.*, 1996	----	Yang *et al.*, 1996
Bufo verrucosissimus	Litvinchuck *et al.*, 2008	Litvinchuck *et al.*, 2008	----
Bufotes balearicus	----	Boettger, 1880	----
Bufotes oblongus	Stock *et al.*, 2001	Stock *et al.*, 2001	----
Bufotes pewzowi	Stock *et al.*, 2001	Stock *et al.*, 2001	----
Bufotes siculus	Stock *et al.*, 2008	Stock *et al.*, 2008	----
Bufotes variabilis	Andren & Nilson, 1979	Andren & Nilson, 1979	----
Bufotes viridis	Boulenger, 1882, 1890, 1897; Pramuk, 2006	Boulenger, 1882, 1890, 1897; Pramuk, 2006	Boulenger, 1897; Pramuk, 2006; Vorobieva & Smirnov, 1987
Capensibufo rosei	Hewitt, 1926a; du Preez & Carruthers, 2009; Tolley *et al.*, 2010	Tolley *et al.*, 2010	MCW pers. obs.; Grandison, 1980; Grandison, 1981; Tolley *et al.*, 2010
Capensibufo tradouwi	du Preez & Carruthers, 2009; Grandison, 1980; Hewitt, 1926b	du Preez & Carruthers, 2009; Hewitt, 1926b	Grandison, 1980, 1981
Churamiti maridadi	Channing & Stanley, 2002	Channing & Stanley, 2002	Channing & Stanley, 2002
Dendrophryniscus berthalutzae	Izecksohn, 1993b	----	----

Dendrophryniscus brevipollicatus	MOP pers. obs.; Cochran, 1955; Izecksohn, 1968; McDiarmid, 1971; Nussbaum & Wu, 2007	McDiarmid, 1971	MCW pers. obs.; McDiarmid, 1971; Nussbaum & Wu, 2007
Dendrophryniscus carvalhoi	Izecksohn, 1993b	----	----
Dendrophryniscus krausae	Cruz & Fusinatto, 2008	----	----
Dendrophryniscus leucomystax	Izecksohn, 1968	MOP pers. obs.	MOP pers. obs.
Dendrophryniscus proboscideus	Izecksohn, 1976	Izecksohn, 1976	----
Didynamipus sjostedti	Andersson, 1903	Grandison, 1981	MCW pers. obs.; Grandison, 1978, 1981
Duttaphrynus atukoralei	----	Bogert & Senanayake, 1966; Manamendra-Arachchi & Pethiyagoda, 1998	----
Duttaphrynus brevirostris	----	Rao, 1937	----
Duttaphrynus crocus	Wogan *et al.*, 2003; Das *et al.*, 2013	Wogan *et al.*, 2003	----
Duttaphrynus himalayanus	Boulenger, 1882, 1890; Das *et al.*, 2013	Boulenger, 1882, 1890; Das *et al.*, 2013	----
Duttaphrynus hololius	Günther, 1875; Boulenger, 1882, 1890	Günther, 1875	----
Duttaphrynus melanostictus	Boulenger, 1882, 1890; van Kampen, 1923; Taylor, 1962; Inger, 1966; Manamendra-Arachchi & Pethiyagoda, 1998	Parker, 1881; Taylor, 1962; Pramuk, 2006; Das *et al.*, 2013	Parker, 1881; Ramaswami, 1936; Vorobieva & Smirnov, 1987; Mendelson, 1997c; Pramuk, 2006
Duttaphrynus parietalis	Boulenger, 1882, 1890	Ramaswami, 1936	Ramaswami, 1936

Duttaphrynus scaber	Das *et al.*, 2013	Das *et al.*, 2013	MCW pers. obs.
Duttaphrynus stomaticus	Boulenger, 1890; Das *et al.*, 2013	Boulenger, 1890; Das *et al.*, 2013	MCW pers. obs.
Duttaphrynus stuarti	Wogan *et al.*, 2003; Das *et al.*, 2013	Das *et al.*, 2013	----
Epidalea calamita	MOP pers. obs.; Boulenger, 1882, 1897	MOP pers. obs.; Boulenger, 1882, 1897	MCW pers. obs.; Parker, 1881; Boulenger, 1897; Mendelson, 1997c
Ghatophryne ornata	Günther, 1875; Boulenger, 1882; Inger, 1960; Biju *et al.*, 2009	Inger, 1960; Biju *et al.*, 2009	----
Incilius alvarius	Cope, 1889; Wright & Wright, 1949	Cope, 1889; Wright & Wright, 1949; Pramuk, 2006	Pramuk, 2006; Mendelson *et al.*, 2011
Incilius aucoinae	O'Neill & Mendelson, 2004	O'Neill & Mendelson, 2004	Mendelson *et al.*, 2011
Incilius bocourti	Brocchi, 1877; Boulenger, 1882	----	Mendelson *et al.*, 2011
Incilius campbelli	Mendelson, 1994	Mendelson, 1994	MCW pers. obs.; Mendelson *et al.*, 2011
Incilius canaliferus	Boulenger, 1882	Boulenger, 1882	MCW pers. obs.; Mendelson *et al.*, 2011
Incilius cavifrons	Firschein, 1950	Firschein, 1950	Mendelson *et al.*, 2011
Incilius chompipe	Vaughan & Mendelson, 2007	----	----
Incilius coccifer	Taylor, 1951; Savage, 2002; Mendelson *et al.*, 2005	Savage, 2002; Pramuk, 2006	Pramuk, 2006; Mendelson *et al.*, 2011
Incilius coniferus	Boulenger, 1882; Taylor, 1951; Cochran & Goin, 1970	Pramuk, 2006	MCW pers. obs.; Pramuk, 2006; Mendelson *et al.*, 2011
Incilius cristatus	Boulenger, 1882; Firschein, 1950; Mendelson, 1997a	Boulenger, 1882; Firschein, 1950; Mendelson, 1997a	Mendelson *et al.*, 2011

Incilius cycladen	Lynch & Smith, 1966; Mendelson *et al.*, 2005	----	----
Incilius fastidiosus	Boulenger, 1882; Savage, 1972	Savage, 1972	Mendelson *et al.*, 2011; Savage, 1972
Incilius ibarrai	Mendelson, 2001; Mendelson *et al.*, 2005	Mendelson, 2001; Mendelson *et al.*, 2005	MCW pers. obs.; Mendelson *et al.*, 2011
Incilius leucomyos	McCranie & Wilson, 2000	McCranie & Wilson, 2000	Mendelson *et al.*, 2011
Incilius luetkenii	Taylor, 1951	Pramuk, 2006	Pramuk, 2006; Mendelson *et al.*, 2011
Incilius macrocristatus	Mendelson, 1997a, b	Mendelson, 1997a, b	Mendelson, 1997a, b
Incilius marmoreus	Taylor, 1943	Taylor, 1943	Mendelson *et al.*, 2011
Incilius mazatlanensis	Taylor, 1943	Taylor, 1943	MCW pers. obs.; Mendelson *et al.*, 2011
Incilius melanochlorus	Boulenger, 1882; Taylor, 1951; Gredin, 1972	Boulenger, 1882; Taylor, 1951; Gredin, 1972	Mendelson *et al.*, 2011
Incilius nebulifer	----	----	Mendelson *et al.*, 2011
Incilius occidentalis	Santos-Barrera, 2014	Santos-Barrera, 2014	MCW pers. obs.; Mendelson *et al.*, 2011
Incilius perplexus	Taylor, 1943	----	Mendelson, 1997c; Mendelson *et al.*, 2011
Incilius pisinnus	Mendelson *et al.*, 2005	Mendelson *et al.*, 2005	----
Incilius porteri	Mendelson *et al.*, 2005	----	----
Incilius signifer	Mendelson *et al.*, 2005	Mendelson *et al.*, 2005	----
Incilius spiculatus	Mendelson, 1997a	Mendelson, 1997a	Mendelson *et al.*, 2011
Incilius tacanensis	Mendelson, 1997b	----	----
Incilius tutelarius	Mendelson, 1997b	Mendelson, 1997b	Mendelson *et al.*, 2011

Incilius valliceps	Boulenger, 1882; Cope, 1889; Taylor, 1936; Wright & Wright, 1949; Firschein, 1950; Mendelson, 1997b	Wright & Wright, 1949; Mendelson, 1997b; Pramuk, 2006	Baldauf, 1959; Pramuk, 2006; Mendelson *et al.*, 2011
Ingerophrynus biporcatus	Boulenger, 1882, 1890; van Kampen, 1923; Inger, 1966	Boulenger, 1890; van Kampen, 1923; Inger, 1966	----
Ingerophrynus celebensis	Boulenger, 1882; van Kampen, 1923	van Kampen, 1923	MCW pers. obs.
Ingerophrynus divergens	Boulenger, 1882; Inger, 1966	Inger, 1966	----
Ingerophrynus galeatus	Boulenger, 1882; Inger *et al.*, 1999	Inger *et al.*, 1999	----
Ingerophrynus macrotis	Boulenger, 1890; van Kampen, 1923; Taylor, 1962; Inger, 1966; Inger *et al.*, 1999; Das *et al.*, 2013	Boulenger, 1890; van Kampen, 1923; Taylor, 1962; Inger, 1966; Inger *et al.*, 1999; Das *et al.*, 2013	Pramuk, 2006
Ingerophrynus philippinicus	van Kampen, 1923	van Kampen, 1923	----
Leptophryne borbonica	MOP pers. obs.; Boulenger, 1882; van Kampen, 1923; Davis, 1935; Taylor, 1962; Inger, 1966	MOP pers. obs.; Boulenger, 1882; van Kampen, 1923; Davis, 1935; Taylor, 1962; Inger, 1966	Davis, 1935
Melanophryniscus devincenzii	DB pers. obs.; Klappenbach, 1968	DB pers. obs.	DB pers. obs.
Melanophryniscus fulvoguttatus	DB pers. obs.	DB pers. obs.	DB & MCW pers. obs.
Melanophryniscus klappenbachi	MOP pers. obs.; Prigioni & Langone, 2000; Nussbaum & Wu, 2007	MOP pers. obs.	MOP pers. obs.

Melanophryniscus pachyrhynus	DB pers. obs.; Caramaschi & Cruz, 2002	Baldo *et al.*, 2012	Baldo *et al.*, 2012
Melanophryniscus rubriventris	DB pers. obs.; McDiarmid, 1971; Cei, 1980	McDiarmid, 1971; Pramuk, 2006	McDiarmid, 1971; Pramuk, 2006
Melanophryniscus stelzneri	McDiarmid, 1971; Cei, 1980	McDiarmid, 1971	McDiarmid, 1971
Mertensophryne anotis	Loveridge, 1932; Poynton, 1964, 1991; Poynton & Broadley, 1988; Poynton & Clarke, 1999; du Preez & Carruthers, 2009	Poynton, 1991	Tihen, 1960; Poynton & Broadley, 1988; Poynton, 1991; Poynton & Clarke, 1999
Mertensophryne lindneri	Poynton & Broadley, 1988; Clarke, 1989	Poynton & Broadley, 1988; Clarke, 1989	Clarke, 1989
Mertensophryne loveridgei	Poynton & Clarke, 1999; Harper *et al.*, 2010	----	Poynton & Clarke, 1999
Mertensophryne micranotis	Loveridge, 1932; Harper *et al.*, 2010	----	----
Mertensophryne taitana	Boulenger, 1882; Loveridge, 1932; Schmidt & Inger, 1959; Poynton & Broadley, 1988; Harper *et al.*, 2010	Schmidt & Inger, 1959; Grandison, 1972; Poynton & Broadley, 1988	MCW pers. obs.; Grandison, 1972
Mertensophryne uzunguensis	Loveridge, 1932; Harper *et al.*, 2010	Grandison, 1972	Grandison, 1972
Nannophryne cophotis	Boulenger, 1900b, Vellard, 1959	----	Pramuk, 2006
Nannophryne variegata	MOP pers. obs.; Boulenger,	MOP pers. obs.; Pramuk, 2006	MOP & MCW pers. obs.;

	1882; Gallardo, 1962b; Cei, 1980		Pramuk, 2006
Nectophryne afra	Boulenger, 1882; Tihen, 1960	Grandison, 1981; Tihen, 1960	Grandison, 1978, 1981; Tihen, 1960
Nectophryne batesii	Boulenger, 1913	----	MCW pers. obs.; Grandison, 1978, 1981
Nectophrynoides minutus	Menegon *et al.*, 2004; Perret, 1972	Grandison, 1978; Menegon *et al.*, 2004	Grandison, 1978; Menegon *et al.*, 2004
Nectophrynoides tornieri	MOP pers. obs.; Perret, 1972; Menegon *et al.*, 2004	Grandison, 1978; Menegon *et al.*, 2004	Grandison, 1978, 1981; Menegon *et* *al.*, 2004
Nectophrynoides viviparus	Perret, 1972; Menegon *et al.*, 2004; Nussbaum & Wu, 2007; Loader *et al.*, 2009; Harper *et al.*, 2010	Perret, 1972; Grandison, 1978; Menegon *et al.*, 2004	Tihen, 1960; Grandison, 1978, 1981; Menegon *et al.*, 2004; Nussbaum & Wu, 2007
Nimbaphrynoides occidentalis	Perret, 1972; Sandberg *et al.*, 2010	Grandison, 1978	Grandison, 1978,1981
Osornophryne antisana	Hoogmoed, 1987	Hoogmoed, 1987	Hoogmoed, 1987
Osornophryne bufoniformis	Cochran & Goin, 1970; Ruiz-Carranza & Hernandez-Camacho, 1976	Ruiz-Carranza & Hernandez-Camacho, 1976	MCW pers. obs.; Ruiz-Carranza & Hernandez-Camacho, 1976; Pramuk, 2006
Osornophryne guacamayo	MOP pers. obs.	MOP pers. obs.	MOP pers. obs.
Osornophryne puruanta	Gluesenkamp & Guayasamin, 2008	----	Gluesenkamp & Guayasamin, 2008
Osornophryne sumacoensis	Gluesenkamp, 1995	----	----
Pedostibes tuberculosus	Günther, 1875; Boulenger, 1882,	Boulenger, 1882	----

	1890; Dahanakur *et al.*, 2004		
Pelophryne brevipes	Inger, 1966; Das, 2008	Inger, 1966	----
Pelophryne misera	van Kampen, 1923; Inger, 1966	van Kampen, 1923; Ramaswami, 1936; Inger, 1966	Ramaswami, 1936
Pelophryne signata	van Kampen, 1923; Das, 2008	van Kampen, 1923	----
Peltophryne empusa	MOP pers. obs.; Boulenger, 1882; Ruibal, 1959; Diaz & Cadiz, 2008	MOP pers. obs.; Diaz & Cadiz, 2008	----
Peltophryne fustiger	Schwartz, 1960	Schwartz, 1960	MCW pers. obs.;
Peltophryne guentheri	Boulenger, 1882; Ruibal, 1959	Ruibal, 1959	----
Peltophryne gundlachi	Ruibal, 1959	Ruibal, 1959	----
Peltophryne lemur	Ruibal, 1959	Pramuk, 2006	Pramuk, 2006
Peltophryne longinasus	Ruibal, 1959; Valdes de la Osa & Ruiz, 1980	----	----
Peltophryne peltocephala	MOP pers. obs.; Boulenger, 1882; Ruibal, 1959	MOP pers. obs.	Pramuk, 2002
Peltophryne taladai	Schwartz, 1960	Schwartz, 1960	Pramuk, 2002
Phrynoidis asper	Boulenger, 1882, 1890; van Kampen, 1923; Taylor, 1962; Inger, 1966	van Kampen, 1923; Taylor, 1962; Inger, 1966; Pramuk, 2006	Griffiths, 1954; Mendelson, 1997c; Pramuk, 2006
Phrynoidis juxtasper	Inger, 1964, 1966	Inger, 1964, 1966; Pramuk, 2006	Pramuk, 2006
Poyntonophrynus damaranus	Channing & Vences, 1999; du Preez & Carruthers, 2009	du Preez & Carruthers, 2009	----

Poyntonophrynus dombensis	Poynton, 1964; Channing & Vences, 1999; du Preez & Carruthers, 2009	Poynton, 1964; du Preez & Carruthers, 2009	----
Poyntonophrynus fenoulheti	Poynton, 1964; Poynton & Broadley, 1988	Poynton, 1964; Poynton & Broadley, 1988	----
Poyntonophrynus vertebralis	Poynton, 1964; du Preez & Carruthers, 2009	Poynton, 1964; du Preez & Carruthers, 2009	----
Rentapia hosii	MOP pers. obs.; van Kampen, 1923; Taylor, 1962; Inger, 1966	MOP pers. obs.; van Kampen, 1923; Taylor, 1962	Tihen, 1960; Pramuk, 2006
Rentapia rugosa	Inger, 1966	Inger, 1966	----
Rhaebo ecuadorensis	Mueses-Cisneros *et al.*, 2012	Mueses-Cisneros *et al.*, 2012	----
Rhaebo glaberrimus	MOP pers. obs.; Cochran & Goin, 1970; Mueses-Cisneros *et al.*, 2012	MOP pers. obs.; Mueses-Cisneros *et al.*, 2012	----
Rhaebo guttatus	MOP pers. obs.; Jimenez de la Espada, 1875; Boulenger, 1882; Melin, 1941	MOP pers. obs.; Pramuk, 2006	Pramuk, 2006
Rhaebo nasicus	Kok & Kalamandeen, 2008	Kok & Kalamandeen, 2008	----
Rhinella achavali	Maneyro *et al.*, 2004	Maneyro *et al.*, 2004	----
Rhinella amboroensis	Harvey & Smith, 1993	----	----
Rhinella arenarum	MOP pers. obs.; Gallardo, 1965; Cei, 1980	MOP pers. obs.; Pramuk, 2006	MCW pers. obs.; Pramuk, 2006
Rhinella arequipensis	Vellard, 1959;Urra, 2013	Pramuk, 2006	Pramuk, 2006
Rhinella arunco	Urra, 2013	Pramuk, 2006	Pramuk, 2006
Rhinella atacamensis	Correa-Quesada *et al.*, 2008	Pramuk, 2006	----
Rhinella castaneotica	Caldwell, 1991; Avila *et al.*, 2010	Caldwell, 1991; Avila *et al.*, 2010	MCW pers. obs.
Rhinella chavin	Lehr *et al.*, 2001	Lehr *et al.*, 2001	Pramuk & Lehr, 2005; Pramuk, 2006

Rhinella dapsilis	Myers & Carvalho, 1945	Myers & Carvalho, 1945	MCW pers. obs.
Rhinella festae	Trueb, 1971	Trueb, 1971	Trueb, 1971
Rhinella granulosa	Narvaes & Rodrigues, 2009	Narvaes & Rodrigues, 2009	----
Rhinella humboldti	Kenny, 1969; Cochran & Goin, 1970; Narvaes & Rodrigues, 2009	Pramuk, 2006	Pramuk, 2006
Rhinella icterica	Cei, 1980; Heyer *et al.*, 1990	Pramuk, 2006	MCW pers. obs.; Pramuk, 2006
Rhinella limensis	Vellard, 1959	Pramuk, 2006	Pramuk, 2006
Rhinella macrorhina	Trueb, 1971	Trueb, 1971	Trueb, 1971
Rhinella manu	Chaparro *et al.*, 2007	Chaparro *et al.*, 2007	Chaparro *et al.*, 2007
Rhinella margaritifera	Lavilla *et al.*, 2013	Lavilla *et al.*, 2013	Pramuk, 2006; Mendelson *et al.*, 2011
Rhinella marina	Boulenger, 1882; Melin, 1941; Kenny, 1969; Cochran & Goin, 1970	Pramuk, 2006	Goodrich, 1930; Baldauf, 1959; Pramuk, 2006; Mendelson *et al.*, 2011
Rhinella nesiotes	Duellman & Toft, 1979	Duellman & Toft, 1979	----
Rhinella ocellata	Leão & Cochran, 1952	Pramuk, 2006	MCW pers. obs.
Rhinella ornata	Jimenez de la Espada, 1875; Heyer *et al.*, 1990; Baldissera *et al.*, 2004	Parker, 1881; Baldissera *et al.*, 2004; Pramuk, 2006	MCW pers. obs.; Parker, 1881; Pramuk, 2006
Rhinella poeppigii	de la Riva, 2002b	de la Riva, 2002b; Pramuk, 2006	MCW pers. obs.; Pramuk, 2006
Rhinella rostrata	Cochran & Goin, 1970; Noble, 1920; Trueb, 1971	Trueb, 1971	Trueb, 1971; Trueb, 1973
Rhinella schneideri	Cei, 1980	Pramuk, 2006	MCW pers. obs.; Pramuk, 2006
Rhinella spinulosa	MOP pers. obs.; Vellard, 1959; Gallardo, 1965; Cei, 1972, 1980	MOP pers. obs.; Pramuk, 2006	MOP pers. obs.; Mendelson, 1997c; Pramuk, 2006
Rhinella vellardi	----	Pramuk, 2006; Vellard, 1959	Pramuk, 2006
Rhinella veraguensis	Boulenger, 1882; Harvey &	----	Pramuk & Lehr, 2005; Pramuk,

	Smith, 1993; Savage, 1969		2006
Sabahphrynus maculatus	van Kampen, 1923; Inger, 1966; Grismer, 2006; Matsui *et al.*, 2007; Matsui *et al.*, 2012	Inger, 1966 Grismer, 2006;; Matsui *et al.*, 2007	Matsui *et al.*, 2007
Schismaderma carens	MOP pers. obs.; Boulenger, 1882; Poynton, 1964; Poynton & Broadley, 1988	MOP pers. obs.; Poynton, 1964; Poynton & Broadley, 1988; Pramuk, 2006	MCW pers. obs.; Pramuk, 2006
Sclerophrys brauni	Harper *et al.*, 2010	Harper *et al.*, 2010	----
Sclerophrys garmani	Keith, 1968; Poynton & Broadley, 1988	Keith, 1968; Poynton & Broadley, 1988	----
Sclerophrys gracilipes	Boulenger, 1899	Boulenger, 1899	MCW pers. obs.
Sclerophrys gutturalis	Poynton & Broadley, 1988	Poynton & Broadley, 1988	----
Sclerophrys kisoloensis	Keith, 1968; Loveridge, 1932; Poynton & Broadley, 1988	Keith, 1968; Poynton & Broadley, 1988	----
Sclerophrys latifrons	Boulenger, 1900c	Boulenger, 1900c; Inger & Menzies, 1961; Perret & Amiet, 1971	----
Sclerophrys lemairii	Inger & Menzies, 1961; Poynton & Broadley, 1988	Inger & Menzies, 1961; Poynton & Broadley, 1988	----
Sclerophrys maculata	Perret & Amiet, 1971; Poynton & Broadley, 1988	Perret & Amiet, 1971; Poynton & Broadley, 1988	Mendelson, 1997c, Pramuk, 2006
Sclerophrys mauritanica	Boulenger, 1882	Boulenger, 1882	MCW pers. obs.
Sclerophrys pantherina	Parker, 1981	Parker, 1981	Parker, 1981
Sclerophrys pardalis	du Preez & Carruthers, 2009	Pramuk, 2006; du Preez & Carruthers, 2009	----

Sclerophrys poweri	du Preez & Carruthers, 2009	du Preez & Carruthers, 2009	----
Sclerophrys regularis	Boulenger, 1882; Sedra & Michael, 1959; Inger & Menzies, 1961; Poynton, 1964	Sedra & Michael, 1959; Inger & Menzies, 1961	Sedra & Michael, 1959; Pramuk, 2006
Sclerophrys steindachneri	Pfeffer, 1893	Pfeffer, 1893	----
Sclerophrys tuberosa	Boulenger, 1882	Boulenger, 1882	MCW pers. obs.
Sclerophrys xeros	Tandy *et al.*, 1976	Pramuk, 2006; Channing *et al.*, 2012	Pramuk, 2006
Strauchbufo raddei	Boulenger, 1882	Vorobieva & Smirnov, 1987	MCW pers. obs.; Vorobieva & Smirnov, 1987
Vandijkophrynus amatolicus	du Preez & Carruthers, 2009	du Preez & Carruthers, 2009	----
Vandijkophrynus angusticeps	MOP pers. obs.; Boulenger, 1882; du Preez & Carruthers, 2009	Schoonees, 1930; du Preez & Carruthers, 2009	MCW pers. obs.; Schoonees, 1930
Vandijkophrynus gariepensis	du Preez & Carruthers, 2009	du Preez & Carruthers, 2009	MCW pers. obs.
Vandijkophrynus inyangae	Poynton & Broadley, 1988; du Preez & Carruthers, 2009	Poynton & Broadley, 1988; du Preez & Carruthers, 2009	----
Vandijkophrynus robinsoni	du Preez & Carruthers, 2009	du Preez & Carruthers, 2009	----
Werneria bambutensis	Rödel *et al.*, 2004	----	----
Werneria mertensiana	Rödel *et al.*, 2004	----	MCW pers. obs.
Werneria tandyi	Rödel *et al.*, 2004	----	----
Wolterstorffina parvipalmata	Tihen, 1960; Perret, 1972; Boistel & Amiet, 2001	----	MCW pers. obs.; Grandison, 1978, 1981; Tihen, 1960
Xanthophryne koynayensis	Biju *et al.*, 2009	Biju *et al.*, 2009	----
Bufonidae not included in Pyron (2014)			

Species	Tympanic membrane	Tympanic annulus	Columella
Adenomus kandianus	Günther, 1872; Manamendra-Arachchi & Pethiyagoda, 1998; Gabadage *et al.*, 2014	Günther, 1872; Manamendra-Arachchi & Pethiyagoda, 1998; Gabadage *et al.*, 2014; Meegaskumbura *et al.*, 2015	Meegaskumbura *et al.*, 2015
Altiphrynoides malcolmi	----	Grandison, 1978	Grandison, 1978, 1981
Altiphrynoides osgoodi	Loveridge, 1932	Grandison, 1978	Grandison, 1978, 1981
Amazophrynella amazonicola	Rojas *et al.*, 2015	----	----
Amazophrynella bokermanni	Izecksohn, 1993a	----	----
Amazophrynella javierbustamantei	Rojas *et al.*, 2016	----	----
Amazophrynella manaos	Rojas *et al.*, 2014	----	----
Amazophrynella matses	Rojas *et al.*, 2015	----	----
Amazophrynella vote	Avila *et al.*, 2012	----	----
Anaxyrus compactilis	Cope, 1889; Brocchi, 1877; Wright & Wright, 1949	Cope, 1889; Wright & Wright, 1949	----
Anaxyrus kelloggi	----	Taylor, 1936	----
Anaxyrus mexicanus	Brocchi, 1879	Brocchi, 1879	----
Ansonia echinata	Inger & Stuebing, 2009	Inger & Stuebing, 2009	----
Ansonia glandulosa	Iskandar & Mumpuni, 2004	Iskandar & Mumpuni, 2004	----
Ansonia jeetsukumarani	Wood *et al.*, 2008	Wood *et al.*, 2008	----
Ansonia latidisca	Inger, 1966; Matsui *et al.*, 2012	Matsui *et al.*, 2012	Matsui *et al.*, 2012
Ansonia latiffi	Wood *et al.*, 2008	Wood *et al.*, 2008	----
Ansonia lumut	Chan *et al.*, 2014	Chan *et al.*, 2014	----
Ansonia thinthinae	Wilkinson *et al.*, 2012	Wilkinson *et al.*, 2012	----
Ansonia vidua	Hertwig *et al.*, 2014	Hertwig *et al.*, 2014	----
Atelopus angelito	Ardila-Robayo & Ruiz-Carranza,	Ardila-Robayo & Ruiz-Carranza,	Ardila-Robayo & Ruiz-Carranza, 1998

	1998	1998	
Atelopus ardila	Coloma *et al.*, 2010	Coloma *et al.*, 2010	Coloma *et al.*, 2010
Atelopus arthuri	Peters, 1973; Coloma, 1997	Coloma, 1997	Coloma, 1997
Atelopus balios	Peters, 1973; Coloma, 1997	Coloma, 1997	Coloma, 1997
Atelopus barbotini	Lescure & Marty, 2000	----	Lötters *et al.*, 2011
Atelopus boulengeri	McDiarmid, 1971; Peters, 1973	McDiarmid, 1971	McDiarmid, 1971
Atelopus carbonerensis	Rivero, 1974	Coloma, 1997	Coloma, 1997
Atelopus carrikeri	Ruthven, 1916; McDiarmid, 1971; Ruiz-Carranza *et al.*, 1994	McDiarmid, 1971; Ruiz-Carranza *et al.*, 1994	McDiarmid, 1971; Ruiz-Carranza *et al.*, 1994;
Atelopus certus	McDiarmid, 1971	McDiarmid, 1971	McDiarmid, 1971
Atelopus chirripoensis	Savage & Bolaños, 2009	Savage & Bolaños, 2009	----
Atelopus chrysocorallus	La Marca, 1996 ―1994‖	----	----
Atelopus coynei	Miyata, 1980; Coloma, 1997	Coloma, 1997	Coloma, 1997
Atelopus cruciger	McDiarmid, 1971; Lötters *et al.*, 2004	MOP pers. obs.; McDiarmid, 1971; Lötters *et al.*, 2004	MOP pers. obs.; McDiarmid, 1971; Lötters *et al.*, 2004
Atelopus dimorphus	Lötters, 2003	Lötters, 2003	Lötters, 2003
Atelopus ebenoides	Cochran & Goin, 1970; McDiarmid, 1971	McDiarmid, 1971	McDiarmid, 1971
Atelopus elegans	McDiarmid, 1971; Peters, 1973	McDiarmid, 1971	McDiarmid, 1971
Atelopus epikeisthos	Lötters *et al.*, 2005 ―2004‖	----	----
Atelopus eusebianus	Rivero & Granados Diaz, 1983	Rivero & Granados Diaz, 1983	Rivero & Granados Diaz, 1983
Atelopus eusebiodiazi	Venegas *et al.*, 2008	Venegas *et al.*, 2008	----
Atelopus exiguus	McDiarmid, 1971; Coloma *et al.*, 2000	McDiarmid, 1971; Coloma *et al.*, 2000	McDiarmid, 1971; Coloma *et al.*, 2000
Atelopus farci	Lynch, 1993	Lynch, 1993	Lynch, 1993
Atelopus gigas	Coloma *et al.*, 2010	Coloma *et al.*, 2010	Coloma *et al.*, 2010
Atelopus glyphus	McDiarmid, 1971	McDiarmid, 1971	McDiarmid, 1971

Atelopus guanujo	Coloma, 2002	Coloma, 2002	Coloma, 2002
Atelopus guitarraensis	Osorno-Muñoz *et al.*, 2001	Osorno-Muñoz *et al.*, 2001	Osorno-Muñoz *et al.*, 2001
Atelopus hoogmoedi	Lescure & Marty, 2000	----	Lötters *et al.*, 2011
Atelopus laetissimus	Ruiz-Carranza *et al.*, 1994	Ruiz-Carranza *et al.*, 1994	Ruiz-Carranza *et al.*, 1994
Atelopus limosus	Ibañez *et al.*, 1995	Ibañez *et al.*, 1995	
Atelopus loettersi	de la Riva *et al.*, 2011	de la Riva *et al.*, 2011	de la Riva *et al.*, 2011
Atelopus longibrachius	Rivero, 1963; Coloma, 1997	Coloma, 1997	Coloma, 1997
Atelopus lozanoi	Osorno-Muñoz *et al.*, 2001	Osorno-Muñoz *et al.*, 2001	Osorno-Muñoz *et al.*, 2001
Atelopus lynchi	Cannatella, 1981	Cannatella, 1981	Cannatella, 1981
Atelopus mandingues	Osorno-Muñoz *et al.*, 2001	Osorno-Muñoz *et al.*, 2001	Osorno-Muñoz *et al.*, 2001
Atelopus marinkellei	Cochran & Goin, 1970	----	----
Atelopus mindoensis	Peters, 1973; Coloma, 1997	Coloma, 1997	Coloma, 1997
Atelopus mittermeieri	Acosta Galvis *et al.*, 2006	Acosta Galvis *et al.*, 2006	----
Atelopus monohernandezii	Ardila-Robayo *et al.*, 2002	Ardila-Robayo *et al.*, 2002	Ardila-Robayo *et al.*, 2002
Atelopus mucubajiensis	Rivero, 1974; Coloma, 1997	Coloma, 1997	Coloma, 1997
Atelopus muisca	Rueda-Almonacid & Hoyos, 1992 —1991"	----	Hoyos *et al.*, 2015
Atelopus nahumae	Ruiz-Carranza *et al.*, 1994	Ruiz-Carranza *et al.*, 1994	Ruiz-Carranza *et al.*, 1994
Atelopus nepiozomus	Peters, 1973	----	----
Atelopus nicefori	Rivero, 1963; Cochran & Goin, 1970; Coloma, 1997	Coloma, 1997	Coloma, 1997
Atelopus nocturnus	Bravo-Valencia & Rivera-Correa, 2011	Bravo-Valencia & Rivera-Correa, 2011	Bravo-Valencia & Rivera-Correa, 2011
Atelopus onorei	Coloma *et al.*, 2007	Coloma *et al.*, 2007	----
Atelopus orcesi	Coloma *et al.*, 2010	Coloma *et al.*, 2010	Coloma *et al.*, 2010
Atelopus oxyrhynchus	McDiarmid, 1971; Rivero, 1974	McDiarmid, 1971	McDiarmid, 1971

Atelopus pachydermus	McDiarmid, 1971; Peters, 1973; Coloma *et al.*, 2007	McDiarmid, 1971	McDiarmid, 1971
Atelopus palmatus	Peters, 1973	----	----
Atelopus pastuso	Coloma *et al.*, 2010	Coloma *et al.*, 2010	Coloma *et al.*, 2010
Atelopus patazensis	Venegas *et al.*, 2008	Venegas *et al.*, 2008	----
Atelopus pedimarmoratus	Cochran & Goin, 1970	Cochran & Goin, 1970	----
Atelopus petersi	Coloma *et al.*, 2007	Coloma *et al.*, 2007	Coloma *et al.*, 2007
Atelopus petriruizi	Ardila-Robayo, 1999	Ardila-Robayo, 1999	Ardila-Robayo, 1999
Atelopus pictiventris	Kattan, 1986	----	----
Atelopus planispina	Jimenez de la Espada, 1875; Peters, 1973; Coloma, 1997	Coloma, 1997	Coloma, 1997
Atelopus podocarpus	Coloma *et al.*, 2010	Coloma *et al.*, 2010	Coloma *et al.*, 2010
Atelopus pyrodactylus	Venegas & Barrio, 2006	----	----
Atelopus reticulatus	Lötters *et al.*, 2002a	----	----
Atelopus sanjosei	Rivero & Serna, 1989; Coloma, 1997	Coloma, 1997	Coloma, 1997
Atelopus sernai	Ruiz-Carranza & Osorno-Muñoz, 1994	Ruiz-Carranza & Osorno-Muñoz, 1994	Ruiz-Carranza & Osorno-Muñoz, 1994
Atelopus simulatus	Ruiz-Carranza & Osorno-Muñoz, 1994	Ruiz-Carranza & Osorno-Muñoz, 1994	Ruiz-Carranza & Osorno-Muñoz, 1994
Atelopus siranus	Lötters & Henzl, 2000	Lötters & Henzl, 2000	----
Atelopus sonsonensis	Vélez-Rodríguez & Ruiz-Carranza, 1997	Vélez-Rodríguez & Ruiz-Carranza, 1997	Vélez-Rodríguez & Ruiz-Carranza, 1997
Atelopus sorianoi	La Marca, 1983; Coloma, 1997	Coloma, 1997	Coloma, 1997
Atelopus subornatus	Coloma, 1997	Coloma, 1997	Coloma, 1997
Atelopus tamaense	La Marca *et al.*, 1990 ―1989‖	----	----

Atelopus vogli	Lötters *et al.*, 2004	Lötters *et al.*, 2004	Lötters *et al.*, 2004
Atelopus walkeri	Rivero, 1963; Cochran & Goin, 1970; McDiarmid, 1971	McDiarmid, 1971	McDiarmid, 1971
Blythophryne beryet	Chandramouli *et al.*, 2016	Chandramouli *et al.*, 2016	Chandramouli *et al.*, 2016
Bufo ailaoanus	Kou, 1984	----	----
Bufo pageoti	Wogan *et al.*, 2003; Das *et al.*, 2013	Wogan *et al.*, 2003; Das *et al.*, 2013	----
Bufoides meghalayana	Pillai & Yazdani, 1973	----	----
Bufotes latastii	Boulenger, 1882, 1890; Stock *et al.*, 2001	Stock *et al.*, 2001	----
Bufotes luristanicus	Stock *et al.*, 2001c, Javari & Torki, 2009	Stock *et al.*, 2001c, Javari & Torki, 2009	----
Bufotes pseudoraddei	----	Stock *et al.*, 1999; Stock *et al.*, 2001	----
Bufotes surdus	Stock *et al.*, 2001	----	----
Bufotes turanensis	Stock *et al.*, 2001	Stock *et al.*, 2001	----
Bufotes zugmayeri	Stock *et al.*, 2001	Stock *et al.*, 2001	----
Dendrophryniscus oreites	Recoder *et al.*, 2010	----	----
Dendrophryniscus organensis	Carvalho-e-Silva *et al.*, 2010	----	----
Dendrophryniscus skuki	Caramaschi, 2012	----	----
Dendrophryniscus stawiarskyi	Izecksohn, 1993b	----	----
Duttaphrynus beddomii	Günther, 1875; Boulenger, 1882, 1890	Günther, 1875; Boulenger, 1882, 1890	----
Duttaphrynus chandai	Das *et al.*, 2013	Das *et al.*, 2013	----
Duttaphrynus kiphirensis	Das *et al.*, 2013	Das *et al.*, 2013	----

Duttaphrynus kotagamai	Fernando *et al.*, 1994; Manamendra-Arachchi & Pethiyagoda, 1998	Fernando *et al.*, 1994	----
Duttaphrynus mamitensis	Das *et al.*, 2013	Das *et al.*, 2013	----
Duttaphrynus manipurensis	Mathew & Sen, 2009	Mathew & Sen, 2009	----
Duttaphrynus microtympanum	----	Boulenger, 1882, 1890; Shah & Gruber, 1994; Manamendra-Arachchi & Pethiyagoda, 1998	----
Duttaphrynus mizoramensis	Das *et al.*, 2013	Das *et al.*, 2013	----
Duttaphrynus nagalandensis	Das *et al.*, 2013	Das *et al.*, 2013	----
Duttaphrynus noellerti	Manamendra-Arachchi & Pethiyagoda, 1998	Manamendra-Arachchi & Pethiyagoda, 1998	----
Duttaphrynus olivaceus	Boulenger, 1882, 1890	----	----
Duttaphrynus sumatranus	Boulenger, 1882; Teynie *et al.*, 2010; Das *et al.*, 2013	Das *et al.*, 2013	----
Duttaphrynus totol	Teynie *et al.*, 2010	Teynie *et al.*, 2010	----
Duttaphrynus valhallae	Meade-Waldo, 1909; van Kampen, 1923	Meade-Waldo, 1909; van Kampen, 1923	----
Duttaphrynus wokhaensis	Boulenger, 1890	Boulenger, 1890	----
Frostius erythrophthalmus	Pimenta & Caramaschi, 2007	----	----
Frostius pernambucensis	MOP pers. obs.; Cannatella, 1986	MOP pers. obs.	Cannatella, 1986
Ghatophryne rubigina	Pillai & Pattabiraman, 1981	----	----
Incilius aurarius	Mendelson *et al.*, 2012	Mendelson *et al.*, 2012	----
Incilius epioticus	Boulenger, 1882; Savage & Kluge, 1961; Savage, 1972; Vaughan	Savage & Kluge, 1961; Savage, 1972	Savage & Kluge, 1961; Savage, 1972; Pramuk, 2006; Mendelson *et al.*, 2011

	& Mendelson, 2007		
Incilius guanacaste	Vaughan & Mendelson, 2007	----	----
Incilius holdridgei	Savage, 1972	Savage, 1972	Savage, 1972
Incilius intermedius	Boulenger, 1882	Boulenger, 1882	----
Incilius karenlipsae	Mendelson & Mulcahy, 2010	Mendelson & Mulcahy, 2010	----
Incilius majordomus	Savage *et al.*, 2013	Savage *et al.*, 2013	Savage *et al.*, 2013
Incilius mccoyi	Santos-Barrera & Flores-Villela, 2011	Santos-Barrera & Flores-Villela, 2011	----
Incilius periglenes	Savage, 1972; Savage, 2002	Savage, 1972; Savage, 2002	Savage, 1972; Savage, 2002
Incilius peripatetes	Taylor, 1951; Savage, 1972	Taylor, 1951; Savage, 1972	Savage, 1972
Ingerophrynus claviger	Boulenger, 1882; van Kampen, 1923	van Kampen, 1923	----
Ingerophrynus gollum	Grismer, 2007	----	----
Ingerophrynus kumquat	Grismer, 2007	----	----
Ingerophrynus parvus	van Kampen, 1923; Taylor, 1962	van Kampen, 1923; Taylor, 1962	----
Ingerophrynus quadriporcatus	van Kampen, 1923; Inger, 1966	van Kampen, 1923; Inger, 1966	----
Laurentophryne parkeri	Tihen, 1960	Tihen, 1960	Tihen, 1960; Grandison, 1978, 1981
Leptophryne cruentata	van Kampen, 1923	van Kampen, 1923	----
Melanophryniscus admirabilis	di Bernardo *et al.*, 2006	----	----
Melanophryniscus alipioi	Langone *et al.*, 2008	----	----
Melanophryniscus atroluteus	DB pers. obs.	DB pers. obs.	DB pers. obs.
Melanophryniscus biancae	Bornschein *et al.*, 2015	----	----
Melanophryniscus	DB pers. obs.	----	----

cambaraensis			
Melanophryniscus cupreuscapularis	DB pers. obs.; Cespedez & Alvarez, 2000	----	----
Melanophryniscus dorsalis	DB pers. obs.	----	----
Melanophryniscus estebani	DB pers. obs.; Cespedez, 2008	----	----
Melanophryniscus krauczuki	Baldo & Basso, 2004	Baldo & Basso, 2004	Baldo & Basso, 2004
Melanophryniscus langonei	Maneyro *et al.*, 2008	----	----
Melanophryniscus macrogranulosus	DB pers. obs.	DB pers. obs.	DB pers. obs.
Melanophryniscus milanoi	Bornschein *et al.*, 2015	----	----
Melanophryniscus montevidensis	DB pers. obs.	DB pers. obs.	DB pers. obs.
Melanophryniscus moreirae	Badenhorst, 1945; Cochran, 1955; McDiarmid, 1971	Badenhorst, 1945; McDiarmid, 1971	Badenhorst, 1945; McDiarmid, 1971; Mendelson, 1997c
Melanophryniscus paraguayensis	Cespedez & Motte, 2007	----	----
Melanophryniscus peritus	Caramaschi & Cruz, 2011	----	----
Melanophryniscus sanmartini	Klappenbach, 1968	----	----
Melanophryniscus setiba	MOP pers. obs.; Peloso *et al.*, 2012	Peloso *et al.*, 2012	Peloso *et al.*, 2012
Melanophryniscus simplex	DB pers. obs.; Caramaschi & Cruz, 2002	----	----
Melanophryniscus spectabilis	DB pers. obs.; Caramaschi & Cruz, 2002	----	----

Melanophryniscus tumifrons	McDiarmid, 1971; Caramaschi & Cruz, 2002	McDiarmid, 1971	McDiarmid, 1971
Melanophryniscus vilavelhensis	DB pers. obs.	----	----
Melanophryniscus xanthostomus	Bornschein *et al.*, 2015	----	----
Mertensophryne howelli	Poynton & Clarke, 1999	----	Poynton & Clarke, 1999
Mertensophryne lonnbergi	Loveridge, 1932; Poynton & Broadley, 1988	Grandison, 1972; Poynton & Broadley, 1988	Grandison, 1972
Mertensophryne melanopleura	Schmidt & Inger, 1959; Poynton & Broadley, 1988	Poynton & Broadley, 1988	----
Mertensophryne mocquardi	Loveridge, 1932	----	----
Mertensophryne nairobiensis	Loveridge, 1932	----	----
Mertensophryne nyikae	Loveridge, 1953	----	----
Mertensophryne schmidti	Grandison, 1972	Grandison, 1972	Grandison, 1972
Mertensophryne usambarae	Poynton & Clarke, 1999; Harper *et al.*, 2010	----	Poynton & Clarke, 1999
Metaphryniscus sosai	Señaris *et al.*, 1994	Señaris *et al.*, 1994	----
Nannophryne apolobambica	de la Riva *et al.*, 2005	de la Riva *et al.*, 2005	----
Nannophryne corynetes	Duellman & Ochoa, 1991	Duellman & Ochoa, 1991	Duellman & Ochoa, 1991; Pramuk, 2006
Nectophrynoides asperginis	Arch *et al.*, 2011	----	Arch *et al.*, 2011
Nectophrynoides cryptus	Perret, 1972	Grandison, 1978	Perret, 1972; Grandison, 1978, 1981

Nectophrynoides frontierei	Menegon *et al.*, 2004	Menegon *et al.*, 2004	Menegon *et al.*, 2004
Nectophrynoides laevis	Menegon *et al.*, 2004	----	----
Nectophrynoides laticeps	Harper *et al.*, 2010	Harper *et al.*, 2010	----
Nectophrynoides paulae	Menegon *et al.*, 2007	Menegon *et al.*, 2007	----
Nectophrynoides poyntoni	Menegon *et al.*, 2004	Menegon *et al.*, 2004	Menegon *et al.*, 2004
Nectophrynoides pseudotornieri	Menegon *et al.*, 2004	----	----
Nectophrynoides vestergaardi	Menegon *et al.*, 2004	Menegon *et al.*, 2004	Menegon *et al.*, 2004
Nectophrynoides wendyae	Menegon *et al.*, 2004	----	----
Oreophrynella cryptica	Señaris, 1995 ―1993‖	----	----
Oreophrynella dendronastes	Lathrop & MacCulloch, 2007	----	----
Oreophrynella huberi	Diego-Aransay & Gorzula, 1990	----	----
Oreophrynella nigra	Señaris *et al.*, 1994	----	----
Oreophrynella quelchii	Boulenger, 1895; McDiarmid, 1971; Nussbaum & Wu, 2007	McDiarmid, 1971; Nussbaum & Wu, 2007	McDiarmid, 1971; Nussbaum & Wu, 2007
Oreophrynella seegobini	Kok, 2009	----	----
Oreophrynella vasquezi	Señaris *et al.*, 1994	----	----
Oreophrynella weiassipuensis	Señaris *et al.*, 2005	----	----
Osornophryne angel	Yanez-Munoz *et al.*, 2011	----	----
Osornophryne cofanorum	Mueses-Cisneros *et al.*, 2010	----	----
Osornophryne occidentalis	Cisneros-Heredia & Gluesenkamp, 2010	Cisneros-Heredia & Gluesenkamp, 2010	----
Osornophryne percrassa	Ruiz-Carranza & Hernandez-Camacho, 1976	Ruiz-Carranza & Hernandez-Camacho, 1976	Ruiz-Carranza & Hernandez-Camacho, 1976

Osornophryne simpsoni	Páez-Moscoso *et al.*, 2011	Páez-Moscoso *et al.*, 2011	Páez-Moscoso *et al.*, 2011
Osornophryne talipes	MOP pers. obs.	----	----
Parapelophryne scalpta	Liu *et al.*, 1973	Fei *et al.*, 2003	Fei *et al.*, 2003
Pedostibes kempi	Boulenger, 1919	----	----
Pelophryne albotaeniata	Tihen, 1960; Das, 2008	Tihen, 1960	Tihen, 1960
Pelophryne api	Das, 2008	Das, 2008	----
Pelophryne guentheri	Boulenger, 1882; van Kampen, 1923; Inger, 1966; Das, 2008	Boulenger, 1882; van Kampen, 1923; Inger, 1966	----
Pelophryne lighti	Das, 2008	Das, 2008	----
Pelophryne linanitensis	Das, 2008	Das, 2008	----
Pelophryne murudensis	Das, 2008	Das, 2008	----
Pelophryne rhopophilia	Das, 2008	Das, 2008	----
Pelophryne saravacensis	Inger & Stuebing, 2009	Inger & Stuebing, 2009	----
Peltophryne cataulaciceps	Schwartz, 1959	Schwartz, 1959	----
Peltophryne florentinoi	Moreno & Rivalta, 2007	Moreno & Rivalta, 2007	----
Peltophryne fluviatica	----	Schwartz, 1972	----
Peltophryne fracta	----	Schwartz, 1972	----
Poyntonophrynus beiranus	Loveridge, 1932; Poynton & Broadley, 1988; du Preez & Carruthers, 2009	Poynton & Broadley, 1988; du Preez & Carruthers, 2009	----
Poyntonophrynus grandisonae	Poynton & Haacke, 1993	Poynton & Haacke, 1993	Poynton & Haacke, 1993
Poyntonophrynus hoeschi	Poynton, 1964; du Preez & Carruthers, 2009	du Preez & Carruthers, 2009	----
Poyntonophrynus kavangensis	Poynton & Broadley, 1988; Channing & Vences, 1999; du Preez & Carruthers, 2009	Poynton & Broadley, 1988; du Preez & Carruthers, 2009	----
Poyntonophrynus lughensis	Loveridge, 1932	----	----
Poyntonophrynus parkeri	----	Loveridge, 1932; Poynton *et al.*,	----

		2005	
Pseudobufo subasper	Boulenger, 1882; van Kampen, 1923; Inger, 1966	van Kampen, 1923; Inger, 1966	Tihen, 1960
Rentapia everetti	van Kampen, 1923; Inger, 1966	van Kampen, 1923	----
Rhaebo andinophrynoides	MOP pers. obs.; Mueses-Cisneros, 2009	MOP pers. obs.; Mueses-Cisneros, 2009	----
Rhaebo atelopoides	Lynch & Ruiz-Carranza, 1981	Lynch & Ruiz-Carranza, 1981	Lynch & Ruiz-Carranza, 1981
Rhaebo blombergi	Myers & Funkhouser, 1951; Cochran & Goin, 1970	Pramuk, 2006	Pramuk, 2006
Rhaebo caeruleostictus	Boulenger, 1882; Hoogmoed, 1989; Pramuk & Kadivar, 2003	Hoogmoed, 1989; Pramuk, 2006	Hoogmoed, 1989; Pramuk, 2006
Rhaebo colomai	Hoogmoed, 1985; Ron *et al.*, 2015	Hoogmoed, 1985; Ron *et al.*, 2015	Hoogmoed, 1985
Rhaebo haematiticus	MOP pers. obs.; Boulenger, 1882; Cochran & Goin, 1970; Pramuk, 2006; Mueses-Cisneros, 2009	MOP pers. obs.; Pramuk, 2006	MOP pers. obs.; Pramuk, 2006; Mendelson *et al.*, 2011
Rhaebo hypomelas	Hoogmoed, 1989; Mueses-Cisneros, 2009	Hoogmoed, 1989; Mueses-Cisneros, 2009	----
Rhaebo lynchi	Mueses-Cisneros, 2007	----	----
Rhaebo olallai	Hoogmoed, 1985; Ron *et al.*, 2015	Hoogmoed, 1985; Ron *et al.*, 2015	Hoogmoed, 1985
Rhinella abei	Baldissera *et al.*, 2004	Baldissera *et al.*, 2004	----
Rhinella achalensis	Cei, 1972, 1980	MOP pers. obs.; Cei, 1972	MOP pers. obs.
Rhinella acrolopha	Trueb, 1971	Trueb, 1971	Trueb, 1971
Rhinella acutirostris	Lötters & Köhler, 2000	Lötters & Köhler, 2000	----
Rhinella alata	Santos *et al.*, 2015	Santos *et al.*, 2015	----

Rhinella amabilis	Pramuk & Kadivar, 2003	Pramuk & Kadivar, 2003; Pramuk, 2006	Pramuk & Kadivar, 2003; Pramuk, 2006
Rhinella arborescandens	Duellman & Schulte, 1992	Duellman & Schulte, 1992	Duellman & Schulte, 1992
Rhinella azarai	Narvaes & Rodrigues, 2009	Narvaes & Rodrigues, 2009	----
Rhinella bergi	Narvaes & Rodrigues, 2009	Narvaes & Rodrigues, 2009	----
Rhinella bernardoi	Sanabria *et al.*, 2010	Sanabria *et al.*, 2010	----
Rhinella casconi	Roberto *et al.*, 2014	Roberto *et al.*, 2014	----
Rhinella centralis	Narvaes & Rodrigues, 2009	Narvaes & Rodrigues, 2009	----
Rhinella ceratophrys	Boulenger, 1882; Cochran & Goin, 1970; Fenolio *et al.*, 2012	Fenolio *et al.*, 2012	----
Rhinella cerradensis	Maciel *et al.*, 2007	Maciel *et al.*, 2007	----
Rhinella chrysophora	McCranie *et al.*, 1989	McCranie *et al.*, 1989	McCranie *et al.*, 1989; Pramuk & Lehr, 2005
Rhinella cristinae	Vélez-Rodríguez & Ruiz-Carranza, 2002	Vélez-Rodríguez & Ruiz-Carranza, 2002	Vélez-Rodríguez & Ruiz-Carranza, 2002
Rhinella crucifer	Baldissera *et al.*, 2004	Baldissera *et al.*, 2004	Mendelson, 1997c
Rhinella diptycha	----	Cope, 1862a	----
Rhinella dorbignyi	MOP pers. obs.; Boulenger, 1882; Cei, 1980; Narvaes & Rodrigues, 2009	MOP pers. obs.	----
Rhinella fernandezae	MOP pers. obs.; Cei, 1980; Narvaes & Rodrigues, 2009	MOP pers. obs.	----
Rhinella fissipes	Boulenger, 1903b, Gallardo, 1967	----	----
Rhinella gallardoi	Carrizo, 1992	Carrizo, 1992	----

Rhinella gildae	Vaz-Silva *et al.*, 2015	Vaz-Silva *et al.*, 2015	----
Rhinella gnustae	Gallardo, 1967; Cei, 1980	Gallardo, 1967; Cei, 1980	----
Rhinella henseli	Baldissera *et al.*, 2004	Baldissera *et al.*, 2004	----
Rhinella hoogmoedi	Caramaschi & Pombal, 2006	Caramaschi & Pombal, 2006	----
Rhinella inca	Gallardo, 1967	Gallardo, 1967	----
Rhinella inopina	Vaz-Silva *et al.*, 2012	Vaz-Silva *et al.*, 2012	----
Rhinella iserni	Jimenez de la Espada, 1875	Jimenez de la Espada, 1875	Jimenez de la Espada, 1875
Rhinella jimi	Stevaux, 2002	Stevaux, 2002	----
Rhinella justinianoi	Harvey & Smith, 1994	----	----
Rhinella leptoscelis	Vellard, 1959; Gallardo, 1967; Padial *et al.*, 2009	Vellard, 1959; Gallardo, 1967; Padial *et al.*, 2009	----
Rhinella lescurei	Fouquet *et al.*, 2007	Fouquet *et al.*, 2007	----
Rhinella lindae	Rivero & Castaño, 1990	Rivero & Castaño, 1990	Rivero & Castaño, 1990
Rhinella magnussoni	Lima *et al.*, 2007	Lima *et al.*, 2007	----
Rhinella major	MOP pers. obs.; Cei, 1980; Narvaes & Rodrigues, 2009	MOP pers. obs.; Pramuk, 2006	Pramuk, 2006
Rhinella martyi	Fouquet *et al.*, 2007	Fouquet *et al.*, 2007	----
Rhinella merianae	Narvaes & Rodrigues, 2009	Narvaes & Rodrigues, 2009	MCW pers. obs.
Rhinella mirandaribeiroi	Narvaes & Rodrigues, 2009	Pramuk, 2006	Pramuk, 2006
Rhinella multiverrucosa	Lehr *et al.*, 2005	Lehr *et al.*, 2005	Lehr *et al.*, 2005; Pramuk, 2006
Rhinella nattereri	Narvaes & Rodrigues, 2009	Narvaes & Rodrigues, 2009	----
Rhinella nicefori	Cochran & Goin, 1970; Trueb, 1971	Trueb, 1971	Trueb, 1971, 1973
Rhinella paraguas	Grant & Bolivar-G, 2014	Grant & Bolivar-G, 2014	Grant & Bolivar-G, 2014
Rhinella paraguayensis	Avila *et al.*, 2010	Avila *et al.*, 2010	----
Rhinella proboscidea	Jimenez de la Espada, 1875	Jimenez de la Espada, 1875	Jimenez de la Espada, 1875
Rhinella pygmaea	Narvaes & Rodrigues, 2009	Narvaes & Rodrigues, 2009	Mendelson, 1997c
Rhinella quechua	Gallardo, 1961; Harvey & Smith, 1993	----	----

Rhinella roqueana	Melin, 1941	----	----
Rhinella rubescens	Cei, 1980	Pramuk, 2006	Pramuk, 2006
Rhinella rubropunctata	Vellard, 1959; Gallardo, 1962a, Cei, 1980	Pramuk, 2006	Pramuk, 2006
Rhinella ruizi	Grant, 2000	Grant, 2000	Grant, 2000
Rhinella rumbolli	Carrizo, 1992	Carrizo, 1992	----
Rhinella scitula	Caramaschi & Niemeyer, 2003; Avila *et al.*, 2010	----	----
Rhinella sclerocephala	Mijares-Urrutia & Arends, 2001	Mijares-Urrutia & Arends, 2001	----
Rhinella sebbeni	Vaz Silva *et al.*, 2015	Vaz Silva *et al.*, 2015	----
Rhinella stanlaii	Lötters & Köhler, 2000	Lötters & Köhler, 2000	Lötters & Köhler, 2000
Rhinella sternosignata	Boulenger, 1882; Cochran & Goin, 1970; La Marca & Mijares-Urrutia, 1996	La Marca & Mijares-Urrutia, 1996; Vélez-Rodríguez, 2005	Vélez-Rodríguez, 2005
Rhinella tacana	Padial *et al.*, 2006	Padial *et al.*, 2006	
Rhinella tenrec	Lynch & Renjifo, 1990	Lynch & Renjifo, 1990	Lynch & Renjifo, 1990
Rhinella truebae	Lynch & Renjifo, 1990	----	----
Rhinella veredas	Brandao *et al.*, 2007	Brandao *et al.*, 2007	----
Rhinella yanachaga	Lehr *et al.*, 2007	Lehr *et al.*, 2007	Lehr *et al.*, 2007
Rhinella yunga	Moravec *et al.*, 2014	----	----
Sclerophrys arabica	Stock *et al.*, 2001	Stock *et al.*, 2001	----
Sclerophrys asmarae	Tandy *et al.*, 1982	Tandy *et al.*, 1982	----
Sclerophrys blanfordii	----	Boulenger, 1882	----
Sclerophrys buchneri	Peters, 1882	Peters, 1882	----
Sclerophrys capensis	MOP pers. obs.; Poynton, 1964; du Preez & Carruthers, 2009	MOP pers. obs.; Poynton, 1964; du Preez & Carruthers, 2009	----
Sclerophrys channingi	Barej *et al.*, 2011	Barej *et al.*, 2011	----

Sclerophrys chudeaui	Chabanaud, 1919	Chabanaud, 1919	----
Sclerophrys cristiglans	Inger & Menzies, 1961	Inger & Menzies, 1961	----
Sclerophrys danielae	Perret, 1977	Perret, 1977	----
Sclerophrys dodsoni	Boulenger, 1895	Boulenger, 1895	----
Sclerophrys fuliginata	Poynton & Broadley, 1988	Poynton & Broadley, 1988	----
Sclerophrys funerea	----	----	Mendelson, 1997c
Sclerophrys kassasii	Baha El Din, 1993	Baha El Din, 1993	----
Sclerophrys kerinyagae	Keith, 1968	Keith, 1968	----
Sclerophrys pentoni	----	Anderson, 1893	----
Sclerophrys perreti	Onadeko *et al.*, 2014	Onadeko *et al.*, 2014	----
Sclerophrys reesi	Poynton, 1977; Harper *et al.*, 2010	Poynton, 1977	----
Sclerophrys superciliaris	Perret & Amiet, 1971; Barej *et al.*, 2011	Perret & Amiet, 1971; Barej *et al.*, 2011	----
Sclerophrys taiensis	Rödel & Ernst, 2000	Rödel & Ernst, 2000	----
Sclerophrys urunguensis	Loveridge, 1932; Poynton & Broadley, 1988; Poynton *et al.*, 2005	Poynton & Broadley, 1988	----
Sclerophrys vittata	Loveridge, 1932	Loveridge, 1932	----
Truebella skoptes	Graybeal & Cannatella, 1995	Graybeal & Cannatella, 1995	Graybeal & Cannatella, 1995; Pramuk, 2006
Truebella tothastes	Graybeal & Cannatella, 1995	Graybeal & Cannatella, 1995	Graybeal & Cannatella, 1995; Pramuk, 2006
Werneria iboundji	Rödel *et al.*, 2004	----	----
Werneria preussi	Perret & Amiet, 1971; Tandy & Keith, 1972; Rödel *et al.*, 2004	Perret & Amiet, 1971; Tandy & Keith, 1972	Grandison, 1978; Perret & Amiet., 1971
Werneria submontana	Rödel *et al.*, 2004	----	----
Wolterstorffina mirei	Perret, 1972; Boistel & Amiet, 2001	Perret, 1972	Perret, 1972; Grandison, 1978, 1981

Xanthophryne tigerina	Biju *et al.*, 2009	Biju *et al.*, 2009	----
Anura included in Pyron (2014)			
Family	**Species**	**Tympanic membrane**	**Tympanic annulus**
Allophrynidae	*Allophryne ruthveni*	Kok & Kalamandeen, 2008	Kok & Kalamandeen, 2008
Alsodidae	*Alsodes barrioi*	Veloso *et al.*, 1981	Veloso *et al.*, 1981
	Alsodes coppingeri	Grandison, 1961; Formas *et al.*, 2008	Grandison, 1961; Formas *et al.*, 2008
	Alsodes gargola	MOP pers. obs.	MOP pers. obs.
	Alsodes nodosus	Grandison, 1961; Penna *et al.*, 1983	Grandison, 1961; Penna *et al.*, 1983
	Alsodes pehuenche	----	----
	Alsodes tumultuosus	Penna *et al.*, 1983	Penna *et al.*, 1983
	Alsodes valdiviensis	Formas *et al.*, 2002	Formas *et al.*, 2002
	Alsodes vanzolinii	----	----
	Eupsophus calcaratus	----	----
	Eupsophus contulmoensis	Ortiz *et al.*, 1989	----
	Eupsophus emiliopugini	----	Formas, 1989
	Eupsophus roseus	Grandison, 1961	Grandison, 1961
	Eupsophus septentrionalis	Ibarra-Vidal *et al.*, 2004	-----
	Eupsophus vertebralis	Grandison, 1961	Grandison, 1961
	Limnomedusa macroglossa	DB pers. obs.	DB pers. obs.; Boulenger, 1882
Alytidae	*Alytes cisternasii*	----	Boulenger, 1882
	Alytes obstetricans	Wever, 1985	Wever, 1985; Boulenger, 1882
	Discoglossus montalentii	----	Lanza *et al.*, 1984

	Discoglossus pictus	Beukema *et al.*, 2013	Smirnov, 1991; Beukema *et* *al.*, 2013
	Discoglossus sardus	----	Lanza *et al.*, 1984
	Discoglossus scovazzi	----	Lanza *et al.*, 1984
Aromobatidae	*Allobates brunneus*	Lima *et al.*, 2009	Lima *et al.*, 2009
	Allobates femoralis	----	TG pers. obs.
	Allobates granti	----	Kok *et al.*, 2006
	Allobates insperatus	----	TG pers. obs.
	Allobates juanii	----	TG pers. obs.
	Allobates kingsburyi	----	TG pers. obs.
	Allobates talamancae	Savage, 2002	Savage, 2002; TG pers. obs.
	Allobates undulatus	----	----
	Anomaloglossus baebatrachus	Boistel & de Massary, 1999	Boistel & de Massary, 1999
	Anomaloglossus beebei	----	TG pers. obs.
	Anomaloglossus kaiei	Kok & Kalamandeen, 2008	Kok & Kalamandeen, 2008
	Aromobates nocturnus	----	TG pers. obs.
	Mannophryne collaris	----	TG pers. obs.
	Mannophryne herminae	Nussbaum & Wu, 2007	Nussbaum & Wu, 2007; TG pers. obs.
	Mannophryne trinitatis	----	TG pers. obs.
	Rheobates palmatus	----	TG pers. obs.
Arthroleptidae	*Arthroleptis adolfifriederici*	----	-----
	Arthroleptis affinis	Spawls *et al.*, 2006	Spawls *et al.*, 2006
	Arthroleptis poecilonotus	----	Boulenger, 1882
	Arthroleptis reichi	----	-----
	Arthroleptis schubotzi	----	-----

	Arthroleptis stenodactylus	Scott, 2005; Spawls *et al.*, 2006; Nussbaum & Wu, 2007; du Preez & Carruthers, 2009	Scott, 2005; Nussbaum & Wu, 2007; du Preez & Carruthers, 2009
	Arthroleptis taeniatus	Scott, 2005	Scott, 2005
	Arthroleptis tanneri	Spawls *et al.*, 2006	Spawls *et al.*, 2006
	Arthroleptis variabilis	Scott, 2005	Scott, 2005
Aromobatidae (cont.)	*Arthroleptis wahlbergii*	----	Boulenger, 1882
	Arthroleptis xenodactyloides	du Preez & Carruthers, 2009	du Preez & Carruthers, 2009
	Astylosternus batesii	Boulenger, 1900c	Boulenger, 1900c
	Astylosternus diadematus	Scott, 2005	Scott, 2005
	Cardioglossa gracilis	Scott, 2005	Scott, 2005
	Cardioglossa leucomystax	Boulenger, 1903a	Boulenger, 1903a
	Cardioglossa manengouba	Blackburn, 2008	Blackburn, 2008
	Cardioglossa oreas	Blackburn, 2008	Blackburn, 2008
	Leptodactylodon bicolor	Amiet, 1980	----
	Leptopelis argenteus	----	Spawls *et al.*, 2006
	Leptopelis bocagii	du Preez & Carruthers, 2009	Drewes, 1984; du Preez & Carruthers, 2009
	Leptopelis calcaratus	----	Laurent, 1941b
	Leptopelis kivuensis	Spawls *et al.*, 2006	Spawls *et al.*, 2006
	Leptopelis millsoni	----	Laurent, 1941b
	Leptopelis vermiculatus	Scott, 2005	Scott, 2005
	Nyctibates corrugatus	Scott, 2005	Scott, 2005
	Scotobleps gabonicus	Scott, 2005	Scott, 2005
	Trichobatrachus robustus	Scott, 2005	Scott, 2005
Ascaphidae	*Ascaphus truei*	Wever, 1985	Wever, 1985
Batrachylidae	*Atelognathus patagonicus*	----	----

	Atelognathus salai	----	----
	Batrachyla leptopus	BLB pers. obs.	BLB pers. obs.
	Batrachyla taeniata	----	----
	Hylorina sylvatica	BLB pers. obs.	Boulenger, 1882; BLB pers. obs.
Bombinatoridae	*Barbourula busuangensis*	Lynch, 1973; Laurent, 1986	----
	Bombina bombina	Wever, 1985	Wever, 1985
	Bombina maxima	----	----
	Bombina orientalis	Wever, 1985	Wever, 1985
	Bombina pachypus	----	----
	Bombina variegata	Wever, 1985	Wever, 1985
Brachycephalidae	*Brachycephalus alipioi*	Pombal & Gasparini, 2006	Pombal & Gasparini, 2006
	Brachycephalus brunneus	Nussbaum & Wu, 2007; da Silva *et al.*, 2007	Nussbaum & Wu, 2007; da Silva *et al.*, 2007
	Brachycephalus didactylus	da Silva *et al.*, 2007	da Silva *et al.*, 2007
	Brachycephalus ephippium	da Silva *et al.*, 2007; Haddad *et al.*, 2010	da Silva *et al.*, 2007; Haddad *et al.*, 2010
	Brachycephalus ferruginus	Alves *et al.*, 2006	Alves *et al.*, 2006
	Brachycephalus hermogenesi	Haddad *et al.*, 2010; Giaretta & Sawaya, 1998	Haddad *et al.*, 2010; Giaretta & Sawaya, 1998
	Brachycephalus izeckshoni	Haddad *et al.*, 2010; Ribeiro *et al.*, 2005	Haddad *et al.*, 2010; Ribeiro *et al.*, 2005
	Brachycephalus nodoterga	da Silva *et al.*, 2007;	da Silva *et al.*, 2007

		Haddad *et al.*, 2010	
	Brachycephalus pernix	da Silva *et al.*, 2007; Haddad *et al.*, 2010	Haddad *et al.*, 2010; da Silva *et al.*, 2007
	Brachycephalus pitanga	Alves *et al.*, 2009	Alves *et al.*, 2009
	Brachycephalus pombali	Alves *et al.*, 2006	Alves *et al.*, 2006
	Brachycephalus vertebralis	da Silva *et al.*, 2007; Pombal, 2001	da Silva *et al.*, 2007
	Ischnocnema bolbodactyla	Cochran, 1955	Cochran, 1955
	Ischnocnema erythromera	Heyer, 1984	Heyer, 1984
Brachycephalidae (cont.)	*Ischnocnema guentheri*	Heyer *et al.*, 1990	Heyer *et al.*, 1990; Lynch, 1971
	Ischnocnema hoehnei	Heyer *et al.*, 1990	Heyer *et al.*, 1990
	Ischnocnema holti	Targino & Carvalho-e-Silva, 2008	Targino & Carvalho-e-Silva, 2008
	Ischnocnema izecksohni	Caramaschi & Kisteumacher, 1989	Caramaschi & Kisteumacher, 1989
	Ischnocnema juipoca	Haddad *et al.*, 2013	Haddad *et al.*, 2013
	Ischnocnema lactea	Miranda-Ribeiro, 1926	Miranda-Ribeiro, 1926
	Ischnocnema nasuta	Haddad *et al.*, 2013	Haddad *et al.*, 2013
	Ischnocnema octavioi	Vrcibradic *et al.*, 2008	Vrcibradic *et al.*, 2008
	Ischnocnema oea	Heyer, 1984	Heyer, 1984
	Ischnocnema parva	Nussbaum & Wu, 2007; Heyer *et al.*, 1990	Nussbaum & Wu, 2007; Heyer *et al.*, 1990
	Ischnocnema sambaqui	Castanho & Haddad, 2000	Castanho & Haddad, 2000
	Ischnocnema spanios	Heyer, 1985	----

	Ischnocnema venancioi	Lutz, 1958	Lutz, 1958
	Ischnocnema verrucosa	Lynch, 1972	Lynch, 1972
Brevicipitidae	*Balebreviceps hillmani*	Largen & Drewes, 1989	Largen & Drewes, 1989
	Breviceps fuscus	du Preez & Carruthers, 2009	----
	Breviceps mossambicus	Scott, 2005	Parker, 1934; Scott, 2005
	Callulina kreffti	----	Parker, 1934
	Probreviceps loveridgei	Harper *et al.*, 2010	Harper *et al.*, 2010; Parker, 1934
	Probreviceps macrodactylus	Harper *et al.*, 2010	Harper *et al.*, 2010; Parker, 1934
	Probreviceps rungwensis	Harper *et al.*, 2010	Harper *et al.*, 2010; Parker, 1934
	Probreviceps uluguruensis	Harper *et al.*, 2010	Harper *et al.*, 2010; Parker, 1934
	Spelaeophryne methneri	----	Harper *et al.*, 2010; Parker, 1934
Calyptocephalellidae	*Calyptocephalella gayi*	----	Parker, 1881; Boulenger, 1882
	Telmatobufo bullocki	Formas *et al.*, 2001	Formas *et al.*, 2001
	Telmatobufo venustus	Formas *et al.*, 2001	Formas *et al.*, 2001
Centrolenidae	*Celsiella revocata*	----	Guayasamin *et al.*, 2009
	Celsiella vozmedianoi	----	Ayarzagüena & Señaris, 1997; Guayasamin *et al.*, 2009
	Centrolene altitudinale	Guayasamin *et al.*, 2006	Guayasamin *et al.*, 2006
	Centrolene bacatum	Guayasamin *et al.*, 2006	Guayasamin *et al.*, 2006
	Centrolene ballux	----	Duellman & Burrowes, 1989

	Centrolene buckleyi	Guayasamin *et al.*, 2006	Boulenger, 1882; Lynch & Renjifo, 2001; Guayasamin *et al.*, 2006
	Centrolene condor	Cisneros-Heredia & Morales-Mite, 2008	Cisneros-Heredia & Morales-Mite, 2008
	Centrolene daidaleum	Guayasamin *et al.*, 2009	Guayasamin *et al.*, 2009
	Centrolene geckoideum	Rueda-Almonacid, 1994; Lynch & Renjifo, 2001	Boulenger, 1882; Rueda-Almonacid, 1994; Lynch & Renjifo, 2001
	Centrolene heloderma	----	Duellman, 1981
	Centrolene peristictum	Lynch & Duellman, 1973	Lynch & Duellman, 1973
	Centrolene pipilatum	Lynch & Duellman, 1973	Lynch & Duellman, 1973
	Centrolene venezuelense	----	Rivero, 1968b
	Cochranella euknemos	Wever, 1985	Wever, 1985
	Cochranella litoralis	----	Ruiz-Carranza & Lynch, 1996
	Cochranella nola	----	Guayasamin *et al.*, 2009
	Espadarana andina	Ruiz-Carranza & Lynch, 1995	Ruiz-Carranza & Lynch, 1995; Lynch & Renjifo, 2001
	Espadarana callistomma	Guayasamin & Trueb, 2007	Guayasamin & Trueb, 2007
Centrolenidae (cont.)	*Espadarana prosoblepon*	MOP pers. obs.; Ruiz-Carranza & Lynch, 1995	MOP pers. obs.; Ruiz-Carranza & Lynch, 1995
	Hyalinobatrachium aureoguttatum	Barrera-Rodríguez, 1999	Barrera-Rodríguez, 1999; Cisneros & McDiarmid, 2007
	Hyalinobatrachium bergeri	Cannatella, 1980	Cannatella, 1980
	Hyalinobatrachium colymbiphyllum	Savage, 2002	Barrera-Rodríguez, 1999; Savage, 2002

	Hyalinobatrachium eccentricum	----	Cisneros & McDiarmid, 2007
	Hyalinobatrachium fleischmanni	Wever, 1985 present, Savage, 2002 absent	Wever, 1985
	Hyalinobatrachium iaspidiense	Castroviejo-Fisher *et al.*, 2011	Castroviejo-Fisher *et al.*, 2011
	Hyalinobatrachium ibama	----	Ruiz-Carranza & Lynch, 1998
	Hyalinobatrachium ignioculus	----	Guayasamin *et al.*, 2009
	Hyalinobatrachium mondolfii	Castroviejo-Fisher *et al.*, 2011	Castroviejo-Fisher *et al.*, 2011
	Hyalinobatrachium munozorum	Lynch & Duellman, 1973	Lynch & Duellman, 1973
	Hyalinobatrachium orocostale	Rivero, 1968b; Castroviejo-Fisher *et al.*, 2011	Castroviejo-Fisher *et al.*, 2011
	Hyalinobatrachium talamancae	Savage, 2002	Savage, 2002
	Hyalinobatrachium taylori	Castroviejo-Fisher *et al.*, 2011	Castroviejo-Fisher *et al.*, 2011
	Ikakogi tayrona	Ruiz-Carranza & Lynch, 1991	Ruiz-Carranza & Lynch, 1991; Cisneros & McDiarmid, 2007
	Nymphargus bejaranoi	Cannatella, 1980	Cannatella, 1980
	Nymphargus cochranae	Lynch & Duellman, 1973	Lynch & Duellman, 1973
	Nymphargus grandisonae	----	Lynch & Duellman, 1973; Cisneros & McDiarmid, 2007
	Nymphargus griffithsi	----	Lynch & Duellman, 1973
Centrolenidae (cont.)	*Nymphargus megacheirus*	----	Lynch & Duellman, 1973

	Nymphargus posadae	Guayasamin *et al.*, 2006	Guayasamin *et al.*, 2006
	Nymphargus siren	Lynch & Duellman, 1973	Lynch & Duellman, 1973; Cisneros & McDiarmid, 2007
	Nymphargus wileyi	Guayasamin *et al.*, 2006	Guayasamin *et al.*, 2006
	Rulyrana adiazeta	----	Guayasamin *et al.*, 2009
	Rulyrana flavopunctata	----	Lynch & Duellman, 1973
	Sachatamia albomaculata	Savage, 2002	Savage, 2002
	Sachatamia ilex	Savage, 2002	Savage, 2002
	Teratohyla midas	Lynch & Duellman, 1973	Lynch & Duellman, 1973; Beirne & Witworth, 2011
	Teratohyla pulverata	Savage, 2002	Boulenger, 1882; Savage, 2002
	Vitreorana antisthenesi	Rivero, 1968b	Rivero, 1968b
	Vitreorana gorzulae	Kok & Kalamandeen, 2008	Kok & Kalamandeen, 2008
	Vitreorana ritae	Lima *et al.*, 2006	Lima *et al.*, 2006
	Vitreorana uranoscopa	DB pers. obs.; Wever, 1985	DB pers. obs.; Wever, 1985
Ceratobatrachidae	*Alcalus baluensis*	----	Inger, 1966
	Cornufer guentheri	----	Fuiten, 2012
	Cornufer guppyi	----	Fuiten, 2012
	Cornufer papuensis	Menzies, 2006	Menzies, 2006
	Cornufer vertebralis	Scott, 2005	Scott, 2005 Fuiten, 2012
	Platymantis corrugatus	Scott, 2005	Scott, 2005
	Platymantis dorsalis	----	Fuiten, 2012
	Platymantis hazelae	----	Fuiten, 2012 Inger, 1954
Ceratophryidae	*Ceratophrys cornuta*	Lima *et al.*, 2006	Boulenger, 1882; Lima *et al.*, 2006
	Ceratophrys ornata	DB pers. obs.	DB pers. obs.
	Chacophrys pierottii	DB pers. obs.	DB pers. obs.
	Lepidobatrachus laevis	MOP pers. obs.	MOP pers. obs.

Conrauidae	*Conraua crassipes*	Boulenger, 1882; Scott, 2005	Scott, 2005
	Conraua goliath	----	Scott, 2005
Craugastoridae	*Barycholos pulcher*	Heyer, 1969	Heyer, 1969
	Bryophryne cophites	Lynch, 1975b	Lynch, 1975b
	Ceuthomantis smaragdinus	Heinicke *et al.*, 2009	Heinicke *et al.*, 2009
	Craugastor alfredi	Boulenger, 1898	Boulenger, 1898
	Craugastor andi	Savage, 2002	Savage, 2002
	Craugastor angelicus	Savage, 1975	Savage, 1975
	Craugastor augusti	Zweifel, 1956b	Zweifel, 1956b
	Craugastor bocourti	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Craugastor bransfordii	Savage, 2002	Savage, 2002
	Craugastor crassidigitus	Lynch & Myers, 1983	Lynch & Myers, 1983
	Craugastor cuaquero	Savage, 2002	Savage, 2002
	Craugastor daryi	Ford & Savage, 1984	Ford & Savage, 1984
	Craugastor emcelae	Lynch, 1985	Lynch, 1985
	Craugastor fitzingeri	Lynch & Myers, 1983	Lynch & Myers, 1983
	Craugastor fleischmanni	Campbell & Savage, 2000	Campbell & Savage, 2000
	Craugastor laticeps	Savage, 1987	Savage, 1987
	Craugastor lineatus	Savage, 1987	Savage, 1987
	Craugastor loki	Lynch, 2000	Lynch, 2000
	Craugastor longirostris	Wever, 1985; Lynch & Myers, 1983	Wever, 1985; Lynch & Myers, 1983
	Craugastor megacephalus	Savage & Myers, 2002	Savage & Myers, 2002
	Craugastor melanostictus	Savage & DeWeese, 1981	Savage & DeWeese, 1981
	Craugastor mexicanus	Lynch, 2000	Lynch, 2000
	Craugastor montanus	Taylor, 1942	Taylor, 1942
	Craugastor obesus	Campbell & Savage, 2000	Campbell & Savage, 2000
	Craugastor podiciferus	Savage, 2002	Savage, 2002

	Craugastor punctariolus	Campbell & Savage, 2000	Campbell & Savage, 2000
Craugastoridae (cont.)	*Craugastor pygmaeus*	Taylor, 1937 —1936‖	Taylor, 1937 —1936‖
	Craugastor raniformis	Lynch & Myers, 1983	Lynch & Myers, 1983
	Craugastor ranoides	Campbell & Savage, 2000	Campbell & Savage, 2000
	Craugastor rhodopis	Lynch, 2000	Lynch, 2000
	Craugastor rugulosus	Campbell & Savage, 2000	Campbell & Savage, 2000
	Craugastor rupinius	Campbell & Savage, 2000	Campbell & Savage, 2000
	Craugastor sandersoni	Campbell & Savage, 2000	Campbell & Savage, 2000
	Craugastor spatulatus	Smith, 1939	Smith, 1939
	Craugastor stuarti	Lynch, 1965b	Lynch, 1965b
	Craugastor tabasarae	Savage *et al.*, 2004	Savage *et al.*, 2004
	Craugastor talamancae	Savage, 2002	Savage, 2002
	Craugastor tarahumaraensis	Taylor, 1940a	Taylor, 1940a
	Craugastor uno	Streicher *et al.*, 2011	Streicher *et al.*, 2011
	Euparkerella brasiliensis	Izecksohn & de Carvalho-e-Silva, 2001	Izecksohn & de Carvalho-e-
	Haddadus binotatus	MOP pers. obs.	MOP pers. obs.
	Holoaden bradei	Hedges *et al.*, 2008; Lutz, 1958	Hedges *et al.*, 2008;
	Holoaden luederwaldti	Hedges *et al.*, 2008; Miranda-Ribeiro, 1920	Hedges *et al.*, 2008
	Hypodactylus brunneus	Lynch, 1975b	Lynch, 1975b
	Hypodactylus dolops	Lynch & Duellman, 1980	Lynch & Duellman, 1980
	Hypodactylus elassodiscus	Lynch, 1973	Lynch, 1973
	Hypodactylus peraccai	Lynch, 1975b	Lynch, 1975b
	Lynchius flavomaculatus	Parker, 1938	Lynch, 1975b
	Lynchius nebulanastes	Cannatella, 1984	Cannatella, 1984
	Lynchius parkeri	Lynch, 1975b	Lynch, 1975b

	Lynchius simmonsi	Lynch, 1974b	Lynch, 1974b
	Noblella heyeri	Lynch, 1986	Lynch, 1986
	Noblella lochites	Lynch, 1976b	Lynch, 1976b
Silva, 2001			
Craugastoridae (cont.)	*Noblella myrmecoides*	Lynch, 1976b	Lynch, 1976b
	Noblella peruviana	Bokermann, 1975; Noble, 1921	Bokermann, 1975; Noble, 1921
	Oreobates barituensis	Pereyra *et al.*, 2014; Vaira & Ferrari, 2008	Pereyra *et al.*, 2014; Vaira & Ferrari, 2008
	Oreobates choristolemma	Harvey & Sheehy, 2005	Harvey & Sheehy, 2005
	Oreobates cruralis	Boulenger, 1902	Boulenger, 1902
	Oreobates discoidalis	Lynch, 1989; Pereyra *et al.*, 2014	Lynch, 1989; Pereyra *et al.*, 2014
	Oreobates granulosus	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Oreobates heterodactylus	Padial & de la Riva, 2005	Padial & de la Riva, 2005
	Oreobates ibischi	Reichle *et al.*, 2001	Reichle *et al.*, 2001
	Oreobates lehri	Padial *et al.*, 2007	Padial *et al.*, 2007
	Oreobates madidi	Padial *et al.*, 2005a	Padial *et al.*, 2005a
	Oreobates pereger	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Oreobates quixensis	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Oreobates sanctaecrucis	Harvey & Keck, 1995	Harvey & Keck, 1995
	Oreobates sanderi	Padial *et al.*, 2005b	Padial *et al.*, 2005b
	Oreobates saxatilis	Duellman, 1990	Duellman, 1990
	Phrynopus barthlenae	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Phrynopus bracki	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Phrynopus bufoides	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Phrynopus horstpauli	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Phrynopus juninensis	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Phrynopus kauneorum	Duellman & Lehr, 2009	Duellman & Lehr, 2009

	Phrynopus pesantesi	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Phrynopus tautzorum	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis acatallelus	Lynch & Ruiz-Carranza, 1983	Lynch & Ruiz-Carranza, 1983
	Pristimantis acerus	Lynch & Duellman, 1980	Lynch & Duellman, 1980
Craugastoridae (cont.)	*Pristimantis achatinus*	Lynch & Myers, 1983	Lynch & Myers, 1983
	Pristimantis actites	Lynch, 1979c	Lynch, 1979c
	Pristimantis acuminatus	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis altae	Savage, 2002	Savage, 2002
	Pristimantis altamazonicus	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis angustilineatus	Lynch, 1998	Lynch, 1998
	Pristimantis aniptopalmatus	----	Duellman & Hedges, 2005
	Pristimantis appendiculatus	Lynch & Duellman, 1997	Lynch & Duellman, 1997
	Pristimantis ardalonychus	Duellman & Pramuk, 1999	Duellman & Pramuk, 1999
	Pristimantis bipunctatus	----	Duellman & Hedges, 2005
	Pristimantis bogotensis	Avilan & Hoyos, 2006	Avilan & Hoyos, 2006
	Pristimantis brevifrons	Lynch, 1981b	Lynch, 1981b
	Pristimantis bromeliaceus	Lynch, 1979b	Lynch, 1979b
	Pristimantis buccinator	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis buckleyi	Lynch, 1981a	Lynch, 1981a
	Pristimantis cajamarcensis	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis calcaratus	Lynch, 1996	Ospina-Sarria *et al*., 2011
	Pristimantis calcarulatus	Lynch & Duellman, 1997	Lynch & Duellman, 1997
	Pristimantis caprifer	Lynch & Duellman, 1997	Lynch & Duellman, 1997
	Pristimantis caryophyllaceus	Savage, 2002	Savage, 2002
	Pristimantis celator	Lynch, 1976a	Lynch, 1976a

	Pristimantis cerasinus	Savage, 1981	----
	Pristimantis ceuthospilus	Duellman & Wild, 1993	Duellman & Wild, 1993
	Pristimantis chalceus	Lynch & Duellman, 1997	Lynch & Duellman, 1997
	Pristimantis chiastonotus	Lynch & Hoogmoed, 1977	Lynch & Hoogmoed, 1977
	Pristimantis chloronotus	Lynch, 1969	Lynch, 1969
	Pristimantis citriogaster	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis colomai	Lynch & Duellman, 1997	Lynch & Duellman, 1997
Craugastoridae (cont.)	*Pristimantis condor*	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis conspicillatus	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis cremnobates	Lynch & Duellman, 1980	Lynch & Duellman, 1980
	Pristimantis crenunguis	Lynch, 1976a	Lynch, 1976a
	Pristimantis croceoinguinis	Lynch, 1968	Lynch, 1968
	Pristimantis crucifer	Lynch, 1976a	Lynch, 1976a
	Pristimantis cruentus	Savage, 1981	Savage, 1981
	Pristimantis cryophilius	Lynch, 1979b	Lynch, 1979b
	Pristimantis curtipes	Lynch, 1981a	Lynch, 1981a
	Pristimantis danae	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis devillei	Lynch, 1969	Lynch, 1969
	Pristimantis diadematus	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis dissimulatus	Lynch & Duellman, 1997	Lynch & Duellman, 1997
	Pristimantis duellmani	Lynch, 1980c	Lynch, 1980c
	Pristimantis eriphus	Lynch & Duellman, 1980	Lynch & Duellman, 1980
	Pristimantis erythropleura	Lynch, 1994	Lynch, 1994
	Pristimantis euphronides	Kaiser *et al.*, 1994b	Kaiser *et al.*, 1994b
	Pristimantis fenestratus	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis frater	Pyburn & Lynch, 1981	Pyburn & Lynch, 1981
	Pristimantis gaigei	Wever, 1985; Lynch, 1980a	Wever, 1985; Lynch, 1980a
	Pristimantis galdi	Lynch & Duellman, 1980	Lynch & Duellman, 1980
	Pristimantis gentry	----	MTR pers. obs.

	Pristimantis glandulosus	Lynch, 1969	Lynch, 1969
	Pristimantis gutturalis	Hoogmoed *et al.*, 1977	Hoogmoed *et al.*, 1977
	Pristimantis hectus	Lynch & Duellman, 1997	Lynch & Duellman, 1997
	Pristimantis imitatrix	Duellman, 1978	Duellman, 1978
	Pristimantis inguinalis	----	Parker, 1940
	Pristimantis inusitatus	Lynch & Duellman, 1980	Lynch & Duellman, 1980
Craugastoridae (cont.)	*Pristimantis juanchoi*	JJOS pers. obs.	Lynch, 1996
	Pristimantis jubatus	García-R & Lynch, 2006	García-R & Lynch, 2006
	Pristimantis kelephus	Lynch, 1998	Lynch, 1998
	Pristimantis koehleri	Padial & de la Riva, 2009	Padial & de la Riva, 2009
	Pristimantis labiosus	Lynch & Duellman, 1997	Lynch & Duellman, 1997
	Pristimantis lanthanites	Lynch, 1975a	Lynch, 1975a
	Pristimantis latidiscus	Lynch & Duellman, 1997	Lynch & Duellman, 1997
	Pristimantis leoni	Lynch & Duellman, 1997	Lynch & Duellman, 1997
	Pristimantis librarius	----	Flores & Vigle, 1994
	Pristimantis lirellus	Duellman & Pramuk, 1999	Duellman & Pramuk, 1999
	Pristimantis llojsintuta	Köhler & Lötters, 1999	Köhler & Lötters, 1999
	Pristimantis luteolateralis	----	Lynch, 1976a
	Pristimantis lymani	Lynch & Duellman, 1997	Lynch & Duellman, 1997
	Pristimantis malkini	Lynch, 1980b	Lynch, 1980b
	Pristimantis marmoratus	Ouboter & Jairam, 2012	Ouboter & Jairam, 2012
	Pristimantis martiae	Lynch, 1974a	Lynch, 1974a
	Pristimantis melanogaster	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis miyatai	Lynch, 1984	Lynch, 1984
	Pristimantis moro	Savage, 2002	----
	Pristimantis museosus	Ibañez *et al.*, 1994	Ibañez *et al.*, 1994
	Pristimantis myops	Lynch, 1998	Lynch, 1998
	Pristimantis nervicus	Lynch, 1994	Lynch, 1994
	Pristimantis nyctophylax		Lynch, 1976a
	Pristimantis ockendeni	Duellman & Lehr, 2009	Duellman & Lehr, 2009

	Pristimantis ocreatus	Lynch, 1981a	Lynch, 1981a
	Pristimantis orcesi	Lynch, 1981a	Lynch, 1981a
	Pristimantis orestes	Lynch, 1979b	Lynch, 1979b
	Pristimantis paisa	Lynch & Ardila-Robayo, 1999	Lynch & Ardila-Robayo, 1999
Craugastoridae (cont.)	*Pristimantis palmeri*	JJOS pers. obs.	Lynch, 1996
	Pristimantis pardalis	Savage, 2002	Savage, 2002
	Pristimantis parvillus	Lynch, 1976a	Lynch, 1976a
	Pristimantis peruvianus	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis petrobardus	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis phoxocephalus	Lynch, 1979b	Lynch, 1979b
	Pristimantis pirrensis	Ibañez & Crawford, 2004	Ibañez & Crawford, 2004
	Pristimantis platydactylus	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis prolatus	Lynch & Duellman, 1980	Lynch & Duellman, 1980
	Pristimantis ptochus	----	Lynch, 1998
	Pristimantis pulvinatus	Rivero, 1968a	Rivero, 1968a
	Pristimantis pycnodermis	Lynch, 1979b	Lynch, 1979b
	Pristimantis pyrrhomerus	Lynch & Duellman, 1997	Lynch & Duellman, 1997
	Pristimantis quantus	Lynch, 1998	Lynch, 1998
	Pristimantis quaquaversus	Lynch, 1974a	Lynch, 1974a
	Pristimantis quinquagesimus	Lynch & Duellman, 1997	Lynch & Duellman, 1997
	Pristimantis ramagii	Boulenger, 1888	Boulenger, 1888
	Pristimantis reichlei	Padial & de la Riva, 2009	Padial & de la Riva, 2009
	Pristimantis rhabdocnemus	Duellman & Hedges, 2005	Duellman & Hedges, 2005
	Pristimantis rhabdolaemus	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis rhodoplichus	Duellman & Wild, 1993	Duellman & Wild, 1993
	Pristimantis ridens	Savage, 2002	Savage, 2002

	Pristimantis riveti	Lynch, 1979b	Lynch, 1979b
	Pristimantis rozei	Rivero, 1961	Rivero, 1961
	Pristimantis sagittulus	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis samaipatae	Köhler & Jungfer, 1995	Köhler & Jungfer, 1995
	Pristimantis savagei	Pyburn & Lynch, 1981	Pyburn & Lynch, 1981
	Pristimantis schultei	Duellman & Lehr, 2009	Duellman & Lehr, 2009
Craugastoridae (cont.)	*Pristimantis shrevei*	Kaiser *et al.*, 1994b	Kaiser *et al.*, 1994b
	Pristimantis simonbolivari	Lynch & Duellman, 1997	Lynch & Duellman, 1997
	Pristimantis simonsii	Lynch, 1975b	Lynch, 1975b
	Pristimantis skydmainos	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis spinosus	Lynch, 1979b	Lynch, 1979b
	Pristimantis stictogaster	Duellman & Hedges, 2005	Duellman & Hedges, 2005
	Pristimantis subsigillatus	Lynch & Duellman, 1997	Lynch & Duellman, 1997
	Pristimantis suetus	Lynch & Rueda-Almonacid, 1998	Lynch & Rueda-Almonacid, 1998
	Pristimantis supernatis	Lynch, 1979a	Lynch, 1979a
	Pristimantis surdus	Lynch, 1980c	Lynch, 1980c
	Pristimantis taeniatus	Lynch, 1980a	Lynch, 1980a
	Pristimantis terraebolivaris	Rivero, 1961	Rivero, 1961
	Pristimantis thectopternus	Lynch, 1975a	Lynch, 1975a
	Pristimantis thymalopsoides	LAC pers. obs.	Lynch, 1976a
	Pristimantis thymelensis	Lynch, 1981a	Lynch, 1981a
	Pristimantis toftae	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Pristimantis truebae	Lynch & Duellman, 1997	Lynch & Duellman, 1997
	Pristimantis unistrigatus	Lynch & Duellman, 1980	Lynch & Duellman, 1980
	Pristimantis urichi	Kaiser *et al.*, 1994b	Kaiser *et al.*, 1994b
	Pristimantis ventrimarmoratus	Lynch & Duellman, 1980	Lynch & Duellman, 1980

	Pristimantis verecundus	Lynch & Burrowes, 1990	Lynch & Burrowes, 1990
	Pristimantis versicolor	Lynch, 1979b	Lynch, 1979b
	Pristimantis vertebralis	Lynch, 1979a	Lynch, 1979a
	Pristimantis viejas	Lynch & Rueda-Almonacid, 1999	Lynch & Rueda-Almonacid, 1999
	Pristimantis walkeri	Lynch, 1974a	Lynch, 1974a
	Pristimantis wiensi	----	Duellman & Wild, 1993
	Pristimantis wnigrum	Lynch & Duellman, 1997	Lynch & Duellman, 1997
Craugastoridae (cont.)	*Pristimantis zophus*	Lynch & Ardila-Robayo, 1999	Lynch & Ardila-Robayo, 1999
	Psychrophrynella iatamasi	Aguayo-Vedia & Harvey, 2001	----
	Psychrophrynella wettsteini	Lehr, 2006	----
	Strabomantis anomalus	Lynch & Myers, 1983	Lynch & Myers, 1983
	Strabomantis biporcatus	Savage & Myers, 2002	Savage & Myers, 2002
	Strabomantis bufoniformis	Lynch, 2000	Lynch, 2000
	Strabomantis necerus	Lynch, 1975c	Lynch, 1975c
	Strabomantis sulcatus	Duellman & Lehr, 2009	Duellman & Lehr, 2009
	Yunganastes ashkapara	Köhler, 2000b	Köhler, 2000b
	Yunganastes bisignatus	Köhler, 2000a	Köhler, 2000a
	Yunganastes fraudator	Lynch & McDiarmid, 1987	Lynch & McDiarmid, 1987
	Yunganastes mercedesae	Lynch & McDiarmid, 1987	Padial *et al.*, 2007
	Yunganastes pluvicanorus	de la Riva & Lynch, 1997	Padial *et al.*, 2007
Cycloramphidae	*Cycloramphus boraceiensis*	MOP pers. obs.; Heyer *et al.*, 1990	----
	Cycloramphus eleutherodactylus	Verdade, 2005	Verdade, 2005
	Thoropa miliaris	----	Boulenger, 1882
	Thoropa taophora	MOP pers. obs.	MOP pers. obs.

	Zachaenus parvulus	Verdade, 2005	Verdade, 2005
Dendrobatidae	*Adelphobates castaneoticus*	----	----
	Adelphobates galactonotus	----	----
	Ameerega bassleri	----	TG pers. obs.
	Ameerega bilinguis	Beirne & Witworth, 2011	TG pers. obs.; Beirne & Witworth, 2011
	Ameerega hahneli	----	TG pers. obs.
	Ameerega macero	----	Rodríguez & Myers, 1993
	Ameerega parvula	----	Boulenger, 1882
Dendrobatidae (cont.)	*Ameerega petersi*	----	TG pers. obs.; Lynch & Renjifo, 2001
	Ameerega picta	----	TG pers. obs.
	Ameerega silverstonei	TG pers. obs.	TG pers. obs.
	Ameerega simulans	Myers *et al.*, 1998	Myers *et al.*, 1998
	Ameerega trivittata	----	TG pers. obs.; Boulenger, 1882
	Andinobates claudiae	----	TG pers. obs.
	Andinobates fulguritus	----	TG pers. obs.
	Colostethus fugax	----	Coloma, 1995
	Colostethus inguinalis	Wever, 1985	Wever, 1985; Boulenger, 1882
	Colostethus latinasus	----	Boulenger, 1882
	Colostethus panamensis	----	TG pers. obs.
	Colostethus pratti	----	TG pers. obs.
	Dendrobates auratus	Nussbaum & Wu, 2007; Wever, 1985; Savage, 2002	Nussbaum & Wu, 2007; Wever, 1985
	Dendrobates tinctorius	----	TG pers. obs.; Boulenger, 1882
	Dendrobates truncatus	----	TG pers. obs.
	Epipedobates anthonyi	----	----

	Epipedobates boulengeri	----	TG pers. obs.
	Epipedobates espinosai	----	TG pers. obs.
	Excidobates captivus	----	TG pers. obs.
	Excidobates mysteriosus	----	Myers, 1982
	Hyloxalus awa	----	TG pers. obs.
	Hyloxalus bocagei	Beirne & Witworth, 2011	TG pers. obs.; Boulenger, 1882; Beirne & Witworth, 2011
	Hyloxalus chlorocraspedus	----	Caldwell, 2005
	Hyloxalus elachyhistus	----	TG pers. obs.
(cont.)	*Hyloxalus nexipus*	----	Frost, 1986
	Hyloxalus pulchellus	----	TG pers. obs.; Boulenger, 1882
	Hyloxalus sauli	----	TG pers. obs.
	Hyloxalus subpunctatus	Lynch & Renjifo, 2001	TG pers. obs.
	Hyloxalus sylvaticus	----	TG pers. obs.
	Hyloxalus vertebralis	----	TG pers. obs.
	Minyobates steyermarki	----	TG pers. obs.
	Oophaga arborea	----	TG pers. obs.
	Oophaga granulifera	----	TG pers. obs.
	Oophaga histrionica	----	TG pers. obs.
	Oophaga lehmanni	----	TG pers. obs.
	Oophaga pumilio	Savage, 2002	TG, Boulenger, 1882; Savage, 2002
	Oophaga speciosa	----	TG pers. obs.
	Oophaga sylvatica	----	TG pers. obs.
	Oophaga vicentei	----	TG pers. obs.
	Phyllobates aurotaenia	----	TG pers. obs.
	Phyllobates bicolor	----	TG pers. obs.; Boulenger,

			1882
	Phyllobates lugubris	----	TG pers. obs.
	Phyllobates terribilis	----	TG pers. obs.
	Phyllobates vittatus	----	TG pers. obs.
	Ranitomeya amazonica	----	Brown *et al.*, 2011
	Ranitomeya imitator	----	TG pers. obs.
	Ranitomeya reticulata	----	TG pers. obs.
	Ranitomeya ventrimaculata	Beirne & Witworth, 2011	TG pers. obs.; Beirne & Witworth, 2011
	Silverstoneia flotator	----	TG pers. obs.
	Silverstoneia nubicola	----	TG pers. obs.
Dicroglossidae	*Euphlyctis cyanophlyctis*	Scott, 2005	Scott, 2005; Parker, 1881; Boulenger, 1882
	Euphlyctis hexadactylus	Boulenger, 1882	Boulenger, 1882
	Fejervarya cancrivora	Zhao & Adler, 1993	Inger, 1966; Zhao & Adler, 1993
	Fejervarya caperata	Kuramoto *et al.*, 2007	Kuramoto *et al.*, 2007
	Fejervarya granosa	Kuramoto *et al.*, 2007	Kuramoto *et al.*, 2007
	Fejervarya kudremukhensis	Kuramoto *et al.*, 2007	Kuramoto *et al.*, 2007
	Fejervarya iskandari	----	Veith *et al.*, 2001
	Fejervarya limnocharis	----	Liu, 1950; Inger, 1966
	Fejervarya mudduraja	Kuramoto *et al.*, 2007	Kuramoto *et al.*, 2007; Chandramouli & Dutta, 2015
	Fejervarya rufescens	----	Boulenger, 1882
	Fejervarya sahyadris	----	Chandramouli & Dutta, 2015
	Hoplobatrachus occipitalis	Scott, 2005	Boulenger, 1882; Scott, 2005

	Hoplobatrachus rugulosus	----	Inger & Stuebing, 1997
	Hoplobatrachus tigerinus	Glaw & Vences, 2007	Boulenger, 1882; Glaw & Vences, 2007
	Ingerana tenasserimensis	----	Iskandar *et al.*, 2011
	Limnonectes asperatus	----	Inger *et al.,* 1996
	Limnonectes blythii	Scott, 2005; Emerson & Berrigan, 1993	Scott, 2005; Emerson & Berrigan, 1993
	Limnonectes dabanus	----	Stuart *et al.*, 2006
	Limnonectes doriae	----	Boulenger, 1920
	Limnonectes finchi	Emerson & Berrigan, 1993	Emerson & Berrigan, 1993
	Limnonectes hascheanus	Emerson & Berrigan, 1993	Emerson & Berrigan, 1993
	Limnonectes ibanorum	----	Inger, 1966
	Limnonectes kuhlii	Inger, 1966; Boulenger, 1882	Inger, 1966
	Limnonectes laticeps	Inger, 1966; Boulenger, 1882	Inger, 1966
	Limnonectes leporinus	Inger & Stuebing, 1997	Inger & Stuebing, 1997
Dicroglossidae (cont.)	*Limnonectes leytensis*	Emerson & Berrigan, 1993	Emerson & Berrigan, 1993
	Limnonectes macrodon	----	Inger, 1966; Boulenger, 1882
	Limnonectes magnus	----	Boulenger, 1920
	Limnonectes malesianus	Inger & Stuebing, 1997	Inger & Stuebing, 1997
	Limnonectes microdiscus	----	Inger, 1966
	Limnonectes microtympanum	----	Boulenger, 1920
	Limnonectes modestus	----	Boulenger, 1882
	Limnonectes palavanensis	Inger & Stuebing, 1997	Inger & Stuebing, 1997
	Limnonectes paramacrodon	Inger & Stuebing, 1997	Inger & Stuebing, 1997
	Limnonectes plicatellus	Emerson & Berrigan, 1993	Emerson & Berrigan, 1993
	Limnonectes woodworthi	----	Inger, 1954

	Nannophrys ceylonensis	Scott, 2005	Scott, 2005
	Nannophrys marmorata	----	----
	Nanorana aenea	----	Dubois & Ohler, 2005
	Nanorana arnoldi	----	Dubois, 1975
	Nanorana liebigii	Ohler & Dubois, 2006	Boulenger, 1882; Günther, 1860
	Nanorana parkeri	Scott, 2005	Scott, 2005
	Nanorana pleski	Günther, 1896; Liu, 1950; Lu & Yang, 1995	Günther, 1896; Liu, 1950; Lu & Yang, 1995
	Nanorana quadranus	----	Ohler & Dubois, 2006
	Nanorana ventripunctata	Lu & Yang, 1995	----
	Nanorana yunnanensis	Zhao & Adler, 1993	Boulenger, 1882
	Occidozyga baluensis		Inger, 1966
	Occidozyga laevis	Boulenger, 1882 absent; Scott, 2005 present	Inger, 1966; Scott, 2005
	Occidozyga lima	Zhao & Adler, 1993	----
	Quasipaa delacouri	Dubois, 1975	----
	Quasipaa shini	Zhao & Adler, 1993	Zhao & Adler, 1993
Dicroglossidae (cont.)	*Quasipaa spinosa*	----	----
	Sphaerotheca breviceps	----	Boulenger, 1882
	Sphaerotheca dobsonii	----	Boulenger, 1882
Eleutherodactylidae	*Adelophryne adiastola*	Hoogmoed & Lescure, 1984	Hoogmoed & Lescure, 1984
	Adelophryne baturitensis	Hoogmoed *et al.*, 1994	Hoogmoed *et al.*, 1994
	Adelophryne gutturosa	Hoogmoed & Lescure, 1984; Kok & Kalamandeen, 2008	Hoogmoed & Lescure, 1984; Kok & Kalamandeen, 2008
	Adelophryne maranguapensis	Hoogmoed *et al.*, 1994	Hoogmoed *et al.*, 1994

	Adelophryne pachydactyla	Hoogmoed *et al.*, 1994	Hoogmoed *et al.*, 1994
	Adelophryne patamona	MacCulloch *et al.*, 2008; Kok & Kalamandeen, 2008	MacCulloch *et al.*, 2008; Kok & Kalamandeen, 2008
	Diasporus diastema	Savage, 2002	Savage, 2002
	Diasporus hylaeformis	Savage, 2002	Savage, 2002
	Diasporus vocator	Savage, 2002; Taylor, 1955	Savage, 2002
	Eleutherodactylus abbotti	Cochran, 1923	Cochran, 1923
	Eleutherodactylus acmonis	Díaz & Cádiz, 2008	Díaz & Cádiz, 2008
	Eleutherodactylus adelus	Diaz *et al.*, 2003	Diaz *et al.*, 2003
	Eleutherodactylus albipes	Barbour & Shreve, 1937	Barbour & Shreve, 1937
	Eleutherodactylus alcoae	Schwartz, 1976b	Schwartz, 1976b
	Eleutherodactylus alticola	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus amadeus	Hedges *et al.*, 1987	Hedges *et al.*, 1987
	Eleutherodactylus amplinympha	Kaiser *et al.*, 1994a	Kaiser *et al.*, 1994a
	Eleutherodactylus andrewsi	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus antillensis	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus apostates	Schwartz, 1973	Schwartz, 1973
	Eleutherodactylus armstrongi	Noble & Hassler, 1933	Noble & Hassler, 1933
	Eleutherodactylus atkinsi	Dunn, 1925; Nussbaum & Wu, 2007	Dunn, 1925; Nussbaum & Wu, 2007
	Eleutherodactylus audanti	Schwartz, 1966	Schwartz, 1966
Eleutherodactylidae (cont.)	*Eleutherodactylus auriculatoides*	Cope, 1862b, Noble, 1923	Cope, 1862b, Noble, 1923

	Eleutherodactylus auriculatus	Cope, 1862b	Cope, 1862b
	Eleutherodactylus bakeri	Cochran, 1935	Cochran, 1935
	Eleutherodactylus barlagnei	Lynch, 1965a	Lynch, 1965a
	Eleutherodactylus bartonsmithi	Díaz & Cádiz, 2008	Díaz & Cádiz, 2008
	Eleutherodactylus blairhedgesi	Estrada *et al.*, 1998	Estrada *et al.*, 1998
	Eleutherodactylus bothroboans	Schwartz, 1965b	Schwartz, 1965b
	Eleutherodactylus bresslerae	Díaz & Cádiz, 2008	Díaz & Cádiz, 2008
	Eleutherodactylus brevirostris	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus brittoni	Schmidt, 1920	Schmidt, 1920
	Eleutherodactylus caribe	Hedges & Thomas, 1992a	Hedges & Thomas, 1992a
	Eleutherodactylus casparii	Díaz & Cádiz, 2008	Díaz & Cádiz, 2008
	Eleutherodactylus cavernicola	Lynn, 1954	Lynn, 1954
	Eleutherodactylus chlorophenax	Schwartz, 1976a	Schwartz, 1976a
	Eleutherodactylus cochranae	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus cooki	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus coqui	Zug, 2013	Zug, 2013
	Eleutherodactylus corona	Hedges & Thomas, 1992b	Hedges & Thomas, 1992b
	Eleutherodactylus counouspeus	Schwartz, 1964	Schwartz, 1964
	Eleutherodactylus cubanus	Barbour & Shreve, 1937	Barbour & Shreve, 1937
	Eleutherodactylus cundalli	Hedges *et al.*, 2008	Hedges *et al.*, 2008

	Eleutherodactylus cuneatus	Cope, 1862b	Cope, 1862b
	Eleutherodactylus darlingtoni	Cochran, 1935	Cochran, 1935
	Eleutherodactylus dimidiatus	Cope, 1862b	Cope, 1862b
Eleutherodactylidae (cont.)	*Eleutherodactylus dolomedes*	Hedges & Thomas, 1992b	Hedges & Thomas, 1992b
	Eleutherodactylus eileenae	Dunn, 1926	Dunn, 1926
	Eleutherodactylus emiliae	Dunn, 1926	Dunn, 1926
	Eleutherodactylus eneidae	Rivero, 1959	Rivero, 1959
	Eleutherodactylus etheridgei	Schwartz, 1958b	Schwartz, 1958b
	Eleutherodactylus eunaster	Schwartz, 1973	Schwartz, 1973
	Eleutherodactylus flavescens	Noble, 1923	Noble, 1923
	Eleutherodactylus fowleri	Schwartz, 1973	Schwartz, 1973
	Eleutherodactylus furcyensis	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus fuscus	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus glamyrus	Estrada & Hedges, 1997b	Estrada & Hedges, 1997b
	Eleutherodactylus glandulifer	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus glanduliferoides	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus glaphycompus	Schwartz, 1973	Schwartz, 1973
	Eleutherodactylus glaucoreius	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus goini	Díaz & Cádiz, 2008	Díaz & Cádiz, 2008

	Eleutherodactylus gossei	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus grabhami	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus grahami	Schwartz, 1979	Schwartz, 1979
	Eleutherodactylus greyi	Díaz & Cádiz, 2008	Díaz & Cádiz, 2008
	Eleutherodactylus griphus	Crombie, 1986	Crombie, 1986
	Eleutherodactylus gryllus	Schmidt, 1920	Schmidt, 1920
	Eleutherodactylus guanahacabibes	Díaz & Cádiz, 2008	Díaz & Cádiz, 2008
	Eleutherodactylus guantanamera	Hedges *et al.*, 1992	Hedges *et al.*, 1992
	Eleutherodactylus gundlachi	Barbour, 1914	Barbour, 1914
	Eleutherodactylus haitianus	Cochran, 1941	Cochran, 1941
Eleutherodactylidae (cont.)	*Eleutherodactylus hedricki*	Rivero, 1963	Rivero, 1963
	Eleutherodactylus heminota	Hedges *et al.*, 2008; Nussbaum & Wu, 2007	Hedges *et al.*, 2008; Nussbaum & Wu, 2007
	Eleutherodactylus hypostenor	Schwartz, 1965b	Schwartz, 1965b
	Eleutherodactylus iberia	Estrada & Hedges, 1996	Estrada & Hedges, 1996
	Eleutherodactylus inoptatus	Barbour, 1914	Barbour, 1914
	Eleutherodactylus intermedius	Díaz & Cádiz, 2008	Díaz & Cádiz, 2008
	Eleutherodactylus ionthus	Díaz & Cádiz, 2008	Díaz & Cádiz, 2008
	Eleutherodactylus jamaicensis	Barbour, 1910	Barbour, 1910
	Eleutherodactylus jaumei	Estrada & Alonso, 1997	Estrada & Alonso, 1997
	Eleutherodactylus	Barbour, 1914	Barbour, 1914

	johnstonei		
	Eleutherodactylus jugans	Cochran, 1935	Cochran, 1935
	Eleutherodactylus junori	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus klinikowskii	Díaz & Cádiz, 2008	Díaz & Cádiz, 2008
	Eleutherodactylus lamprotes	Schwartz, 1973	Schwartz, 1973
	Eleutherodactylus leberi	Díaz & Cádiz, 2008	Díaz & Cádiz, 2008
	Eleutherodactylus lentus	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus leoncei	Hedges, 1992	Hedges, 1992
	Eleutherodactylus limbatus	Cope, 1862b, Nussbaum & Wu, 2007	Cope, 1862b, Nussbaum & Wu, 2007
	Eleutherodactylus locustus	Schmidt, 1920	Schmidt, 1920
	Eleutherodactylus luteolus	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus maestrensis	Diaz *et al.*, 2005	Diaz *et al.*, 2005
	Eleutherodactylus mariposa	Hedges *et al.*, 1992	Hedges *et al.*, 1992
	Eleutherodactylus marnockii	Hedges *et al.*, 1992	Hedges *et al.*, 1992
	Eleutherodactylus martinicensis	Lynch, 1965a	Lynch, 1965a
	Eleutherodactylus melacara	Hedges *et al.*, 1992	Hedges *et al.*, 1992
	Eleutherodactylus minutus	Noble, 1923	Noble, 1923
Eleutherodactylidae (cont.)	*Eleutherodactylus monensis*	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus nitidus	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus nortoni	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus nubicola	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus orcutti	Hedges *et al.*, 2008	Hedges *et al.*, 2008

	Eleutherodactylus orientalis	Díaz & Cádiz, 2008	Díaz & Cádiz, 2008
	Eleutherodactylus oxyrhyncus	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus pantoni	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus parabates	Schwartz, 1964	Schwartz, 1964
	Eleutherodactylus parapelates	Hedges & Thomas, 1987	Hedges & Thomas, 1987
	Eleutherodactylus patriciae	Schwartz, 1965 "1964"	Schwartz, 1965 "1964"
	Eleutherodactylus paulsoni	Schwartz, 1964	Schwartz, 1964
	Eleutherodactylus pentasyringos	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus pezopetrus	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus pictissimus	Cochran, 1935	Cochran, 1935
	Eleutherodactylus pinarensis	Dunn, 1926	Dunn, 1926
	Eleutherodactylus pinchoni	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus pipilans	Taylor, 1940b	Taylor, 1940b
	Eleutherodactylus pituinus	Schwartz, 1965a	Schwartz, 1965a
	Eleutherodactylus planirostris	Cope, 1862b	Cope, 1862b
	Eleutherodactylus poolei	Cochran, 1938	Cochran, 1938
	Eleutherodactylus portoricensis	Schmidt, 1927	Schmidt, 1927
	Eleutherodactylus principalis	Estrada & Hedges, 1997c	Estrada & Hedges, 1997c
	Eleutherodactylus probalaeus	Schwartz, 1976b	Schwartz, 1976b

	Eleutherodactylus rhodesi	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus richmondi	Schmidt, 1920	Schmidt, 1920
	Eleutherodactylus ricordii	Díaz & Cádiz, 2008	Díaz & Cádiz, 2008
Eleutherodactylidae (cont.)	*Eleutherodactylus riparius*	Diaz *et al.*, 2001	Diaz *et al.*, 2001
	Eleutherodactylus rivularis	Diaz *et al.*, 2001	Diaz *et al.*, 2001
	Eleutherodactylus rogersi	Goin, 1955	Goin, 1955
	Eleutherodactylus ronaldi	Diaz *et al.*, 2001	Diaz *et al.*, 2001
	Eleutherodactylus rufifemoralis	Noble & Hassler, 1933	Noble & Hassler, 1933
	Eleutherodactylus ruthae	Cochran, 1941	Cochran, 1941
	Eleutherodactylus schmidti	Noble, 1923	Noble, 1923
	Eleutherodactylus schwartzi	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus sciagraphus	Schwartz, 1973	Schwartz, 1973
	Eleutherodactylus simulans	Díaz & Fong, 2001	Díaz & Fong, 2001
	Eleutherodactylus sisyphodemus	Crombie, 1977	Crombie, 1977
	Eleutherodactylus sommeri	Schwartz, 1977	Schwartz, 1977
	Eleutherodactylus symingtoni	Schwartz, 1957	Schwartz, 1957
	Eleutherodactylus thomasi	Schwartz, 1959	Schwartz, 1959
	Eleutherodactylus thorectes	Hedges, 1988	Hedges, 1988
	Eleutherodactylus toa	Estrada & Hedges, 1991	Estrada & Hedges, 1991
	Eleutherodactylus tonyi	Estrada & Hedges, 1997a	Estrada & Hedges, 1997a
	Eleutherodactylus turquinensis	Barbour & Shreve, 1937	Barbour & Shreve, 1937
	Eleutherodactylus unicolor	Hedges *et al.*, 2008	Hedges *et al.*, 2008

	Eleutherodactylus varians	Díaz & Cádiz, 2008	Díaz & Cádiz, 2008
	Eleutherodactylus varleyi	Dunn, 1925; Nussbaum & Wu, 2007	Dunn, 1925; Nussbaum & Wu, 2007
	Eleutherodactylus ventrilineatus	Hedges *et al.*, 2008	Hedges *et al.*, 2008
	Eleutherodactylus weinlandi	Barbour, 1914	Barbour, 1914
	Eleutherodactylus wetmorei	Cochran, 1932	Cochran, 1932
Eleutherodactylidae (cont.)	*Eleutherodactylus wightmanae*	Schmidt, 1920	Schmidt, 1920
	Eleutherodactylus zeus	Schwartz, 1958a	Schwartz, 1958a
	Eleutherodactylus zugi	Schwartz, 1958a	Schwartz, 1958a
	Phyzelaphryne miriamae	Heyer, 1977	Heyer, 1977
Heleophrynidae	*Hadromophryne natalensis*	du Preez & Carruthers, 2009	----
	Heleophryne purcelli	Scott, 2005; du Preez & Carruthers, 2009	Scott, 2005
Hemiphractidae	*Flectonotus fitzgeraldi*		
	Flectonotus pygmaeus	----	Duellman *et al.*, 2011
	Gastrotheca argenteovirens	----	Cochran & Goin, 1970
	Gastrotheca atympana	Duellman, 2015	Duellman, 2015
	Gastrotheca aureomaculata	Duellman, 2015	Cochran & Goin, 1970; Duellman, 2015
	Gastrotheca christiani	Laurent *et al.*, 1986	Laurent *et al.*, 1986
	Gastrotheca chrysosticta	Laurent *et al.*, 1986	Laurent *et al.*, 1986
	Gastrotheca cornuta	Cochran & Goin, 1970	Cochran & Goin, 1970
	Gastrotheca dendronastes	----	Duellman, 2015
	Gastrotheca dunni	----	Duellman, 2015

	Gastrotheca excubitor	Catenazzi *et al.*, 2013	Catenazzi *et al.*, 2013
	Gastrotheca fissipes	Mendes *et al.*, 2012	Mendes *et al.*, 2012
	Gastrotheca galeata	----	Duellman, 2015
	Gastrotheca gracilis	Laurent *et al.*, 1986	Laurent *et al.*, 1986
	Gastrotheca griswoldi	----	Duellman, 2015
	Gastrotheca guentheri	----	Duellman, 2015
	Gastrotheca helenae	Duellman, 2015	Cochran & Goin, 1970
	Gastrotheca litonedis	----	Duellman, 2015
	Gastrotheca longipes	----	Duellman, 2015
	Gastrotheca marsupiata	----	Boulenger, 1882
Hemiphractidae (cont.)	*Gastrotheca monticola*	----	Duellman, 2015
	Gastrotheca nicefori	Lynch & Renjifo, 2001; Cochran & Goin, 1970	Lynch & Renjifo, 2001; Cochran & Goin, 1970
	Gastrotheca ochoai	----	Duellman, 2015
	Gastrotheca orophylax	----	Duellman, 2015
	Gastrotheca peruana	----	Duellman, 2015
	Gastrotheca plumbea	----	Boulenger, 1882
	Gastrotheca pseustes	----	Duellman, 2015
	Gastrotheca psychrophila	----	Duellman, 2015
	Gastrotheca riobambae	MOP pers. obs.; Duellman, 2015	MOP pers. obs.; Duellman, 2015
	Gastrotheca ruizi	----	Duellman, 2015
	Gastrotheca stictopleura	----	Duellman, 2015
	Gastrotheca trachyceps	----	Duellman, 2015
	Gastrotheca weinlandii	----	Duellman, 2015
	Gastrotheca zeugocystis	----	Duellman, 2015
	Gastrotheca walkeri	Duellman, 2015	Mendelson *et al.*, 2000
	Hemiphractus bubalus	----	----
	Hemiphractus helioi	----	Duellman, 2015
	Hemiphractus	----	Trueb, 1974

	proboscideus		
	Hemiphractus scutatus	----	Trueb, 1974
	Stefania evansi	Kok & Kalamandeen, 2008	Kok & Kalamandeen, 2008
	Stefania ginesi	Señaris *et al.*, 2014	Señaris *et al.*, 2014
	Stefania scalae	----	----
	Stefania schuberti	Señaris *et al.*, 2014	Señaris *et al.*, 2014
Hemisotidae	*Hemisus marmoratus*	Scott, 2005; du Preez & Carruthers, 2009	Scott, 2005
Hylidae	*Acris crepitans*	----	Boulenger, 1882
	Acris gryllus	----	Boulenger, 1882
Hylidae (cont.)	*Agalychnis annae*	----	Duellman, 1963
	Agalychnis aspera	----	Boulenger, 1882
	Agalychnis callidryas	Wever, 1985	Boulenger, 1882
	Agalychnis dacnicolor	Wever, 1985; Boulenger, 1882	Boulenger, 1882
	Agalychnis granulosa	----	----
	Agalychnis hulli	Beirne & Witworth, 2011	Beirne & Witworth, 2011
	Agalychnis lemur	----	Boulenger, 1882
	Agalychnis litodryas	----	Duellman & Trueb, 1967
	Agalychnis moreletii	----	Boulenger, 1882
	Agalychnis saltator	----	Savage & Heyer, 1967
	Agalychnis spurrelli	----	----
	Anotheca spinosa	Savage, 2002	Boulenger, 1882; Savage, 2002
	Aparasphenodon brunoi	----	----
	Aplastodiscus albofrenatus	Lutz, 1973	Lutz, 1973
	Aplastodiscus albosignatus	Lutz, 1973	Lutz, 1973
	Aplastodiscus arildae	----	Cruz & Peixoto, 1987 "1985"

	Aplastodiscus cavicola	----	Cruz & Peixoto, 1985 "1984"
	Aplastodiscus eugenioi	----	Carvalho-e-Silva & Carvalho- e-Silva, 2006
	Aplastodiscus leucopygius	----	Cruz & Peixoto, 1985 "1984"
	Aplastodiscus perviridis	MOP pers. obs.	MOP pers. obs.
	Aplastodiscus weygoldti	----	Cruz & Peixoto, 1987 "1985"
	Argenteohyla siemersi	Trueb, 1970c	Trueb, 1970c
	Bokermannohyla astartea	----	Bokermann, 1967a
	Bokermannohyla circumdata	Lutz, 1973	Boulenger, 1882; Lutz, 1973
	Bokermannohyla hylax	----	Heyer, 1985
	Bokermannohyla martinsi	----	Bokermann, 1964a
Hylidae (cont.)	*Bromeliohyla bromeliacia*	----	Duellman, 1970b
	Charadrahyla nephila	----	Mendelson & Campbell, 1999
	Charadrahyla taeniopus	----	Duellman, 1970b
	Corythomantis greeningi	----	----
	Cruziohyla calcarifer	McCranie & Wilson, 2002	Boulenger, 1882; McCranie & Wilson, 2002
	Dendropsophus anceps	Lutz, 1973	Lutz, 1973
	Dendropsophus berthalutzae	Lutz, 1973	Lutz, 1973
	Dendropsophus bifurcus	----	Duellman, 1974
	Dendropsophus bipunctatus	Lutz, 1973	Boulenger, 1882; Lutz, 1973
	Dendropsophus branneri	Lutz, 1973	Lutz, 1973

	Dendropsophus brevifrons	----	Duellman & Crump, 1974
	Dendropsophus ebraccatus	Wever, 1985	----
	Dendropsophus elegans	----	Lutz, 1973
	Dendropsophus gaucheri	----	Lescure & Marty, 2000
	Dendropsophus juliani	----	Moravec *et al.*, 2006
	Dendropsophus koechlini	----	Duellman & Trueb, 1989
	Dendropsophus labialis	----	Boulenger, 1882
	Dendropsophus marmoratus	Lutz, 1973	Boulenger, 1882; Lutz, 1973
	Dendropsophus melanargyreus	----	Bokermann, 1964b
	Dendropsophus microcephalus	Wever, 1985	Wever, 1985
	Dendropsophus minutus	Lima *et al.*, 2006	Lima *et al.*, 2006
	Dendropsophus miyatai	----	Vigle & Goberdhan-Vigle, 1990
	Dendropsophus nanus	Lutz, 1973	Lutz, 1973
	Dendropsophus parviceps	----	Boulenger, 1882
	Dendropsophus pelidna	----	Duellman, 1989
Hylidae (cont.)	*Dendropsophus rhodopeplus*	----	Duellman, 1972a
	Dendropsophus robertmertensi	----	Duellman, 1970b
	Dendropsophus rubicundulus	----	Boulenger, 1882
	Dendropsophus sarayacuensis	----	Duellman, 1974
	Dendropsophus sartoti	----	Duellman, 1970b
	Dendropsophus schubarti	Duellman, 2005	Duellman, 2005
	Dendropsophus seniculus	Lutz, 1973	Boulenger, 1882; Lutz, 1973

	Dendropsophus timbeba	Duellman, 2005	Duellman, 2005
	Dendropsophus triangulum	----	Boulenger, 1882
	Dendropsophus tritaeniatus	----	Bokermann, 1965
	Diaglena spatulata	----	Duellman, 1970b
	Duellmanohyla rufioculis	----	Duellman, 1970b
	Duellmanohyla soralia	McCranie & Wilson, 2002	McCranie & Wilson, 2002
	Ecnomiohyla miliaria	Savage, 2002	Savage, 2002
	Ecnomiohyla miotympanum	----	Duellman, 1970b
	Exerodonta abdivita	----	Duellman, 2001
	Exerodonta chimalaà	----	Mendelson & Campbell, 1994
	Exerodonta melanomma	----	----
	Exerodonta perkinsi	----	Duellman, 2001
	Exerodonta smaragdina	----	Duellman, 1970b
	Exerodonta sumichrasti	----	Boulenger, 1882
	Exerodonta xera	----	Duellman, 2001
	Hyla annectans	----	Liu, 1950
	Hyla andersonii	Dood, 2013	Dood, 2013
	Hyla arborea	----	Boulenger, 1882
	Hyla arenicolor	----	----
	Hyla avivoca	Dood, 2013	Dood, 2013
	Hyla chinensis	----	Boulenger, 1882
Hylidae (cont.)	*Hyla chrysoscelis*	Dood, 2013	Dood, 2013
	Hyla cinerea	Wever, 1985	Boulenger, 1882
	Hyla euphorbiacea	----	Duellman, 1970b
	Hyla eximia	----	----
	Hyla femoralis	Dood, 2013	Dood, 2013

	Hyla gratiosa	Dood, 2013	Dood, 2013
	Hyla meridionalis	Schleich *et al.*, 1996	Schleich *et al.*, 1996
	Hyla plicata	----	Duellman, 1970b
	Hyla squirella	Dood, 2013	Dood, 2013
	Hyla versicolor	Wever, 1985	----
	Hyla walkeri	----	Duellman, 1970b
	Hyla wrightorum	Dood, 2013	Dood, 2013
	Hyloscirtus alytolylax	----	Duellman, 1972a
	Hyloscirtus armatus	----	Duellman *et al.*, 1997
	Hyloscirtus colymba	----	----
	Hyloscirtus larinopygion	----	Rivera-Correa & Faivovich, 2013
	Hyloscirtus lindae	----	----
	Hyloscirtus pacha	----	----
	Hyloscirtus palmeri	Savage, 2002	Savage, 2002
	Hyloscirtus pantostictus	----	----
	Hyloscirtus phyllognathus	----	Duellman, 1972a
	Hyloscirtus psarolaimus	----	----
	Hyloscirtus ptychodactylus	----	----
	Hyloscirtus simmonsi	----	Duellman, 1989
	Hyloscirtus staufferorum	----	----
	Hyloscirtus tapichalaca	----	Kizirian *et al.*, 2003
	Hyloscirtus tigrinus	----	Mueses-Cisneros & Anganoy-Criollo, 2008
Hylidae (cont.)	*Hypsiboas albomarginatus*	Lutz, 1973	Lutz, 1973
	Hypsiboas albopunctatus	----	Lutz, 1973
	Hypsiboas andinus	----	Barrio, 1965
	Hypsiboas balzani	----	Duellman *et al.*, 1997
	Hypsiboas bischoffi	Lutz, 1973	Lutz, 1973

	Hypsiboas boans	Lima *et al.*, 2006	Boulenger, 1882; Lima *et al.*, 2006
	Hypsiboas caingua	----	Carrizo, 1990
	Hypsiboas calcaratus		Caminer & Ron, 2014
	Hypsiboas cinerascens	Lima *et al.*, 2006	Lima *et al.*, 2006
	Hypsiboas cordobae	----	Barrio, 1965
	Hypsiboas crepitans	----	Lutz, 1973
	Hypsiboas dentei	----	Bokermann, 1967b
	Hypsiboas ericae	----	Caramaschi & Cruz, 2000
	Hypsiboas faber	Lutz, 1973	Boulenger, 1882
	Hypsiboas fasciatus	----	Boulenger, 1882
	Hypsiboas geographicus	Boulenger, 1882	Boulenger, 1882
	Hypsiboas guentheri	----	Langone, 1997
	Hypsiboas heilprini	----	Trueb & Tyler, 1974
	Hypsiboas joaquini	----	Garcia *et al.*, 2003
	Hypsiboas lanciformis	Lutz, 1973; Lima *et al.*, 2006	Boulenger, 1882; Lutz, 1973; Lima *et al.*, 2006
	Hypsiboas latistriatus	----	Caramaschi & Cruz, 2004
	Hypsiboas leptolineatus	----	Braun & Braun, 1977
	Hypsiboas lundii	----	Bokermann & Sazima, 1978
	Hypsiboas marginatus	----	Garcia *et al.*, 2001
	Hypsiboas marianitae	----	Duellman *et al.*, 1997
	Hypsiboas melanopleura	----	Duellman *et al.*, 1997
	Hypsiboas microderma	----	Pyburn, 1977
Hylidae (cont.)	*Hypsiboas multifasciatus*	----	de Sá, 1996
	Hypsiboas nympha	----	Faivovich *et al.*, 2006
	Hypsiboas ornatissimus	Kok & Kalamandeen, 2008	Kok & Kalamandeen, 2008

	Hypsiboas pardalis	----	Lutz, 1973
	Hypsiboas pellucens	----	Duellman, 1971
	Hypsiboas picturatus	MOP pers. obs.	MOP pers. obs.
	Hypsiboas polytaenius	Lutz, 1973	Boulenger, 1882; Lutz, 1973
	Hypsiboas prasinus	----	Lutz, 1973
	Hypsiboas pulchellus	DB pers. obs.; Lutz, 1973	DB pers. obs.; Boulenger, 1882; Lutz, 1973
	Hypsiboas punctatus	Duellman, 2005	Duellman, 2005
	Hypsiboas raniceps	Lutz, 1973	Lutz, 1973
	Hypsiboas riojanus	Lutz, 1973	Lutz, 1973
	Hypsiboas roraima	----	Duellman & Hoogmoed, 1992
	Hypsiboas rosenbergi	----	----
	Hypsiboas rufitelus	----	----
	Hypsiboas semiguttatus	García *et al.*, 2007	García *et al.*, 2007
	Hypsiboas semilineatus	----	Lutz, 1973
	Hypsiboas sibleszi	----	Hoogmoed, 1979
	Isthmohyla pseudopuma	Savage, 2002	Savage, 2002
	Isthmohyla rivularis	Savage, 2002	Savage, 2002
	Isthmohyla tica	----	Boulenger, 1882
	Itapothyla langsdorfii	Lutz, 1973	Boulenger, 1882; Lutz, 1973
	Litoria adelaidensis	Barker *et al.*, 1995	Boulenger, 1882; Barker *et al.*, 1995
	Litoria alboguttata	----	Anstis, 2013
	Litoria amboinensis	----	Menzies, 2006
	Litoria andiirrmalin	----	Anstis, 2013
	Litoria angiana	----	----
Hylidae (cont.)	*Litoria arfakiana*	----	Boulenger, 1882

	Litoria aurea	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria australis	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria barringtonensis	----	Anstis, 2013
	Litoria bicolor	Barker *et al.*, 1995	Boulenger, 1882; Barker *et al.*, 1995
	Litoria booroolongensis	----	Anstis, 2013
	Litoria brevipes	Barker *et al.*, 1995	Boulenger, 1882; Barker *et al.*, 1995
	Litoria burrowsi	----	Anstis, 2013
	Litoria caerulea	Barker *et al.*, 1995	Boulenger, 1882; Barker *et al.*, 1995
	Litoria cavernicola	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria chloris	----	Anstis, 2013
	Litoria citropa	Barker *et al.*, 1995	Barker *et al.*, 1995; Anstis, 2013
	Litoria congenita	----	Menzies, 2006
	Litoria coplandi	----	Anstis, 2013
	Litoria cryptotis	----	Anstis, 2013
	Litoria cultripes	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria cyclorhyncha	----	Anstis, 2013
	Litoria dahlii	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria darlingtoni	----	Menzies, 2006
	Litoria daviesae	----	Anstis, 2013
	Litoria dayi	Barker *et al.*, 1995	Barker *et al.*, 1995; Anstis, 2013
	Litoria dentata	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria electrica	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria eucnemis	----	Anstis, 2013

	Litoria ewingii	Barker *et al.*, 1995	Boulenger, 1882
Hylidae (cont.)	*Litoria fallax*	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria freycineti	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria genimaculata	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria gilleni	----	Anstis, 2013
	Litoria gracilenta	----	Boulenger, 1882
	Litoria havina	----	Menzies, 2006
	Litoria impura	----	Menzies, 2006
	Litoria inermis	----	Davies *et al.*, 1983
	Litoria jervisiensis	----	Anstis, 2013
	Litoria jungguy	----	Anstis, 2013
	Litoria kumae	----	Menzies, 2006
	Litoria latopalmata	----	----
	Litoria lesueurii	Barker *et al.*, 1995	----
	Litoria longipes	----	Anstis, 2013
	Litoria longirostris	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria maculosa	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria maini	----	Anstis, 2013
	Litoria manya	----	Anstis, 2013
	Litoria meiriana	----	Anstis, 2013
	Litoria microbelos	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria micromembrana	----	----
	Litoria modica	----	----
	Litoria moorei	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria nannotis	Barker *et al.*, 1995	----
	Litoria nasuta	----	Anstis, 2013
	Litoria nigrofrenata	Barker *et al.*, 1995	Boulenger, 1882
	Litoria novaehollandiae	----	Anstis, 2013
	Litoria nudidigita	----	Anstis, 2013
Hylidae (cont.)	*Litoria nyakalensis*	Barker *et al.*, 1995	Barker *et al.*, 1995

	Litoria pallida	----	Davies *et al.*, 1983
	Litoria paraewingi	----	Anstis, 2013
	Litoria pearsoniana	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria peronii	Barker *et al.*, 1995	Boulenger, 1882
	Litoria personata	----	Anstis, 2013
	Litoria phyllochroa	Barker *et al.*, 1995	Boulenger, 1882; Barker *et al.*, 1995
	Litoria platycephala	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria pronimia	----	Menzies, 2006
	Litoria raniformis	----	Anstis, 2013
	Litoria revelata	----	Anstis, 2013
	Litoria rheocola	----	Anstis, 2013
	Litoria rothi	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria rubella	----	Anstis, 2013
	Litoria splendida	----	Anstis, 2013
	Litoria subglandulosa	Barker *et al.*, 1995	Barker *et al.*, 1995
	Litoria tornieri	----	Davies *et al.*, 1983
	Litoria tyleri	----	Anstis, 2013
	Litoria vagitus	----	Anstis, 2013
	Litoria verreauxii	Barker *et al.*, 1995	----
	Litoria verrucosa	----	Anstis, 2013
	Litoria watjulumensis	----	Anstis, 2013
	Litoria wilcoxii	----	Anstis, 2013
	Litoria xanthomera	Barker *et al.*, 1995	Barker *et al.*, 1995; Anstis, 2013
	Lysapsus limellum	MOP pers. obs.	MOP pers. obs.; Boulenger, 1882
	Megastomatohyla mixe	----	Duellman, 1970b
Hylidae (cont.)	*Myersiohyla imparquesi*	Ayarzagüena & Señaris,	Ayarzagüena & Señaris,

		1993	1993
	Myersiohyla kanaima	----	Duellman & Hoogmoed, 1992
	Nyctimantis rugiceps	----	Duellman & Trueb, 1976
	Nyctimystes brevipalmatus	Barker *et al.*, 1995	Barker *et al.*, 1995
	Nyctimystes foricula	----	----
	Nyctimystes infrafrenatus	Barker *et al.*, 1995	Boulenger, 1882; Barker *et al.*, 1995
	Nyctimystes kubori	----	----
	Nyctimystes narinosus	----	----
	Nyctimystes papua	----	----
	Nyctimystes pulcher	----	----
	Nyctymistes zweifeli	----	----
	Osteocephalus alboguttatus	----	Boulenger, 1882
	Osteocephalus buckleyi	Jungfer *et al.*, 2013; Lima *et al.*, 2006	Jungfer *et al.*, 2013; Lima *et al.*, 2006
	Osteocephalus cabrerai	----	Jungfer, 2010
	Osteocephalus deridens	----	Jungfer *et al.*, 2000
	Osteocephalus fuscifascies	----	Jungfer *et al.*, 2000
	Osteocephalus leprieurii	Kok & Kalamandeen, 2008	Boulenger, 1882; Kok & Kalamandeen, 2008
	Osteocephalus mutabor	Kok & Kalamandeen, 2008	Kok & Kalamandeen, 2008
	Osteocephalus planiceps	----	Jungfer *et al.*, 2000
	Osteocephalus oophagus	Jungfer *et al.*, 2013; Lima *et al.*, 2006	Jungfer *et al.*, 2013; Lima *et al.*, 2006
	Osteocephalus taurinus	----	----
	Osteocephalus verruciger	----	Trueb & Duellman, 1971
	Osteocephalus yasuni	----	Jungfer *et al.*, 2013
	Osteopilus brunneus	----	Trueb & Tyler, 1974

	Osteopilus crucialis	----	Boulenger, 1882
	Osteopilus dominicensis	----	Trueb & Tyler, 1974
Hylidae (cont.)	*Osteopilus marianae*	----	Trueb & Tyler, 1974
	Osteopilus pulchrilineatus	----	Trueb & Tyler, 1974
	Osteopilus septentrionalis	Wever, 1985; Diaz & Cadiz, 2008	Diaz & Cadiz, 2008
	Osteopilus vastus	----	Boulenger, 1882
	Osteopilus wilderi	----	Trueb & Tyler, 1974
	Phasmahyla cochranae	----	Bokermann, 1966
	Phasmahyla cruzi	----	Carvalho-e-Silva *et al.,* 2009
	Phasmahyla exilis	----	Cruz, 1980
	Phasmahyla guttata	----	----
	Phasmahyla jandaia	----	Bokermann & Sazima, 1978
	Phrynomedusa marginata	----	Izecksohn & Cruz, 1976
	Phyllodytes auratus	----	Kenny, 1969
	Phyllodytes luteolus	----	----
	Phyllomedusa atelopoides	----	Duellman, 2005
	Phyllomedusa ayeaye	----	Lutz, 1966
	Phyllomedusa azurea	MOP pers. obs.	MOP pers. obs.
	Phyllomedusa bahiana	----	Lutz & Lutz, 1939
	Phyllomedusa baltea	----	Duellman & Toft, 1979
	Phyllomedusa bicolor	Lima *et al.*, 2006; Kok & Kalamandeen, 2008	Boulenger, 1882; Lima *et al.*, 2006; Kok & Kalamandeen, 2008
	Phyllomedusa boliviana	----	Cei, 1980
	Phyllomedusa burmeisteri	----	Izecksohn & Carvalho-e-Silva, 2001

	Phyllomedusa camba	Duellman, 2005	Duellman, 2005
	Phyllomedusa centralis	----	Bokermann, 1965
	Phyllomedusa duellmani	----	Cannatella, 1982
	Phyllomedusa hypochondrialis	----	Caramaschi, 2006
Hylidae (cont.)	*Phyllomedusa iheringii*	----	Langone, 1994
	Phyllomedusa megacephala	----	Caramaschi, 2006
	Phyllomedusa neildi	----	Barrio-Amorós, 2006
	Phyllomedusa nordestina	----	Caramaschi, 2006
	Phyllomedusa oreades	----	Brandão, 2002
	Phyllomedusa palliata	Boulenger, 1882	Boulenger, 1882
	Phyllomedusa perinesos	----	Duellman, 1973
	Phyllomedusa rohdei	----	Izecksohn & Carvalho-e-Silva, 2001
	Phyllomedusa sauvagii	MOP pers. obs.	MOP pers. obs.
	Phyllomedusa tarsius	Lima *et al.*, 2006	Boulenger, 1882; Lima *et al.*, 2006
	Phyllomedusa tetraploidea	----	Pombal & Haddad, 1992
	Phyllomedusa tomopterna	Lima *et al.*, 2006	Lima *et al.*, 2006
	Phyllomedusa trinitatis	----	Funkhouser, 1957
	Phyllomedusa vaillanti	----	Funkhouser, 1957
	Plectrohyla ameibothalame	----	Canseco-Márquez *et al.*, 2002
	Plectrohyla arborescandens	----	Duellman, 2001
	Plectrohyla bistincta	----	Boulenger, 1882
	Plectrohyla calthula	----	Duellman, 2001
	Plectrohyla chrysopleura	----	Duellman, 2001

	Plectrohyla cyclada	----	Duellman, 2001
	Plectrohyla glandulosa	----	Duellman, 1970b
	Plectrohyla guatemalensis	----	Boulenger, 1882
	Plectrohyla mutadai	----	Duellman, 1970b
	Plectrohyla pentheter	----	Duellman, 1970b
	Plectrohyla siopela	----	Duellman, 1970b
	Pseudacris brachypona	Dood, 2013	Dood, 2013
	Pseudacris brimleyi	Dood, 2013	Dood, 2013
Hylidae (cont.)	*Pseudacris cadaverina*	----	Duellman, 1970b
	Pseudacris clarkii	----	----
	Pseudacris crucifer	Dood, 2013	Dood, 2013
	Pseudacris feriarum	Dood, 2013	Dood, 2013
	Pseudacris fouquetti	----	Elliot *et al.*, 2009
	Pseudacris illinoensis	Dood, 2013	Dood, 2013
	Pseudacris kalmi	----	Elliot *et al.*, 2009
	Pseudacris maculata	----	Elliot *et al.*, 2009
	Pseudacris nigrita	----	Boulenger, 1882
	Pseudacris ocularis	----	Boulenger, 1882
	Pseudacris ornata	----	Boulenger, 1882
	Pseudacris regilla	----	Boulenger, 1882
	Pseudacris streckeri	Wever, 1985	----
	Pseudacris triseriata	----	Boulenger, 1882
	Pseudis bolbodactyla	----	Caramaschi & Cruz, 1998
	Pseudis cardosoi	----	Kwet, 2000
	Pseudis fusca	----	Caramaschi & Cruz, 1998
	Pseudis minuta	MOP pers. obs.	MOP pers. obs.; Boulenger, 1882
	Pseudis paradoxa	Duellman, 2005	Boulenger, 1882; Duellman, 2005

	Pseudis tocantins	----	Caramaschi & Cruz, 1998
	Ptychohyla dendrophasma	----	Duellman, 2001
	Ptychohyla euthysanota	----	Duellman, 1970b
	Ptychohyla hypomykter	----	McCranie & Wilson, 1993
	Ptychohyla leonhardschultzei	----	Duellman, 1970b
	Ptychohyla spinipollex	----	----
	Ptychohyla zophodes	----	Duellman, 2001
	Scarthyla goinorum	Duellman, 2005	Duellman, 2005
Hylidae (cont.)	*Scinax acuminatus*	DB pers. obs.	DB pers. obs.; Boulenger, 1882
	Scinax berthae	Barrio, 1962	Barrio, 1962
	Scinax boesemani	Lima *et al.*, 2006; Kok & Kalamandeen, 2008	Lima *et al.*, 2006; Kok & Kalamandeen, 2008
	Scinax boulengeri	Wever, 1985	----
	Scinax catharinae	----	JF pers. obs.
	Scinax crospedospilus	----	Heyer *et al.*, 1990
	Scinax cruentommus	----	JF pers. obs.
	Scinax elaeochrous	----	Boulenger, 1882
	Scinax faivovichi	Brasileiro *et al.*, 2007	Brasileiro *et al.*, 2007
	Scinax fuscovarius	DB pers. obs.; Lutz, 1973	DB pers. obs.; Lutz, 1973
	Scinax garbei	Lima *et al.*, 2006	JF pers. obs.; Lima *et al.*, 2006
	Scinax nasicus	----	Boulenger, 1882
	Scinax nebulosus	----	JF pers. obs.
	Scinax perpusillus	Lutz, 1973	JF pers. obs.; Lutz, 1973
	Scinax rostratus	----	Boulenger, 1882
	Scinax ruber	----	JF pers. obs.
	Scinax squalirostris	----	JF pers. obs.
	Scinax staufferi	----	Boulenger, 1882

	Scinax uruguayus	Giraudo *et al.*, 2005	Giraudo *et al.*, 2005
	Smilisca baudinii	Savage, 2002	Boulenger, 1882; Savage, 2002
	Smilisca cyanosticta	----	Duellman, 1970b
	Smilisca fodiens	----	----
	Smilisca phaeota	Wever, 1985; Savage, 2002	Savage, 2002
	Smilisca puma	----	Duellman, 1970b
	Smilisca sila	----	Duellman, 1970b
	Smilisca sordida	----	Boulenger, 1882
Hylidae (cont.)	*Sphaenorhynchus lacteus*	Duellman, 2005	Duellman, 2005
	Tepuhyla talbergae	Kok & Kalamandeen, 2008	Kok & Kalamandeen, 2008
	Tepuihyla aecii	----	Ayarzagüena *et al.*, 1992
	Tepuihyla exophthalma	Smith & Noonan (2001)	Smith & Noonan (2001)
	Tepuihyla edelcae	----	Ayarzagüena *et al.*, 1992
	Tepuihyla rodriguezi	----	Ayarzagüena *et al.*, 1992
	Tlalocohyla godmani	----	Duellman, 1970b
	Tlalocohyla loquax	Savage, 2002	Savage, 2002
	Tlalocohyla picta	----	Duellman, 1970b
	Tlalocohyla smithtii	----	Duellman, 1970b
	Trachycephalus hadroceps	----	Duellman & Hoogmoed, 1992
	Trachycephalus jordani	----	----
	Trachycephalus mesophaeus	Boulenger, 1882	Boulenger, 1882
	Trachycephalus nigromaculatus	----	----
	Trachycephalus resinifictrix	Lima *et al.*, 2006	Lima *et al.*, 2006
	Trachycephalus typhonius	Lutz, 1973	Lutz, 1973
	Triprion petasatus	----	Duellman, 1970b

	Xenohyla truncata	Lutz, 1973	Lutz, 1973
Hylodidae	*Crossodactylus schmidti*	MOP pers. obs.	MOP pers. obs.
	Hylodes ornatus	----	Bokermann, 1967c
	Megaelosia goeldii	----	----
Hyperoliidae	*Acanthixalus spinosus*	Drewes, 1984	Amiet, 2012
	Afrixalus dorsalis	----	Drewes, 1984
	Afrixalus fornasini	du Preez & Carruthers, 2009	du Preez & Carruthers, 2009
	Afrixalus laevis	----	----
	Alexteroon obstetricans	----	Amiet, 2012
Hyperoliidae (cont.)	*Cryptothylax gresshoffi*	----	Drewes, 1984
	Heterixalus alboguttatus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Heterixalus betsileo	Glaw & Vences, 2007	----
	Heterixalus boettgeri	Glaw & Vences, 2007	Glaw & Vences, 2007
	Heterixalus carbonei	Vences *et al.*, 2000	Vences *et al.*, 2000
	Heterixalus madagascariensis	Glaw & Vences, 2007	Vences *et al.*, 2002; Glaw & Vences, 2007
	Heterixalus punctatus	----	Vences *et al.*, 2002
	Heterixalus tricolor	----	Glaw & Vences, 2007
	Hyperolius benguellensis	du Preez & Carruthers, 2009	----
	Hyperolius castaneus	----	Laurent, 1944
	Hyperolius chlorosteus	----	Boulenger, 1915
	Hyperolius concolor	----	Amiet, 2012
	Hyperolius guttulatus	----	Boulenger, 1882
	Hyperolius nasutus	Drewes, 1984; du Preez & Carruthers, 2009; Harper *et al.*, 2010	Harper *et al.*, 2010
	Hyperolius ocellatus	----	Laurent, 1944

	Hyperolius phantasticus	----	Drewes, 1984
	Hyperolius puncticulatus	----	Schiotz, 1975
	Hyperolius pusillus	Drewes, 1984; du Preez & Carruthers, 2009	----
	Hyperolius tuberilinguis	du Preez & Carruthers, 2009	du Preez & Carruthers, 2009
	Hyperolius viridiflavus	Wever, 1985	Wever, 1985
	Kassina maculata	du Preez & Carruthers, 2009	Drewes, 1984; du Preez & Carruthers, 2009
	Kassina senegalensis	Scott, 2005; du Preez & Carruthers, 2009	Scott, 2005; Boulenger, 1882; Drewes, 1984; du Preez & Carruthers, 2009
Hyperoliidae (cont.)	*Morerella cyanophthalma*	Rödel *et al.*, 2009	Rödel *et al.*, 2009
	Opisthotylax immaculatus	Drewes, 1984	----
	Phlyctimantis leonardi	----	Drewes, 1984
	Phlyctimantis verrucosus	Spawls *et al.*, 2006	Spawls *et al.*, 2006
	Semnodactylus wealii	du Preez & Carruthers, 2009	Drewes, 1984; Boulenger, 1882
	Tachycnemis seychellensis	----	Drewes, 1984; Boulenger, 1882
Leiopelmatidae	*Leiopelma archeyi*	----	----
	Leiopelma hochstetteri	Wever, 1985	Wever, 1985
Leptodactylidae	*Adenomera andreae*	Lima *et al.*, 2006	Lima *et al.*, 2006
	Adenomera heyeri	Boistel *et al.*, 2006	Boistel *et al.*, 2006
	Adenomera hylaedactyla	Lima *et al.*, 2006	Lima *et al.*, 2006
	Edalorhina perezi	Beirne & Witworth, 2011	Boulenger, 1882; Beirne & Witworth, 2011
	Engystomops coloradum	Nacimento *et al.*, 2005	----
	Engystomops guayaco	Nacimento *et al.*, 2005	----
	Engystomops montubio	Nacimento *et al.*, 2005	----

	Engystomops petersi	Nacimento *et al.*, 2005	DB pers. obs.
	Engystomops pustulatus	DB pers. obs.	DB pers. obs.
	Engystomops pustulosus	Nacimento *et al.*, 2005	----
	Engystomops randi	Nacimento *et al.*, 2005	----
	Leptodactylus albilabris	----	Ponssa, 2008.
	Leptodactylus bolivianus	----	----
	Leptodactylus bufonius	DB pers. obs.	DB pers. obs.; Ponssa, 2008
	Leptodactylus chaquensis	DB pers. obs.	DB pers. obs.
	Leptodactylus diedrus	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Leptodactylus discodactylus	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Leptodactylus didymus	de Sá *et al.*, 2014	de Sá *et al.*, 2014
Leptodactylidae (cont.)	*Leptodactylus elenae*	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Leptodactylus fallax	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Leptodactylus fuscus	Lima *et al.*, 2006	Ponssa, 2008; Lima *et al.*, 2006
	Leptodactylus gracilis	Boulenger, 1882	Boulenger, 1882; Ponssa, 2008
	Leptodactylus griseigularis	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Leptodactylus knudseni	Lima *et al.*, 2006	Lima *et al.*, 2006
	Leptodactylus labyrinthicus	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Leptodactylus latrans	DB pers. obs.	DB pers. obs.
	Leptodactylus leptodactyloides	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Leptodactylus longirostris	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Leptodactylus melanonotus	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Leptodactylus myersi	de Sá *et al.*, 2014	de Sá *et al.*, 2014

	Leptodactylus mystaceus	Lima *et al.*, 2006	Ponssa, 2008; Lima *et al.*, 2006
	Leptodactylus mystacinus	MOP pers. obs.	MOP pers. obs.; Ponssa, 2008
	Leptodactylus notoaktites	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Leptodactylus pentadactylus	Lima *et al.*, 2006	Boulenger, 1882; Lima *et al.*, 2006
	Leptodactylus plaumanni	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Leptodactylus podicipinus	DB pers. obs.	DB pers. obs.
	Leptodactylus rhodonotus	Duellman, 2005	Duellman, 2005
	Leptodactylus rhodomystax	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Leptodactylus riveroi	Lima *et al.*, 2006	Lima *et al.*, 2006
	Leptodactylus silvanimbus	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Leptodactylus spixi	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Leptodactylus stenodema	Lima *et al.*, 2006	Lima *et al.*, 2006
	Leptodactylus syphax	DB pers. obs.	DB pers. obs.
	Leptodactylus validus	de Sá *et al.*, 2014	de Sá *et al.*, 2014
Leptodactylidae (cont.)	*Leptodactylus vastus*	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Leptodactylus wagneri	de Sá *et al.*, 2014	de Sá *et al.*, 2014
	Lithodytes lineatus	Lima *et al.*, 2006	Lima *et al.*, 2006
	Paratelmatobius cardosoi	----	----
	Paratelmatobius poecilogaster	----	----
	Physalaemus albonotatus	DB pers. obs.	DB pers. obs.
	Physalaemus biligonigerus	Boulenger, 1882	DB pers. obs.
	Physalaemus centralis	DB pers. obs.	DB pers. obs.
	Physalaemus cuvieri	DB pers. obs.	DB pers. obs.
	Physalaemus gracilis	----	Boulenger, 1882
	Physalaemus nattereri	DB pers. obs.	DB pers. obs.

	Physalaemus signifer	----	----
	Pleurodema brachyops	Wever, 1985	Wever, 1985
	Pleurodema cinereum	DB pers. obs.	DB pers. obs.; Boulenger, 1882
	Pleurodema diplolister	----	Boulenger, 1882
	Pleurodema kriegi	----	MOP pers. obs.
	Pleurodema marmoratum	DB pers. obs.	DB pers. obs.
	Pleurodema tucumanum	----	MOP pers. obs.
	Pseudopaludicola falcipes	DB pers. obs.; Boulenger, 1882	DB pers. obs.
	Pseudopaludicola mystacalis	DB pers. obs.	DB pers. obs.
	Scythrophrys sawayae	Lynch, 1971	
Limnodynastidae	*Adelotus brevis*	Boulenger, 1882	----
	Heleioporus australiacus	Barker *et al.*, 1995	Barker *et al.*, 1995
	Lechriodus fletcheri	Barker *et al.*, 1995	Barker *et al.*, 1995
	Lechriodus melanopyga	Boulenger, 1882	Boulenger, 1882
	Limnodynastes depressus	Barker *et al.*, 1995	Barker *et al.*, 1995
	Limnodynastes dorsalis	Barker *et al.*, 1995	----
Limnodynastidae (cont.)	*Limnodynastes dumerilii*	Barker *et al.*, 1995	Barker *et al.*, 1995
	Limnodynastes fletcheri	Barker *et al.*, 1995	----
	Limnodynastes lignarius	Barker *et al.*, 1995	Barker *et al.*, 1995
	Limnodynastes peronii	Barker *et al.*, 1995	Boulenger, 1882
	Limnodynastes salmini	Barker *et al.*, 1995	Boulenger, 1882; Barker *et al.*, 1995
	Limnodynastes tasmaniensis	Boulenger, 1882; Barker *et al.*, 1995	----
	Neobatrachus pelobatoides	Anstis, 2013	Anstis, 2013
	Neobatrachus pictus	Barker *et al.*, 1995	----

	Neobatrachus sudelli	Barker *et al.*, 1995	----
	Notaden bennettii	Barker *et al.*, 1995	----
	Philoria sphagnicolus	Barker *et al.*, 1995	----
	Platyplectrum ornatum	Barker *et al.*, 1995	Boulenger, 1882; Barker *et al.*, 1995
Mantellidae	*Aglyptodactylus madagascariensis*	Glaw & Vences, 2007	Boulenger, 1882; Glaw & Vences, 2007
	Blommersia blommersae	Glaw & Vences, 2007	Glaw & Vences, 2007
	Blommersia domerguei	Glaw & Vences, 2007	Glaw & Vences, 2007
	Blommersia grandisonae	Glaw & Vences, 2007	Glaw & Vences, 2007
	Blommersia madinika	Glaw & Vences, 2007	Glaw & Vences, 2007
	Blommersia sarotra	Glaw & Vences, 2007	Glaw & Vences, 2007
	Boehmantis microtympanum	Glaw & Vences, 2007	Glaw & Vences, 2007
	Boophis ankaratra	Glaw & Vences, 2007	Glaw & Vences, 2007
	Boophis axelmeyeri	Glaw & Vences, 2007	Glaw & Vences, 2007
	Boophis bottae	Glaw & Vences, 2007	Glaw & Vences, 2007
	Boophis englaenderi	Glaw & Vences, 2007	Glaw & Vences, 2007
	Boophis goudotii	Boulenger, 1882	Boulenger, 1882
	Boophis idae	Glaw & Vences, 2007	Glaw & Vences, 2007
	Boophis madagascariensis	----	Boulenger, 1882
Mantellidae (cont.)	*Boophis mandraka*	Glaw & Vences, 2007	Glaw & Vences, 2007
	Boophis marojezensis	Glaw & Vences, 2007	Glaw & Vences, 2007
	Boophis pauliani	Glaw & Vences, 2007	Glaw & Vences, 2007
	Boophis phyrrus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Boophis picturatus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Boophis rufioculis	Glaw & Vences, 2007	Glaw & Vences, 2007
	Boophis sambirano	----	Vences & Glaw, 2005
	Boophis sibilans	Glaw & Vences, 2007	Glaw & Vences, 2007

	Boophis tephraeomystax	Glaw & Vences, 2007	Glaw & Vences, 2007; Boulenger, 1882
	Boophis vittatus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Boophis williamsi	Glaw & Vences, 2007	Guibe, 1974; Glaw & Vences, 2007
	Gephyromantis asper	Glaw & Vences, 2007	Glaw & Vences, 2007
	Gephyromantis azurrae	Glaw & Vences, 2007	Glaw & Vences, 2007
	Gephyromantis blanci	----	Glaw & Vences, 2007
	Gephyromantis boulengeri	Glaw & Vences, 2007	Glaw & Vences, 2007
	Gephyromantis cornutus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Gephyromantis corvus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Gephyromantis eiselti	Glaw & Vences, 2007	Glaw & Vences, 2007
	Gephyromantis granulatus	----	Boulenger, 1882
	Gephyromantis horridus	Glaw & Vences, 2007	Vences *et al.*, 2002
	Gephyromantis klemmeri	Glaw & Vences, 2007	Guibe, 1974; Glaw & Vences, 2007
	Gephyromantis luecocephalus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Gephyromantis leucomaculatus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Gephyromantis luteus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Gephyromantis malagasius	Glaw & Vences, 2007	Glaw & Vences, 2007
Mantellidae (cont.)	*Gephyromantis plicifer*	Glaw & Vences, 2007	Glaw & Vences, 2007
	Gephyromantis pseudoasper	Glaw & Vences, 2007	Guibe, 1974; Glaw & Vences, 2007
	Gephyromantis redimitus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Gephyromantis rivicola	Glaw & Vences, 2007	Glaw & Vences, 2007
	Gephyromantis salegy	Glaw & Vences, 2007	Glaw & Vences, 2007

	Gephyromantis sculpturatus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Gephyromantis striatus	Glaw & Vences, 2007	Vences *et al.*, 2002
	Gephyromantis ventrimaculatus	Vences *et al.*, 2002; Glaw & Vences, 2007	Vences *et al.*, 2002; Glaw & Vences, 2007
	Gephyromantis zavona	Glaw & Vences, 2007	Glaw & Vences, 2007
	Guibemantis albolineatus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Guibemantis bicalcaratus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Guibemantis liber	Glaw & Vences, 2007	Glaw & Vences, 2007
	Guibemantis pulcher	----	Boulenger, 1882
	Guibemantis punctatus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Guibemantis tornieri	Glaw & Vences, 2007	Glaw & Vences, 2007
	Laliostoma labrosum	Glaw & Vences, 2007	Glaw & Vences, 2007
	Mantella aurantiaca	Scott, 2005	Vences *et al.*, 2002
	Mantella baroni	Glaw & Vences, 2007	Glaw & Vences, 2007
	Mantella betsileo	----	Boulenger, 1882
	Mantella bernhardi	Glaw & Vences, 2007	Glaw & Vences, 2007
	Mantella crocea	----	Vences *et al.*, 2002
	Mantella ebenaui	----	Boulenger, 1882
	Mantella expectata	Glaw & Vences, 2007	Glaw & Vences, 2007
	Mantella laevigata	----	Vences *et al.*, 2002
	Mantella madagascariensis	----	Boulenger, 1882
	Mantella nigricans	----	Glaw & Vences, 2007
	Mantella viridis	Glaw & Vences, 2007	Glaw & Vences, 2007
Mantellidae (cont.)	*Mantidactylus aerumnalis*	Glaw & Vences, 2007	Glaw & Vences, 2007
	Mantidactylus ambreensus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Mantidactylus argenteus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Mantidactylus betsileanus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Mantidactylus biporus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Mantidactylus charlotteae	Glaw & Vences, 2007	Glaw & Vences, 2007

	Mantidactylus curtus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Mantidactylus femoralis	Scott, 2005; Glaw & Vences, 2007	Glaw & Vences, 2007
	Mantidactylus lugubris	----	Boulenger, 1882
	Mantidactylus majori	Glaw & Vences, 2007	Glaw & Vences, 2007
	Mantidactylus mocquardi	Glaw & Vences, 2007	Glaw & Vences, 2007
	Mantidactylus opiparis	Glaw & Vences, 2007	Glaw & Vences, 2007
	Mantidactylus ulcerosus	Glaw & Vences, 2007	Glaw & Vences, 2007
	Spinomantis aglavei	----	Vences *et al.*, 2002
	Spinomantis guibei	----	Guibe, 1974
	Tsingymantis antitra	Glaw & Vences, 2007	Glaw & Vences, 2007
Megophryidae	*Brachytarsophrys feae*	Boulenger, 1887	----
	Leptobrachium banae	----	Lathrop *et al.*, 1998a
	Leptobrachium chapaense	Delorme *et al.*, 2006	Delorme *et al.*, 2006
	Leptobrachium echinatum	Delorme *et al.*, 2006	Delorme *et al.*, 2006
	Leptobrachium hasseltii	Delorme *et al.*, 2006	Delorme *et al.*, 2006; Cannatella & Trueb, 1988
	Leptobrachium hendricksoni	Delorme *et al.*, 2006	Delorme *et al.*, 2006
	Leptobrachium mouhoti	----	Stuart *et al.*, 2006
	Leptobrachium montanum	Delorme *et al.*, 2006	Delorme *et al.*, 2006
	Leptobrachium nigrops	Delorme *et al.*, 2006	Delorme *et al.*, 2006
	Leptobrachium pullum	Delorme *et al.*, 2006	Delorme *et al.*, 2006
	Leptobrachium smithi	Delorme *et al.*, 2006	Delorme *et al.*, 2006
Megophryidae (cont.)	*Leptolalax arayai*	Lathrop *et al.*, 1998b	Lathrop *et al.*, 1998b
	Leptolalax bourreti	Ohler *et al.*, 2011	Ohler *et al.*, 2011
	Leptolalax oshanensis	----	Liu, 1950
	Leptolalax pelodytoides	Lathrop *et al.*, 1998b	Lathrop *et al.*, 1998b
	Leptolalax pictus	Inger & Stuebing, 1997	Inger & Stuebing, 1997

	Leptolalax pluvialis	Ohler *et al.*, 2011	Ohler *et al.*, 2011
	Leptolalax ventripunctatus	Ohler *et al.*, 2011	Ohler *et al.*, 2011
	Megophrys baluensis	----	Wang *et al.*, 2012
	Megophrys longipes	----	Wang *et al.*, 2012
	Megophrys major	----	Wang *et al.*, 2012
	Megophrys minor	----	Wang *et al.*, 2012
	Megophrys nasuta	Wever, 1985	Wever, 1985; Delorme *et al.*, 2006
	Megophrys parva	----	Wang *et al.*, 2012; Boulenger, 1882
	Megophrys shapingensis	----	Wang *et al.*, 2012
	Megophrys spinata	----	Wang *et al.*, 2012
	Ophryophryne hansi	----	Stuart *et al.*, 2006
	Ophryophryne microstoma	----	Wang *et al.*, 2012; Delorme *et al.*, 2006
	Oreolalax chuanbeiensis	Wu *et al.*, 1993	----
	Oreolalax jiandongensis	Wei *et al.*, 2009	----
	Oreolalax liangbeiensis	Wei *et al.*, 2009	Wei *et al.*, 2009
	Oreolalax lichuanensis	Wei *et al.*, 2009	Wei *et al.*, 2009; Wu *et al.*, 1993
	Oreolalax major	Wu *et al.*, 1993; Wei *et al.*, 2009	Wu *et al.*, 1993; Wei *et al.*, 2009
	Oreolalax multipunctatus	Wei *et al.*, 2009	Wei *et al.*, 2009
	Oreolalax nanjiangensis	Wei *et al.*, 2009	Wei *et al.*, 2009
	Oreolalax omeimontis	Wei *et al.*, 2009	Wei *et al.*, 2009
Megophryidae (cont.)	*Oreolalax pingii*	Delorme *et al.*, 2006; Wei *et al.*, 2009	Delorme *et al.*, 2006; Wei *et al.*, 2009

	Oreolalax popei	Delorme *et al.*, 2006; Wei *et al.*, 2009	Delorme *et al.*, 2006; Wei *et al.*, 2009
	Oreolalax rhodostigmatus	Wu *et al.*, 1993; Delorme *et al.*, 2006; Wei *et al.*, 2009	Wu *et al.*, 1993; Delorme *et al.*, 2006; Wei *et al.*, 2009
	Oreolalax rugosus	Wu *et al.*, 1993; Wei *et al.*, 2009	Wu *et al.*, 1993; Wei *et al.*, 2009
	Oreolalax schmidti	Delorme *et al.*, 2006; Wei *et al.*, 2009	Delorme *et al.*, 2006; Wei *et al.*, 2009
	Oreolalax xiangchengensis	Wei *et al.*, 2009	----
	Scutiger boulengeri	----	----
	Scutiger chintingensis	----	----
	Scutiger mammatus	----	Günther, 1896
	Scutiger muliensis	----	----
	Scutiger tuberculatus	----	----
Micrixalidae	*Micrixalus fuscus*	----	Boulenger, 1882; Biju *et al.*, 2014a
	Micrixalus kottigeharensis	----	Rao, 1937; Biju *et al.*, 2014a
	Micrixalus saxicola	----	Biju *et al.*, 2014a; Chandramouli & Dutta, 2015
Microhylidae	*Anodonthyla boulengerii*	Glaw & Vences, 2007	Glaw & Vences, 2007; Parker, 1934
	Anodonthyla montana	Glaw & Vences, 2007	Glaw & Vences, 2007; Parker, 1934
	Anodonthyla moramora	Glaw & Vences, 2007	Glaw & Vences, 2007

	Anodonthyla rouxae	Glaw & Vences, 2007	Guibe, 1974; Glaw & Vences, 2007
	Apantophryne pansa	----	Parker, 1934
	Asterophrys turpicola	Zweifel, 1972	Zweifel, 1972
	Austrochaperina palmipes	Zweifel, 1956a	Zweifel, 1956a
Microhylidae (cont.)	*Barygenys flavigularis*	Zweifel, 1972	Zweifel, 1972
	Calluela guttulata	Boulenger, 1882	Parker, 1934
	Calluela minuta	----	Parker, 1934
	Calluela yunnanensis	Zhao & Adler, 1993	Parker, 1934
	Callulops robustus	Zweifel, 1972	Parker, 1934; Zweifel, 1972
	Chaperina fusca	Inger, 1966	Inger, 1966; Parker, 1934
	Chiasmocleis albopunctata	----	Parker, 1934
	Chiasmocleis hudsoni	Lima *et al.*, 2006	Lima *et al.*, 2006
	Choerophryne rostellifer	----	Parker, 1934
	Cophixalus ornatus	----	----
	Cophyla berara	----	Glaw & Vences, 2007
	Cophyla phyllodactyla	Glaw & Vences, 2007	Boulenger, 1882; Glaw & Vences, 2007; Parker, 1934
	Copiula derongo	Zweifel, 2000	Zweifel, 2000
	Copiula guttata	----	----
	Ctenophryne aequatorialis	MT pers. obs.	MT pers. obs.
	Ctenophryne geayi	MT pers. obs.; Parker, 1934	MT pers. obs.; Parker, 1934
	Dasypops schirchi	MT pers. obs.	MT pers. obs.; Parker, 1934
	Dermatonotus muelleri	DB & MT pers. obs.	MT pers. obs.

	Dyscophus antongilii	Nussbaum & Wu, 2007	Boulenger, 1882; Nussbaum & Wu, 2007; Parker, 1934
	Dyscophus guineti	MT pers. obs.; Glaw & Vences, 2007	MT pers. obs.; Glaw & Vences, 2007
	Dyscophus insularis	Boulenger, 1882; Glaw & Vences, 2007	Glaw & Vences, 2007; Parker, 1934
	Elachistocleis bicolor	MT pers. obs.; Boulenger, 1882	MT pers. obs.
	Gastrophryne carolinensis	MT pers. obs.; Wever, 1985	MT pers. obs.; Parker, 1934; Wever, 1985
Microhylidae (cont.)	*Gastrophryne elegans*	----	Parker, 1934
	Genyophryne thomsoni	----	Parker, 1934
	Glyphoglossus molossus	Boulenger, 1882	Parker, 1934
	Hamptophryne boliviana	MT pers. obs.	MT pers. obs.; de Sa & Trueb, 1991
	Hoplophryne rogersi	Parker, 1934	Parker, 1934
	Hoplophryne uluguruensis	Parker, 1934	Parker, 1934
	Hylophorbus picoides	Kraus, 2013	Kraus, 2013
	Hylophorbus rufescens	Zweifel, 1972	Zweifel, 1972
	Hypopachus variolosus	MT pers. obs.; Wever, 1985; Boulenger, 1882	MT pers. obs.; Wever, 1985
	Kalophrynus baluensis	----	Inger & Stuebing, 1997
	Kalophrynus interlineatus	----	Parker, 1934
	Kalophrynus intermedius	----	Inger, 1966
	Kalophrynus pleurostigma	Zhao & Adler, 1993	Boulenger, 1882; Parker, 1934; Zhao & Adler, 1993

	Kaloula borealis	----	Parker, 1934
	Kaloula conjuncta	----	Parker, 1934
	Kaloula mediolineata	----	Parker, 1934
	Kaloula picta	----	Parker, 1934
	Kaloula pulchra	MT pers. obs.; Wever, 1985	MT pers. obs.; Wever, 1985
	Liophryne rhododactyla	----	Parker, 1934
	Liophryne schlaginhaufeni	----	Parker, 1934
	Mantophryne lateralis	----	Zweifel, 1972
	Melanobatrachus indicus	Parker, 1934; Boulenger, 1882	Parker, 1934
	Metamagnusia slateri	----	Günther, 2009
	Metaphrynella pollicaris	----	Parker, 1934
	Metaphrynella sundana	----	Inger, 1966; Parker, 1934
	Microhyla achatina	----	Parker, 1934
Microhylidae (cont.)	*Microhyla annectens*	Inger, 1966	Parker, 1934
	Microhyla berdmorei	Parker, 1934	Inger, 1966; Parker, 1934
	Microhyla borneensis	Parker, 1934	Parker, 1934
	Microhyla butleri	Parker, 1934	Parker, 1934 present; Vorobieva & Smirnov, 1987 absent
	Microhyla heymonsi	----	Parker, 1934 present; Vorobieva & Smirnov, 1987 absent
	Microhyla okinavensis	Parker, 1934	Parker, 1934
	Microhyla ornata	----	Smirnov, 1991
	Microhyla palmipes	Parker, 1934	Parker, 1934
	Microhyla pulchra	Parker, 1934	Smirnov, 1991

	Microhyla superciliaris	Parker, 1934	Parker, 1934
	Micryletta inornata	----	Parker, 1934
	Oreophryne monticola	----	Parker, 1934
	Oreophryne sibilans	Günther, 2003	Günther, 2003
	Oreophryne unicolor	Günther, 2003	Günther, 2003
	Otophryne pyburni	Boulenger, 1900a	Boulenger, 1900a
	Oxydactyla crassa	----	----
	Paradoxophyla palmata	Guibe, 1974	Guibe, 1974
	Phrynella pulchra	----	Parker, 1934
	Phrynomantis bifasciatus	Scott, 2005 Boulenger, 1882	Scott, 2005; Harper *et al.*, 2010
	Phrynomantis microps	MT pers. obs.	MT pers. obs.
	Platypelis grandis	----	Parker, 1934
	Platypelis milloti	Glaw & Vences, 2007	Glaw & Vences, 2007
Microhylidae (cont.)	*Platypelis pollicaris*	Glaw & Vences, 2007	Glaw & Vences, 2007; Parker, 1934
	Platypelis tuberifera	----	Parker, 1934
	Plethodonthyla bipunctata	----	Guibe, 1974
	Plethodonthyla guentheri	----	Glaw & Vences, 2007
	Plethodonthyla inguinalis	Glaw & Vences, 2007	Glaw & Vences, 2007; Parker, 1934
	Plethodonthyla mihanika	Glaw & Vences, 2007	Glaw & Vences, 2007
	Plethodonthyla notosticta	Glaw & Vences, 2007	Boulenger, 1882; Glaw & Vences, 2007; Parker, 1934
	Plethodonthyla ocellata	Glaw & Vences, 2007	Glaw & Vences, 2007; Parker, 1934
	Plethodonthyla tuberata	----	Parker, 1934

	Pseudocallulops eurydactylus	Günther, 2009	Günther, 2009; Zweifel, 1972
	Ramanella montana	----	Parker, 1934
	Ramanella obscura	----	Parker, 1934
	Ramanella variegata	----	Parker, 1934
	Rhombophryne alluaudi	Glaw & Vences, 2007	Glaw & Vences, 2007
	Rhombophryne coronata	Vences & Glaw, 2003	Vences & Glaw, 2003
	Rhombophryne coudreaui	Glaw & Vences, 2007	Glaw & Vences, 2007
	Rhombophryne grandis	----	Guibe, 1974
	Rhombophryne coudreaui	----	Glaw & Vences, 2007
	Rhombophryne psologlossa	----	Parker, 1934
	Rhombophryne serratopalpebrosa	Scherz *et al.*, 2014	Scherz *et al.*, 2014
	Rhombophryne testudo	Glaw & Vences, 2007	Glaw & Vences, 2007; Parker, 1934
	Rhombophryne tetradactyla	Glaw & Vences, 2007	Glaw & Vences, 2007
	Rhombophryne tridactyla	Glaw & Vences, 2007	Glaw & Vences, 2007
	Scaphiophryne calcarata	Nussbaum & Wu, 2007	Nussbaum & Wu, 2007
Microhylidae (cont.)	*Scaphiophryne marmorata*	MT pers. obs.; Glaw & Vences, 2007	MT pers. obs.; Glaw & Vences, 2007
	Scaphiophryne menabensis	Glaw & Vences, 2007	Glaw & Vences, 2007
	Sphenophryne cornuta	----	Boulenger, 1882; Parker, 1934
	Synapturanus mirandaribeiroi	MT pers. obs.	MT pers. obs.; Nelson & Lescure, 1975
	Uperodon systoma	Boulenger, 1882	Parker, 1934
	Xenorhina bouwensi	----	Parker, 1934
	Xenorhina obesa	Zweifel, 1960	Zweifel, 1960
	Xenorhina oxycephala	----	Menzies, 2006

Myobatrachidae	*Assa darlingtoni*	Barker *et al.*, 1995	Tyler, 1972
	Crinia deserticola	----	----
	Crinia parinsignifera	----	----
	Crinia riparia	----	----
	Crinia signifera	Boulenger, 1882	----
	Crinia tinnula	----	----
	Geocrinia victoriana	MOP pers. obs.	MOP pers. obs.
	Metacrinia nichollsi	----	----
	Mixophyes carbinensis	Anstis, 2013	Anstis, 2013
	Mixophyes coggeri	Anstis, 2013	Anstis, 2013
	Mixophyes fasciolatus	MOP pers. obs.; Barker *et al.*, 1995	MOP pers. obs.; Boulenger, 1882; Barker *et al.*, 1995
	Mixophyes schevilli	Nussbaum & Wu, 2007; Barker *et al.*, 1995	Nussbaum & Wu, 2007; Barker *et al.*, 1995
	Myobatrachus gouldii	----	----
	Pseudophryne bibronii	Barker *et al.*, 1995	Barker *et al.*, 1995
	Pseudophryne coriacea	Barker *et al.*, 1995	Barker *et al.*, 1995
Myobatrachidae (cont.)	*Rheobatrachus silus*	Barker *et al.*, 1995	----
	Spicospina flammocaerulea	Roberts *et al.*, 1997	Roberts *et al.*, 1997
	Taudactylus acutirostris	Barker *et al.*, 1995	----
	Uperoleia aspera	Barker *et al.*, 1995	----
	Uperoleia borealis	----	----
	Uperoleia crassa	----	----
	Uperoleia fusca	----	----

	Uperoleia glandulosa	----	----
	Uperoleia inundata	----	----
	Uperoleia laevigata	Barker *et al.*, 1995	----
	Uperoleia lithomoda	----	----
	Uperoleia littlejohni	----	----
	Uperoleia micromeles	----	----
	Uperoleia minima	----	----
	Uperoleia mjobergii	----	----
	Uperoleia rugosa	Barker *et al.*, 1995	----
	Uperoleia russelli	Barker *et al.*, 1995	----
	Uperoleia talpa	----	----
	Uperoleia trachyderma	----	----
	Uperoleia tyleri	----	----
Nasikabatrachidae	*Nasikabatrachus sahyadrensis*	Biju & Bossuyt, 2003	----
Nyctibatrachidae	*Nyctibatrachus beddomii*	----	Inger *et al.*, 1984
	Nyctibatrachus deccanensis	Boulenger, 1882	----
	Nyctibatrachus kempholeyensis	----	Rao, 1937
	Nyctibatrachus major	Boulenger, 1882	----
Nyctibatrachidae (cont.)	*Nyctibatrachus minimus*	----	Biju *et al.*, 2007
	Nyctibatrachus minor	----	Inger *et al.*, 1984
	Nyctibatrachus sylvaticus	----	Rao, 1937; Chandramouli & Dutta, 2015
Odontophrynidae	*Macrogenioglottus alipioi*	DB pers. obs.	DB pers. obs.
	Odontophrynus achalensis	MOP pers. obs.	MOP pers. obs.
	Odontophrynus	DB pers. obs.	DB pers. obs.

	americanus		
	Odontophrynus carvalhoi	DB pers. obs.	DB pers. obs.
	Odontophrynus cultripes	DB pers. obs.	DB pers. obs.
	Proceratophrys appendiculata	Dias *et al.*, 2013	Boulenger, 1882; Dias *et al.*, 2013
	Proceratophrys avelinoi	DB pers. obs.	BLB pers. obs.
	Proceratophrys boiei	DB pers. obs.	Boulenger, 1882
	Proceratophrys concavitympanum	----	Giaretta *et al.*, 2000
	Proceratophrys cristiceps	DB pers. obs.	DB pers. obs.
	Proceratophrys laticeps	----	----
	Proceratophrys melanopogon	----	----
Pelodytidae	*Pelobates cultripes*	----	----
	Pelobates fuscus	Laurent, 1986	----
	Pelobates syriacus	----	----
	Pelobates varaldii	----	----
	Pelodytes caucasicus	----	----
	Pelodytes ibericus	----	----
	Pelodytes punctatus	----	----
Petropedetidae	*Arthroleptides martiensseni*	Scott, 2005	Scott, 2005
	Arthroleptides yakusini	Harper *et al.*, 2010	Harper *et al.*, 2010
	Aubria subsigillata	Scott, 2005	Boulenger, 1882; Scott, 2005
Petropedetidae (cont.)	*Petropedetes cameronensis*	Scott, 2005	Scott, 2005
	Petropedetes newtoni	Scott, 2005	Scott, 2005
	Petropedetes parkeri	Scott, 2005	Scott, 2005

Phrynobatrachidae	*Phrynobatrachus acridoides*	Scott, 2005; du Preez & Carruthers, 2009; Spawls *et al.*, 2006	Scott, 2005; du Preez & Carruthers, 2009; Spawls *et al.*, 2006
	Phrynobatrachus africanus	Scott, 2005	Scott, 2005
	Phrynobatrachus calcaratus	Boulenger, 1882	----
	Phrynobatrachus cricogaster	Scott, 2005	Scott, 2005
	Phrynobatrachus dispar	----	Boulenger, 1882
	Phrynobatrachus krefftii	Scott, 2005	Scott, 2005
	Phrynobatrachus natalensis	Scott, 2005; du Preez & Carruthers, 2009	Scott, 2005; du Preez & Carruthers, 2009
	Phrynobatrachus sandersoni	Scott, 2005	Scott, 2005
Pipidae	*Hymenochyrus boettgeri*	----	Rabb & Rabb, 1963
	Pipa carvalhoi	----	----
	Pipa parva	----	Cannatella & Trueb, 1988
	Pipa pipa	Wever, 1985	Wever, 1985
	Xenopus borealis	Wever, 1985	Wever, 1985; Cannatella & Trueb, 1988
	Xenopus epitropicalis	----	Cannatella & Trueb, 1988
	Xenopus fraseri	----	Evans *et al.*, 2015
	Xenopus laevis	Wever, 1985	Wever, 1985; Cannatella & Trueb, 1988
	Xenopus muelleri	----	Cannatella & Trueb, 1988
	Xenopus tropicalis	Cannatella & Trueb, 1988	Cannatella & Trueb, 1988
Ptychadenidae	*Hildebrandtia ornata*	Scott, 2005; du Preez & Carruthers, 2009	Scott, 2005; Boulenger, 1882; du Preez & Carruthers,

			2009
	Ptychadena aequiplicata	----	Boulenger, 1900c
	Ptychadena anchietae	Scott, 2005; du Preez & Carruthers, 2009	Scott, 2005; du Preez & Carruthers, 2009
	Ptychadena mascareniensis	Scott, 2005; du Preez & Carruthers, 2009	Scott, 2005; du Preez & Carruthers, 2009
	Ptychadena oxyrhynchus	du Preez & Carruthers, 2009	Boulenger, 1882; du Preez & Carruthers, 2009
	Ptychadena porosissima	du Preez & Carruthers, 2009	du Preez & Carruthers, 2009
	Ptychadena taenioscelis	Harper *et al.*, 2010	Harper *et al.*, 2010
Pyxicephalidae	*Amietia angolensis*	Scott, 2005; du Preez & Carruthers, 2009; Spawls *et al.*, 2006	Scott, 2005; du Preez & Carruthers, 2009; Spawls *et al.*, 2006
	Amietia fuscigula	Scott, 2005	Scott, 2005; Boulenger, 1882
	Anhydrophryne rattrayi	Scott, 2005	Scott, 2005
	Arthroleptella landdrosia	Scott, 2005; du Preez & Carruthers, 2009	Scott, 2005; du Preez & Carruthers, 2009
	Arthroleptella lightfooti	----	-----
	Cacosternum boettgeri	Scott, 2005; Nussbaum & Wu, 2007; du Preez & Carruthers, 2009	Scott, 2005; Nussbaum & Wu, 2007; du Preez & Carruthers, 2009
	Cacosternum capense	Scott, 2005; du Preez & Carruthers, 2009	Scott, 2005
	Cacosternum nanum	Scott, 2005	Scott, 2005
	Microbatrachella capensis	Scott, 2005	Scott, 2005

	Natalobatrachus bonebergi	Scott, 2005; du Preez & Carruthers, 2009	Scott, 2005; du Preez & Carruthers, 2009
	Poyntonia paludicola	Scott, 2005; du Preez & Carruthers, 2009	Scott, 2005
Pyxicephalidae (cont.)	*Pyxicephalus adspersus*	Scott, 2005; du Preez & Carruthers, 2009	Scott, 2005; Haas, 1999; Boulenger, 1882; du Preez & Carruthers, 2009
	Pyxicephalus edulis	Scott, 2005; du Preez & Carruthers, 2009	Scott, 2005; du Preez & Carruthers, 2009
	Strongylopus fasciatus	du Preez & Carruthers, 2009	Boulenger, 1882; du Preez & Carruthers, 2009
	Strongylopus grayii	Scott, 2005	Boulenger, 1882; Scott, 2005
	Tomopterna delalandii	du Preez & Carruthers, 2009; Boulenger, 1882	Boulenger, 1882
	Tomopterna marmorata	Scott, 2005	Scott, 2005
	Tomopterna natalensis	du Preez & Carruthers, 2009	Boulenger, 1882
	Tomopterna tandyi	Scott, 2005	Scott, 2005
	Tomopterna tuberculosa	du Preez & Carruthers, 2009	Boulenger, 1882
Ranidae	*Abavorana luctuosa*	Inger & Stuebing, 1997	Inger, 1966; Inger & Stuebing, 1997
	Amnirana albolabris	Scott, 2005; Spawls *et al.*, 2006	Boulenger, 1882; Scott, 2005; Spawls *et al.*, 2006
	Amnirana galamensis	Scott, 2005; du Preez & Carruthers, 2009; Spawls *et al.*,	Boulenger, 1882; Scott, 2005; du Preez & Carruthers,

		2006	2009; Spawls *et al.*, 2006
	Amolops chunganensis	----	Yang, 1991
	Amolops daorum	Bain *et al.*, 2003	Bain *et al.*, 2003
	Amolops granulosus	----	Yang, 1991
	Amolops hainanensis	----	Yang, 1991
	Amolops hongkongensis	----	Yang, 1991
	Amolops jinjiangensis	----	Yang, 1991
	Amolops larutensis	----	Yang, 1991
	Amolops loloensis	----	Yang, 1991
	Amolops montzorum	----	Yang, 1991
	Amolops ricketti	Scott, 2005	Inger *et al.*, 1999; Scott, 2005
Ranidae (cont.)	*Amolops spinapectoralis*	Inger *et al.*, 1999	Inger *et al.*, 1999
	Amolops viridimaculatus	Zhao & Adler, 1993	Zhao & Adler, 1993
	Babina adenopleura	----	Liu, 1936
	Babina okinavana	----	Boettger, 1895
	Babina pleuraden	----	Liu, 1950
	Chalcorana chalconota	Inger & Stuebing, 1997	Boulenger, 1882; Inger & Stuebing, 1997
	Chalcorana eschatia	----	Inger *et al.*, 2009
	Chalcorana megalonesa	----	Inger *et al.*, 2009
	Chalcorana parvaccola	----	Inger *et al.*, 2009
	Chalcorana raniceps	----	Inger *et al.*, 2009
	Clinotarsus alticola	----	Boulenger, 1882
	Clinotarsus curtipes	----	Boulenger, 1882
	Glandirana rugosa	----	Boulenger, 1882
	Glandirana tientaiensis	Zhao & Adler, 1993	Zhao & Adler, 1993
	Huia cavitympanum	Inger, 1966	Inger, 1966

	Huia masonii	----	Iskandar, 1998
	Hydrophylax gracilis	Parker, 1881	Parker, 1881
	Hydrophylax malabaricus	Biju *et al.*, 2014b	Boulenger, 1882; Biju *et al.*, 2014b
	Hylarana erythrea	Teynie *et al.*, 2010	Inger, 1966; Boulenger, 1882
	Hylarana macrodactyla	----	Liu, 1936; Boulenger, 1882
	Hylarana taipehensis	Zhao & Adler, 1993	Inger *et al.*, 1999; Zhao & Adler, 1993
	Indosylvirana aurantiaca	Biju *et al.*, 2014b	Biju *et al.*, 2014b
	Indosylvirana milleti	----	Inger *et al.*, 1999
	Lithobates areolatus	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Lithobates berlandieri	----	McCranie & Wilson, 2002
	Lithobates blairi	Elliot *et al.*, 2009	Elliot *et al.*, 2009
Ranidae (cont.)	*Lithobates bwana*	Hillis & de Sá, 1988	Hillis & de Sá, 1988
	Lithobates capito	----	Boulenger, 1882
	Lithobates catesbeianus	Wever, 1985	Wever, 1985; Boulenger, 1882
	Lithobates chiricahuensis	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Lithobates clamitans	Wever, 1985	Wever, 1985; Boulenger, 1882
	Lithobates fisheri	Dood, 2013	Dood, 2013
	Lithobates forreri	Savage, 2002	Savage, 2002
	Lithobates grylio	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Lithobates heckscheri	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Lithobates juliani	Hillis & de Sá, 1988	Hillis & de Sá, 1988
	Lithobates macroglossa	----	Boulenger, 1882; Inger, 1966
	Lithobates maculatus	Hillis & de Sá, 1988	Hillis & de Sá, 1988
	Lithobates montezumae	----	Boulenger, 1882

	Lithobates okaloosae	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Lithobates onca	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Lithobates palmipes	Kok & Kalamandeen, 2008	Kok & Kalamandeen, 2008
	Lithobates palustris	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Lithobates pipiens	Scott, 2005	Scott, 2005
	Lithobates septentrionalis	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Lithobates sevosus	Dood, 2013	Dood, 2013
	Lithobates sierramadrensis	Hillis & de Sá, 1988	Hillis & de Sá, 1988
	Lithobates sphenocephalus	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Lithobates sylvaticus	----	Boulenger, 1882
	Lithobates tarahumarae	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Lithobates taylori	Savage, 2002	Savage, 2002
	Lithobates vaillanti	Savage, 2002	Savage, 2002
	Lithobates vibicarius	Savage, 2002	Savage, 2002
	Lithobates virgatipes	Wever, 1985	Wever, 1985
Ranidae (cont.)	*Lithobates warszewitschii*	Jaslow *et al.*, 1988; Savage, 2002	Jaslow *et al.*, 1988; Boulenger, 1882; Savage, 2002
	Lithobates yavapaiensis	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Meristogenys jerboa	----	Inger, 1966; Boulenger, 1882
	Meristogenys kinabaluensis	Inger & Stuebing, 1997	Inger & Stuebing, 1997
	Meristogenys phaeomerus	Inger & Stuebing, 1997	Yang, 1991
	Meristogenys poecilus	----	Yang, 1991
	Meristogenys whiteheadi	----	Inger & Stuebing, 2009
	Odorrana andersonii	----	Liu, 1936; Boulenger, 1882
	Odorrana bacboensis	Bain *et al.*, 2003	Bain *et al.*, 2003
	Odorrana chloronota	Bain *et al.*, 2003	Inger, 1966; Boulenger, 1882

	Odorrana grahami	----	Bain *et al.*, 2003
	Odorrana hosii	----	Bain *et al.*, 2003
	Odorrana ishikawae	----	Stejneger, 1901
	Odorrana jingdongensis	----	Bain *et al.*, 2003
	Odorrana junlianensis	----	Bain *et al.*, 2003
	Odorrana khalam	Stuart *et al.*, 2005	Stuart *et al.*, 2005
	Odorrana livida	Bain *et al.*, 2003	Bain *et al.*, 2003
	Odorrona margaretae	Zhao & Adler, 1993	Liu, 1950; Zhao & Adler, 1993
	Odorrana morafkai	----	Bain *et al.*, 2003
	Odorrana schmackeri	Zhao & Adler, 1993	Zhao & Adler, 1993
	Odorrana swinhoana	Zhao & Adler, 1993	Zhao & Adler, 1993
	Odorrana tiannanensis	Zhao & Adler, 1993	Zhao & Adler, 1993
	Odorrana tormota	Gridi-Papp *et al.*, 2008	Gridi-Papp *et al.*, 2008
	Papurana arfaki	----	Boulenger, 1882
	Papurana daemeli	Barker *et al.*, 1995	Barker *et al.*, 1995
	Pelophylax cerigensis	Beerli *et al.*, 1994	Beerli *et al.*, 1994
	Pelophylax cretensis	Beerli *et al.*, 1994	Beerli *et al.*, 1994
	Pelophylax epeiroticus	----	Schneider *et al.*, 1984
Ranidae (cont.)	*Pelophylax esculentus*	Boulenger, 1882	Ecker, 1889
	Pelophylax fukienensis	Zhao & Adler, 1993	Zhao & Adler, 1993
	Pelophylax nigromaculatus	Zhao & Adler, 1993	Liu, 1950; Zhao & Adler, 1993
	Pelophylax plancyi	Zhao & Adler, 1993	Zhao & Adler, 1993; Boulenger, 1882
	Pelophylax ridibundus	Wever, 1985	Wever, 1985
	Pelophylax saharicus	Schleich *et al.*, 1996	Schleich *et al.*, 1996
	Pulchrana baramica	----	Iskandar, 1998; Inger, 1966
	Pulchrana glandulosa	----	Inger, 1966; Boulenger,

			1882
	Pulchrana signata	----	Inger, 1966; Boulenger, 1882
	Rana arvalis	Boulenger, 1882	Boulenger, 1882
	Rana aurora	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Rana boylii	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Rana cascadae	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Rana chaochiaoensis	----	Liu, 1950
	Rana chensinensis	----	Liu, 1950
	Rana dalmatina	----	Boulenger, 1882
	Rana hanluica	----	Shen et *al.*, 2007
	Rana iberica	----	Boulenger, 1882
	Rana japonica	----	Liu, 1936; Boulenger, 1882
	Rana johnsi	----	Smith, 1921
	Rana latastei	----	Boulenger, 1882
	Rana longicrus	Zhao & Adler, 1993	Zhao & Adler, 1993
	Rana luteiventris	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Rana macrocnemis	----	Picariello *et al.*, 1999
	Rana muscosa	Elliot *et al.*, 2009	Elliot *et al.*, 2009
	Rana pirica	Matsui, 1991	Matsui, 1991
	Rana pretiosa	----	Boulenger, 1882
	Rana sauteri	Zhao & Adler, 1993	Zhao & Adler, 1993
Ranidae (cont.)	*Rana shuchinae*	----	Liu, 1950
	Rana tagoi	----	Ryuzaki *et al.*, 2014
	Rana temporaria	----	Boulenger, 1882
	Sanguina sanguinea	Inger, 1954	Inger, 1954
	Staurois latopalmatus	----	Inger & Stuebing, 1997
	Staurois natator	Scott, 2005	Scott, 2005 Boulenger, 1882
	Staurois tuberilinguis	----	Inger, 1966

	Sylvirana guentheri	Zhao & Adler, 1993	Zhao & Adler, 1993; Boulenger, 1882
	Sylvirana maosonensis	----	Inger *et al.*, 1999
	Sylvirana nigrovittata	----	Smith, 1921
Ranixalidae	*Indirana beddomi*	----	Inger *et al.*, 1984; Boulenger, 1882
	Indirana brachytarsus	----	Inger *et al.*, 1984
	Indirana diplosticta	----	Inger *et al.*, 1984
	Indirana semipalmata	----	Inger *et al.*, 1984; Chandramouli & Dutta, 2015
Rhacophoridae	*Buergeria buergeri*	----	Boulenger, 1882
	Buergeria japonica	Zhao & Adler, 1993	Zhao & Adler, 1993
	Buergeria robusta	Zhao & Adler, 1993	Zhao & Adler, 1993
	Chiromantis doriae	----	Zhao & Adler, 1993
	Chiromantis petersii	----	Boulenger, 1882
	Chiromantis rufescens	----	Boulenger, 1882
	Chiromantis vittatus	----	Orlov *et al.*, 2012
	Chiromantis xerampelina	du Preez & Carruthers, 2009; Scott, 2005	du Preez & Carruthers, 2009; Scott, 2005
	Feihyla kajau	----	Inger & Stuebing, 1997
	Feihyla palpebralis	----	Inger *et al.*, 2012
	Ghatixalus variabilis	----	----
	Gracixalus gracilipes	----	Rowley *et al.*, 2011
Rhacophoridae (cont.)	*Gracixalus supercornutus*	----	Rowley *et al.*, 2011
	Kurixalus appendiculatus	----	Inger, 1966; Boulenger, 1882
	Kurixalus banaensis	----	Orlov *et al.*, 2012
	Kurixalus eiffingeri	Zhao & Adler, 1993	Zhao & Adler, 1993

	Kurixalus idiooticus	Wu *et al.*, 2016	Wu *et al.*, 2016
	Kurixalus odontotarsus	----	Orlov *et al.*, 2012
	Liuixalus romeri	Zhao & Adler, 1993	Zhao & Adler, 1993
	Nyctixalus pictus	Inger & Stuebing, 1997	Inger & Stuebing, 1997
	Philautus acutirostris	Boulenger, 1882	----
	Philautus acutus	Dring, 1987	Dring, 1987
	Philautus aurantium	----	Inger & Stuebing, 1997
	Philautus aurifasciatus	----	Inger, 1966; Boulenger, 1882
	Philautus bunitus	Inger & Stuebing, 1997	Inger & Stuebing, 1997
	Philautus hosii	----	Inger, 1966
	Philautus petersi	Inger & Stuebing, 1997	Inger & Stuebing, 1997
	Philautus surdus	Scott, 2005; Boulenger, 1882	Scott, 2005
	Philautus umbra	----	Dring, 1987
	Polypedates colletti	----	Inger, 1966
	Polypedates leucomystax	----	Inger, 1966
	Polypedates macrotis	----	Inger, 1966
	Polypedates maculatus	Wever, 1985	Wever, 1985; Boulenger, 1882
	Polypedates otilophus	----	Inger, 1966
	Pseudophilautus alto	----	Manamendra-Arachchi & Pethiyagoda, 2005
	Pseudophilautus amboli	Biju & Bossuyt, 2009	Biju & Bossuyt, 2009
	Pseudophilautus cavirostris	----	Boulenger, 1882; Manamendra-Arachchi & Pethiyagoda, 2005
	Pseudophilautus decoris	Wickramasinghe *et al.*, 2013	Wickramasinghe *et al.*, 2013
Rhacophoridae (cont.)	*Pseudophilautus femoralis*	----	Günther, 1864
	Pseudophilautus folicola	----	Wickramasinghe *et al.*,

			2013
	Pseudophilautus hoffmanni	Wickramasinghe *et al.*, 2013	Wickramasinghe *et al.*, 2013
	Pseudophilautus jayarami	Biju & Bossuyt, 2009	Biju & Bossuyt, 2009
	Pseudophilautus kani	Biju & Bossuyt, 2009	Biju & Bossuyt, 2009
	Pseudophilautus leucorhinus	----	Boulenger, 1882
	Pseudophilautus lunatus	----	Manamendra-Arachchi & Pethiyagoda, 2005
	Pseudophilautus mooreorum	----	Meegaskumbara & Manamendra-Arachchi, 2005
	Pseudophilautus microtympanum	----	Manamendra-Arachchi & Pethiyagoda, 2005
	Pseudophilautus ocularis	----	Manamendra-Arachchi & Pethiyagoda, 2005
	Pseudophilautus papillosus	----	Manamendra-Arachchi & Pethiyagoda, 2005
	Pseudophilautus pleurotaenia	----	Manamendra-Arachchi & Pethiyagoda, 2005
	Pseudophilautus popularis	----	Manamendra-Arachchi & Pethiyagoda, 2005
	Pseudophilautus reticulatus	----	Boulenger, 1882
	Pseudophilautus sarasinorum	----	Manamendra-Arachchi & Pethiyagoda, 2005
	Pseudophilautus schmarda	----	Boulenger, 1882
	Pseudophilautus tanu	Wickramasinghe *et al.*, 2013	Wickramasinghe *et al.*, 2013
	Pseudophilautus zorro	----	Wickramasinghe *et al.*, 2013
	Raorchestes anili	----	Seshadri *et al.*, 2012

	Raorchestes beddomii	----	Boulenger, 1882
	Raorchestes charius	----	Rao, 1937
	Raorchestes chlorosoma	----	Seshadri *et al.*, 2012
	Raorchestes chotta	Seshadri *et al.*, 2012	----
Rhacophoridae (cont.)	*Raorchestes chromasynchysi*	----	Seshadri *et al.*, 2012
	Raorchestes coonoorensis	----	Seshadri *et al.*, 2012
	Raorchestes dubois	----	Seshadri *et al.*, 2012
	Raorchestes glandulosus	Boulenger, 1882	Seshadri *et al.*, 2012
	Raorchestes graminirupes	----	Seshadri *et al.*, 2012
	Raorchestes griet	----	Seshadri *et al.*, 2012
	Raorchestes luteolus	----	Kuramoto & Joshy, 2003
	Raorchestes marki	----	Seshadri *et al.*, 2012
	Raorchestes munnarensis	----	Seshadri *et al.*, 2012
	Raorchestes nerostagona	----	Seshadri *et al.*, 2012
	Raorchestes ponmudi	----	Seshadri *et al.*, 2012
	Raorchestes sushili	----	Seshadri *et al.*, 2012
	Raorchestes tinniens	----	Boulenger, 1882; Rao, 1937; Seshadri *et al.*, 2012
	Raorchestes tuberohumerus	----	Kuramoto & Joshy, 2003
	Rhacophorus annamensis	----	Stuart *et al.*, 2006
	Rhacophorus angulirostris	Inger & Stuebing, 1997	Inger & Stuebing, 1997
	Racophorus calcaneus	----	Stuart *et al.*, 2006
	Rhacophorus chenfui	Zhao & Adler, 1993	Liu, 1950; Zhao & Adler, 1993
	Rhacophorus dennysi	----	Boulenger, 1882
	Rhacophorus dugritei	Zhao & Adler, 1993	Liu, 1950; Boulenger, 1882
	Rhacophorus dulitensis	----	Inger, 1966

	Rhacophorus fasciatus	----	Inger, 1966
	Rhacophorus gauni	----	Inger, 1966
	Rhacophorus harrisoni	Inger & Stuebing, 1997	Inger & Stuebing, 1997
	Rhacophorus maximus	----	Günther, 1858
	Rhacophorus minimus	Rao *et al.*, 2006	Rao *et al.*, 2006
	Rhacophorus nigropalmatus	Wever, 1985; Inger, 1966	Wever, 1985
	Rhacophorus omeimontis	Zhao & Adler, 1993	Liu, 1950; Zhao & Adler, 1993
Rhacophoridae (cont.)	*Rhacophorus orlovi*	Ziegler & Köhler, 2001	Ziegler & Köhler, 2001
	Rhacophorus pardalis	Inger & Stuebing, 1997	Inger & Stuebing, 1997
	Rhacophorus reindwartii	Zhao & Adler, 1993	Inger *et al.*, 1999; Zhao & Adler, 1993
	Rhacophorus rhodopus	Zhao & Adler, 1993	Zhao & Adler, 1993
	Rhacophorus rufipes	Inger & Stuebing, 1997	Inger & Stuebing, 1997
	Rhacophorus schlegelii	----	Boulenger, 1882
	Taruga eques	----	Boulenger, 1882; Meegaskumbura *et al.*, 2010
	Taruga fastigo	----	Meegaskumbura *et al.*, 2010
	Taruga longinasus	----	Meegaskumbura *et al.*, 2010
	Theloderma asperum	Zhao & Adler, 1993	Zhao & Adler, 1993
	Theloderma corticale	----	Zhao & Adler, 1993
	Theloderma moloch	-----	Annandale, 1912
	Theloderma stellatum	----	Zhao & Adler, 1993
Rhinodermatidae	*Insuetophrynus acarpicus*	Barrio, 1970	Barrio, 1970
	Rhinoderma darwinii	Nussbaum & Wu, 2007	Nussbaum & Wu, 2007; Boulenger, 1882

Rhinophrynidae	*Rhinophrynus dorsalis*	Wever, 1985	Wever, 1985
Scaphiopodidae	*Scaphiopus couchii*	Wever, 1985; Nussbaum & Wu, 2007	Wever, 1985; Nussbaum & Wu, 2007
	Scaphiopus holbrookii	Laurent, 1986;	Laurent, 1986
	Scaphiopus hurteri	Wever, 1985	Wever, 1985
	Spea bombifrons	Wever, 1985	Wever, 1985
	Spea hammondi	Wever, 1985; Boulenger, 1882	Wever, 1985
	Spea intermontana	----	Hall & Larsen, 1998
	Spea multiplicata	----	----
Sooglossidae	*Sechellophryne gardineri*	Boistel *et al.*, 2013; Nussbaum & Wu, 2007	Nussbaum & Wu, 2007
	Sooglosus sechellensis	Scott, 2005; Nussbaum & Wu, 2007	Scott, 2005; Nussbaum & Wu, 2007
	Sooglosus thomasseti	Nussbaum & Wu, 2007	Nussbaum & Wu, 2007
Telmatobiidae	*Telmatobius bolivianus*	Lavilla & Ergueta Sandoval, 1999	Parker, 1940; Lavilla & Ergueta Sandoval, 1999
	Telmatobius culeus	JSB pers. obs.	JSB pers. obs.; Jaslow *et al.*, 1988
	Telmatobius gigas	de la Riva, 2002a	----
	Telmatobius hintoni	JSB pers. obs.	JSB pers. obs.
	Telmatobius huayra	Lavilla & Ergueta Sandoval, 1995	Lavilla & Ergueta Sandoval, 1995
	Telmatobius marmoratus	JSB pers. obs.	JSB pers. obs.
	Telmatobius niger	Trueb, 1979	Trueb, 1979
	Telmatobius sibiricus	JSB pers. obs;.de la Riva & Harvey, 2003	JSB pers. obs.

	Telmatobius simonsi	JSB pers. obs;.de la Riva & Harvey, 2003	JSB pers. obs;.de la Riva & Harvey, 2003
	Telmatobius truebae	----	----
	Telmatobius vellardi	Trueb, 1979	Trueb, 1979
	Telmatobius verrucosus	JSB pers. obs.	JSB pers. obs.
	Telmatobius vilamensis	Formas *et al.*, 2003	Formas *et al.*, 2003
	Telmatobius yuracare	de la Riva & Harvey, 2003	JSB pers. obs.
	Telmatobius zapahuirensis	Veloso *et al.*, 1982	Veloso *et al.*, 1982
Anura not included in Pyron (2014)			
Family	**Species**	**Tympanic membrane**	**Tympanic annulus**
Alsodidae	*Eupsophus altor*	----	----
Arthroleptidae	*Arthroleptis phrynoides*	Liu, 1950	Liu, 1950
	Cardioglossa escalaerae	Scott, 2005	Scott, 2005
	Letodactylodon ventrimarmoratus	Scott, 2005	Scott, 2005
	Leptopelis mossambicus	Scott, 2005	Scott, 2005
Batrachylidae	*Atelognathus nitoi*	----	----
	Atelognathus praebasalticus	----	----
	Atelognathus reverberii	----	----
	Atelognathus solitarius	----	----
	Chaltenobatrachus grandisonae	Basso *et al.*, 2011	Basso *et al.*, 2011
Brachycephalidae	*Ischnocnema nigriventris*	----	----
Callyptocephalellidae	*Telmatobufo australis*	Formas *et al.*, 2001	Formas *et al.*, 2001
Ceratobatrachidae	*Alcalus mariae*	----	Fuiten, 2012
	Cornufer bufoniformis	Scott, 2005	Scott, 2005
Ceratophryidae	*Ceratophrys aurita*	----	----
	Ceratophrys calcarata	----	----

	Ceratophrys cranwelli	MOP pers. obs.	MOP pers. obs.
Craugastoridae	*Bryophryne abramalagae*	Lehr & Catenazzi, 2010	Lehr & Catenazzi, 2010
	Bryophryne bakersfield	Chaparro *et al.*, 2015	Chaparro *et al.*, 2015
	Bryophryne bustamantei	Chaparro *et al.*, 2007	Chaparro *et al.*, 2007
	Bryophryne flammiventris	Lehr & Catenazzi, 2010	Lehr & Catenazzi, 2010
	Bryophryne gymnotis	Lehr & Catenazzi, 2010	Lehr & Catenazzi, 2010
	Bryophryne hanssaueri	Lehr & Catenazzi, 2009	Lehr & Catenazzi, 2009
	Bryophryne nubilosus	Lehr & Catenazzi, 2008	Lehr & Catenazzi, 2008
	Bryophryne zonalis	Lehr & Catenazzi, 2009	Lehr & Catenazzi, 2009
Craugastoridae (cont.)	*Euparkerella cochranae*	----	----
	Euparkerella cryptica	----	----
	Euparkerella robusta	----	----
	Euparkerella tridactyla	----	----
	Hypodactylus nigrovittatus	----	----
Cycloramphidae	*Cycloramphus asper*	Verdade, 2005	----
	Cycloramphus dubius	----	----
	Cycloramphus granulosus	----	----
	Cycloramphus ohausi	Verdade, 2005	----
	Cycloramphus stejnegeri	Verdade, 2005	----
	Thoropa lutzi	----	----
	Thoropa petropolitana	----	----
Eleutherodactylidae	*Eleutherodactylus albolabris*	----	----
	Eleutherodactylus grandis	----	----
	Eleutherodactylus guttilatus	----	----
	Eleutherodactylus karlschmidti	----	----
	Eleutherodactylus leprus	----	----
	Eleutherodactylus pallidus	----	----

	Eleutherodactylus rubrimaculatus	----	----
	Phrynopus montium	----	----
	Pristimantis festae	----	----
	Pristimantis ornatissimus	----	----
	Pristimantis variabilis	----	----
Hemiphractidae	*Cryptobatrachus conditus*	----	----
	Cryptobatrachus fuhrmanni	----	----
	Fritziana fissilis	----	----
	Fritziana goeldii	----	----
	Fritziana ohausi	----	----
	Fritziana ulei	----	----
Hylidae	*Duellmanohyla uranochroa*	----	Boulenger, 1882
	Hyla hallowellii	----	----
	Hyloscirtus bogotensis	Lynch & Renjifo, 2001	Lynch & Renjifo, 2001
Hylodidae	*Crossodactylus dispar*	----	----
	Crossodactylus grandis	----	----
	Crossodactylus gaudichaudii	----	----
	Hylodes asper	----	----
	Hylodes dactylocinus	Pavan *et al.*, 2001	Pavan *et al.*, 2001
	Hylodes glaber	----	----
	Hylodes lateristrigatus	----	----
	Hylodes magalhaesi	----	----
	Hylodes nasus	----	----
	Hylodes perplicatus	----	Miranda Ribero, 1926
	Hylodes phyllodes	Heyer & Cocroft, 1986	Heyer & Cocroft, 1986
Hyperoliidae	*Callixalus pictus*	----	Drewes, 1984

	Hyperolius horstockii	Boulenger, 1882; du Preez & Carruthers, 2009	----
	Kassinula wittei	----	Drewes, 1984
Leptodactylidae	*Crossodactylodes bokermanni*	Barata *et al.*, 2013	----
	Crossodactylodes izecksohni	Barata *et al.*, 2013	----
	Crossodactylodes pintoi	Barata *et al.*, 2013	----
	Crossodactylodes septentrionalis	Teixeira *et al.*, 2013	Teixeira *et al.*, 2013
	Hydrolaetare schmidti	Cochran & Goin, 1959	Cochran & Goin, 1959
	Leptodactylus latinasus	DB pers. obs.	DB pers. obs.; Ponssa, 2008
	Leptodactylus macrosternum	----	----
	Leptodactylus poecilochilus	----	Boulenger, 1882
	Leptodactylus pustulatus	----	----
	Paratelmatobius lutzii	Barata *et al.*, 2013	----
Leptodactylidae (cont.)	*Paratelmatobius mantiqueira*	----	Pombal & Haddad, 1999
	Paratelmatobius yepiranga	Garcia *et al.*, 2009	Garcia *et al.*, 2009
	Physalaemus ephippifer	DB pers. obs.	DB pers. obs.
	Physalaemus maculiventris	Heyer *et al.*, 1990	----
	Physalaemus nanus	----	----
	Pseudopaludicola boliviana	DB pers. obs.	DB pers. obs.
	Pseudopaludicola saltica	DB pers. obs.	DB pers. obs.
	Pseudopaludicola pusilla	----	----
	Rupirana cardosoi	----	----

Limnodynastidae	*Heleioporus albopunctatus*	----	----
	Heleioporus eyrei	----	----
	Notaden nichollsi	Nussbaum & Wu, 2007	Nussbaum & Wu, 2007
	Philoria frosti	----	----
Mantellidae	*Boophis rhodoscelis*	----	----
	Tsingymantis antitra	Glaw & Vences, 2007	Glaw & Vences, 2007
Megophryidae	*Leptobrachella mjobergi*	Inger & Stuebing, 1997	Inger & Stuebing, 1997
Microhylidae	*Adelastes hylonomus*	----	Zweiffel, 1986
	Arcovomer passarelii	MT pers. obs.	MT pers. obs.
	Callulops glandulosus	Zweifel, 1972	Zweifel, 1972
	Chiasmocleis avilapiresae	MT pers. obs.	MT pers. obs.
	Chiasmocleis capixaba	MT pers. obs.	MT pers. obs.
	Chiasmocleis carvalhoi	MT pers. obs.	MT pers. obs.
	Chiasmocleis leucosticta	MT pers. obs.	MT pers. obs.
	Chiasmocleis schubarti	MT pers. obs.	MT pers. obs.
	Cophixalus saxatilis	----	----
	Ctenophryne aterrima	MT pers. obs.	MT pers. obs.
	Myersiella microps	MT pers. obs.	MT pers. obs.
	Otophryne pyburni	----	----
Microhylidae (cont.)	*Otophryne steyermarki*	Kok & Kalamandeen, 2008	Kok & Kalamandeen, 2008
	Oxydactyla coggeri	----	----
	Stereocyclops histrio	MT pers. obs.	MT pers. obs.
	Stereocyclops incrassatus	MT pers. obs.	MT pers. obs.
	Stereocyclops parkeri	MT pers. obs.	MT pers. obs.
	Uperodon mormorata	----	Chandramouli & Dutta, 2015
Myobatrachidae	*Arenophryne rotunda*	----	----
	Crinia bilingua	----	----
	Crinia georgiana	----	Heyer & Liem, 1976

	Crinia glauerti	----	----
	Crinia insignifera	----	----
	Crinia tasmaniensis	----	----
	Crinia subinsignifera	----	----
	Pseudophryne australis	----	----
	Pseudophryne corroboree	----	----
	Pseudophryne dendyi	----	----
	Pseudophryne douglasi	----	----
	Pseudophryne guentheri	----	----
	Pseudophryne major	----	----
	Pseudophryne occidentalis	----	----
	Pseudophryne semimarmorata	Loftus-Hill, 1973	Loftus-Hill, 1973
	Taudactylus diurnus	Nussbaum & Wu, 2007	Nussbaum & Wu, 2007
Odontobatrachidae	*Odontobatrachus natator*	Scott, 2005	Scott, 2005; Barej *et al.*, 2014
Phrynobatrachidae	*Phrynobatrachus plicatus*	Scott, 2005	Scott, 2005
Pyxicephalidae	*Anhydrophryne hewitti*	Scott, 2005	Scott, 2005
	Arthroleptella lightfooti	Scott, 2005	Scott, 2005
	Ericabatrachus baleensis	----	Scott, 2005
	Nothophryne broadleyi	Scott, 2005	Scott, 2005
Ranidae	*Hydrophylax gracilis*	Biju *et al.*, 2014b	Biju *et al.*, 2014b
	Indosylvirana temporalis	Biju *et al.*, 2014b	Biju *et al.*, 2014b
	Indosylvirana flavescens	----	Chandramouli & Dutta, 2015
Ranixalidae	*Indirana temporalis*	----	Boulenger, 1882
Rhacophoridae	*Pseudophilautus silus*	----	----
	Theloderma pictum	----	----
Telmatobiidae	*Telmatobius*	----	----

	brachydactylus		
	Telmatobius laticeps	----	----
	Telmatobius macrostomus	----	----
Incertae sedis (Brachycephaloidea)	*Atopophrynus syntomopus*	----	----
	Geobatrachus walkeri	Ardila-Robayo, 1979	Ardila-Robayo, 1979

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SUPPLEMENTARY INFORMATION 2.2

Additional information on clades or species of Anura in which tympanic middle ear structures were completely lost (as evidenced by the lack of columella).

Clades in which the lack of columella is a putative synapomorphy. Numbers given in brackets are scored species/total species in the genus

Ascaphus [1/2] (Ascaphidae) + *Leiopelma* [2/4] (Leiopelmatidae): As was noted in the Discussion section, the lack of tympanic middle ear structures is a synapomorphy of the most basal extant anuran clade (see Section S2.1).

Atelognathus [6/7] + *Chaltenobatrachus* [1/1] (Batrachylidae): The only two species included by Pyron (2014) lack a columella, as well as *A. nitoi*, *A. praebasalticus*, *A. reverberii*, and *A. solitarius* (see Section S2.1).

Chaltenobatrachus grandisonae was not included by Pyron (2014) but Basso *et al*. (2011) recovered *Atelognathus* and *Chaltenobatrachus* as highly supported sister genera.

Brachycephalus [8/29] (Brachycephalidae): The eight scored species that were included by Pyron (2014) lack a columella. The remaining four sampled species have unknown character states.

Hoplophryne [2/2] (Microhylidae): Both species of this genus lack a columella.

Pseudophryne [10/14] (Myobatrachidae): The only two species included by Pyron (2014) lack a columella. In addition eight species not included in that hypothesis lack this structure (see Section S2.1), and the condition is unknown in the remaining four species.

Telmatobufo [3/4] (Calyptocephalellidae): The only two species included by Pyron (2014) lack a columella, as well as *T. australis* (see Section S2.1). The character state in the remaining species (*T. ignotus*) is unknown.

Species in which the lack of a columella is autapomorphic according to the phylogenetic hypothesis of Pyron (2014)

Balebreviceps hilmani (Brevicipitidae): Monotypic genus.

Melanobatrachus indicus (Microhylidae): Monotypic genus.

Rhinophrynus dorsalis (Rhinophrynidae): Monotypic family.

Pristimantis duellmani, *P. simonsii*, and *P. surdus* (Craugastoridae): The lack of a columella in these species represents three independent autapomorphies within *Pristimantis*.

Species where a more exhaustive phylogenetic or/and osteological data are necessary to better understand the evolution of tympanic middle ear

Alsodes (Alsodidae): The plesiomorphic condition in this genus is recovered as ambiguous. The revision of the sequences employed in the phylogenetic analysis of Pyron (2014) revealed some chimeric terminals (B. L. Blotto, obs. pers.). Despite having considered more terminals for *Alsodes*, the phylogenetic hypothesis of Blotto *et al*. (2013) differs in the position of only a few terminals, and optimization of the columella results in the same ambiguities as Pyron's hypothesis. Nevertheless, a rather complex pattern of evolution for the occurrence of columella is evident (see Section S2.1). Thus, the coding of columella condition in additional species of *Alsodes* may help to solve the ambiguities.

Atopophrynus syntomopus (Brachycephaloidea): This species lacks a columella. Unfortunately, its phylogenetic relationships within Brachycephaloidea are uncertain (see Padial *et al*., 2014), so it is not possible to interpret the significance of this condition in a phylogenetic context.

Bombina (Bombinatoridae): As was noted by Ramaswami (1942) and Wever (1985) the pattern of morphological and developmental variation of the columella in this genus is complex. In some species this element was reported to be a cartilaginous structure connected to the hyoid laterally (see Wever, 1985) or as a small independent cartilage that was interpreted as a remnant of the columella (Stadtmüller, 1931). Based on the presence or absence of these cartilages, we score the columella as present in *B. maxima*, *B. orientalis*, *B. pachypus*, and *B. variegata* and absent in *B. bombina*.

Crinia riparia (Myobatrachidae): This species is deeply nested in *Crinia* (see Appendix S2.1). The inclusion of the remaining species not sampled by Pyron (2014) in a phylogenetic analysis, as well as additional description of the columella in this genus, will help to understand if this condition represents an apomorphy of this species or of a subclade of *Crinia*.

Euparkerella + *Holoaden* and *Bryophryne* (Craugastoridae): all five species of *Euparkerella*, the two scored species of *Holoaden*, and the only species of *Bryophryne* included by Pyron (2014) lack a columella. The phylogenetic relationships among these genera result in an ambiguity for columella condition within Craugastoridae (see Section S2.1). As *Bryophryne* includes eight additional species, some of which have a columella (see Section S2.1), a more inclusive phylogeny of this clade, and new morphological data will help to understand the pattern of tympanic middle ear evolution in Craugastoridae.

Hemisus (Hemisotidae): The only included species of this genus lacks a columella. The study of the remaining species will help to understand if this condition represents an autapomorphy of this species or a synapomorphy of *Hemisus* (or a subclade).

Microhyla (Microhylidae): Parker (1934) indicates that all the species of *Microhyla* he studied have a complete middle ear except for lacking an external tympanic membrane. However, Vorobyeva and Smirnov (1987), who specifically studied this character system, found *Microhyla butleri* and *M. heymonsi* to lack a columella. Subsequently, Smirnov (1991) states that *M. ornata* possesses a tympanic middle ear whereas *M. heymonsi* lacks it. He also described *M. pulchra* as having a poorly differentiated plectral apparatus in newly metamorphosed individuals. So, it is clear that the columella is both present and absent in *Microhyla*, and more studies are necessary to understand the taxonomic distribution of the different elements of the tympanic middle ear in this genus.

Nanorana (Dicroglossidae): There is an ambiguity in a subclade of this genus (see Section S2.1) for which it is not possible to define the number of transformations in the columella in this genus.

Oreolalax (Megophryidae): Only one species of this genus was included by Pyron (2014), and it lacks a columella; however, the occurrence of a columella varies among species of this genus, so the inclusion of at least some of the remaining 17 species in phylogenetic analyses is necessary to determine if this condition represents an apomorphy of this species or of a subclade of *Oreolalax*.

Phrynopus juninensis and related species (Craugastoridae): The closely related species of *P. juninensis* (e.g. *P. bracki*, *P. tautzorum*) lack a tympanic membrane and annulus, but the condition for the columella is unknown (see Section S2.1). Additional studies are necessary to understand the pattern of evolution of the tympanic middle ear.

Scutiger (Megophryidae): Two independent losses occurred within this genus (see Section S2.1), although only six of the 20 species were included by Pyron (2014) and the columella condition is known for only five of those species (see Section S1).

Telmatobius (Telmatobiidae): Two independent secondary losses and two cases of intraspecific polymorphism occur in this genus (see Section S2.1). Only 17 of the 63 species of the genus were included by Pyron (2014), and columella condition was scored for 15 of those (see Section S2.1). Although the columella was described as absent in *T. yuracare* (de la Riva, 1994), it was scored as present because the examination of the same specimens used for the original osteological description

(MNCN 16645-46) reveal the presence of an extremely small columella. In *Telmatobius,* the columella shows marked differences in shape and size, even intraspecifically and within the same individual (Wiens, 1993).

Additional species with absence of tympanic middle ear not included in Pyron (2014)

Arenophryne rotunda (Myobatrachidae): This species lacks a columella and was recovered as sister of taxon of *Myobatrachus* by Read *et al*. (2001). In the context of this phylogenetic relationship, this condition represents an independent loss in Anura. The condition in the other species of this genus is unknown.

Crossodactylodes and *Paratelmatobius* (Leptodactylidae): *Crossodactylodes septentrionalis* and two additional unnamed species were included in the phylogenetic analysis of Fouquet *et al.* (2013), and the absence of columella was proposed as a synapomorphy of this genus. Four analyzed species lack a columella (see Section S1), whereas this condition is unknown in the remaining species. *Paratelmatobius lutzi* is the only known species of *Paratelmatobius* lacking a columella, whereas it is present in *P. cardosoi*, *P. mantiqueira*, *P. poecilogaster*, and *P. yepiranga*, and the condition is unknown in *P. gaigeae* (see Section S2.1). If *P. lutzi* is recovered nested in *Paratelmatobius* the lack of columella in this species represent another independent loss in Anura. Alternatively, if this species is the sister taxon of all other species of the genus, this can result in an ambiguity for the columella condition within Paratelmatobiinae, according to the relationships proposed by Fouquet *et al*. (2013).

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Results of ancestral reconstructions for Bufonidae

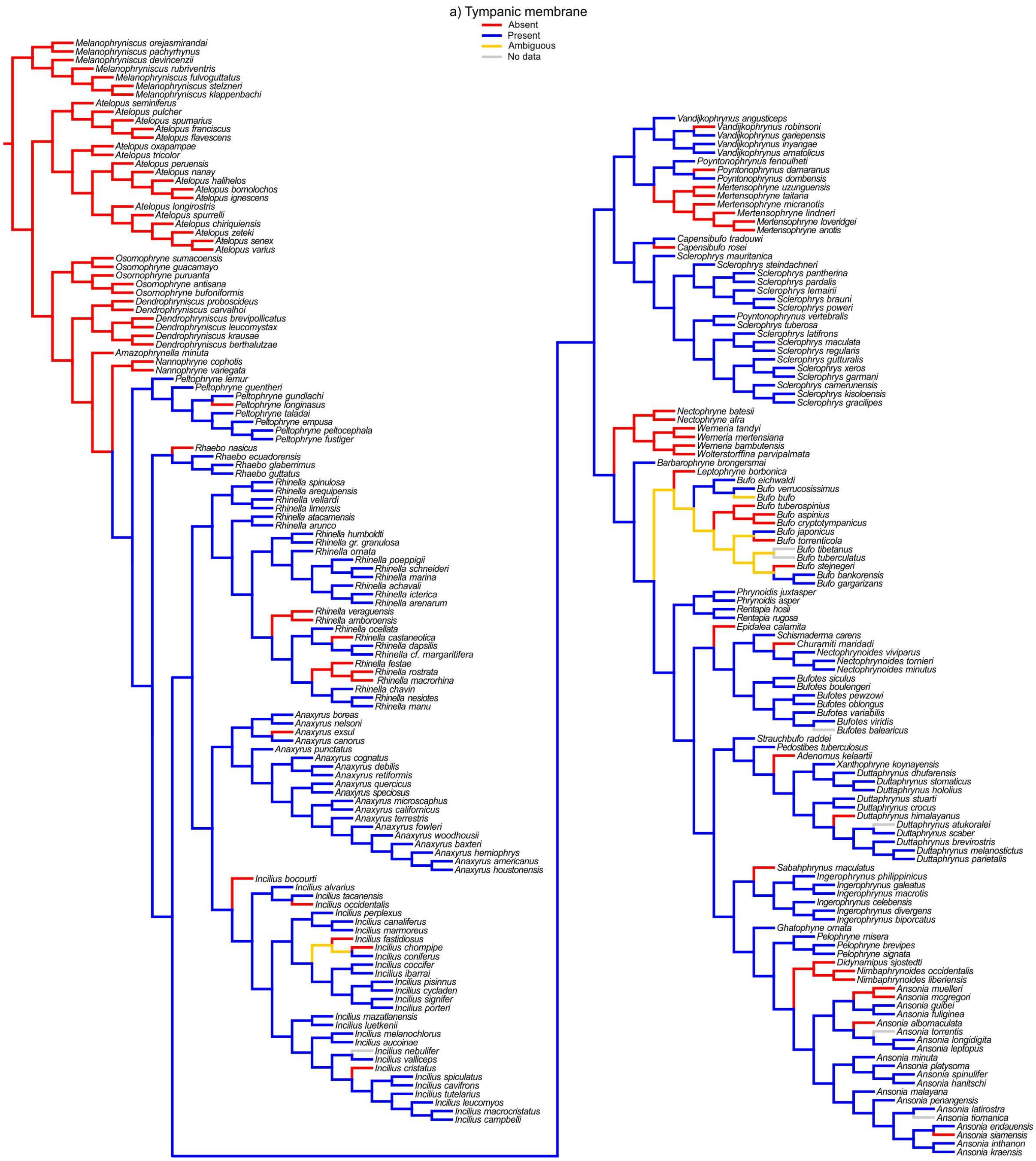

Figure 2.3.1—Partial phylogenetic tree of Pyron (2014) showing ancestral reconstructions for: tympanic membrane with parsimony.

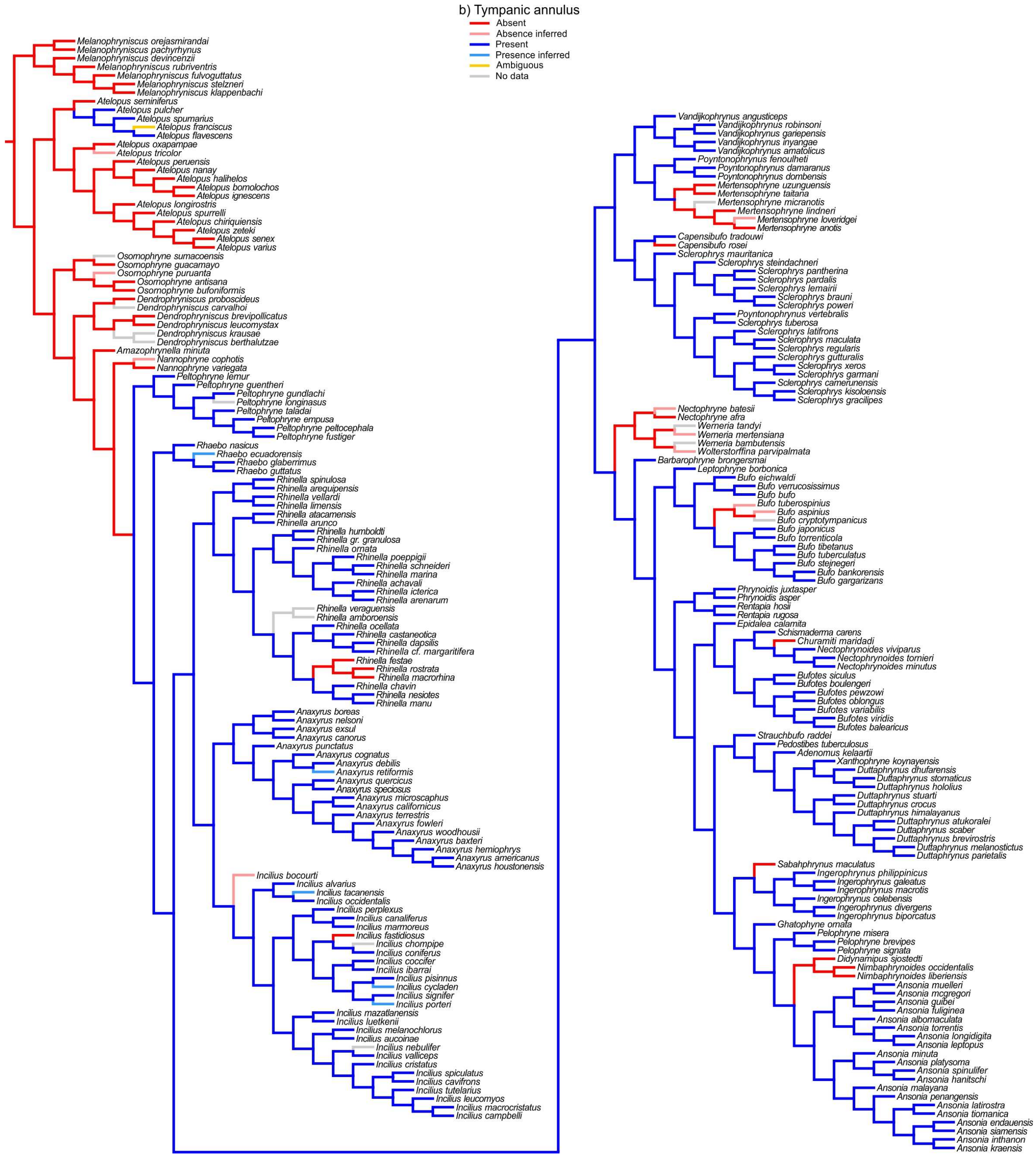

Figure 2.3.2—Partial phylogenetic tree of Pyron (2014) showing ancestral reconstructions for tympanic annulus with parsimony.

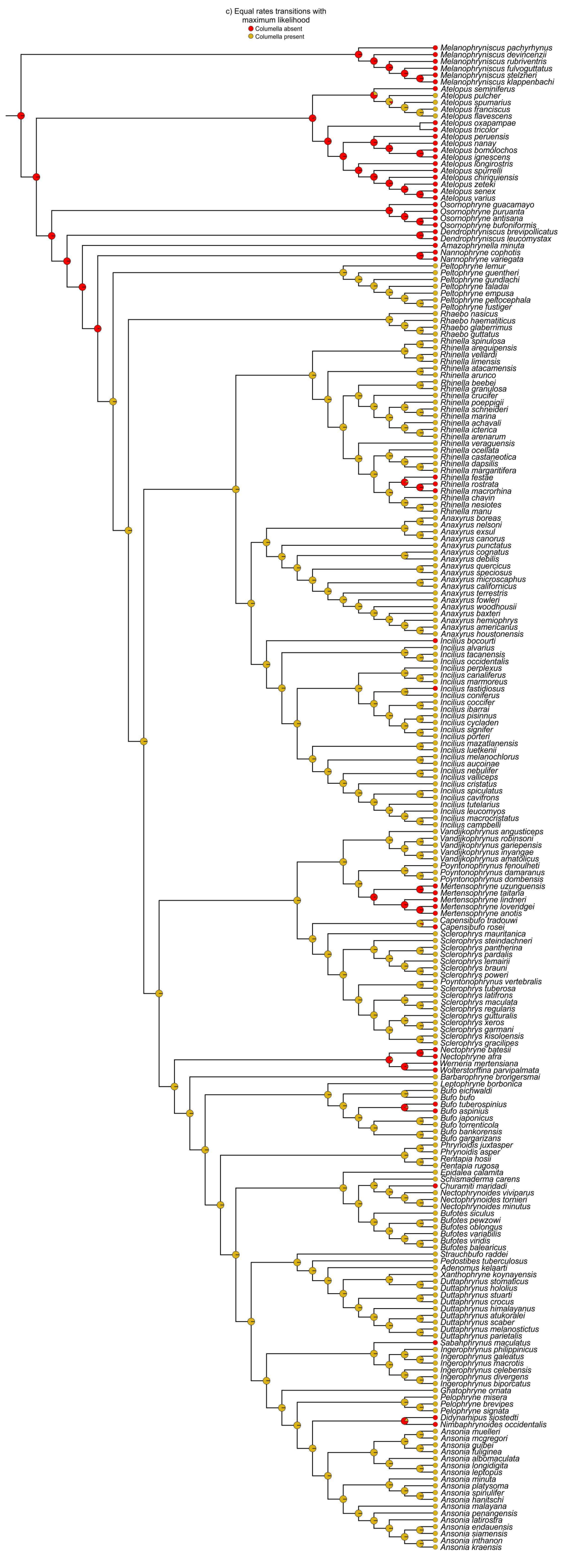

Figure 2.3.3—Partial phylogenetic tree of Pyron (2014) showing ancestral reconstructions for columella considering equal rates transitions with maximum likelihood.

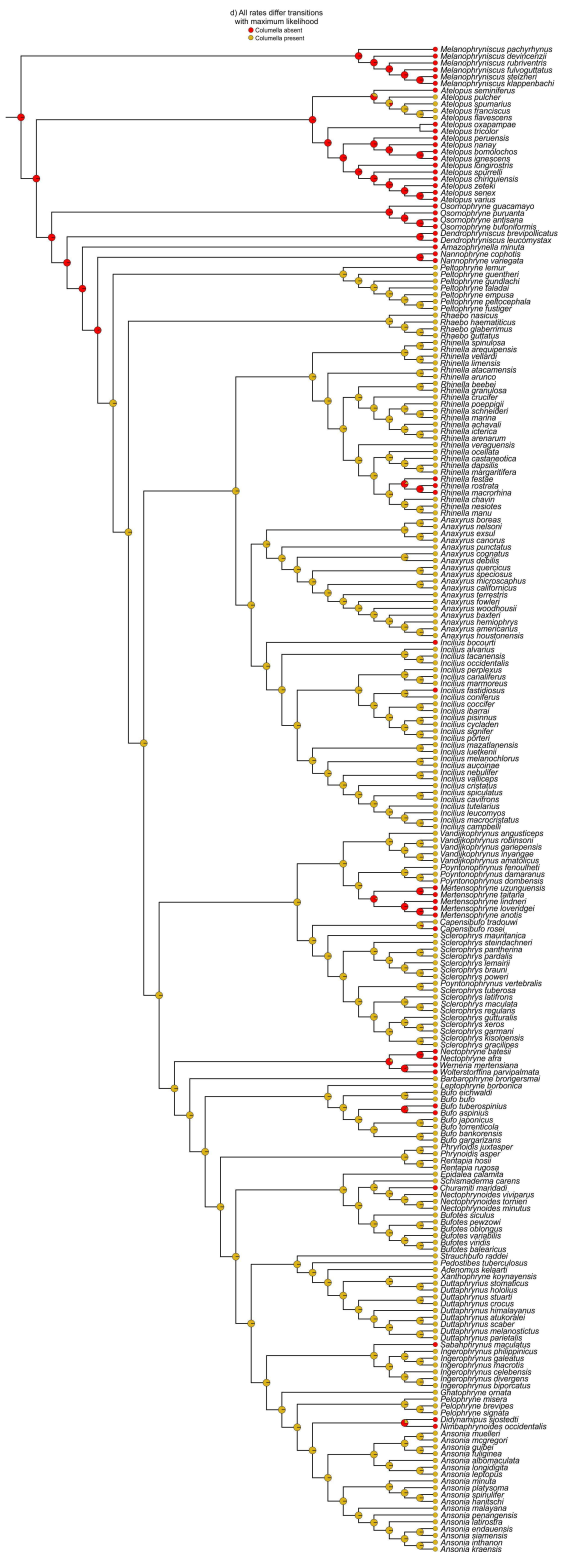

Figure 2.3.4—Partial phylogenetic tree of Pyron (2014) showing ancestral reconstructions for columella considering all rates differ transitions with maximum likelihood.

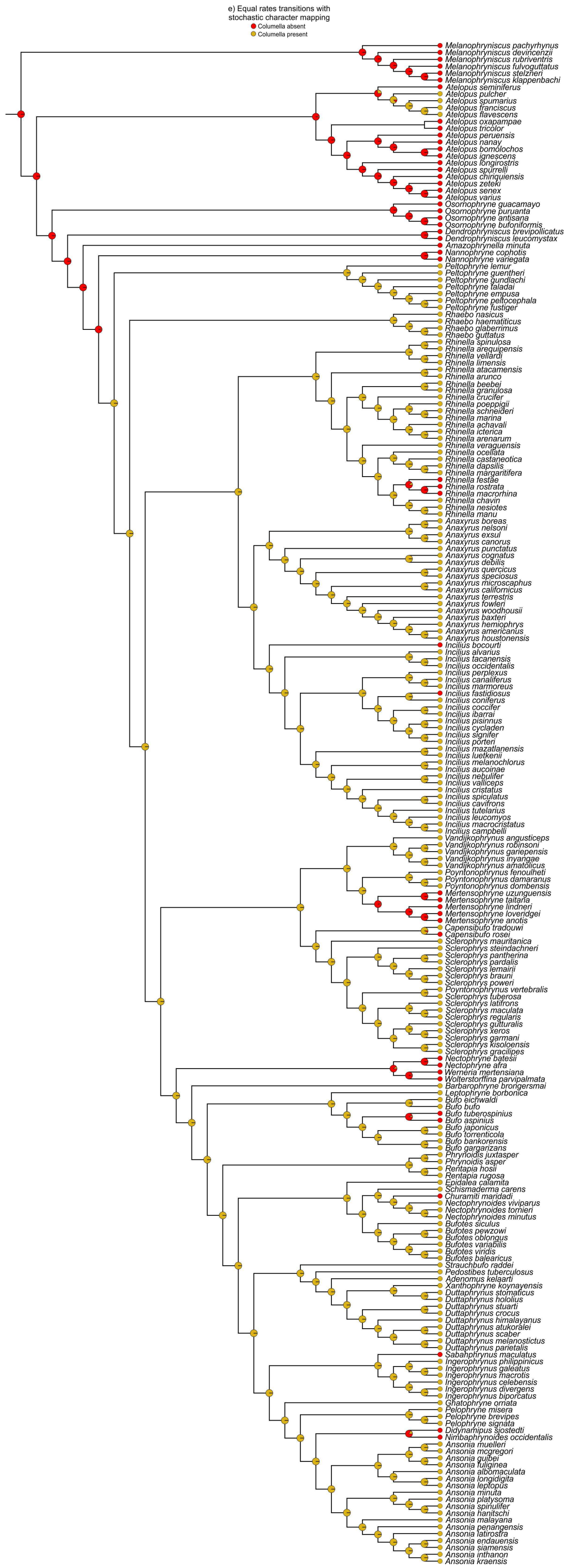

Figure 2.3.5—Partial phylogenetic tree of Pyron (2014) showing ancestral reconstructions for columella considering equal rates transitions with stochasticharacter mapping.

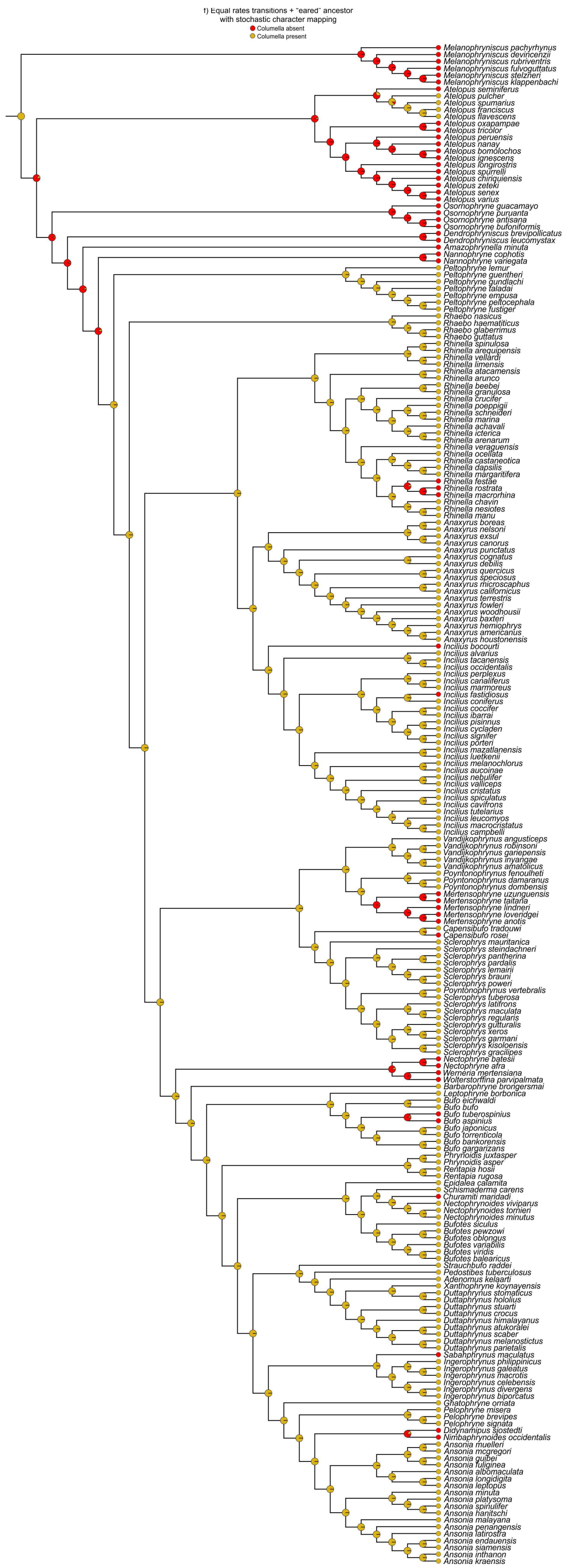

Figure 2.3.6—Partial phylogenetic tree of Pyron (2014) showing ancestral reconstructions for columella considering equal rates transitions + "eared" ancestor with stochastic character mapping.

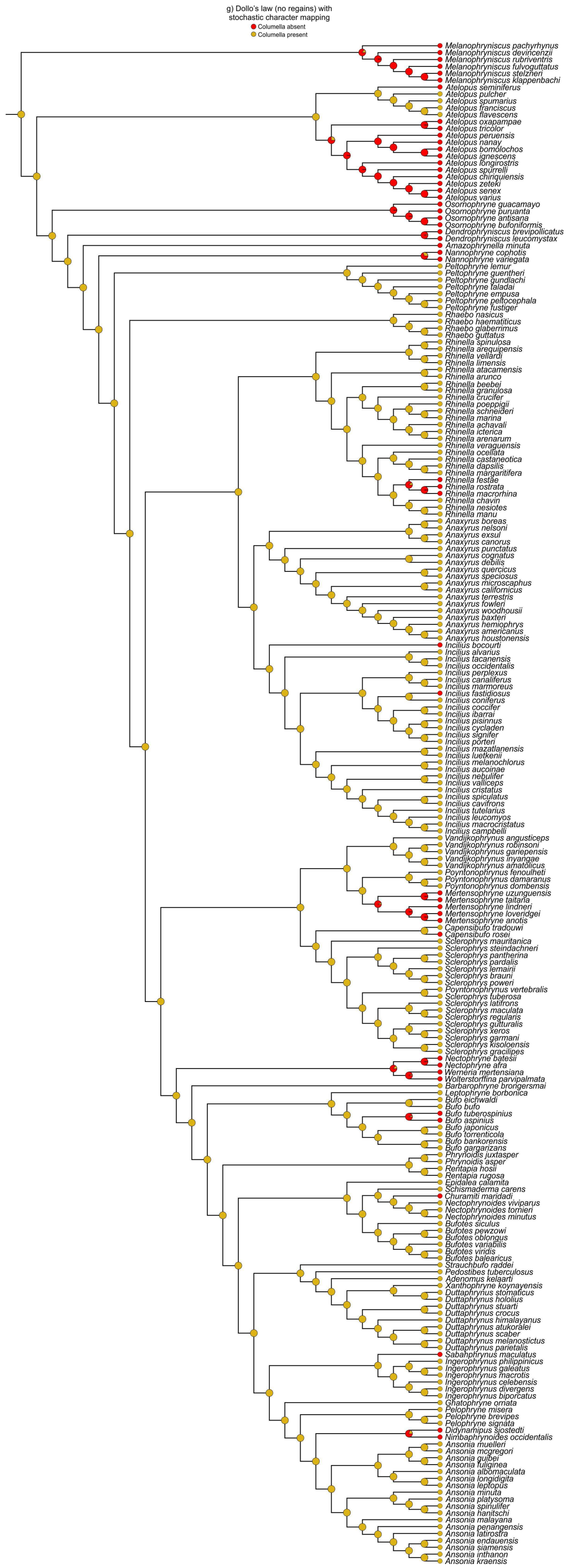

Figure 2.3.7—Partial phylogenetic tree of Pyron (2014) showing ancestral reconstructions for columella considering Dollo's law (no regains) with stochastic character.

Table 2.3.1—Comparison of estimated tympanic middle ear transformations across parsimony, maximum likelihood analyses and Bayesian stochastic mutational mapping analyses on phylogenies. For the maximum likelihood analyses we tested models in which transition rates from presence/absence of columella were allowed to differ across the tree (ARD) and a model in which transition rates were equal (ER). The equal transition rates model had a lower AIC value and was therefore used in all Bayesian models. All the unconstrained analyses (parsimony, ARD and ER maximum likelihood, ER SIMMAP) support an ancestor lacking columella with two subsequent regains in Bufonidae: one within *Atelopus* and one within the sister clade of *Nannophryne*. When the ancestor is constrained to having a complete middle ear, the SIMMAP model supports only one regain of the middle ear within *Atelopus*. When no regains are allowed (Dollo's law), the SIMMAP model supports 17 total losses of columella. N/A: not applicable.

Model	**AIC**	**# of losses**	**# of regains**	**Total transitions**	**Support for earless ancestor (Yes/No,**
Parsimony	N/A	10	2	12	Yes, N/A
ARD	108.362	10	2	12	Yes, 99.499%
ER	106.849	10	2	12	Yes, 99.592%
ER SIMMAP	N/A	10	2	12	Yes, 99.995%
ER + "eared" ancestor	N/A	12	2	14	No by design
Dollo's Law SIMMAP	N/A	17	0	17	Not possible

SUPPLEMENTARY INFORMATION 2.4

Detail of the clades or species of Bufonidae where tympanic middle ear transformations occurred according to the ancestral state reconstructions shown in figure 2 and Section 2.3.

- Tympanic membrane:

Within Bufonidae a regain of this structure occurred in the sister clade of *Nannophryne*. Subsequent independent losses occurred at least 25 times in the following taxa: at least four times (and up to five, depending on alternative resolution of the ambiguity) within *Incilius*, three times in *Ansonia,* three times in *Rhinella*, at least once (and up to four times) in the clade *Leptophryne borbonica* + *Bufo*, once in each of the clades *Didynamipus* + *Nimbaphrynoides*, *Nectophryne* + *Werneria* + *Wolterstorffina*, and *Mertensophryne*, and in each of the species *Adenomus kelaartii*, *Anaxyrus exsul*, *Capensibufo rosei*, *Churamiti maridadi*, *Duttaphrynus himalayanus*, *Epidalea calamita*, *Peltophryne longinasus*, *Poyntonophrynus damaranus*, *Rhaebo nasicus*, *Sabahphrynus maculatus*, and *Vandijkophrynus robinsoni.*

- Tympanic annulus and columella:

From the ancestral condition there were two independent reappearances of these structures: (a) within a derived clade of *Atelopus*, the *Atelopus flavescens-spumarius* clade, composed by *A. flavescens*, *A. franciscus*, *A. pulcher*, and *A.*

spumarius, and (b) in the sister clade of *Nannophryne*. Ten independent secondary losses occurred within the last clade in the following taxa: *Bufo tuberospinius* + *B. aspinius* + *B. cryptotympanicus*, *Capensibufo rosei*, *Churamiti maridadi*, *Didynamipus* + *Nimbaphrynoides*, *Incilius bocourti*, *I. fastidiosus*, *Mertensophryne*, *Nectophryne* + *Werneria* + *Wolterstorffina*, *Rhinella festae* + *R. macrorhina* + *R. rostrata*, and *Sabahphrynus maculatus*.

Inferred transformations in tympanic middle ear structures and relationships in bufonids analyzed in published phylogenetic analyses but not included by Pyron (2014).

- Taxa that affect the number of transformations inferred and disscussed on Section 2.3:

(a) *Frostius erythrophthalmus.* This species (and also its closely related species *F. pernambucensis*), has a tympanic membrane, tympanic annulus, and columella, and was recovered as the sister taxon of *Oreophrynella* by Peloso *et al*. (2012) and Ron *et al*. (2015). The conditions of *Frostius* add one independent regain of tympanic middle ear structures in Bufonidae.

(b) *Rhaebo colomai* and *R. olallai*. Ron *et al*. (2015) synonymized the genus *Andinophryne* with *Rhaebo* based on results of a phylogenetic analysis. *Rhaebo colomai* and *R. olallai* were recovered nested within the remaining species of *Rhaebo*. Both species lack a tympanic membrane but retain a tympanic annulus and columella. This situation left unresolved the number of independent losses of tympanic membrane within *Rhaebo* (once or twice) but does not modify the number of steps for the two transformation series.

(c) *Parapelophryne scalpta*. This species was recovered as sister taxon of *Bufo* in the phylogenetic analysis of Matsui *et al*. (2015). It lacks a tympanic membrane but retains a tympanic annulus and columella. The lack of a tympanic membrane in this species affects the ancestral character reconstruction of this character, because it resolves the ambiguities in *Bufo + Leptophryne borbonica*. Thus, the lack of tympanic membrane is the plesiomorphic condition for the clade *Leptophryne* + *Parapelophryne* + *Bufo*, with three independent regains in *Bufo*. The ancestral character reconstructions for tympanic annulus and columella are not modified.

(d) *Bufotes latastii*, *B. luristanicus*, *B. pseudoraddei*, and *B. surdus* were included in a phylogenetic analysis by Portik and Papenfuss (2015), in which it was recovered nested within a monophyletic *Bufotes*. The lack of a differentiated tympanic membrane in *B. surdus* adds one additional step only in this transformation series.

(e) The clade *Bufoides meghalayanus* + *Blythophryne beryet* was recovered as the sister clade of *Xanthophryne koynayensis* by Chandramouli *et al*. (2016). The lack of a differentiated tympanic membrane in *B. meghalayanus* adds one additional step in this transformation series. The conditions for tympanic annulus and columella in *Bufoides meghalayanus* are unknown.

- Taxa that do not affect the number of transformations inferred and disscussed on Section S4.1:

(a) *Oreophrynella.* Species of this monophyletic genus (Kok *et al*. 2012) lack tympanic middle ear structures and have been recovered as the sister clade of *Atelopus* in the phylogenetic analyses of Pramuk (2006) and van Bocxlaer *et al*. (2010).

(b) *Amazophrynella amazonicola*, *A. bokermanni*, *A. javierbustamantei*, *A. manaos*, *A. matses*, and *A. vote*. All of these species lack at least the tympanic membrane. Phylogenetic studies for these species were done by Rojas *et al*. (2014, 2015, 2016) who recovered *Amazophrynella* as monophyletic.

(c) *Adenomus kandianus*. This species lacks a tympanic membrane but possesses a tympanic annulus and columella. It is the sister taxon to *A. kelaartii* according to Meegaskumbura *et al*. (2015).

(d) *Sclerophrys arabica*, *S. asmarae*, *S. blandfordii*, *S. capensis*, *S. dodsoni*, *S. pentoni*, *Duttaphrynus dhufarensis* and *D. olivaceus.* All these species were included in the phylogenetic analysis of Portik and Papenfuss (2015).

(e) *Ansonia lumut* and *A. vidua*, which were recovered nested in *Ansonia* by Chan *et al*. (2014) and Hertwig *et al*. (2014) respectively. Both species possess a complete tympanic middle

ear.

(f) *Rhinella alata*, which possesses a complete tympanic middle ear, is recovered nested in the *R. margaritifera* group by Santos *et al*. (2015).

(g) *Rhinella azarai*, *R. bernardoi*, *R. bergi*, *R. centralis*, *R. dorbignyi*, *R. fernandezae*, *R. major*, *R. merianae*, *R. mirandaribeiroi*, and *R. pygmaea* were recovered within a monophyletic *R. granulosa* group; *R. henseli* as sister taxon of *R. crucifer*; and *R.*

sternosignata as sister taxon of the clade composed by the species of the *R. margaritifera* + *R. veraguensis* groups by Pereyra *et al*. (2016). All of these species possess complete tympanic middle ears.

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SUPPLEMENTARY INFORMATION 2.5

Table 2.5.1 - Taxonomic distribution of mating system in species of Bufonidae. The distinctions among mating systems are somewhat artificial (see Wells, 2007) and the reproductive mode for many taxa are not well described. Thus we arbitrarily consider prolonged breeders as opposite to species with scramble competition, since we are interested only in the taxonomic distribution of the latter. We consider occurrence of scramble competition when the reproduction is explosive, there is fighting between males for females (but not for the territory) and/or non-choice for pairs. See figure in the last page for the taxonomic distribution of mating systems among the species of Bufonidae included in the phylogenetic analysis of Pyron (2014). Abbreviations: DB, Diego Baldo; LAC, Luis A. Coloma; MOP, Martín O. Pereyra.

Genus (number of species)	**Species**	**Mating system**	**Source**
Adenomus (2 sp.)	*A. kandianus*	scramble	Meegaskumbura *et al*., 2015
Altiphrynoides (2 sp.)	*A. malcolmi*	scramble	Grandison, 1978
Amazophrynella (6 sp.)	*A. minuta*	prolonged	Moreira & Lima, 1996
Anaxyrus (22 sp.)	*A. americanus*	scramble	Wells, 1977
	A. californicus	prolonged	AmphibiaWeb
	A. canorus	scramble	Wright & Wright, 1995
	A. cognatus	scramble	Wells, 1977; Degenhardt *et al*., 1996
	A. debilis	prolonged	Degenhardt *et al*., 1996
	A. exsul	scramble	Wells, 1977
	A. fowleri	prolonged	Wells, 1977; Given, 2002
	A. microscaphus	prolonged	Degenhardt *et al*., 1996
	A. nelsoni	prolonged	Wright & Wright, 1995
	A. punctatus	prolonged	Degenhardt *et al*., 1996
	A. quercicus	prolonged	Wright & Wright, 1995
	A. retiformis	prolonged	Bogert, 1962
	A. terrestris	scramble? explosive	Bartlett & Bartlett, 1999
	A. woodhousii	scramble	Wells, 1977

Ansonia (28 sp.)	*A. malayana*	prolonged	Dring, 1979
Atelopus (96 sp.)	*A. elegans*	scramble	LAC pers. obs.
	A. ignescens	scramble	Peters, 1973
	A. laetissimus	scramble	Granda-Rodriguez *et al.*, 2009
	A. oxyrhynchus	cf. scramble	Dole & Duran, 1974
	nex	prolonged	Savage, 2002
	A. varius	scramble? explosive	Crump, 1988
Barbarophryne (1 sp.)	*B. brongersmai*	scramble	Martinez del Marmol Marin & Jimenez Robles, 2013
Blytophryne (1 sp.)	No data		
Bufo (17 sp.)	*B. bankorensis*	prolonged	Pope, 1931
	B. bufo	scramble	Davies & Halliday, 1978; Hoghlund & Robertson,
	B. gargarizans	scramble	Liu, 1950
	B. stejnegeri	prolonged	Fei *et al.*, 2009
	B. tibetanus	prolonged	Fei *et al.*, 2009
	B. torrenticola	scramble? explosive	Tsuji & Kawamichi, 1996
	B. verrucosissimus	prolonged	Kuzmin, 1999
Bufoides (1 sp.)	No data		
Bufotes (14 sp.)	*B. boulengeri*	explosive	
	B. viridis	prolonged	Salvador, 1996
Capensibufo (2 sp.)	*C. rosei*	scramble	Minter *et al.*, 2004, Wells,1977
Churamiti (1 sp.)	No data		
Dendrophryniscus (10 sp.)	*D. leucomystax*	scramble? explosive	Zina, 2010
Dydinamipus (1 sp.)	No data		
Duttaphrynus (27 sp.)	*D. crocus*	scramble? explosive	Wogan *et al.*, 2003
	D. melanostictus	scramble? explosive	Khan, 2000 in AmphibiaWeb
		prolonged	Church, 1960

Epidalea (1 sp.)	*E. calamita*	prolonged	Sinsch, 1992
Frostius (2 sp.)	No data		
Ghathphryne (2 sp.)	No data		
Incilius (40 sp.)	*I. alvarius*	scramble	Blair & Pettus, 1954, Wells,1977
	I. coniferus	prolonged	Savage, 2002
	I. fastidiosus	scramble	Han & Fu, 2013
	I. luetkenii	prolonged	Savage, 2002
	I. melanochlorus	prolonged	Savage, 2002
	I. nebulifer	prolonged	Savage, 2002
	I. valliceps	prolonged	Wells, 1977
Ingerophrynus (12 sp.)	*I. biporcatus*	prolonged	Márquez & Eekhout, 2006
	I. parvus	prolonged	Shahriza *et al.,* 2012
Laurentophryne (1 sp.)	No		
Leptophryne (2 sp.)	No data		
Melanophryniscus (26 sp.)	*M. alipioi*	scramble	DB pers. obs.
	M. krauczuki	scramble	DB pers. obs.
	M. langonei	scramble	DB pers. obs.
	M. devincenzii	scramble	DB pers. obs.
	M. cambaraensis	scramble	Santos & Grant, 2010
	M. macrogranulosus	scramble	Zaffaroni Caorsi *et al*., 2014
	M. klappenbachi	scramble	MOP pers. obs.
	M. fulvoguttatus	scramble	DB pers. obs.
	M. atroluteus	scramble	MOP pers. obs.
	M. cupreuscapularis	scramble	DB pers. obs.
	M. rubriventris	scramble	Goldberg *et al*., 2006
	M. stelzneri	scramble	DB pers. obs.
	M. fulvogutattus	scramble	DB pers. obs.
Mertensophryne (14 sp.)	*M. taitana*	prolonged	Stewart, 1967
Metaphryniscus (1 sp.)	No data		
Nannophryne (4 sp.)	*N. variegata*	scramble	Formas & Pugin 1978
Nectophryne (2 sp.)	No		

Nectophrynoides (13 sp.)	*N. asperginis*	scramble	Lee *et al*., 2006
Nimbaphrynoides (1 sp.)	No data		
Oreophrynella (9 sp.)	No data		
Osornophryne (11 sp.)	No data		
Parapelophryne (1 sp.)	No data		
Pedostibes (2 sp.)	No data		
Pelophryne (11 sp.)	No data		
Peltophryne (12 sp.)	*P. fustiger*	prolonged	Schwartz, 1991
	P. peltocephala	prolonged	Valdes, 1988
Phrynoidis (2 sp.)	*P. juxtaspera*	prolonged	Inger & Bacon, 1968
Poyntonophrynus (10 sp.)	*P. damaranus*	scramble	Minter *et al.,* 2004
Pseudobufo (1 sp.)	No data		
Rentapia (3 sp.)	No		
Rhaebo (13 sp.)	*R. guttatus*	scramble	Machado & Bernarde, 2011
	R. haematiticus	prolonged	Savage, 2002
Rhinella (90 sp.)	*R. arenarum*	scramble	MOP pers. obs.
	R. azarai	scramble	Pereyra *et al*., 2016
	R. bergi	scramble	Pereyra *et al*., 2016
	R. castaneotica	prolonged	Caldwell & de Araújo2004
	R. chavin	prolonged	Lehr *et al*., 2001
	R. icterica	scramble	MOP pers. obs.
	R. fernandezae	scramble	Pereyra *et al*., 2016
	R. major	scramble	Pereyra *et al*., 2016
	R. margaritifera	scramble	Wells, 1979, Hodl, 1990
	R. marina	scramble	Wells, 1977
	R. ornata	scramble	DB pers. obs.
	R. ocellata	prolonged	Caldwell & Shepard, 2007
	R. rubescens	scramble	Arantes *et al*., 2015
	R. rumbolli	scramble	DB and MOP pers. obs.
	R. schneideri	scramble	Arantes *et al*., 2015
Sabahphrynus (1 sp.)	No		
Schismaderma (1 sp.)	*S. carens*	scramble? explosive	Tandy & Keith, 1972

Sclerophrys (44 sp.)	*S. capensis*	prolonged (female choice)	Minter *et al.,* 2004
		scramble	Tandy & Keith, 1972
	S. garmani	prolonged	Keith, 1968; Minter *et al.,* 2004
	S. gutturalis	scramble	Passmore, 1981; du Preez & Carruters, 2009
	S. kisoloensis	prolonged	Keith, 1968
	S. maculata	prolonged	Tandy & Keith, 1972
	S. mauritanica	prolonged	Salvador, 1996
	S. pantherina	scramble	Poynton & Lambiris, 1998
	S. pardalis	scramble	Poynton & Lambiris, 1998
	S. regularis	scramble	Wells, 1977
	S. xeros	prolonged	Tandy *et al.*, 1976
Strauchbufo (1 sp.)	*S. raddei*	scramble	Liu, 1950
Truebella (2 sp.)	No data		
Vandijkophrynus (5 sp.)	*V. angusticeps*	scramble	Minter *et al.,* 2004, du Preez & Carruters, 2009
	V. gariepensis	prolonged	Tandy & Keith, 1972
Werneria (6 sp.)	No data		
Wolterstorffina (3 sp.)	No data		
Xanthophryne (2 sp.)	*X. koynayensis*	scramble	Gaitonde *et al.*, 2016
	X. tigerina	scramble	Gaitonde *et al.*, 2016

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SUPPLEMENTARY INFORMATION 5.1

Specimens micro-CT scanned from the National Museum of Natural History (USNM), Washington, D.C., United States.

Amietophrynus gracilipes —Congo: Likouala: Impongui (USNM 576239, 576391).

Amietophrynus mauritanica —Morocco: Tetouan: Larache, 20 km SE of (USNM 346809, 346811).

***Anaxyrus canorus* —**United States: California: Tioga Pass Mono-Tuolumne county border (USNM 311300).

Anaxyrus cognatus —United States: New Mexico: Luna: Columbus (USNM 320094, 320103).

Anaxyrus houstonensis —United States: Texas: Harris Fairbanks (USNM 542211).

Anaxyrus microscaphus —United States: New Mexico: Grant: San Lorenzo (USNM 320140); near New Mexico Hwy 35, Mimbres River Drainage (USNM 320144).

Atelopus chiriquiensis —Costa Rica: Limon: Pico Blanco (= Cerro Kamuk) (USNM 30643-4).

Atelopus flavescens —French Guiana: Cayenne, ca. 82 km S of, 3 km W of Kaw (USNM 331415, 331417).

Atelopus franciscus —French Guiana: Cayenne: Crique Gregoire, Inini (USNM 192815).

Atelopus ignescens —Ecuador: Imbabura: near Odovalo (= Otavalo) (USNM 236903–4).

Atelopus longirostris —Ecuador: Pichincha: Llambo (USNM 193825); Tandayapa (USNM 193835).

Atelopus pulcher —Peru: Amazonas: La Poza (USNM 569373); Shiringa (USNM 569381).

Atelopus varius — Costa Rica: San Jose Desamparados, near, along Rio Jorco (USNM 279113, 279119).

Atelopus zeteki —Panama: Coclé: El Valle, Cerro Gaital (USNM 129893, 129896).

Bufo bankorensis —Taiwan: Kaohsiung Hsien: Kosempo (= Chiasien) (USNM 66082–3).

Bufo japonicas —Japan (USNM 11348): Honshu Island: Nagano: Karuizawa (USNM 51998).

Capensibufo rosei —South Africa: Western Cape: Cape Town, Table Mountain (USNM 159110, 159113).

Dendrophryniscus brevipollicatus — Brazil: Parana: Sao Joao da Graciosa (USNM 217659); Espirito Santo: Santa Teresa (USNM 239919).

Duttaphrynus scaber —Sri Lanka: North Eastern Mannar: Marichchukkadi (USNM 254716, 254718).

Duttaphrynus stomaticus —Nepal: Narayani: Chitwan Sauraha, vicinity of Smithsonian Institution Camp, Royal Chitwan National Park (USNM 266829, 266836).

Epidalea calamita — Germany: Bavaria: Nuremberg (USNM 579882, 579890).

Incilius campbelli —Belize: Toledo: Maya Mountain Forest Reserve, Snake Creek (USNM 498198, 498200).

Incilius canaliferus —Mexico: Chiapas: La Esperanza (USNM 116005, 116019).

Incilius coniferus —Panama: Bocas del Toro: Isla Cristobal Bocatorito camp (USNM 348058–9).

Incilius ibarrai —Honduras: Ocotepeque: El Volcan (USNM 523715, 523723).

Incilius mazatlanensis —Mexico: Sonora: Bahia Kino (USNM 214074, 214077).

Incilius occidentalis —Mexico: Puebla: Tecamachalco (USNM 116539, 116541).

Ingerophrynus celebensis —Indonesia: Celebes: Sulawesi Tengah: Toli Toli (USNM 52986); Bada Toeare (USNM 61189).

Melanophryniscus stelzneri —Brazil: Mato Grosso Do Sul: Maracaju (USNM 107712, 107722).

Mertensophryne taitana —Malawi: Rumphi (USNM 153417).

Nannophryne variegata — Chile: Magallanes: Mayne Harbor (USNM 15124).

Nectophryne batesii —Cameroon: Littoral: Nguengue (USNM 571097).

Osornophryne bufoniformis —Ecuador: Sucumbíos: Santa Barbara (USNM 193537, 193540).

Peltophryne fustiger —Cuba: Pinar del Rio: La Mulata (USNM 51864).

Rhinella arenarum — Uruguay: Montevideo (USNM 70620, 70622).

Rhinella castaneotica —Brazil: Para: Itaituba (USNM 518807, 518809).

Rhinella crucifer —Brazil: Río de Janeiro (USNM 70613–4).

Rhinella dapsilis —Ecuador: Pastaza: Río Rutuno, tributary of Río Bobonaza (USNM 196951). Brazil: Amazonas: Borba, Río Madeira (USNM 201814).

Rhinella granulosa —Guyana: East Berbice: Dubulay Ranch (USNM 566017–8).

Rhinella icterica —Brazil: Sâo Paulo, Quarter Parque Jabaquara (USNM 100954, 100957).

Rhinella ocellata —Brazil: Goias: Río Araguaia (USNM 130177).

Rhinella poeppigii —Peru: San Martin (USNM 346829–30).

Rhinella schneideri —Bolivia: Santa Cruz (USNM 281765).

Schismaderma carens —Malawi: Rumphi (USNM 153377, 153380).

Strauchbufo raddei —China: Manchuria: Hei Sui (USNM 53371–2).

Vandijkophrynus angusticeps —South Africa: Cape Of Good Hope: Kommetjie, near Cape Town (USNM 165087, 165089)

Vandijkophrynus gariepensis —Lesotho: Butha-Buthe (USNM 239871, 239873).

Werneria mertensiana —Cameroon: Littoral: Nguengue (USNM 571101, 571105).

Wolterstorffina parvipalmata —Cameroon: Littoral: Nguengue (USNM 571108–9).

SUPPLEMENTARY INFORMATION 5.2

Table 5.2.1- Collection country, sites, and permit numbers for wild-caught animals in the study.

Species	Country	Region	Permit #
Atelopus spumarius	Ecuador	Bred in captivity	Permit: 001-13 IC-FAU-DNB/MA
Osornophryne guacaymayo	Ecuador	Sumaco	Permit: 001-13 IC-FAU-DNB/MA
Rhaebo haematiticus	Ecuador	Mindo Forest Reserve and Rio Guajalito Reserve in Pastaza	Permit: 001-13 IC-FAU-DNB/MA
Rhamphophryne festae	Ecuador	Rio Rutuno, Pastaza	Permit: 001-13 IC-FAU-DNB/MA
Rhinella marina	Ecuador	Canelos, Pastaza and in Mindo Forest Reserve and Maquipucuna Biological Reserve in Pastaza	Permit: 001-13 IC-FAU-DNB/MA
Rhinella spinulosa	Peru	K'iripampa Acopia in Acomayo, Cusco	Permit: 0071-2014-MINAGRI-DGFFS/DGEFFS

SUPPLEMENTAL INFORMATION 5.3

Table 5.3.1 – Ossification level of each species for each character.

Name	Genus_species	Ear	1	2	3	4	5	6	7
30643	Atelopus_chiriquiensis	N	1	1	0	1	1	1	0
30644	Atelopus_chiriquiensis	N	1	1	1	1	1	1	0
236903	Atelopus_ignescens	N	1	1	1	1	0	0	0
236904	Atelopus_ignescens	N	1	1	1	1	0	0	0
193825	Atelopus_longirostris	N	1	0	0	1	1	1	0
193835	Atelopus_longirostris	N	1	0	0	1	1	1	0
279113	Atelopus_varius	N	1	1	1	1	1	1	1
279119	Atelopus_varius	N	1	1	1	1	1	1	1
129893	Atelopus_zeteki	N	1	1	1	1	1	1	1
129896	Atelopus_zeteki	N	1	1	1	1	1	1	1
159113	Capensibufo_rosei	N	0	0	0	1	0	0	0
159110	Capensibufo_rosei	N	1	0	0	1	0	0	0
239919	Dendrophryniscus_brevipollicatus	N	0	0	0	1	1	1	0
217659	Dendrophryniscus_brevipollicatus	N	0	1	0	1	0	1	0
107712	Melanophryniscus_stelzneri	N	1	1	1	1	1	0	0
107722	Melanophryniscus_stelzneri	N	1	1	1	1	1	0	0
153417	Mertensophryne_taitana	N	0	1	1	1	0	1	0
15124	Nannophryne_variegata	N	1	0	0	1	0	1	0
571097	Nectophryne_batesii	N	0	0	0	0	1	0	0
193540	Osornophryne_bufoniformis	N	0	0	0	1	1	1	0
193537	Osornophryne_bufoniformis	N	0	1	0	1	1	1	1
2520	Osornophryne_guacamayo	N	NA	NA	NA	NA	NA	NA	NA
2523	Osornophryne_guacamayo	N	NA	NA	NA	NA	NA	NA	NA
3166	Rhinella_festae	N	NA	NA	NA	NA	NA	NA	NA
3708	Rhinella_festae	N	NA	NA	NA	NA	NA	NA	NA
571101	Werneria_mertensiana	N	1	1	0	1	0	0	1
571105	Werneria_mertensiana	N	1	1	0	1	1	0	1
571108	Wolterstorffina_parvipalmata	N	0	0	0	0	0	0	0

571109	Wolterstorffina_parvipalmata	N	0	0	0	0	0	0	0
576391	Amietophrynus_gracilipes	Y	1	0	0	0	1	0	1
576239	Amietophrynus_gracilipes	Y	1	0	0	1	1	0	1
346809	Amietophrynus_mauritanicus	Y	0	1	0	0	1	0	1
346811	Amietophrynus_mauritanicus	Y	0	1	0	0	1	0	1
311300	Anaxyrus_canorus	Y	1	0	0	0	0	0	0
320094	Anaxyrus_cognatus	Y	1	1	1	1	1	1	1
320103	Anaxyrus_cognatus	Y	1	1	1	1	1	1	1
542211	Anaxyrus_houstonensis	Y	1	1	0	1	1	1	1
320140	Anaxyrus_microscaphus	Y	1	0	0	0	0	0	0
320144	Anaxyrus_microscaphus	Y	1	0	0	0	0	0	0
331415	Atelopus_flavescens	Y	1	1	1	1	1	1	0
331417	Atelopus_flavescens	Y	1	1	1	1	1	1	0
192815	Atelopus_franciscus	Y	1	1	1	1	1	1	1
569373	Atelopus_pulcher	Y	1	1	1	1	1	1	0
569381	Atelopus_pulcher	Y	1	1	1	1	1	1	0
243	Atelopus_spumarius	Y	NA	NA	NA	NA	NA	NA	NA
3720	Atelopus_spumarius	Y	NA	NA	NA	NA	NA	NA	NA
4905	Atelopus_spumarius	Y	NA	NA	NA	NA	NA	NA	NA
66082	Bufo_bankorensis	Y	1	1	1	1	1	1	1
66083	Bufo_bankorensis	Y	1	1	1	1	1	1	1
51998	Bufo_japonicus	Y	1	1	0	1	0	1	0
113484	Bufo_japonicus	Y	1	1	1	1	0	1	1
254716	Duttaphrynus_scaber	Y	1	1	0	1	0	0	1
254718	Duttaphrynus_scaber	Y	1	1	0	1	0	0	1
266829	Duttaphrynus_stomaticus	Y	1	1	0	1	0	1	0
266836	Duttaphrynus_stomaticus	Y	1	1	0	1	0	1	0
579882	Epidalea_calamita	Y	1	0	0	1	0	0	0
579890	Epidalea_calamita	Y	1	0	0	1	0	1	0
498198	Incilius_campbelli	Y	1	1	0	1	1	1	1
498200	Incilius_campbelli	Y	1	1	1	0	1	1	1
116005	Incilius_canaliferus	Y	1	1	1	1	1	1	1
116019	Incilius_canaliferus	Y	1	1	1	1	1	1	1
348058	Incilius_coniferus	Y	1	1	1	1	1	1	1
348059	Incilius_coniferus	Y	1	1	1	1	1	1	1
523715	Incilius_ibarrai	Y	0	1	0	1	1	1	1
523723	Incilius_ibarrai	Y	0	1	0	1	1	1	1
214077	Incilius_mazatlanensis	Y	1	1	1	1	1	1	1

214074	Incilius_mazatlanensis	Y	1	1	1	1	1	1	1
116539	Incilius_occidentalis	Y	1	1	1	1	1	1	1
116541	Incilius_occidentalis	Y	1	1	1	1	1	1	1
52986	Ingerophrynus_celebensis	Y	1	1	1	1	1	1	1
61189	Ingerophrynus_celebensis	Y	1	1	1	1	1	1	1
51864	Peltophryne_fustiger	Y	1	1	1	1	1	1	1
4336	Rhaebo_haematiticus	Y	NA	NA	NA	NA	NA	NA	NA
4337	Rhaebo_haematiticus	Y	NA	NA	NA	NA	NA	NA	NA
674	Rhaebo_haematiticus	Y	NA	NA	NA	NA	NA	NA	NA
70620	Rhinella_arenarum	Y	1	1	1	1	1	1	1
70622	Rhinella_arenarum	Y	1	1	1	1	1	1	1
518809	Rhinella_castaneotica	Y	1	1	0	1	1	1	1
518807	Rhinella_castaneotica	Y	1	1	1	1	1	1	1
70613	Rhinella_crucifer	Y	1	1	1	1	1	1	1
70614	Rhinella_crucifer	Y	1	1	1	1	1	1	1
196951	Rhinella_dapsilis	Y	1	1	1	1	1	1	1
201814	Rhinella_dapsilis	Y	1	1	1	1	1	1	1
566017	Rhinella_granulosa	Y	1	1	1	1	1	1	1
566018	Rhinella_granulosa	Y	1	1	1	1	1	1	1
100954	Rhinella_icterica	Y	1	1	1	1	1	1	1
100957	Rhinella_icterica	Y	1	1	1	1	1	1	1
4343	Rhinella_marina	Y	NA	NA	NA	NA	NA	NA	NA
4344	Rhinella_marina	Y	NA	NA	NA	NA	NA	NA	NA
130177	Rhinella_ocellata	Y	1	1	0	1	1	1	1
346829	Rhinella_poeppigii	Y	1	1	1	1	1	1	1
346830	Rhinella_poeppigii	Y	1	1	1	1	1	1	1
281765	Rhinella_schneideri	Y	1	1	1	1	1	1	1
38	Rhinella_spinulosa	Y	NA	NA	NA	NA	NA	NA	NA
153377	Schismaderma_carens	Y	0	0	0	0	1	0	0
153380	Schismaderma_carens	Y	0	0	0	0	1	0	0
53371	Strauchbufo_raddei	Y	1	0	0	1	1	0	0
53372	Strauchbufo_raddei	Y	1	0	0	1	1	1	0
165087	Vandijkophrynus_angusticeps	Y	1	0	0	1	1	0	1
165089	Vandijkophrynus_angusticeps	Y	1	0	0	1	1	0	1
239871	Vandijkophrynus_gariepensis	Y	1	0	0	0	0	0	0

239873	Vandijkophrynus_gariepensis	Y	1	0	0	1	0	0	0

Name	Genus_species	Ear	8	9	10	11	12	Ossification level total
30643	Atelopus_chiriquiensis	N	1	0	0	0	0	1
30644	Atelopus_chiriquiensis	N	1	0	0	0	0	1
236903	Atelopus_ignescens	N	1	0	1	0	0	2
236904	Atelopus_ignescens	N	1	0	1	0	0	2
193825	Atelopus_longirostris	N	1	0	1	0	0	2
193835	Atelopus_longirostris	N	1	0	1	0	0	2
279113	Atelopus_varius	N	1	1	0	0	0	2
279119	Atelopus_varius	N	1	1	0	0	0	2
129893	Atelopus_zeteki	N	1	1	1	0	0	3
129896	Atelopus_zeteki	N	1	1	1	0	0	3
159113	Capensibufo_rosei	N	1	0	0	0	0	1
159110	Capensibufo_rosei	N	1	0	0	0	0	1
239919	Dendrophryniscus_brevipollicatus	N	0	0	1	0	0	1
217659	Dendrophryniscus_brevipollicatus	N	1	0	1	0	0	2
107712	Melanophryniscus_stelzneri	N	1	0	1	0	1	3
107722	Melanophryniscus_stelzneri	N	1	0	1	0	1	3
153417	Mertensophryne_taitana	N	1	0	1	0	0	2
15124	Nannophryne_variegata	N	1	0	0	0	0	1
571097	Nectophryne_batesii	N	0	0	0	0	0	0
193540	Osornophryne_bufoniformis	N	1	0	1	1	0	3
193537	Osornophryne_bufoniformis	N	1	0	1	1	0	3
2520	Osornophryne_guacamayo	N	NA	NA	NA	NA	NA	0
2523	Osornophryne_guacamayo	N	NA	NA	NA	NA	NA	0
3166	Rhinella_festae	N	NA	NA	NA	NA	NA	0
3708	Rhinella_festae	N	NA	NA	NA	NA	NA	0
571101	Werneria_mertensiana	N	1	0	0	0	0	1
571105	Werneria_mertensiana	N	1	0	0	0	0	1
571108	Wolterstorffina_parvipalmata	N	0	0	0	0	0	0
571109	Wolterstorffina_parvipalmata	N	0	0	0	0	0	0
576391	Amietophrynus_gracilipes	Y	1	0	0	0	0	1
576239	Amietophrynus_gracilipes	Y	1	0	0	0	0	1
346809	Amietophrynus_mauritanicus	Y	1	1	0	0	0	2
346811	Amietophrynus_mauritanicus	Y	1	1	0	0	0	2

311300	Anaxyrus_canorus	Y	0	0	0	0	0	0
320094	Anaxyrus_cognatus	Y	1	1	0	1	0	3
320103	Anaxyrus_cognatus	Y	1	1	0	1	0	3
542211	Anaxyrus_houstonensis	Y	1	1	0	0	0	2
320140	Anaxyrus_microscaphus	Y	0	0	0	0	0	0
320144	Anaxyrus_microscaphus	Y	0	0	0	0	0	0
331415	Atelopus_flavescens	Y	1	1	0	0	0	2
331417	Atelopus_flavescens	Y	1	1	0	0	0	2
192815	Atelopus_franciscus	Y	1	1	0	0	0	2
569373	Atelopus_pulcher	Y	1	0	0	0	0	1
569381	Atelopus_pulcher	Y	1	0	0	0	0	1
243	Atelopus_spumarius	Y	NA	NA	NA	NA	NA	0
3720	Atelopus_spumarius	Y	NA	NA	NA	NA	NA	0
4905	Atelopus_spumarius	Y	NA	NA	NA	NA	NA	0
66082	Bufo_bankorensis	Y	1	1	0	0	1	3
66083	Bufo_bankorensis	Y	1	1	0	0	1	3
51998	Bufo_japonicus	Y	1	1	0	0	0	2
113484	Bufo_japonicus	Y	1	1	0	0	0	2
254716	Duttaphrynus_scaber	Y	1	0	0	0	0	1
254718	Duttaphrynus_scaber	Y	1	0	0	1	0	2
266829	Duttaphrynus_stomaticus	Y	1	0	0	0	1	2
266836	Duttaphrynus_stomaticus	Y	1	0	0	0	1	2
579882	Epidalea_calamita	Y	1	0	0	0	0	1
579890	Epidalea_calamita	Y	1	0	1	0	0	2
498198	Incilius_campbelli	Y	1	1	0	1	0	3
498200	Incilius_campbelli	Y	1	1	0	1	0	3
116005	Incilius_canaliferus	Y	1	1	0	0	0	2
116019	Incilius_canaliferus	Y	1	1	0	0	0	2
348058	Incilius_coniferus	Y	1	1	0	0	1	3
348059	Incilius_coniferus	Y	1	1	0	0	1	3
523715	Incilius_ibarrai	Y	1	0	0	1	1	3
523723	Incilius_ibarrai	Y	1	0	0	1	1	3
214077	Incilius_mazatlanensis	Y	1	1	0	0	1	3
214074	Incilius_mazatlanensis	Y	1	1	0	1	1	4
116539	Incilius_occidentalis	Y	1	1	0	0	0	2
116541	Incilius_occidentalis	Y	1	1	0	0	0	2
52986	Ingerophrynus_celebensis	Y	1	1	0	0	0	2
61189	Ingerophrynus_celebensis	Y	1	1	0	0	1	3
51864	Peltophryne_fustiger	Y	1	1	0	0	1	3
4336	Rhaebo_haematiticus	Y	NA	NA	NA	NA	NA	0
4337	Rhaebo_haematiticus	Y	NA	NA	NA	NA	NA	0

674	Rhaebo_haematiticus	Y	NA	NA	NA	NA	NA	0
70620	Rhinella_arenarum	Y	1	1	0	1	0	3
70622	Rhinella_arenarum	Y	1	1	0	1	0	3
518809	Rhinella_castaneotica	Y	1	1	0	0	0	2
518807	Rhinella_castaneotica	Y	1	1	0	0	0	2
70613	Rhinella_crucifer	Y	1	1	0	1	0	3
70614	Rhinella_crucifer	Y	1	1	0	1	0	3
196951	Rhinella_dapsilis	Y	1	1	0	0	0	2
201814	Rhinella_dapsilis	Y	1	1	0	0	0	2
566017	Rhinella_granulosa	Y	1	1	1	1	0	4
566018	Rhinella_granulosa	Y	1	1	1	1	0	4
100954	Rhinella_icterica	Y	1	1	0	1	0	3
100957	Rhinella_icterica	Y	1	1	0	1	0	3
4343	Rhinella_marina	Y	NA	NA	NA	NA	NA	0
4344	Rhinella_marina	Y	NA	NA	NA	NA	NA	0
130177	Rhinella_ocellata	Y	1	1	0	1	0	3
346829	Rhinella_poeppigii	Y	1	1	0	0	1	3
346830	Rhinella_poeppigii	Y	1	1	0	0	1	3
281765	Rhinella_schneideri	Y	1	1	0	1	1	4
38	Rhinella_spinulosa	Y	NA	NA	NA	NA	NA	0
153377	Schismaderma_carens	Y	0	0	0	0	0	0
153380	Schismaderma_carens	Y	0	0	0	0	0	0
53371	Strauchbufo_raddei	Y	1	0	0	0	0	1
53372	Strauchbufo_raddei	Y	1	1	1	0	0	3
165087	Vandijkophrynus_angusticeps	Y	1	1	0	0	0	2
165089	Vandijkophrynus_angusticeps	Y	1	1	0	0	0	2
239871	Vandijkophrynus_gariepensis	Y	0	0	0	0	0	0
239873	Vandijkophrynus_gariepensis	Y	0	0	0	0	0	0

SUPPLEMENTARY INFORMATION 5.4

Table 5.4.1 – Presence (0) absence (1) of bones for each species.

Name	Genus_species	Ear	Pterygoids	Prevomers	Palatines
30643	Atelopus_chiriquiensis	N	1	1	1
30644	Atelopus_chiriquiensis	N	1	1	1
236903	Atelopus_ignescens	N	1	1	1
236904	Atelopus_ignescens	N	1	1	1
193825	Atelopus_longirostris	N	1	1	1
193835	Atelopus_longirostris	N	1	1	1
279113	Atelopus_varius	N	1	1	1
279119	Atelopus_varius	N	1	1	1
129893	Atelopus_zeteki	N	1	1	1
129896	Atelopus_zeteki	N	1	1	1
159113	Capensibufo_rosei	N	1	1	1
159110	Capensibufo_rosei	N	1	1	1
239919	Dendrophryniscus_brevipollicatus	N	1	1	0
217659	Dendrophryniscus_brevipollicatus	N	1	1	1
107712	Melanophryniscus_stelzneri	N	1	1	1
107722	Melanophryniscus_stelzneri	N	1	1	1
153417	Mertensophryne_taitana	N	1	1	1
15124	Nannophryne_variegata	N	1	1	1
571097	Nectophryne_batesii	N	1	1	0
193540	Osornophryne_bufoniformis	N	1	1	1
193537	Osornophryne_bufoniformis	N	1	1	1
2520	Osornophryne_guacamayo	N	1	1	1
2523	Osornophryne_guacamayo	N	1	1	1
3166	Rhinella_festae	N	1	1	1
3708	Rhinella_festae	N	1	1	1
571101	Werneria_mertensiana	N	1	1	1
571105	Werneria_mertensiana	N	1	1	1
571108	Wolterstorffina_parvipalmata	N	1	1	1
571109	Wolterstorffina_parvipalmata	N	1	1	1
576391	Amietophrynus_gracilipes	Y	1	1	1
576239	Amietophrynus_gracilipes	Y	1	1	1
346809	Amietophrynus_mauritanicus	Y	1	1	1

346811	Amietophrynus_mauritanicus	Y	1	1	1
311300	Anaxyrus_canorus	Y	1	1	1
320094	Anaxyrus_cognatus	Y	1	1	1
320103	Anaxyrus_cognatus	Y	1	1	1
542211	Anaxyrus_houstonensis	Y	1	1	1
320140	Anaxyrus_microscaphus	Y	1	1	1
320144	Anaxyrus_microscaphus	Y	1	1	1
331415	Atelopus_flavescens	Y	1	1	1
331417	Atelopus_flavescens	Y	1	1	1
192815	Atelopus_franciscus	Y	1	1	1
569373	Atelopus_pulcher	Y	1	1	1
569381	Atelopus_pulcher	Y	1	1	1
243	Atelopus_spumarius	Y	1	1	1
3720	Atelopus_spumarius	Y	1	1	1
4905	Atelopus_spumarius	Y	1	1	1
66082	Bufo_bankorensis	Y	1	1	1
66083	Bufo_bankorensis	Y	1	1	1
51998	Bufo_japonicus	Y	1	1	1
113484	Bufo_japonicus	Y	1	1	1
254716	Duttaphrynus_scaber	Y	1	1	1
254718	Duttaphrynus_scaber	Y	1	1	1
266829	Duttaphrynus_stomaticus	Y	1	1	1
266836	Duttaphrynus_stomaticus	Y	1	1	1
579882	Epidalea_calamita	Y	1	1	1
579890	Epidalea_calamita	Y	1	1	1
498198	Incilius_campbelli	Y	1	1	1
498200	Incilius_campbelli	Y	1	1	1
116005	Incilius_canaliferus	Y	1	1	1
116019	Incilius_canaliferus	Y	1	1	1
348058	Incilius_coniferus	Y	1	1	1
348059	Incilius_coniferus	Y	1	1	1
523715	Incilius_ibarrai	Y	1	1	1
523723	Incilius_ibarrai	Y	1	1	1
214077	Incilius_mazatlanensis	Y	1	1	1
214074	Incilius_mazatlanensis	Y	1	1	1
116539	Incilius_occidentalis	Y	1	1	1
116541	Incilius_occidentalis	Y	1	1	1
52986	Ingerophrynus_celebensis	Y	1	1	1
61189	Ingerophrynus_celebensis	Y	1	1	1
51864	Peltophryne_fustiger	Y	1	1	1
4336	Rhaebo_haematiticus	Y	1	1	1

4337	Rhaebo_haematiticus	Y	1	1	1
674	Rhaebo_haematiticus	Y	1	1	1
70620	Rhinella_arenarum	Y	1	1	1
70622	Rhinella_arenarum	Y	1	1	1
518809	Rhinella_castaneotica	Y	1	1	1
518807	Rhinella_castaneotica	Y	1	1	1
70613	Rhinella_crucifer	Y	1	1	1
70614	Rhinella_crucifer	Y	1	1	1
196951	Rhinella_dapsilis	Y	1	1	1
201814	Rhinella_dapsilis	Y	1	1	1
566017	Rhinella_granulosa	Y	1	1	1
566018	Rhinella_granulosa	Y	1	1	1
100954	Rhinella_icterica	Y	1	1	1
100957	Rhinella_icterica	Y	1	1	1
4343	Rhinella_marina	Y	1	1	1
4344	Rhinella_marina	Y	1	1	1
130177	Rhinella_ocellata	Y	1	1	1
346829	Rhinella_poeppigii	Y	1	1	1
346830	Rhinella_poeppigii	Y	1	1	1
281765	Rhinella_schneideri	Y	1	1	1
38	Rhinella_spinulosa	Y	1	1	1
153377	Schismaderma_carens	Y	1	1	1
153380	Schismaderma_carens	Y	1	1	1
53371	Strauchbufo_raddei	Y	1	1	1
53372	Strauchbufo_raddei	Y	1	1	1
165087	Vandijkophrynus_angusticeps	Y	1	1	1
165089	Vandijkophrynus_angusticeps	Y	1	1	1
239871	Vandijkophrynus_gariepensis	Y	1	1	1
239873	Vandijkophrynus_gariepensis	Y	1	1	1

Name	**Genus_species**	**Ear**	**Quadratojugals**	**Sphenethmoid**
30643	Atelopus_chiriquiensis	N	1	1
30644	Atelopus_chiriquiensis	N	1	1
236903	Atelopus_ignescens	N	1	1
236904	Atelopus_ignescens	N	1	1
193825	Atelopus_longirostris	N	1	1
193835	Atelopus_longirostris	N	1	1
279113	Atelopus_varius	N	1	1
279119	Atelopus_varius	N	1	1
129893	Atelopus_zeteki	N	1	1

129896	Atelopus_zeteki	N	1	1
159113	Capensibufo_rosei	N	1	1
159110	Capensibufo_rosei	N	1	1
239919	Dendrophryniscus_brevipollicatus	N	2	1
217659	Dendrophryniscus_brevipollicatus	N	2	1
107712	Melanophryniscus_stelzneri	N	2	1
107722	Melanophryniscus_stelzneri	N	2	1
153417	Mertensophryne_taitana	N	1	1
15124	Nannophryne_variegata	N	1	1
571097	Nectophryne_batesii	N	1	1
193540	Osornophryne_bufoniformis	N	1	1
193537	Osornophryne_bufoniformis	N	1	1
2520	Osornophryne_guacamayo	N	1	1
2523	Osornophryne_guacamayo	N	1	1
3166	Rhinella_festae	N	1	1
3708	Rhinella_festae	N	1	1
571101	Werneria_mertensiana	N	1	1
571105	Werneria_mertensiana	N	1	1
571108	Wolterstorffina_parvipalmata	N	2	1
571109	Wolterstorffina_parvipalmata	N	2	1
576391	Amietophrynus_gracilipes	Y	1	1
576239	Amietophrynus_gracilipes	Y	1	1
346809	Amietophrynus_mauritanicus	Y	1	1
346811	Amietophrynus_mauritanicus	Y	1	1
311300	Anaxyrus_canorus	Y	1	1
320094	Anaxyrus_cognatus	Y	1	1
320103	Anaxyrus_cognatus	Y	1	1
542211	Anaxyrus_houstonensis	Y	1	1
320140	Anaxyrus_microscaphus	Y	1	1
320144	Anaxyrus_microscaphus	Y	1	1
331415	Atelopus_flavescens	Y	1	1
331417	Atelopus_flavescens	Y	1	1
192815	Atelopus_franciscus	Y	1	1
569373	Atelopus_pulcher	Y	1	1
569381	Atelopus_pulcher	Y	1	1
243	Atelopus_spumarius	Y	1	1
3720	Atelopus_spumarius	Y	1	1
4905	Atelopus_spumarius	Y	1	1
66082	Bufo_bankorensis	Y	1	1
66083	Bufo_bankorensis	Y	1	1
51998	Bufo_japonicus	Y	1	1

113484	Bufo_japonicus	Y	1	1
254716	Duttaphrynus_scaber	Y	1	1
254718	Duttaphrynus_scaber	Y	1	1
266829	Duttaphrynus_stomaticus	Y	1	1
266836	Duttaphrynus_stomaticus	Y	1	1
579882	Epidalea_calamita	Y	1	1
579890	Epidalea_calamita	Y	1	1
498198	Incilius_campbelli	Y	1	1
498200	Incilius_campbelli	Y	1	1
116005	Incilius_canaliferus	Y	1	1
116019	Incilius_canaliferus	Y	1	1
348058	Incilius_coniferus	Y	1	1
348059	Incilius_coniferus	Y	1	1
523715	Incilius_ibarrai	Y	1	1
523723	Incilius_ibarrai	Y	1	1
214077	Incilius_mazatlanensis	Y	1	1
214074	Incilius_mazatlanensis	Y	1	1
116539	Incilius_occidentalis	Y	1	1
116541	Incilius_occidentalis	Y	1	1
52986	Ingerophrynus_celebensis	Y	1	1
61189	Ingerophrynus_celebensis	Y	1	1
51864	Peltophryne_fustiger	Y	1	1
4336	Rhaebo_haematiticus	Y	1	1
4337	Rhaebo_haematiticus	Y	1	1
674	Rhaebo_haematiticus	Y	1	1
70620	Rhinella_arenarum	Y	1	1
70622	Rhinella_arenarum	Y	1	1
518809	Rhinella_castaneotica	Y	1	1
518807	Rhinella_castaneotica	Y	1	1
70613	Rhinella_crucifer	Y	1	1
70614	Rhinella_crucifer	Y	1	1
196951	Rhinella_dapsilis	Y	1	1
201814	Rhinella_dapsilis	Y	1	1
566017	Rhinella_granulosa	Y	1	1
566018	Rhinella_granulosa	Y	1	1
100954	Rhinella_icterica	Y	1	1
100957	Rhinella_icterica	Y	1	1
4343	Rhinella_marina	Y	1	1
4344	Rhinella_marina	Y	1	1
130177	Rhinella_ocellata	Y	1	1
346829	Rhinella_poeppigii	Y	1	1

346830	Rhinella_poeppigii	Y	1	1
281765	Rhinella_schneideri	Y	1	1
38	Rhinella_spinulosa	Y	1	1
153377	Schismaderma_carens	Y	1	1
153380	Schismaderma_carens	Y	1	1
53371	Strauchbufo_raddei	Y	1	1
53372	Strauchbufo_raddei	Y	1	1
165087	Vandijkophrynus_angusticeps	Y	1	1
165089	Vandijkophrynus_angusticeps	Y	1	1
239871	Vandijkophrynus_gariepensis	Y	1	1
239873	Vandijkophrynus_gariepensis	Y	1	1