



*Zootaxa* 4104 (1): 001–109  
<http://www.mapress.com/j/zt/>

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# Monograph

ISSN 1175-5326 (print edition)

**ZOOTAXA**

ISSN 1175-5334 (online edition)

<http://doi.org/10.11646/zootaxa.4104.1.1>

<http://zoobank.org/urn:lsid:zoobank.org:pub:D598E724-C9E4-4BBA-B25D-511300A47B1D>

# ZOOTAXA

4104

## **Phylogenetics, classification, and biogeography of the treefrogs (Amphibia: Anura: Arboranae)**

WILLIAM E. DUELLMAN<sup>1,3</sup>, ANGELA B. MARION<sup>2</sup> & S. BLAIR HEDGES<sup>2</sup>

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Magnolia Press  
Auckland, New Zealand

*Accepted by M. Vences: 27 Oct. 2015; published: 19 Apr. 2016*

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(*Zootaxa* 4104)

109 pp.; 30 cm.

19 April 2016

ISBN 978-1-77557-937-3 (paperback)

ISBN 978-1-77557-938-0 (Online edition)

FIRST PUBLISHED IN 2016 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: [magnolia@mapress.com](mailto:magnolia@mapress.com)

<http://www.mapress.com/j/zt>

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ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

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## Abstract

A phylogenetic analysis of sequences from 503 species of hylid frogs and four outgroup taxa resulted in 16,128 aligned sites of 19 genes. The molecular data were subjected to a maximum likelihood analysis that resulted in a new phylogenetic tree of treefrogs. A conservative new classification based on the tree has (1) three families composing an unranked taxon, Arboranae, (2) nine subfamilies (five resurrected, one new), and (3) six resurrected generic names and five new generic names. Using the results of a maximum likelihood timetree, times of divergence were determined. For the most part these times of divergence correlated well with historical geologic events. The arboranan frogs originated in South America in the Late Mesozoic or Early Cenozoic. The family Pelodyadidae diverged from its South American relative, Phyllomedusidae, in the Eocene and invaded Australia via Antarctica. There were two dispersals from South America to North America in the Paleogene. One lineage was the ancestral stock of *Acris* and its relatives, whereas the other lineage, subfamily Hyliinae, differentiated into a myriad of genera in Middle America.

**Key words:** Anura, Hylidae, phylogeny, new classification, new genera (*Callimedusa*, *Colomascirtus*, *Julianus*, *Rheohyla*, *Sarcohyla*), resurrected genera (*Dryophytes*, *Dryopsophus*, *Hyliola*, *Hylomantis*, *Ololygon*, *Pithecopus*), new subfamily (*Scinaxinae*), historical biogeography.

## Resumen

Un análisis filogenético de las secuencias de 503 individuos de ranas hílidos, e individuos de cuatro taxa en grupos externos, dió como resultado 16128 sitios alineados para 19 genes. Los datos moleculares se sometieron a un análisis de máxima verosimilitud que resultó en un nuevo árbol filogenético de las ranas arbóreas. Una nueva clasificación, conservadora, basada en el árbol tiene: (1) tres familias que componen un taxón sin rango taxonómico, Arboranae, (2) nueve subfamilias (cinco resucitadas, una nueva), y (3) seis nombres de géneros resucitados y cinco nuevos géneros. Usando los resultados de un árbol de tiempo de máxima verosimilitud, se estimaron los tiempos de las divergencias. En su mayor parte, estos tiempos se correlacionan bien con eventos geológicos. Las arboranas se originaron en Suramérica en e; Tarde Mesozoico o Temprano Cenozoico. La familia Pelodyadidae divergió de su clado hermano Suramericano, los Phyllomedusidae, en el Eoceno e invadió Australia por la vía de la Antártida. Hubieron dos dispersiones de Sudamérica a Norteamérica en el Paleógeno. Un linaje es el ancestro de *Acris* y sus parientes, y el otro linaje, la subfamilia Hyliinae se diferenció en un gran número de géneros en Mesoamérica.

**Palabras clave:** Anura, Hylidae, filogenia, nueva clasificación, nuevos géneros (*Callimedusa*, *Colomascirtus*, *Julianus*, *Rheohyla*, *Sarcohyla*), resucitados géneros (*Drophytes*, *Dryopsophus*, *Hyliola*, *Hylomantis*, *Ololygon*, *Pithecopus*), nueva subfamilia (*Scinaxinae*), biogeografía histórica

## Resumo

Uma análise filogenética utilizando sequências de 503 táxons de os sapos de los árboles e quatro táxones externos resultou no alinhamento de 16.128 sítios de 19 genes. Os dados moleculares foram submetidos a uma análise de máxima verossimilhança, que resultou em uma nova árvore filogenética para os hílideos. A nova classificação conservadora baseada na árvore, possui (1) três famílias que compõem um táxon sem classificação, (2) um total de nove subfamilias (cinco revalidados, uma nova), e (3) seis nomes de gêneros revalidados e cinco novos nomes de gêneros. Usando os resultados da árvore máxima verossimilhança, tempos de divergência foram determinados. A maior parte destes tempos de divergência tiveram uma boa correlação com eventos históricos geológicos. Os sapos arboranas se originaram na América do Sul no final do Mesozóico ou no início Cenozóico. A família Pelodyadidae divergiu de seu parente sul-americano, Phyllomedusidae, em no Eoceno e invadiu a Austrália via Antártica. Houveram duas dispersões da América do Sul para a América do Norte no Paleógeno. Uma linhagem foi o estoque ancestral de *Acris* e seus parentes, enquanto a outra linhagem, sub-família Hyliinae, se diferenciou em uma infinidade de gêneros na América Central.

**Palavras-chave:** Anura, Hylidae, filogenia, nova classificação, novos nomes de gêneros (*Callimedusa*, *Colomascirtus*, *Julianus*, *Rheohyla*, *Sarcohyla*), nomes de gêneros revalidados (*Drophytes*, *Dryopsophus*, *Hyliola*, *Hylomantis*, *Ololygon*, *Pithecopus*), nova subfamilia (*Scinaxinae*), biogeografia histórica

## Introduction

The so-called treefrogs are plentiful in the Americas and the Australo-Papuan region, and they also occur in Europe, extreme northern Africa, western and eastern Asia, and the Japanese Archipelago. These frogs have been grouped into the family Hylidae that currently contains 951 species or 14.5% of all anurans (AmphibiaWeb, 2015). Hylid frogs of the subfamilies Hylinae and Phyllomedusinae are most speciose in South and Middle America; hylines are moderately diverse in North America, and one genus, *Hyla*, occurs in western Eurasia and eastern Asia. The species-rich subfamily Pelodyadinae is restricted to the Australo-Papuan Region. In the past two decades, classification of the treefrogs has changed dramatically from that based solely on morphological evidence (e.g., Duellman 2001) to arrangements based mainly on molecular evidence (e.g., Faivovich *et al.* 2005; Wiens *et al.* 2010). For example, Duellman (2001) recognized the marsupial frogs and their allies as a subfamily, Hemiphractinae, within Hylidae; he also recognized the subfamily Pseudinae (*Lysapsus* and *Pseudis*) within the Hylidae that also contained the subfamilies Hylinae, Pelodyadinae, and Phyllomedusinae. Despite the highly erroneous disposition of the marsupial frogs and their allies (*Cryptobatrachus*, *Flectonotus*, *Fritziana*, *Gastrotheca*, *Hemiphractus*, and *Stefania*) into three families by Frost *et al.* (2006), molecular data strongly support the monophyly of Hemiphractidae (Castroviejo-Fisher *et al.* 2015) that is the sister taxon to the terraranans (Duellman, 2015; Heinicke *et al.* 2009).

The number of species of hylid frogs has grown steadily since the recognition of the family by Daudin (1802), who recognized 27 species in one genus. Excluding species now placed in other families, Duméril and Bibron (1841) recognized six genera and 43 species; that number increased to 57 in Günther's (1859) catalogue. Twenty-three years later, Boulenger (1882) recognized eight genera and 177 species, while the numbers increased to 11 genera and 286 species in Nieden (1923) and to 29 genera and 492 species in Duellman (1977). In the Version 6.0 of Amphibian Species of the World (Frost 2015), 948 species are contained in 48 genera. Herein we place those species in 60 genera in three families.

For more than 150 years, most treefrogs from Eurasia, the Americas, and the Australo-Papuan Region were placed in the genus *Hyla*. The first major breakup of that genus was Tyler's (1971) recognition of *Litoria* for the "*Hyla*" in the Australo-Papuan Region. A major molecular analysis of hylid frogs by Faivovich *et al.* (2005) resulted in the recognition of 10 new or resurrected genera in the Neotropics (mostly in Central America and Mexico), thereby restricting *Hyla* to Eurasia and North America south to Guatemala. Subsequently, frogs in Phyllomedusinae were subjected to an analysis of a significant set of molecular data; this resulted in the recognition of seven genera in that subfamily (Faivovich *et al.* 2009).

In a review of sampling strategies of a large phylogenetic unit, Hylidae, Wiens *et al.* (2005) recognized Hemiphractidae as separate from Hylidae; they recognized three hylid subfamilies—Hylinae, Pelodyadinae, and Phyllomedusinae. Their results were based on 144 morphological characters and data from sequences of two mitochondrial and two nuclear genes, but for most species, only the 16S gene was used. Their combined data set included only 81 species. They erroneously applied the generic name *Boana* to a large clade in South America for which the generic name was shown earlier to be *Hypsiboas* by Faivovich *et al.* (2005). Wiens *et al.* (2010) presented a maximum likelihood analysis of up to 11 genes of 362 taxa; the results were congruent with those of Faivovich *et al.* (2005).

Herein we present a new molecular phylogeny of treefrogs based on 503 taxa with 16,128 aligned sites of 19 genes. Our classification based on these results places three families in an unranked taxon, thereby rendering the largest family of amphibians more manageable. Taxonomic revision was done for the same purpose in recent years for another, similar-sized group of amphibians (Hedges *et al.* 2008), as well as large groups of lizards and snakes (Gamble *et al.* 2008, Vidal *et al.* 2009, Townsend *et al.* 2011, Hedges & Conn 2012, Hedges 2014). Classifications are intended to be dynamic, and manageability is a recognized criterion for changing taxonomy (Hedges 2013; Vences *et al.* 2013), even if it leads to a short period of instability (revision shock; Hedges 2013). Our classification also includes the resurrection of available names and accounts of new names in order to recognize major clades.

## Material and methods

The taxonomy and content of Hylidae is based on Amphibian Species of the World (Frost 2015), last accessed on September 15, 2015.

We began by assembling all available data in Genbank for two mitochondrial genes which were the best-represented, the large (16S) and small (12S) rRNA subunits. We reviewed both gene alignments in MEGA 5.2 (Tamura *et al.* 2011) and trimmed them to include only sequences of Hylidae (*s.l.*), as well as those of the chosen four outgroup taxa—viz., *Ceuthomantis smaragdinus*, *Dendrobates auratus*, *Haddadus binotatus*, and *Rhinoderma darwini*. We excluded taxa that have since been synonymized with recognized taxa according to Frost (2015).

We also built alignments for an additional 10 genes that were well-represented: cytochrome b (cytb), chemokine receptor 4 (CXCR4), histone 3a (H3A), sodium-calcium exchanger 1 (NCX1), pro-opiomelanocortin (POMC), recombination-activating gene 1 (RAG1), rhodopsin (Rho), seventh-in-absentia (SIA), solute carrier family 8 member 3 (SLC8a3), and tyrosinase precursor (Tyr). To do this, we again queried GenBank for all hylid sequences for each of the 10 genes and examined all available sequences of Hylidae (*s.l.*). Again, we used the latest taxonomy (Frost 2015) and, for each gene, examined all available sequences for each recognized species and chose the longest and most complete (or, if all else equal the first sequence). This approach was similar, but not identical, to that of Pyron & Wiens (2011). However, we added seven additional genes for which there were at least 25 distinct hylid taxa: 28S rRNA (28S), cellular myelocytomatosis exon 2 (cmyc2), cellular myelocytomatosis exon 3 (cmyc3), cytochrome oxidase subunit I (COI), tensin 3 (TNS3), NADH dehydrogenase subunit 1 (ND1), and NADH dehydrogenase subunit 2 (ND2).

All genes were aligned independently in MEGA 5.2, using MUSCLE 3.6 under default parameters (Edgar 2004), and rarely with adjustments made by eye. Protein translations were reviewed for protein-coding genes to ensure correct alignment with respect to reading frame. Individual gene trees were constructed as an additional check on data quality, and a few obviously misplaced sequences (either mislabeled in Genbank, or containing sequence errors) were removed. All 19 genes were concatenated for a total of 503 ingroup taxa (species) and four outgroup taxa, and 16,128 aligned sites. For comparison, Pyron & Wiens (2011) included 1824 sequences of Hylidae (*s.l.*) across the 12 genes in common with our data set whereas we used 2306 sequences across those same genes. We included seven additional genes for a total of 3069 sequences of Hylidae (*s.l.*), which corresponds to 68% more sequences (overall) than in Pyron & Wiens (2011). GenBank accession numbers for all genes of all taxa included in this study are given in Appendix 1 along with a summary of sequence coverage per gene.

Maximum likelihood analyses were performed on the concatenated dataset. As with phylogenetic analyses of other large data sets (Padiál *et al.* 2014; Pyron *et al.* 2011; Pyron *et al.* 2013), Bayesian methods and standard bootstrap analysis were computationally intractable. RAxML 8.0.24 (Stamatakis 2014) was implemented on the CIPRES Science Gateway (Miller *et al.* 2010). The dataset was partitioned by gene (i.e., 19 partitions), and analyzed using the GTRGAMMA model for all partitions (the maximized available model in RAxML). All parameters for the ML analyses were estimated by the program during the run. Branch support in the trees was provided by rapid bootstrap analysis (1000 replicates). The rapid bootstrap method has been shown to produce almost identical values as the standard bootstrap method ( $r = 0.99$ ), but it is many times faster (Stamatakis *et al.* 2008). As a test of the consistency of the rapid bootstrap method, we made five separate runs and determined that 82% of the nodes were identical or varied within 5% and nearly all (99%) of the well-supported nodes (>70% support value) were in this category. This is consistent with the typical pattern of bootstrap support values, where higher support values have smaller variance (Hedges 1992). Alternate partitioning schemes were considered, including the best scheme under the BIC according to PartitionFinder 1.1.1 (Lanfear *et al.* 2012; Lanfear *et al.* 2014). There were no significant changes in topology in the resulting trees between the two schemes.

Divergence times were estimated using RelTime as implemented in MEGA7 (Tamura *et al.* 2013). The full dataset (16,128 aligned sites) was loaded and all sites were analyzed. The topology from the ML analysis was used as the starting tree, with the four outgroup taxa defined manually. Local clocks were used, with a clock stringency of “few clocks” set (clock rates merged on two StdErrors). The GTR+I+G model was implemented with five discrete gamma categories.

Two minimum and two maximum constraints were used as calibrations. The minimum divergence time between Hylinae and Acridinae was set at 16 million years ago (Mya), based on remains of *Hyla* from the Miocene of Austria (1998b). The divergence time between Phyllomedusidae and Pelodyadidae was constrained between 35–70 Mya, based on the timeframe when Australian pelodyadid arboranans (represented by *Litoria*) could disperse from South America through Antarctica (Li & Powell 2001; Sanmartin & Ronquist 2004; Springer *et al.* 1998; Woodburne & Case 1996). The maximum age for the Caribbean genus *Osteopilus* was set at 37.2 Mya, the date at which the Greater and Lesser Antilles became permanently subaerial, based on geologic evidence

(Iturralde-Vinent & MacPhee, 1999). RelTime analyses were also performed with various combinations of minimum and maximum calibrations in order to gauge the effects of each calibration on the inferred divergence times.

Finally, as a check on RelTime estimates, we also estimated divergence times using an uncorrelated relaxed clock model in BEAST v1.8.1 (Drummond & Rambaut 2007) on our maximum likelihood tree with the topology constrained, using default optimization settings for priors and operators and two independent runs. We set uniform priors on the three calibrated nodes, as for the RelTime analyses, then ran the search for 100 million generations, unpartitioned, and discarded the first 10 million generations as the burn-in. We used Tree Annotator v1.8.0 (Drummond & Rambaut 2007) to visualize the inferred phylogeny and the node age estimates. Because the time estimates from BEAST were nearly identical to those of RelTime ( $r = 0.96$ , slope = 1.06) we present only those from RelTime because they have more conservative confidence intervals.

Divergence times were similar across all RelTime analyses calibrated with different sets of maximums and minimums. There were four sets of identical results: (1) those analyses that included the minimum calibration of 35 Mya placed on the split between Phyllomedusidae and Pelodyadidae and maximum of 70 Mya placed on that same split, regardless of whether the other minimum and/or maximum were included; (2) those analyses that included the minimum calibration of 16 Mya placed on the split between Hylinae and Acridinae and the maximum of 70 Mya placed on the split between Phyllomedusidae and Pelodyadidae, regardless of the presence of the 37.2 Mya *Osteopilus* maximum; (3) those analyses that included the minimum calibration of 35 Mya placed on the split between Phyllomedusidae and Pelodyadidae and maximum of 37.2 Mya on *Osteopilus*, regardless of the presence of the 16 Mya minimum placed on the split between Hylinae and Acridinae; and (4) the analysis with the minimum calibration of 16 Mya placed on the split between Hylinae and Acridinae and the maximum of 37.2 Mya placed at the base of *Osteopilus*. Presented in our timetree (Fig. 17) are the divergence times estimated from an analysis with all four calibrations, which corresponded to the results of set one. The date estimates of analyses in set two were ~11% younger than those of set one. The date estimates of analyses in set three were ~17% older than those of set one. The date estimates of the analysis in set four were ~7% older than those of set one. These results showed that no single calibration had a major (e.g., >50%) impact on the resulting time estimates.

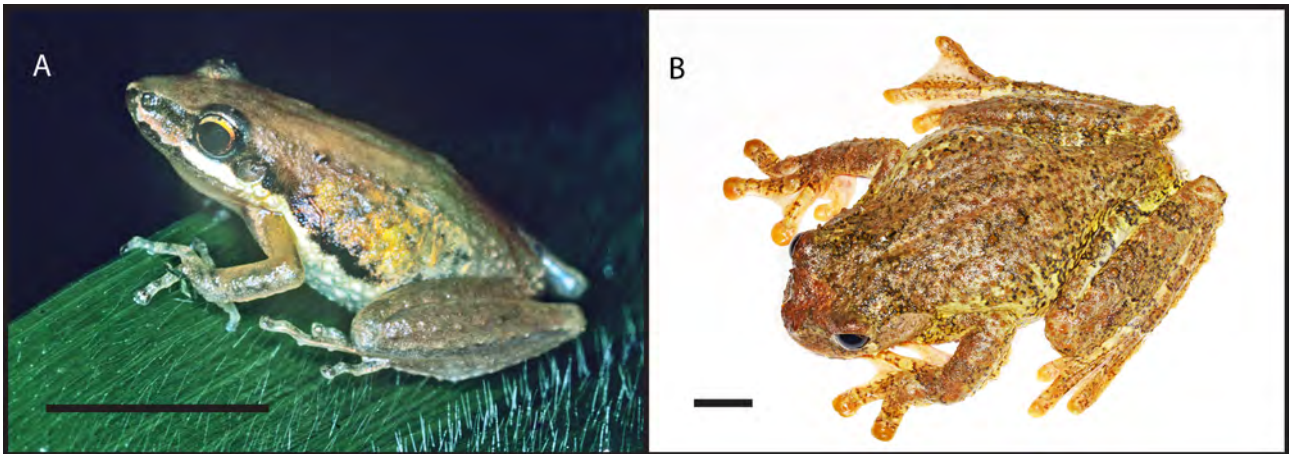
The arrangement of taxonomic accounts follows the phylogenetic tree (Fig. 4). We do not present a generic account if no taxonomic changes have been made within a genus and the substance of the generic account remains the same as that in Amphibian Species of the World (Frost 2015). Family group and generic definitions are only a few statements and are not intended to be full definitions. Synonymies are given if they differ from those in Frost (2015), but those citations are not listed in the References. Snout-vent length is abbreviated SVL; larval labial tooth row formula is abbreviated LTRF, and diploid chromosome number is designated as 2n. Species that were not included in the molecular analysis are noted by an asterisk (\*) in the lists of species in accounts of genera. Specific specimens are referred to by their museum acronyms: AMNH = American Museum of Natural History, New York, USA; BPBM = Bernice P. Bishop Museum, Honolulu, Hawaii, USA; KU = Biodiversity Institute, University of Kansas, Lawrence, Kansas, USA; MNRJ = Museu Nacional de Rio De Janeiro, Brazil; SBH = S. Blair Hedges collection, Philadelphia, Pennsylvania, USA; UMMZ = University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA.

## Classification

### Arboranae new taxon

**Definition.** Species in this unranked taxon have an arciferal pectoral girdle, eight procoelous presacral vertebrae, separate calcaneum and astragalus, intercalary elements (usually cartilaginous) between terminal and penultimate phalanges, claw-shaped terminal phalanges, and SVL from 18 mm in *Litoria microbelos* (Cogger) (Fig. 1A) to 142 mm in *Osteopilus vastus* (Cope) (Fig. 1B); eggs deposited in water or on vegetation above water; aquatic larvae in all species; basic LTRF 2/3 in tadpoles, chromosome complement  $2n = 18-34$ .

**Content.** This taxon contains three families currently containing 934 species: Hylidae, Pelodyadidae, and Phyllomedusidae.



**FIGURE 1.** **A.** The smallest known arboranan, *Litoria microbelos*, KU 179485, AMAX Mining Camp, 300 m, Mitchell Plateau, Western Australia, Australia. W. E. Duellman. **B.** The largest known arboranan, *Osteopilus vastus*, SBH 269439, Mome Deux Mamelles, Grande Anse, Haiti. S. B. Hedges. Bars = 10 mm.

**Distribution.** This taxon ranges throughout temperate North America, Central America, the West Indies, and tropical and subtropical South America; it also occurs in Australia, Tasmania, New Guinea, and the Solomon Islands. Furthermore it exists throughout much of temperate Eurasia, Japan, and extreme northern Africa.

**Etymology.** The name is derived from the Latin *arbor* meaning tree and the Latin *rana* meaning frog. It is applied to this large group in which most of the species are arboreal; notable exceptions are some terrestrial species (e.g. *Acris* and *Pseudacris* in North America and some *Litoria* [formerly *Cyclorana*] in Australia) and aquatic species (Pseudinae) in South America. This name also is complementary to the higher taxon Terraranae (emended from Terrarana), which includes terrestrial breeding "land frogs." Also see the discussion in Heinicke *et al.* (2009) regarding the formation of higher taxa names, which are unregulated by the Code. Hedges *et al.* (2008) discussed why they chose an unranked taxon for landfrogs, and their reasoning applies here to the treefrogs, a similar-sized group (~1,000 species). The numbers of taxa in both groups are growing at a high rate, which will necessitate further taxonomic subdivision. Erection of a superfamily in both cases would constrain that growth, making an unranked taxon more appropriate. For this reason we object to the use of the superfamily Brachycephaloidea in place of Terraranae (Padial *et al.* 2014).

**Remarks.** Three distinct clades are evident in our molecular phylogeny (Fig. 2). Our conservative approach to a classification based on the phylogeny is to propose an unranked name, Arboranae, for what previously had been Hylidae. Within Arboranae, we have elevated the two subfamilial names (Pelodyadinae and Phyllomedusinae) to the family level. The phylogenetic analysis shows that the large conglomerate of South American arboranans is paraphyletic with respect to Nearctic hylids. A more sophisticated analysis based on expanded genomic data is needed to show the relationships of this, the largest assemblage of arboranans, herein still recognized as members of Hylidae.

### Family Hylidae Rafinesque, 1815

Hylarina Rafinesque, 1815:78. Type genus: *Hylaria* Rafinesque, 1814 (an unjustified emendation of *Hyla* Laurenti, 1768 [fide Frost 2015]).

**Definition.** Iris horizontally elliptical; arciferal pectoral girdle, eight procoelous presacral vertebrae, separate calcaneum and astragalus, intercalary cartilages between terminal and penultimate phalanges, claw-shaped terminal phalanges, SVL from 18 mm in *Litoria microbelos* to 142 mm in *Osteopilus vastus*;  $2n = 18-34$  chromosomes; eggs deposited in water or on vegetation over water; aquatic larvae in all species.

**Content.** Seven subfamilies, 49 genera and 676 species.

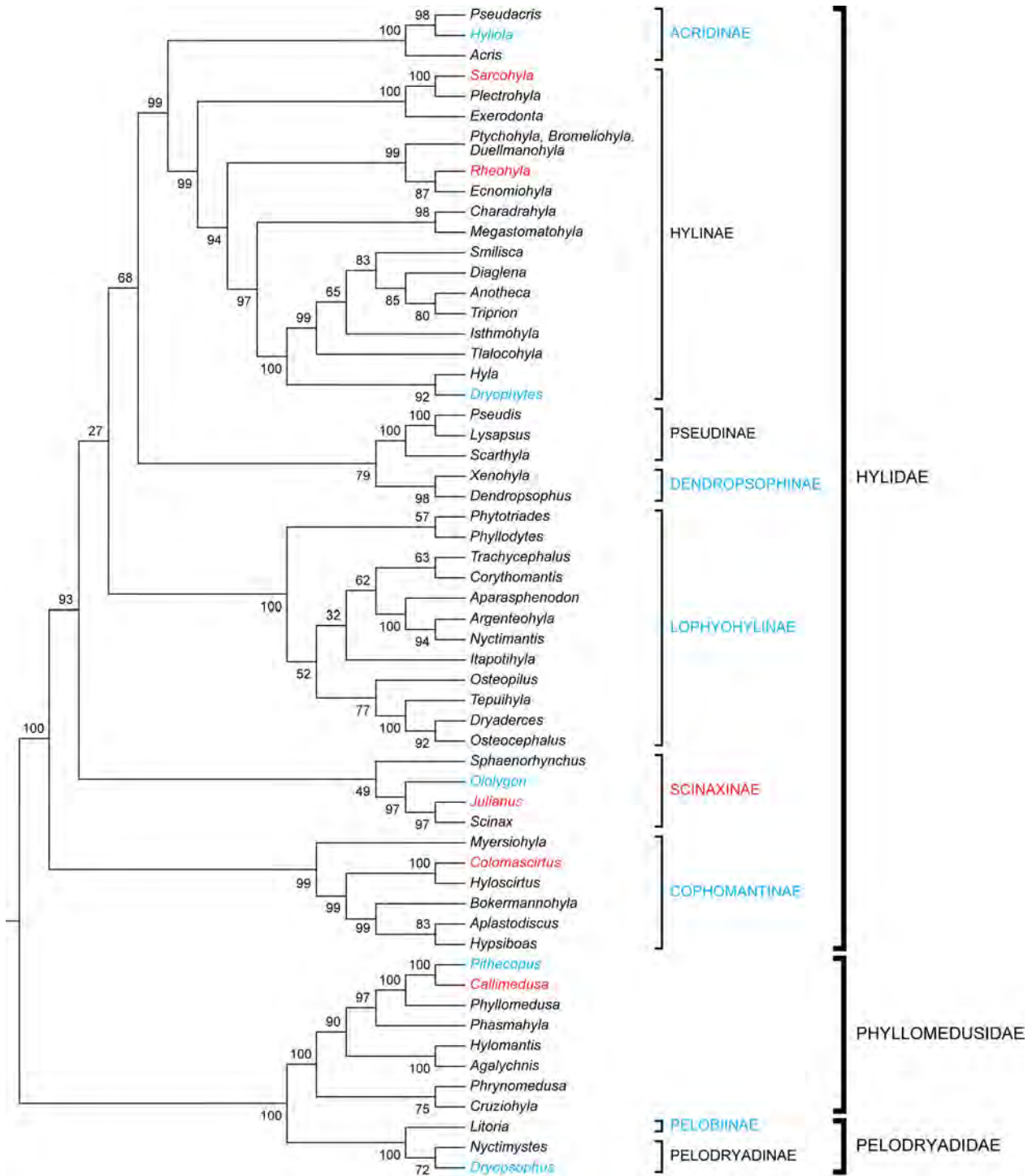
**Distribution.** North America from southern Alaska and Hudson Bay southward throughout Mexico and Central America to subtropical Argentina, the Pacific lowlands from Colombia to northwestern Peru, and the



Andes southward to Bolivia. The family also occurs in the Greater Antilles and throughout much of temperate Eurasia, Japan, and extreme northern Africa.

**Etymology.** The family name is based on the generic name *Hyla* that is derived from the vocative of *Hylas*, the companion of Hercules, in Greek mythology.

**Remarks.** We recognize seven subfamilies within Hylidae. These are based on the molecular tree and do not necessarily have distinguishing morphological characters. The placement of many species is questionable because of the absence of molecular data. These are treated in the remarks of respective genera.



**FIGURE 2.** Phylogenetic tree of the families, subfamilies, and genera of arboran frogs, distilled from the maximum likelihood phylogeny (Fig. 4). Names in red are new and those in blue are resurrected. The tree is rooted with *Ceuthomantis smaragdinus*, *Dendrobates auratus*, *Haddadus binotatus*, and *Rhinoderma darwinii* (not shown). Bootstrap support values are indicated at nodes.

## Subfamily Acridinae Mivart, 1869

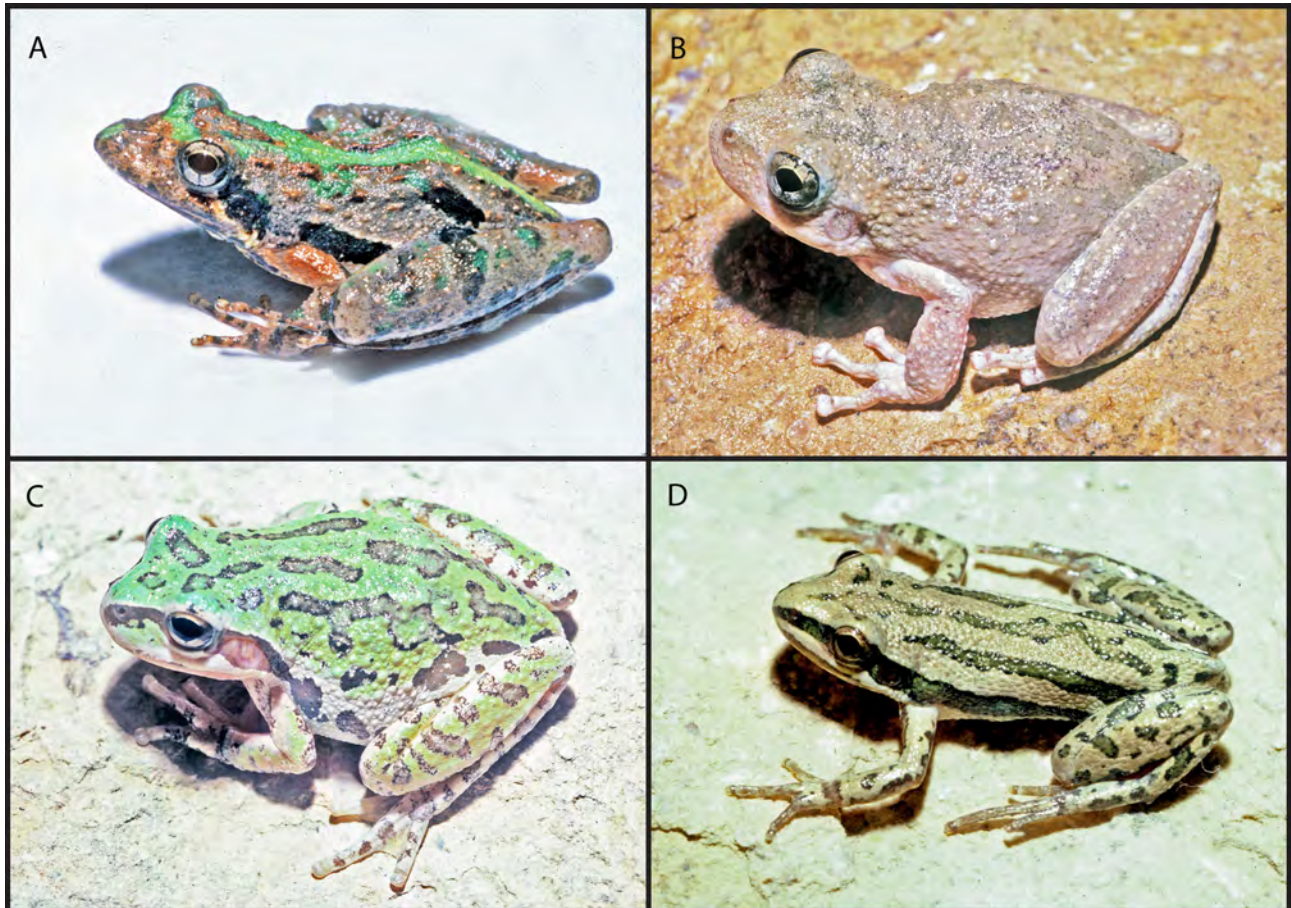
Acridina Mivart, 1869: 292. Type genus *Acris* Duméril and Bibron, 1841:506.

**Definition.** Small to medium-sized (19–48 mm SVL) mainly terrestrial and semi-aquatic frogs; discs on fingers and toes not, or only slightly, expanded (Fig. 3A); chromosome complement  $2n = 22$  or 24.

**Content.** Three genera and 21 species.

**Distribution.** North America from southern Alaska southward to southern Baja California, and east of the Rocky Mountains from Hudson Bay to the Gulf of Mexico.

**Etymology.** The familial name is based on that of the type genus, the Greek *akris*, meaning a kind of grasshopper.



**FIGURE 3.** **A.** *Acris gryllus*, KU 207329, Bluff Lake, Noxubee County, Mississippi, USA. **B.** *Hyliola cadaverina*, KU 207397, Santa Ynez River, Santa Barbara County, California, USA. **C.** *Hyliola regilla*, KU 207467, Sunrise, 32 km S Bend, Deschutes County, Oregon, USA. **D.** *Pseudacris triseriata*, KU 207486, 10 km E Pratt, Pratt County, Kansas, USA. All by W. E. Duellman.

## *Hyliola* Mocquard, 1899

*Hyliola* Mocquard, 1899:337. Type species: *Hyla regilla* Baird and Girard, 1852, by subsequent designation by Stejneger (1907:75).

**Definition.** Medium-sized frogs (30–46 mm SVL) with slightly expanded terminal discs on digits; chromosome complement  $2n = 24$ .

**Content.** Four species: *Hyliola cadaverina* (Cope), *hypochondriaca* (Hallowell), *regilla* (Baird and Girard), and *sierra* (Jameson, Mackey, and Richmond) (Fig. 3B and C).

**Distribution.** Western North America from southern Alaska to southern Baja, California, and eastward to western Texas, USA.

**Etymology.** The generic name is a diminutive form of "*hyla*," apparently alluding to the small size of these species in comparison with species of *Hyla*, a genus of frogs most of which are larger in size.

**Remarks.** Previous phylogenetic analyses of *Pseudacris* (e.g., Hedges 1986; Cocroft 1994) consistently showed *P. cadaverina* and *P. regilla* to be sister species and separated from other species of *Pseudacris*. The generic separation also recognizes the geographic separation of *Hyliola* and *Pseudacris*.

### *Pseudacris* Fitzinger 1843

*Pseudacris* Fitzinger, 1843. Type species.—*Rana nigrita* LeConte 1825:282, by monotypy.

*Chorophilus* Baird, 1854. Type species.—*Rana nigrita* LeConte, 1825:282, by original designation.

*Helocaetes* Baird, 1854. Type species.—*Hyla triseriata* Wied-Neuwied, 1839, by subsequent designation by Schmidt, 1953:73.

*Limnaoedus* Mittleman and List, 1953:83. Type species.—*Hylodes ocellaris* Holbrook, 1838 (= *Hyla ocellaris* Bosc and Daudin, 1901), by original designation.

*Parapseudacris* Hardy and Burrows, 1986: 80.—Type species *Hyla crucifer* Wied-Neuwied, 1838, by original designation.

Synonymy with *Pseudacris* by Hedges, 1986:11.

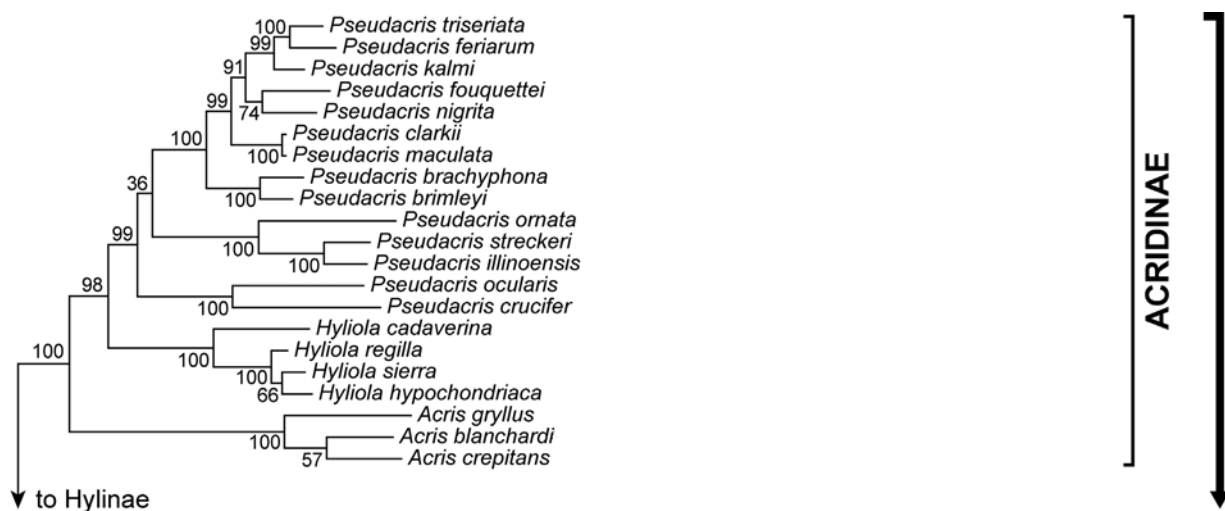
**Definition.** Small, primarily terrestrial frogs (SVL up to 48 mm in *P. streckeri*) (Fig. 3D); chromosome complement  $2n = 24$ .

**Content.** Fourteen species: *Pseudacris brachyphona* (Cope), *brimleyi* Brandt and Walker, *clarkii* (Baird), *crucifer* (Wied-Neuwied), *feriarum* (Baird), *fouquettei* Lemmon, Lemmon, Collins, and Cannatella, *illinoensis* Smith, *kalmi* Harper, *maculata* (Agassiz), *nigrita* (LeConte), *ocularis* (Holbrook), *ornata* (Holbrook), *streckeri* Wright and Wright, and *triseriata* (Wied-Neuwied).

**Distribution.** North America east of the Great Basin from Hudson Bay to the Gulf of Mexico.

**Etymology.** The name is derived from the Greek *pseudes* meaning false and the Greek *akris*, referring to the genus *Acris*.

**Remarks.** Three distinct clades are evident in the tree (Fig. 4). The largest clade contains nine species and includes the type species of the genus. A clade containing the large species (*Pseudacris illinoensis*, *ornata*, and *streckeri*) was recognized as the subgenus *Pycnacris* by Fouquette and Dubois (2014:361). Another clade includes *Pseudacris crucifer* and *P. ocellaris*, the type species of the genera *Parapseudacris* Hardy and Burrows (1986:80) and *Limnaoedus* (Mittleman & List 1953:83), respectively.



**FIGURE 4.** Maximum likelihood phylogeny of arboranan frogs based on DNA sequence data from 19 genes (16,128 aligned sites). The tree is rooted with *Ceuthomantis smaragdinus*, *Dendrobates auratus*, *Haddadus binotatus*, and *Rhinoderma darwini* (not shown). Bootstrap support values are indicated at nodes.

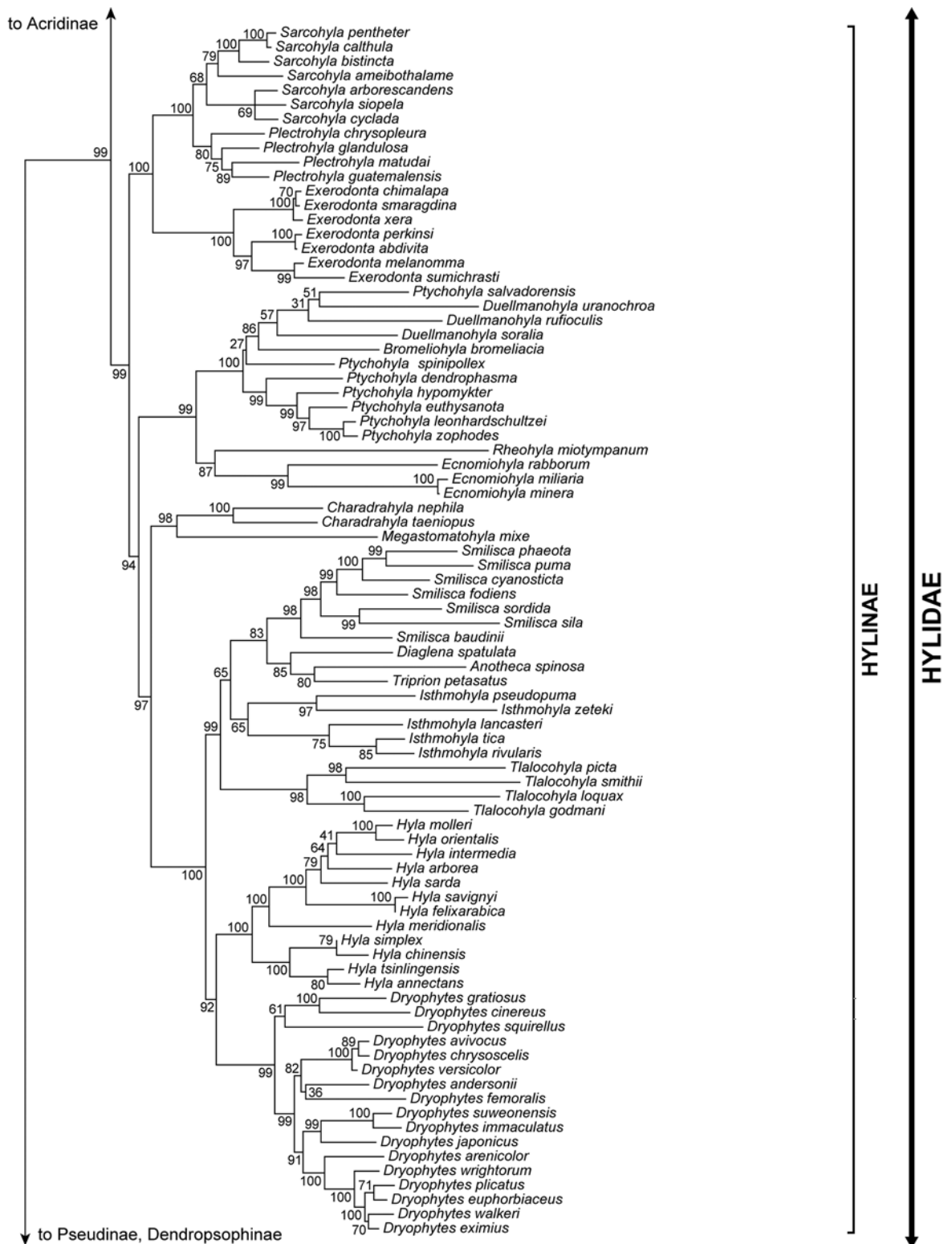


FIGURE 4. (Continued)

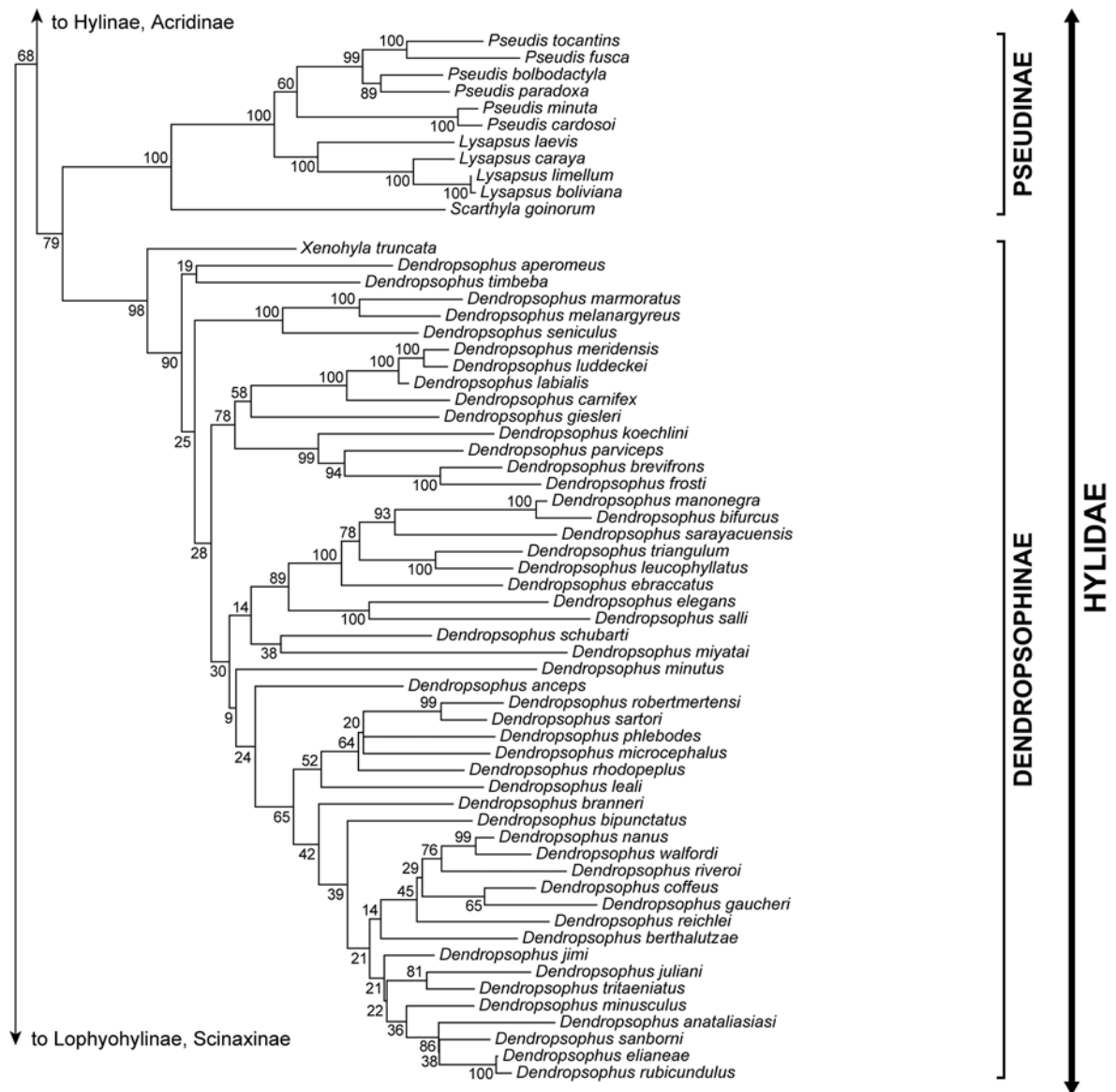


FIGURE 4. (Continued)

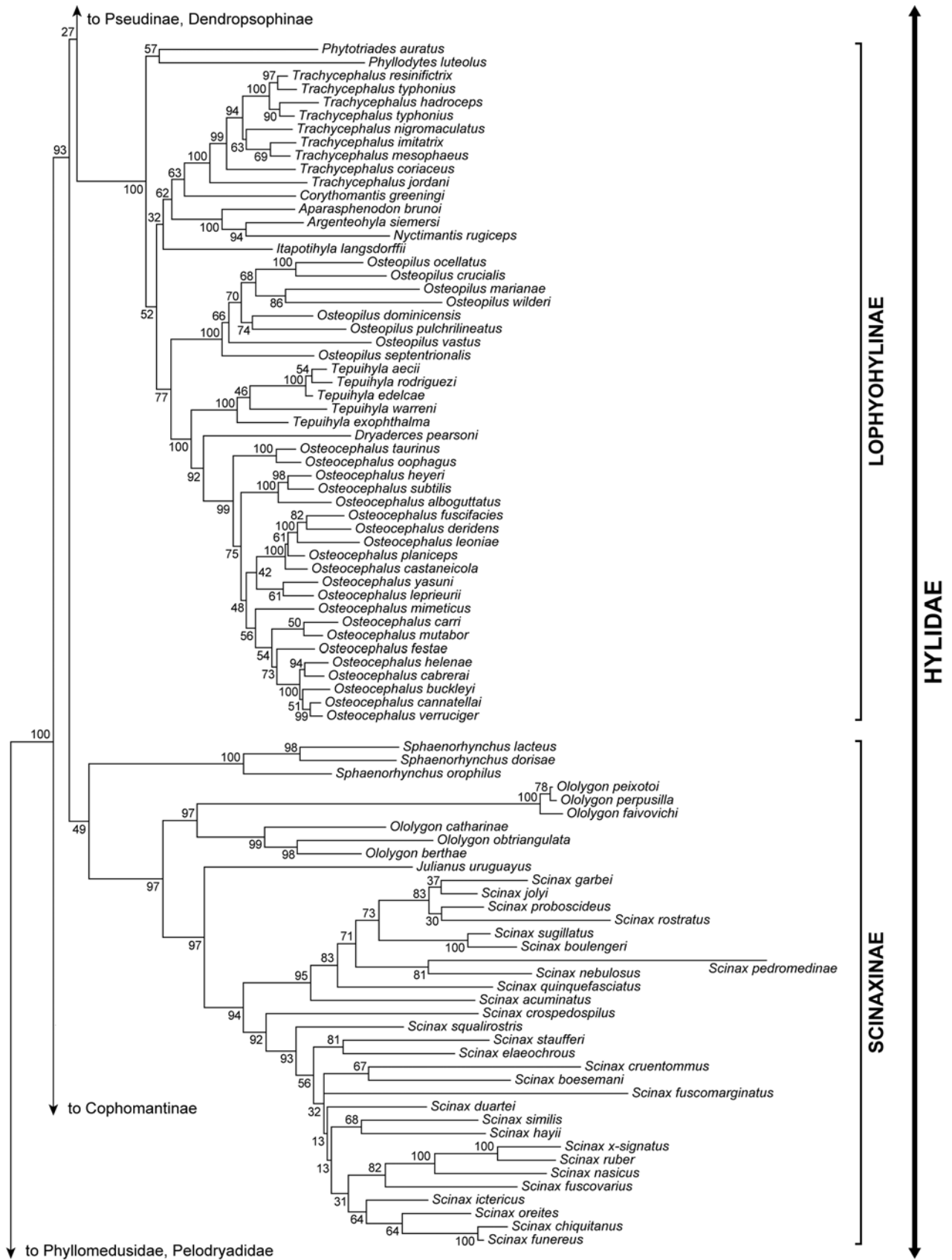


FIGURE 4. (Continued)



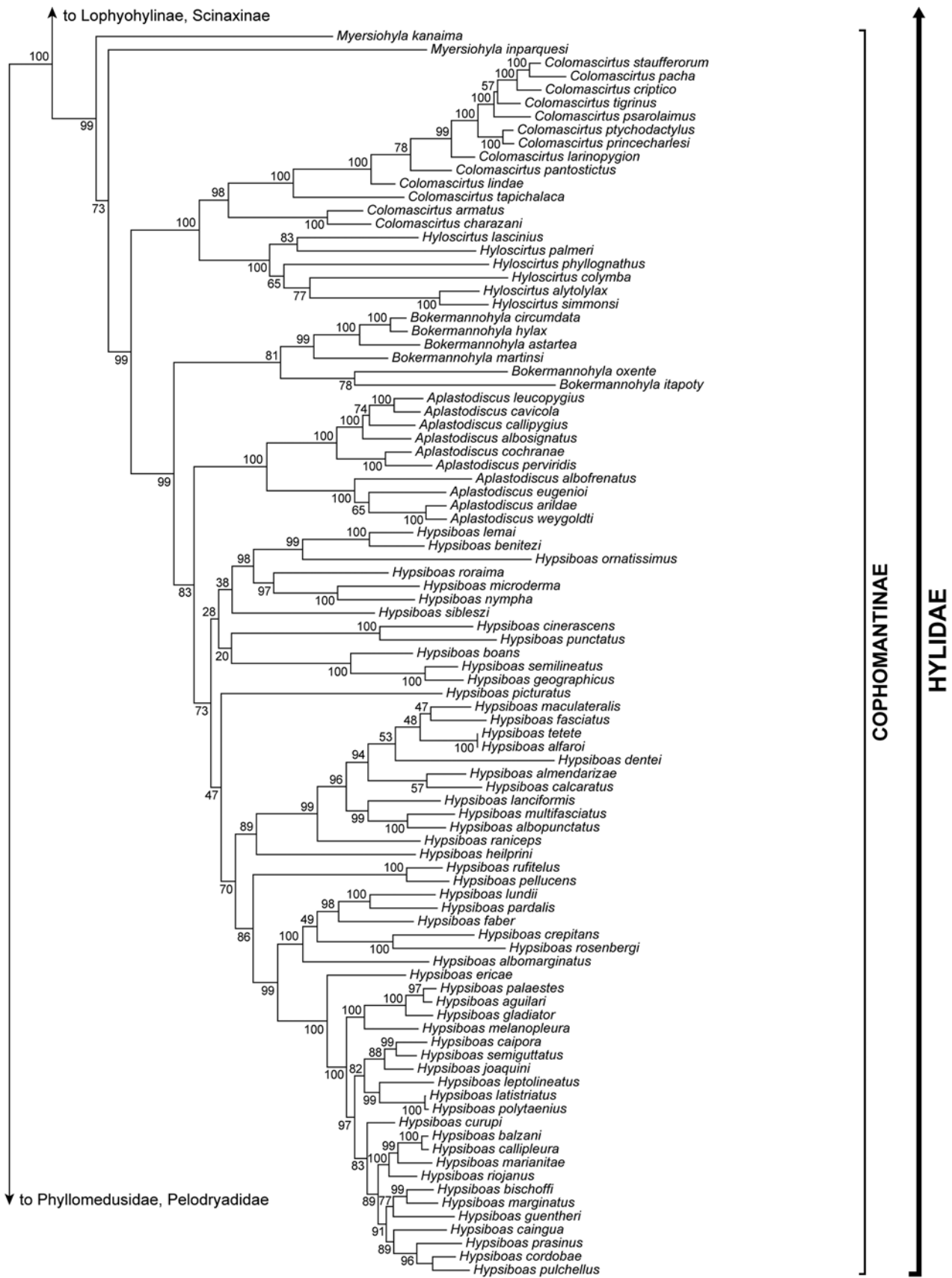


FIGURE 4. (Continued)

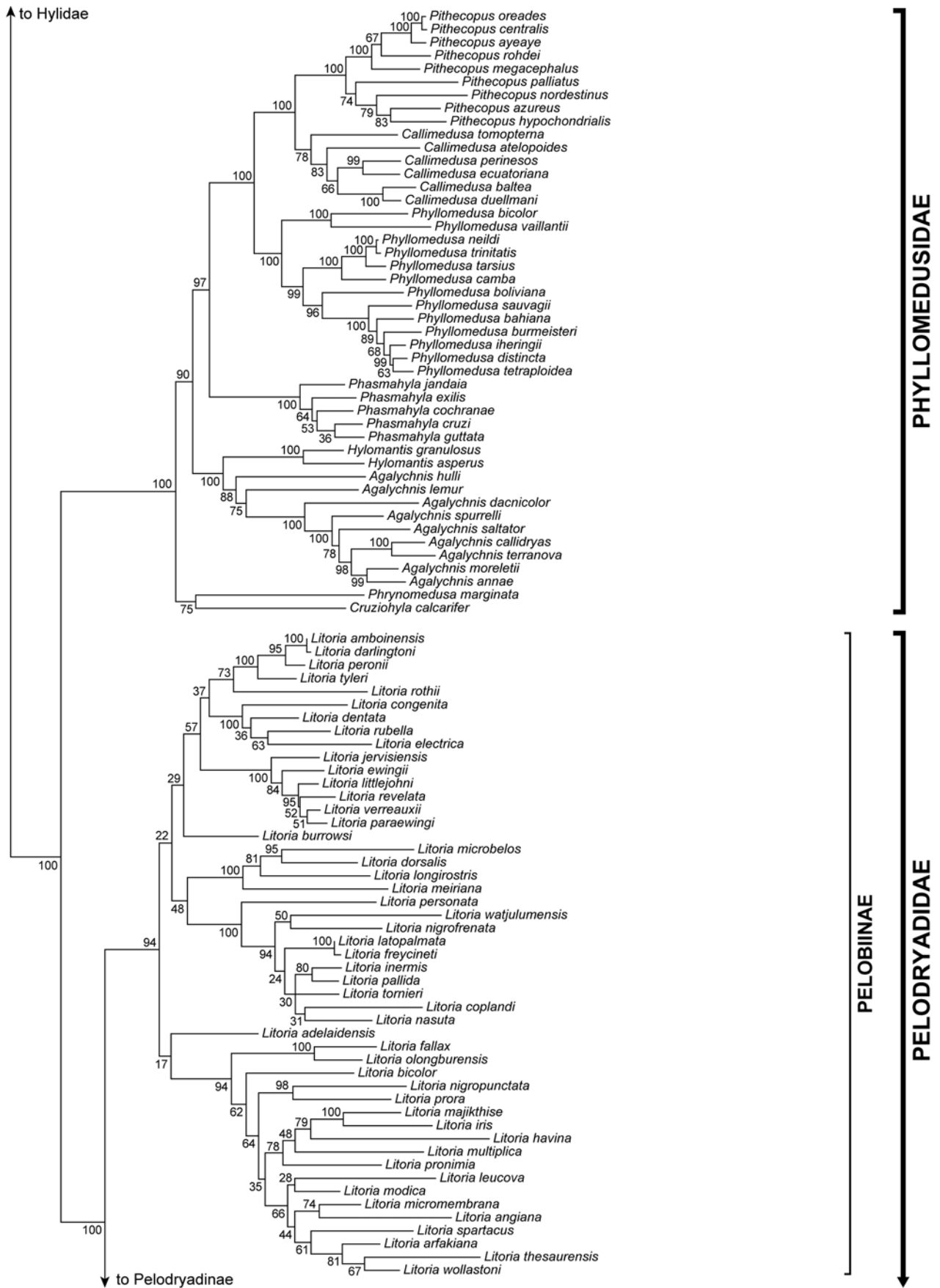


FIGURE 4. (Continued)



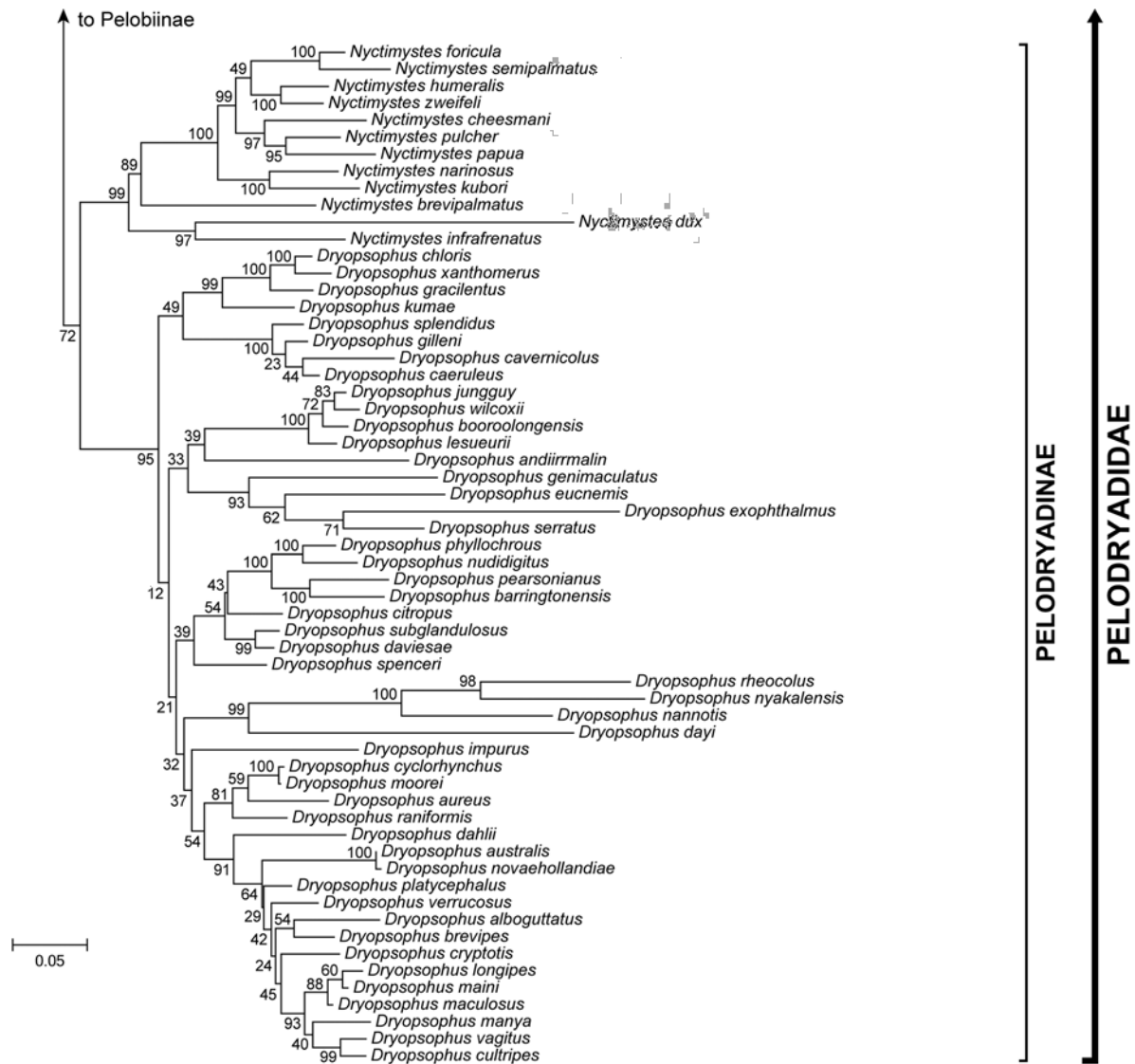


FIGURE 4. (Continued)

### Subfamily Hyalinae Rafinesque, 1815

Hylarinia Rafinesque, 1815:78. Type genus: *Hylaria* Rafinesque, 1814 (an unjustified emendation of *Hyla* Laurenti, 1768 [*vide* Frost 2015]).

**Definition.** As for the family.

**Content.** Eighteen genera and 165 species.

**Distribution.** North America southward throughout Mexico and Central America, and barely entering South America. The subfamily also occurs throughout much of temperate Eurasia, Japan, and extreme northern Africa.

**Etymology.** The family name is based on the generic name *Hyla* that is derived from the vocative of *Hylas*, the companion of Hercules, in Greek mythology.

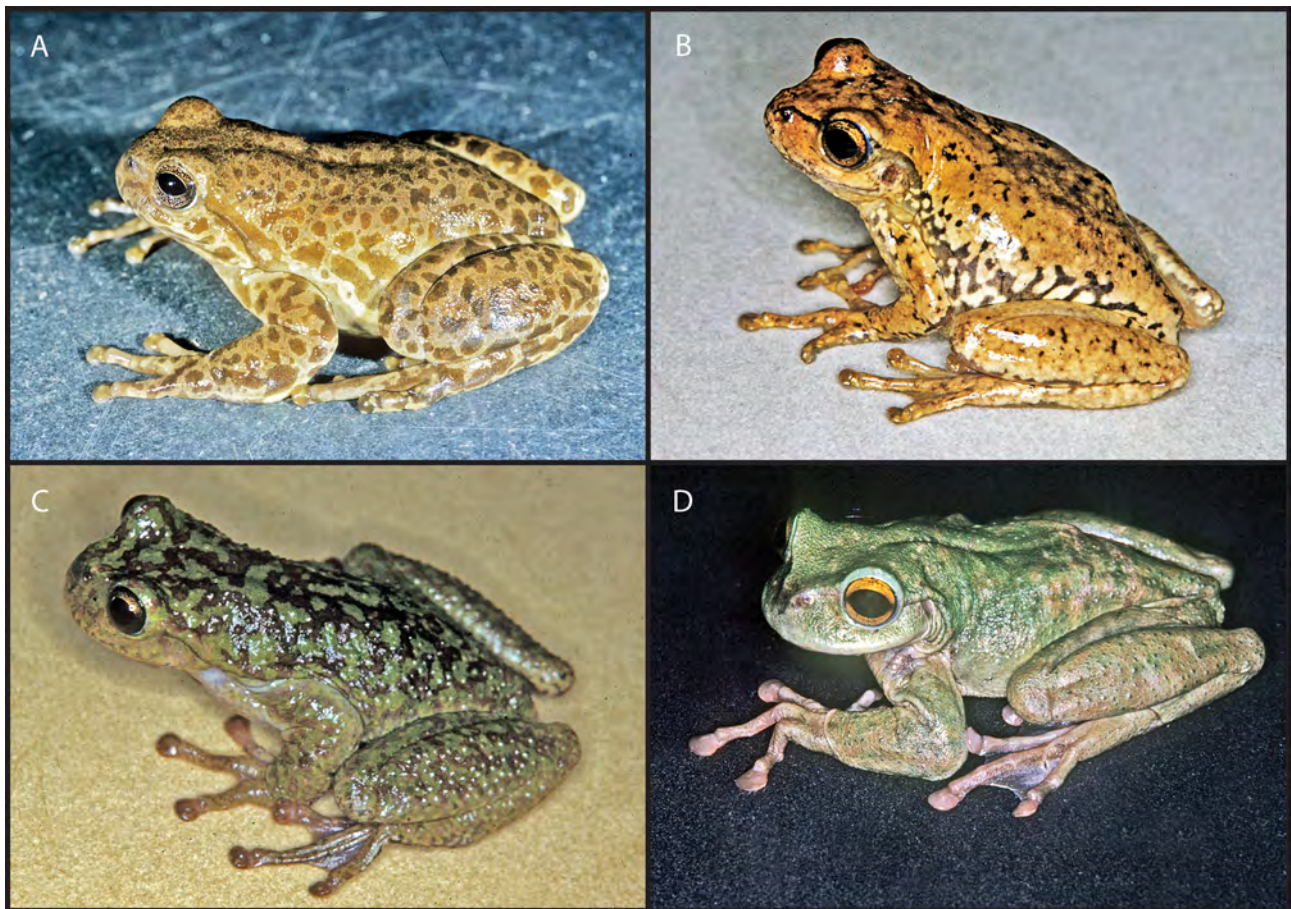
**Remarks.** The monophyly of all of the Nearctic, Mexican, and Central American genera of hylines is strongly supported (Fig. 2). This clade contains 18 genera and 165 species. Except for the Central American *Smilisca phaeota*, *sila*, and *sordida*, the ranges of which extend into northwestern South America, no species in this clade extends into that continent.

## *Sarcohyla* new genus

*Sarcohyla*. Type species: *Cauphias crassus* Brocchi, 1877:130.

**Definition.** Moderate to large frogs having thick, glandular skin and enlarged prepollex without a projecting spine (Figs. 5A and B), and the alary process of the premaxilla not bifurcate posteriorly.

**Content.** Twenty-four species: *Sarcohyla ameibothalame* (Canseco-Márquez, Mendelson, and Gutiérrez-Mayén), *arborescandens* (Taylor), *bistincta* (Cope), *calthula* (Ustach, Mendelson, McDiarmid, and Campbell), *calvicollina*\* (Toal), *celata*\* (Toal and Mendelson), *cembra*\* (Caldwell), *charadricola*\* (Duellman), *chryses*\* (Adler), *crassa*\* (Brocchi), *cyanomma*\* (Caldwell), *cyclada* (Campbell and Duellman), *ephemera*\* (Meik, Canseco-Márquez, Smith, and Campbell), *hazela*\* (Taylor), *labedactyla*\* (Mendelson and Toal), *miahuatlanensis*\* (Meik, Canseco-Márquez, Smith, and Campbell), *mykter*\* (Adler), *pachyderma*\* (Taylor), *pentheter* (Adler), *psarosema*\* (Campbell and Duellman), *robertsorum*\* (Taylor), *sabrina*\* (Caldwell), *siopela* (Duellman), and *thorectes*\* (Adler); all names are new combinations.



**FIGURE 5.** **A.** *Sarcohyla crassa*, KU 148699, 1.9 km S El Estudiante, 1850 m, Oaxaca, Mexico. J. A. Campbell. **B.** *Sarcohyla bistincta*, UMMZ 119193, Dos Aguas, 2100 m, Michoacán, Mexico. W. E. Duellman. **C.** *Plectrohyla guatemalensis*, KU 58834, Panajachel, 1600 m, Sololá, Guatemala. W. E. Duellman. **D.** *Plectrohyla teuchestes*, KU 58831, Finca Los Alpes, 1000 m, Alta Verapaz, Guatemala. W. E. Duellman

**Distribution.** Highlands of Mexico west of the Isthmus of Tehuantepec northward to Durango and San Luis Potosí.

**Etymology.** The generic name is derived from the Greek *sarkodes* meaning fleshy in combination with *Hylas* of Greek mythology. The name refers to the thick, glandular skin characteristic of most of the species in the genus. The gender is feminine.

**Remarks.** For the most part this genus is the *Hyla bistincta* and *Hyla arborescandens* groups of Duellman (2001). The phylogenetic tree by Faivovich *et al.* (2005) included only five species in the *Hyla bistincta* Group,

which they showed as the sister clade to *Plectrohyla*. Faivovich *et al.* (2005:104) stated: “Technically our results are certainly compatible with the recognition of a separate genus for the members of the *H. bistincta* group and the few species from other groups associated with them. However, we are particularly concerned that the present, clean separation between *Plectrohyla* and these exemplars probably will not hold when more species of the two clades, particularly from the *H. bistincta* group, are added.” Contrary to their concern, additional species (Fig. 4) showed a complete separation of *Plectrohyla* from the “*Hyla bistincta* Group” recognized herein as the genus *Sarcohyla*.

### ***Plectrohyla* Brocchi, 1877**

*Plectrohyla* Brocchi, 1877:92. Type species: *Plectrohyla guatemalensis* Brocchi, 1877, by original designation.

**Definition.** Moderate to large frogs having thick, glandular skin and enlarged prepollex with a projecting spine (Figs. 5C and D), and the alary process of the premaxilla bifurcate posteriorly.

**Content.** Eighteen species: *Plectrohyla acanthodes*\* Duellman and Campbell, *avia*\* Stuart, *chrysopleura* Wilson, McCranie, and Cruz-Diaz, *dasyopus*\* McCranie and Wilson, *exquisita*\* McCranie and Wilson, *glandulosa* (Boulenger), *guatemalensis* Brocchi, *hartwegi*\* Duellman, *ixil*\* Stuart, *lacertosa*\* Bumzahem and Smith, *matudai* Hartweg, *pokomchi*\* Duellman and Campbell, *psiloderma*\* McCranie and Wilson, *pycnochila*\* Rabb, *quecchi*\* Stuart, *sagorum*\* Hartweg, *tecunumani*\* Duellman and Campbell, and *teuchestes*\* Duellman and Campbell.

**Distribution.** Northern Central American highlands from Chiapas, Mexico, eastward through Guatemala and northern El Salvador to central and northern Honduras.

**Etymology.** The generic name is derived from the Greek *plektron* meaning spur and *Hylas* of Greek mythology. The name refers to the prepollical spines characteristic of members of the genus.

**Remarks.** Molecular data are available for only four of the 18 species.

### ***Bromeliohyla*, *Duellmanohyla*, and *Ptychohyla***

One clade contains one species of *Bromeliohyla* and seven species of *Ptychohyla*. *Bromeliohyla bromeliacia* (Taylor) is the well-supported sister of the clade of *Ptychohyla salvadorensis* (Mertens) plus three species of *Duellmanohyla*. Moreover, *Ptychohyla spinipollex* Schmidt is sister to that clade of five species. Although not notably different as adults, except in coloration (Fig. 6), egg deposition sites and tadpoles of the species in these three genera are distinctly different (Campbell & Smith 1992; Duellman 2001). *Bromeliohyla* is an inhabitant of arboreal bromeliads where eggs are deposited in water in the axils of the leaves, and tadpoles have small ventral oral discs with a LTRF of 2/3–2/5, long tooth rows, a depressed body, massive caudal musculature, and shallow fins. *Duellmanohyla* breeds in streams, where tadpoles develop in quiet pools and have a large, pendant oral discs with a LTRF of 2/2 or 2/3, short tooth rows, a rounded body, well-developed caudal musculature, and fins nearly as high as the caudal musculature at midlength of the tail. *Ptychohyla* also breeds in streams, where tadpoles develop in riffles and have large ventral oral discs with a LTRF of 3/6–6/9, long tooth rows, a rounded body, well-developed caudal musculature, and fins nearly as high as the caudal musculature at midlength of the tail. The tadpole of *Ptychohyla salvadorensis* has a large ventral mouth with 2/3–2/5, entirely unlike tadpoles of *Duellmanohyla* (McCranie and Wilson 2002).

Low nodal support values in the clade containing *Bromeliohyla*, *Duellmanohyla*, and *Ptychohyla salvadorensis*, indicate that the existing molecular data are unable to resolve their relationships. Although the deep nesting of *P. salvadorensis* in this clade suggests that *Ptychohyla* is paraphyletic, more molecular data are needed to corroborate this. Therefore, we retain this species in the genus *Ptychohyla*.

### ***Rheohyla* new genus**

*Rheohyla*. Type species: *Hyla miotympanum* Cope, 1863:47.

**Definition.** Medium-sized treefrog (SVL in females to 51 mm) with smooth skin on dorsum, fingers about one-

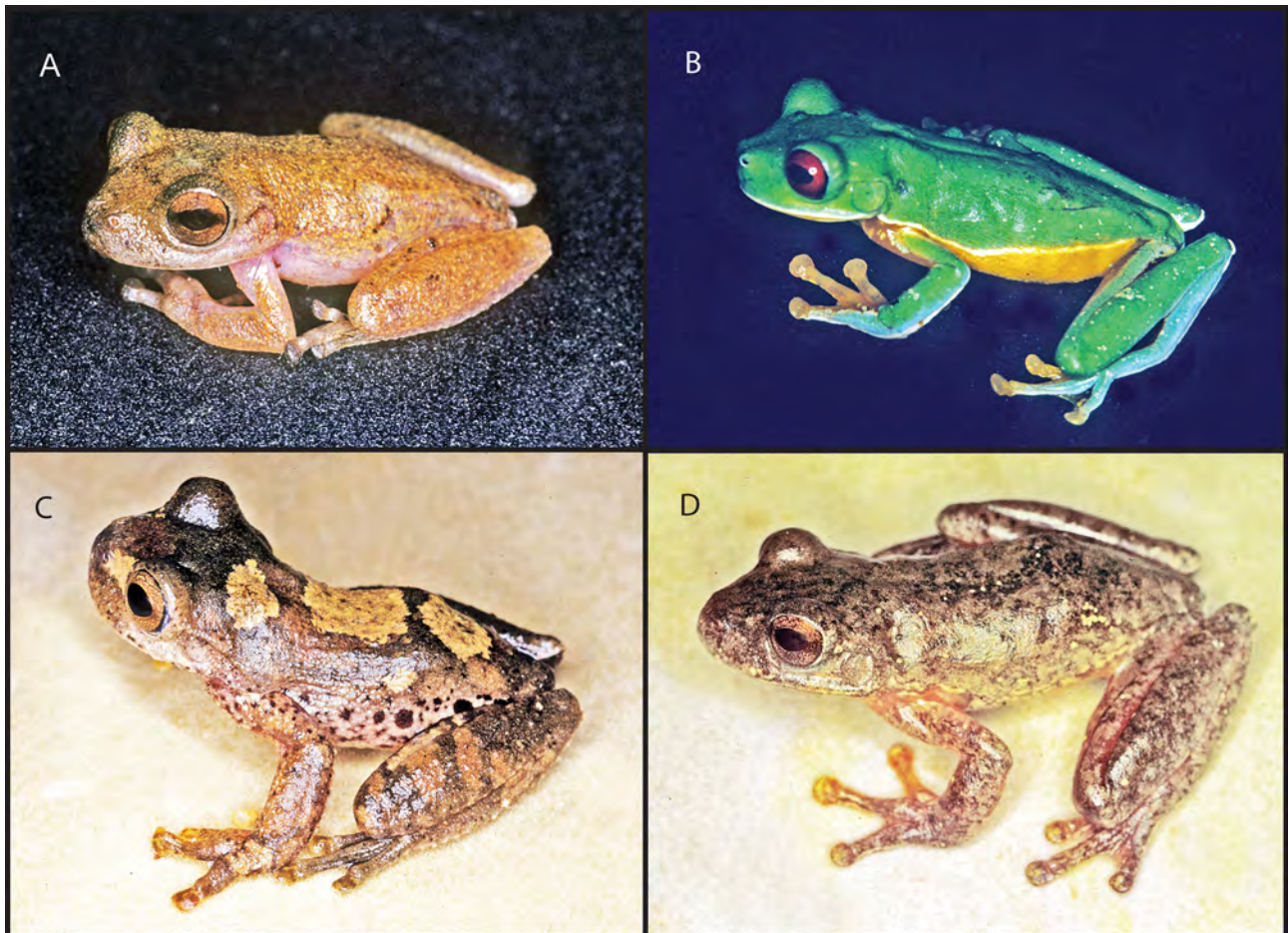


third webbed and toes about three-fourths webbed. Dermal fringes absent on outer edges of forelimbs and feet; prepollex not enlarged (Fig. 7A). Tadpoles being generalized stream inhabitants with a LTRF 2/3.

**Content.** Monotypic; *Rheohyla miotympanum* new combination.

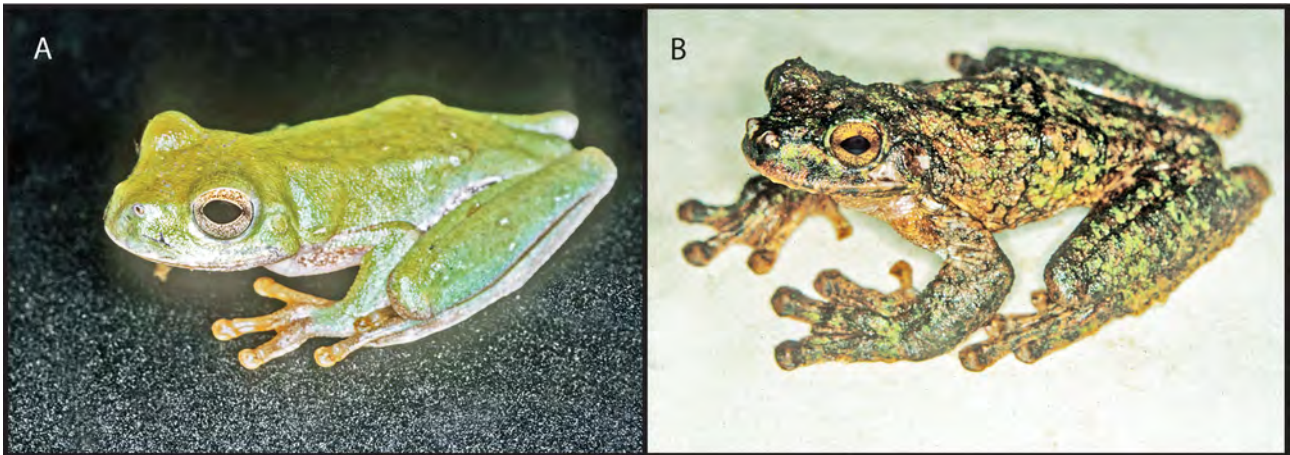
**Distribution.** Eastern Mexico—Cloud forests at elevations of 1000–2800 m on the Atlantic slopes of the Sierra Madre Oriental; disjunct populations in Sierra de Los Tuxtlas and on the northern slopes of the highlands of Chiapas.

**Etymology.** The generic name is a combination of the Greek *rheos* meaning stream and *Hylas* of Greek mythology. The name refers to the breeding site of the species. The gender is feminine.



**FIGURE 6.** **A.** *Bromeliohyla bromeliacia*, KU 57249, Finca Chicoyou, 980 m, Alta Verapaz, Guatemala. **B.** *Duellmanohyla uranochroa*, KU 101727, North slope Cerro Pando, 1450 m, Bocas del Toro, Panama. **C.** *Ptychohyla hypomykter*, KU 58053, Finca Los Alpes, 1000 m, Alta Verapaz, Guatemala. **D.** *Ptychohyla salvadorensis*, KU 103256, West slope Cerro Uyuca, 1650 m, Francisco-Morazán, Honduras. All by W. E. Duellman.

**Remarks.** The molecular phylogenetic tree produced by Faivovich *et al.* (2005) contained one clade with two taxa—*Hyla miotympanum* and *H. miliaria* (Cope); they recognized this clade as a new genus *Ecnomiohyla*. However, these authors noted the morphological differences between the species, a factor emphasized by Mendelson *et al.* (2008), who eliminated *E. miotympanum* from their discussion of species of *Ecnomiohyla*. The analysis of the 16S rRNA gene by Batista *et al.* (2014) resulted in a tree with seven species of *Ecnomiohyla* with *E. miotympanum* well separated from the other species. In our tree (Fig. 4) there are three species of *Ecnomiohyla* plus a well-supported (87%) long branch to *Rheohyla miotympanum*. In contrast to the canopy-dwelling species of *Ecnomiohyla* that breeds in tree holes, the sister genus, *Rheohyla*, breeds in comparatively slow moving streams, whereas members of the genera *Charadrohyla*, *Plectrohyla*, and *Sarcohyla* breed in cascading streams. The tadpoles of *Rheohyla* do not have enlarged ventral mouths, whereas species in the other three genera have tadpoles with enlarged ventral mouths with multiple rows of labial papillae.



**FIGURE 7. A.** *Rheohyla miotympanum*, KU 100965. Salto Cola de Caballo, 710 m, Nuevo León, Mexico. **B.** *Ecnomiohyla miliaria*, KU 101610, Finca Santa Clara, 1200 m, Chiriquí, Panama. Both by W. E. Duellman.

### *Ecnomiohyla* Faivovich, Haddad, Garcia, Frost, Campbell, and Wheeler, 2005

*Ecnomiohyla* Faivovich, Haddad, Garcia, Frost, Campbell, and Wheeler, 2005:100. Type species: *Hypsiboas miliaris* Cope, 1886, by original designation.

**Definition.** Large treefrogs (SVL in males to 110 mm) with dermal fringes on the outer edges of the limbs, extensive webbing on the hands and feet, and an enlarged prepollex (Fig. 7B). Tadpoles with a LTRF of 2/3 and developing in water in tree holes.

**Content.** Twelve species: *Ecnomiohyla bailarina*\* Batista, Hertz, Mebert, Köhler, Lotzkat, Ponce, and Vesely, *echinata*\* (Duellman), *fimbrimembra*\* (Taylor), *miliaria* (Cope), *minera* (Wilson, McCranie, and Williams), *phantasmagoria*\* (Dunn), *raborum* Mendelson, Savage, Griffith, Ross, Kubicki, and Gagliardo, *salvaje*\* (Wilson, McCranie, and Williams), *sukia*\* Savage and Kubicki, *thysanota*\* (Duellman), *valancifer*\* (Firschein and Smith), and *veraguensis*\* Batista, Hertz, Mebert, Köhler, Lotzkat, Ponce, and Vesely.

**Distribution.** Southern Mexico through Central America to western Colombia and northwestern Ecuador.

**Etymology.** According to Faivovich *et al.* (2005:100), “From the Greek, *ecnomios*, meaning marvelous, unusual ...” The gender is feminine.

**Remarks.** Mendelson *et al.* (2008), Savage and Kubicki (2010), and Batista *et al.* (2014) have expanded our knowledge of this genus, which still contains species known only from their holotypes (e.g., *Ecnomiohyla echinata* and *E. thysanota*). For more than half of a century, *E. phantasmagoria* has been known only from the holotype from the Río Cauca in Colombia, but recently was discovered in the Provincia de Esmeraldas in Ecuador (Ortega-Andrade *et al.* 2010).

Our tree (Fig. 4) shows *Ecnomiohyla raborum* as the sister species of *E. malaria* + *E. minera*. The most extensive molecular phylogenetic tree, based only on the 16S rRNA mitochondrial gene, of *Ecnomiohyla* contains six species (Batista *et al.* 2014). In their maximum likelihood consensus tree, two well-supported clades are evident. One contains *E. fimbrimembra* as the sister species of *E. raborum* + *E. bailarina*; the second clade has *E. miliaria* as the sister species of *E. sukia* + *E. veraguensis*.

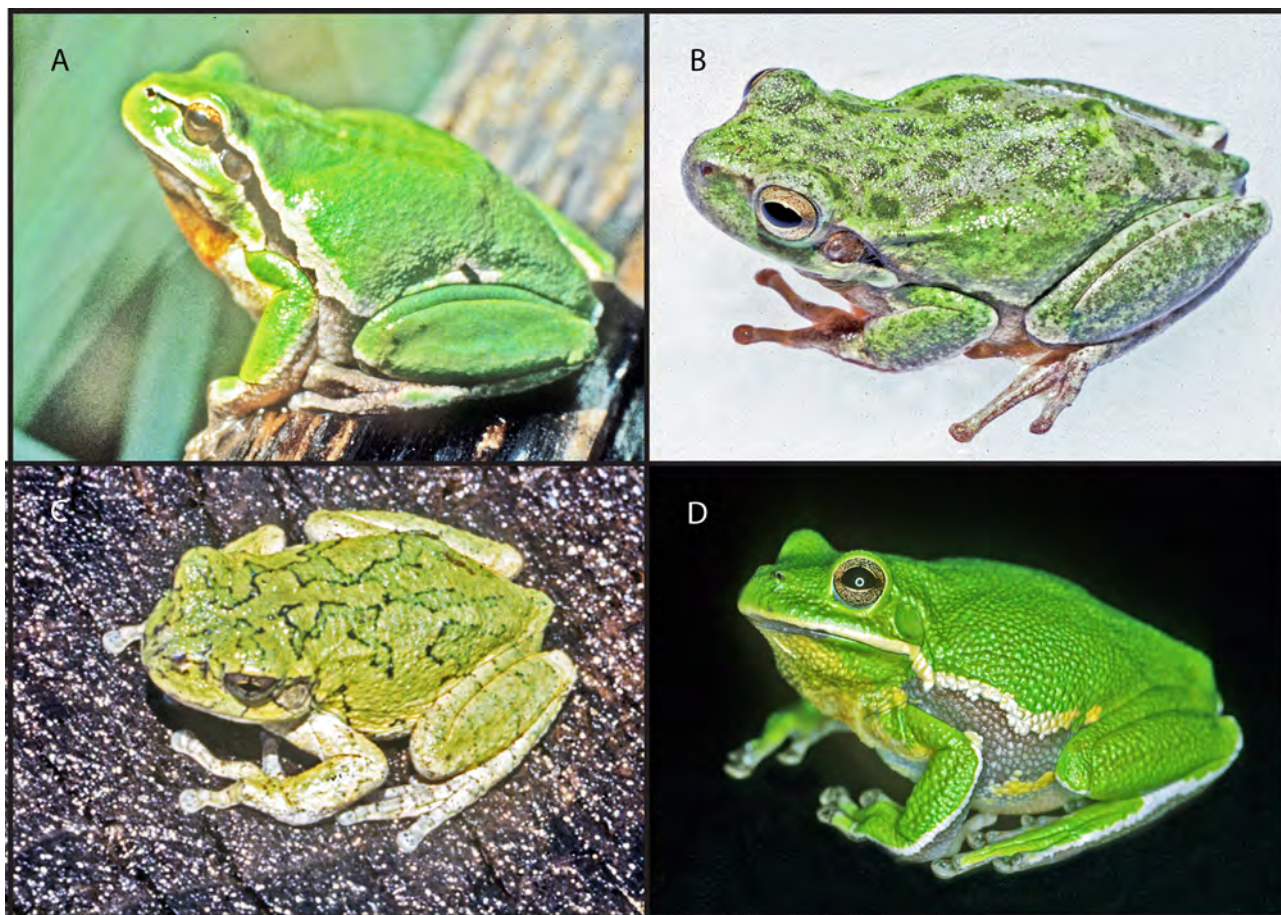
Mendelson *et al.* (2008) emphasized that the Amazonian “*Hyla tuberculosa*” Boulenger is not a member of *Ecnomiohyla* and should be designated *incertae sedis*. Savage and Kubicki (2010) regarded the placement of *tuberculosa* in *Ecnomiohyla* as problematic because it lacked the synapomorphic morphological characters, principally an enlarged prepollex with keratinous spines, of the genus. We await molecular data for this species but herein we consider “*Hyla tuberculosa*” to be a member of the South American catch-all genus, *Hypsiboas*.



## *Hyla Laurenti, 1768*

*Hyla Laurenti, 1768:32*. Type species: *Hyla viridis* Laurenti, 1768 (= *Rana arborea* Linnaeus, 1758) by subsequent designation (Stejneger, 1907:75).

**Definition.** Moderate-sized, arboreal, primarily green frogs with expanded terminal discs on the digits (Figs. 8A and B); no definitive morphological features are known to differentiate *Hyla* from *Dryophytes*.



**FIGURE 8.** **A.** *Hyla arborea*, Tübingen, Baden Württemberg, Germany. **B.** *Hyla sarda*, KU 207373, 2.4 km ESE Musei (near Domusnovas), Cagliari, Sardinia, Italy. **C.** *Dryophytes versicolor*, near Greenville, Darke County, Ohio, USA. **D.** *Dryophytes gratiosus*, KU 109911, Woodland, East Feliciana Parish, Louisiana, USA. All by W. E. Duellman.

**Content.** Sixteen species: *Hyla annectans* (Jerdon), *arborea* (Linnaeus), *chinensis* Günther, *felixarabica* Gvoždík, Kotlík & Moravec, *hallowellii*\* Thompson, *heinzsteinitzi*\* Grach, Plesser & Werner, *intermedia* Boulenger, *meridionalis* Boettger, *molleri* Bedriaga, *orientalis* Bedriaga, *sanchiangensis*\* Pope, *sarda* (De Betta), *savignyi* Audouin, *simplex* Boettger, *tsinlingensis* Liu & Hu, and *zhaopingensis*\* Tang & Zhang.

**Distribution.** Eurasia south of the Baltic Sea eastward with a hiatus between eastern Russia and the Oriental Region from northeastern India to Vietnam, China, and Hainan Island; Sardinia and Corsica, extreme north Africa from Morocco to Tunisia; northeastern Egypt, Turkey, and southern Arabian Peninsula.

**Etymology.** The generic name is derived from *Hylas*, the companion of Hercules, in Greek mythology. The gender is feminine.

**Remarks.** In a tree based on parsimony analysis (Faivovich *et al.* 2005), three Eurasian species (*Hyla annectans*, *arborea*, and *savignyi*) were in a clade sister of a large clade containing the 11 North American species of *Hyla*, plus the Asian *Hyla japonica*. Bayesian and maximum likelihood analyses of a larger number of species (Hua *et al.* 2009) resulted in the recognition of two strongly supported clades—one with nine Eurasian species and another with 13 North American species and three East Asian species—*Hyla immaculata*, *japonica*, and *suweonensis*. Our analysis shows strong support for two clades of Nearctic hylids. One of these is recognized

herein as the genus *Hyla*, restricted to the Old World; the other, herein recognized as the genus *Dryophytes*, is primarily New World but with three species in Asia. These genera are separated geographically.

### ***Dryophytes* Fitzinger, 1843**

*Dryophytes* Fitzinger, 1843:31. Type species: *Hyla versicolor* LeConte, 1825, by original designation.

**Definition.** Moderate-sized, arboreal, primarily green frogs with expanded terminal discs on the digits (Figs. 8C and D); no definitive morphological features are known to separate *Dryophytes* from *Hyla*.

**Content.** Nineteen species: *Dryophytes andersonii* (Baird), *arboricola*\* (Taylor), *arenicolor* (Cope), *avivocus* (Viosca), *bocourti*\* (Mocquard), *chrysofelis* (Cope), *cinereus* (Schneider), *euphorbiaceus* (Günther), *eximius* (Baird), *femoralis* (Daudin), *gratiosus* (LeConte), *immaculatus* Boettger, *japonicus* (Günther), *plicatus* (Brocchi), *squirellus* (Daudin), *suweonensis* (Kuramoto), *versicolor* (LeConte), *walkeri* (Stuart), and *wrightorum* (Taylor); all new combinations.

**Distribution.** North America east of the Sierra Nevada southward from extreme southern Canada to the Gulf of Mexico and on the Mexican Plateau southward to Oaxaca, plus the highlands of Chiapas, Mexico, and adjacent Guatemala. Nearctic Region in far eastern Russia, Korean Peninsula, Japan, eastern China, and Ryukyu Island

**Etymology.** The generic name is derived from the Greek *dryos* meaning tree and the Greek *phytes* meaning plant. This rather redundant epithet presumably refers to the arboreal habits of these frogs. The gender is masculine.

**Remarks.** The inclusion of Asian and North American taxa in the same genus is like the biogeography of *Rana*, a genus with 41 species in Eurasia and seven species in western North America (Frost 2015).

Sixteen species of *Dryophytes* occur in eastern North America, and three species are found in eastern temperate Asia. We purposefully excluded sequences in Genbank (FJ226937, FJ226830) identified as “*Hyla heinzsteinitzi*” because they were labeled incorrectly. They are *Dryophytes japonica*, introduced to Israel, as was determined by the authors of the study that generated the sequences (Stöck *et al.* 2008).

In the trees produced by Faivovich *et al.* (2005) and Hua *et al.* (2009), a sample identified as “*Hyla*” *walkeri*, a species restricted to the highlands of western Guatemala and adjacent Mexico, is the sister species of “*Hyla*” *immaculata*, a species occurring in eastern China. Hua *et al.* (2009:256) examined the voucher specimen of “*Hyla*” *walkeri* used by Faivovich *et al.* (2005); they noted that this specimen (AMNH-A 168406) came from the pet trade, has no locality data, and closely resembled specimens of “*Hyla*” *immaculata* from China. The true “*Hyla*” *walkeri* sample included in Hua *et al.* (2009) falls out in a clade of five Mexican species, all members of the *Hyla eximia* Group recognized by Duellman (2001). In our analysis, we included only those GenBank sequences positively identified as “*Hyla*” *walkeri*, from Hua *et al.* (2009) and Lemmon *et al.* (2007). (Pyron and Wiens [2011] included sequences from both the pet-trade “*walkeri*” sample from Faivovich *et al.* [2005] and the true *walkeri* sample from Hua *et al.* [2009] as a single chimeric taxon.) Thus in our analysis (Fig. 4), *Dryophytes walkeri* is a member of the *Hyla eximia* Group recognized by Duellman (2001).

### **Subfamily Pseudinae Fitzinger, 1843**

Pseudinae Fitzinger, 1843:33. Type genus: *Pseudis* Wagler, 1930, by original designation.

**Definition.** Aquatic and semi-aquatic frogs with elongate (usually mineralized) intercalary elements between the distal and penultimate phalanges. Chromosome complement  $2n = 24$ , but  $2n = 22$  in *Scarthyla goinorum* (Bokermann) and  $2n = 28$  in *Pseudis cardosoi* (Kwet).

**Content.** Three genera and 13 species.

**Distribution.** Tropical and subtropical South America east of the Andes, including Trinidad, southward to Uruguay, Paraguay, and northern Argentina.

**Etymology.** The subfamily name is that of the type genus, *Pseudis*, which is from the Greek, *pseudos*, meaning lie.

**Remarks.** The analysis of molecular data by Faivovich *et al.* (2005) showed *Scarthyla goinorum* Bokermann

to be the sister taxon of two species each of *Lysapsus* + *Pseudis*. Our analysis of four species of *Lysapsus*, six of *Pseudis*, and *Scarthyla goinorum* shows the same arrangement with 100% support of the monophyly of the three lineages (Fig. 4).

### Subfamily Dendropsophinae Fitzinger, 1843

Dendropsophini Fitzinger, 1843:32. Type genus: *Dendropsophus* Fitzinger, 1843, by original designation.

**Definition.** Small to medium-sized primarily arboreal frogs; quadratojugal reduced or absent; reduction LTRF for 1/2 to 0/0 in larvae. Chromosome complement  $2n = 30$  (except in *Xenohyla*).

**Content.** Two genera with 97 species.

**Distribution.** Tropical southern Mexico through Central America and tropical and subtropical South America, including Trinidad, southward to northern Argentina and Uruguay.

**Etymology.** The familial and generic names are derived from the Greek *Dendron* meaning tree and the Greek *psophos* meaning sound or noise. The name refers to the vocalizations of these frogs originating in trees.

**Remarks.** Dendropsophinae is the sister taxon of Pseudinae in the phylogenetic analysis of molecular data. The two subfamilies share no derived morphological characters. The analysis also shows that *Xenohyla truncata* (Izecksohn) (Fig. 9A), an inhabitant of terrestrial bromeliads in the restinga of southeastern Brazil, is the sister species of *Dendropsophus* (Fig. 4). However, *Xenohyla* has  $2n = 24$  chromosomes (Suárez *et al.* 2013), whereas all *Dendropsophus* for which the chromosome number is known have  $2n = 30$  chromosomes.

Our phylogenetic analysis includes only about half (49) of the 95 species of *Dendropsophus*. Within the tree (Fig. 4), four groups are strongly supported—*D. marmoratus* Group (3 species; Fig. 9B), *D. labialis* Group (3 species; Fig. 9C), *D. leucophyllatus* Group (6 species; Fig. 9D) and *D. parviceps* Group (4 species; Fig. 9E). These correspond approximately with the continuous reduction on larval mouthparts as shown by Duellman and Trueb (1983). The Central American (*D. microcephalus*, *phlebodes*, *sartori*, and *robertmertensi*; Fig. 9F) is weakly supported. Further recognition of distinct clades within the burdensomely large genus *Dendropsophus* awaits rigorous analysis of molecular data for many more species.

### Subfamily Lophohylineae Miranda-Ribeiro, 1926

Lophiohylineae Miranda-Ribeiro, 1926:64. Type genus *Lophohyla* Miranda-Ribeiro, 1923 = *Phyllodytes* Wagler, 1830. [As noted by Fouquette and Dubois, 2014:368, Lophiohylineae is an incorrect spelling of *Lophohyla* Miranda Ribeiro, 1923:5.]

**Definition.** Most members of this subfamily (except *Phyllodytes*, *Phytotriades*, and *Tepuihyla*) are casque-headed. Chromosome complement in most genera  $2n = 24$ , but  $2n = 22$  in *Phyllodytes*, 28 in *Osteopilus wilderi* (Dunn), and 34 in *O. ocellatus* (Linnaeus).

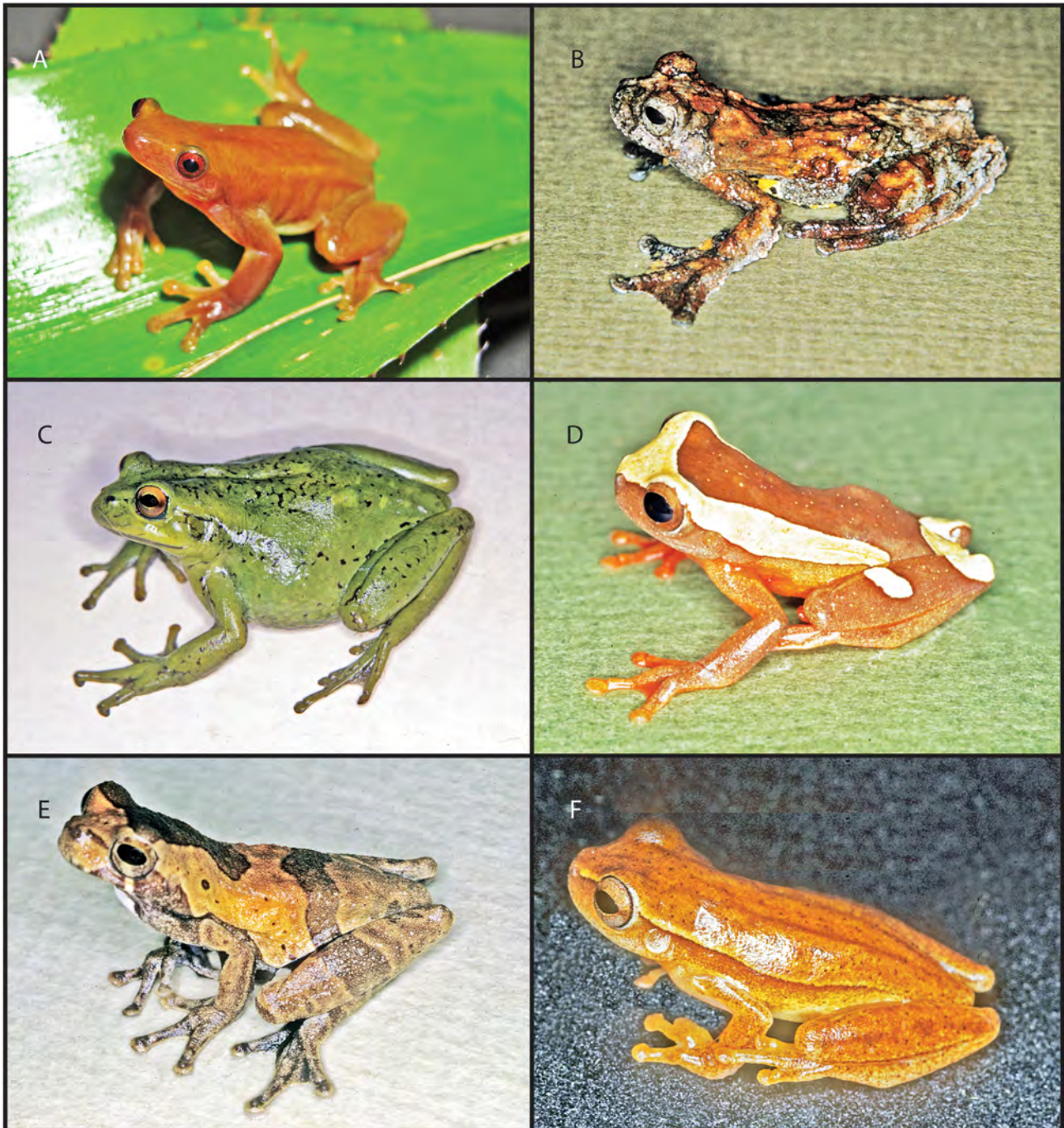
**Content.** Twelve genera and 76 species.

**Distribution.** Tropical and subtropical South America to Uruguay and northern Argentina, including the Pacific lowlands to northwestern Peru and the Guiana Highlands (but not the Andes), Greater Antilles, Bahama Islands, and peninsular Florida, USA; one species, *Trachycephalus typhonius* (Linnaeus), extending northward into Mexico.

**Etymology.** The familial and generic names are derived from the Greek *lophos* meaning mane or crest and from *Hylas* in Greek mythology. The gender is feminine.

**Remarks.** This subfamily has a 100% support value. Distinctive cranial characters help to define the casque-headed genera *Aparasphenodon*, *Argenteohyla*, *Corythomantis*, *Dryaderces*, *Itapotihyla*, *Nyctimantis*, and *Trachycephalus* (Trueb 1970).





**FIGURE 9.** **A.** *Xenohyla truncata*, MNRJ 75594, Restinga da Maricá, 3 m, Rio de Janeiro, Brazil. J. Pombal, Jr. **B–F.** Representatives of the major clades in *Dendropsophus*: **B.** *D. marmoratus*, KU 126436, Lago Agrio, 320 m, Sucumbíos, Ecuador. **C.** *D. labialis*, KU 124867, Jardín del Recuerdo, 2580 m, Cundinamarca, Colombia. **D.** *D. leucophyllatus*, KU 128434, IPEAN, 10 m. Belém, Pará, Brazil. **E.** *D. parviceps*, KU 126476, Santa Cecilia, 340 m, Sucumbíos, Ecuador. **F.** *D. microcephalus*, KU 64591, Palmar Sur, 15 m, Puntarenas, Costa Rica, All by W. E. Duellman.

### Subfamily Scinaxinae New Subfamily

Scinaxinae. Type genus: *Scinax* Wagler, 1830.

**Definition.** Small to medium-sized frogs with sacral diapophyses not expanded; in dorsal view, snout acutely rounded to acute with projecting proboscis.

**Content.** Four genera and 126 species.

**Distribution.** Mostly South America from Uruguay, northern Argentina, and northwestern Peru northward through Central America to southern and eastern Mexico; Islands of Tobago, Trinidad, and Saint Lucia.

**Etymology.** The familial name is derived from the Greek *skinos* meaning quick or nimble, an appropriate name for these agile frogs.

**Remarks.** The support value is high (97%) for the cluster of three of the genera (*Julianus*, *Ololygon*, and *Scinax*), but the placement of *Sphaenorhynchus* as the sister taxon of the others is low (49%); thus, the relationships of *Sphaenorhynchus* are equivocal.

### ***Sphaenorhynchus* Tschudi, 1838**

*Sphaenorhynchus* Tschudi, 1838:71. Type species: *Hyla lactea* Daudin, 1802, by original designation.

**Definition.** Small to medium-sized green treefrogs with rounded discs on the fingers and toes, both of which are extensively webbed.

**Content.** Fourteen species: *Sphaenorhynchus botocudo*\* Caramaschi, Albeida & Gasparini, *bromelicola*\* Bokermann, *caramaschii*\* Toledo, Garcia, Lingnau & Haddad, *carneus*\* (Cope), *dorisae* (Goin), *lacteus* (Daudin), *mirim*\* Caramaschi, Albeida & Gasparini, *orophilus* (Lutz & Lutz), *palustris*\* Bokermann, *pauloalvini*\* Bokermann, *planicola*\* (Lutz & Lutz), *platycephalus*\* (Werner), *prasinus*\* Bokermann, and *surdus*\* (Cochran).

**Distribution.** South America east of the Andes southward to Bolivia and southeastern Brazil; Trinidad.

**Etymology.** The generic name is derived from the Greek *sphenos* meaning wedge and the Greek *rhynchos* meaning snout. The name applies to the flattened snouts of members of this genus.

**Remarks.** Molecular data are available only for the three Amazonian species that are supported at 100% for their monophyly, but data are missing for the 11 species in eastern Brazil.

### ***Ololygon* Fitzinger, 1843**

*Ololygon* Fitzinger, 1843:31. Type species: *Hyla strigilata* Spix, 1824, by original designation.

**Definition.** Small to medium-sized frogs with slightly truncate discs on fingers and toes, webbing reduced between fingers and absent between Fingers I and II (Figs. 10A and B); venter immaculate, eggs deposited in streams or terrestrial bromeliads.

**Content.** Forty-six species: *Ololygon agilis*\* (Cruz & Peixoto), *albicans*\* (Bokermann), *alcetraz*\* (Lutz), *angrensis*\* (Lutz), *arduoa*\* (Peixoto), *argyreornata*\* (Miranda-Ribeiro), *ariadne*\* (Bokermann), *aromothyella*\* (Faivovich), *atrata*\* (Peixoto), *aurata*\* (Wied-Neuwied), *belloni*\* (Faivovich, Gasparini & Haddad), *berthae* (Barrio), *brieni*\* (De Witte), *canastrensis*\* (Cardoso & Haddad), *carnevallii*\* Caramaschi & Kisteumacher, *catharinae* (Boulenger), *centralis*\* (Pombal & Bastos), *cosenzai*\* (Lacerda, Peixoto & Feio), *faivovichii* (Brasileiro, Oyamaguchi & Haddad), *flavoguttata*\* (Lutz & Lutz), *heyeri*\* Peixoto & Weygoldt, *hiemalis*\* (Haddad & Pombal), *humilis*\* (Lutz & Lutz), *insperata*\* (Silva & Alves-Silva), *jureia*\* (Pombal & Gordo), *kautskyi*\* Carvalho-e-Silva & Peixoto, *littoralis*\* (Pombal & Gordo), *littorea*\* Peixoto, *longilinea*\* (Lutz), *luizotavioi*\* Caramaschi & Kisteumacher, *machadoi*\* (Bokermann & Sazima), *melloi*\* Peixoto, *muriciensis*\* (Cruz, Nunes & Lima), *obtriangulata* (Lutz), *peixotoi* (Brasileiro, Haddad, Sawaya & Martins), *perpusilla* (Lutz & Lutz), *pombali*\* (Lourenço, Carvalho, Baêta, Pezzuti & Leite), *ranki*\* (Andrade & Cardoso), *rizibilis*\* (Bokermann), *skaios*\* (Pombal, Carvalho, Canelos & Bastos), *skuki*\* (Lima, Cruz & Azevedo), *strigilata*\* (Spix), *trapicheiroi*\* (Lutz & Lutz), *tripui*\* (Lourenço, Nascimento & Pires), *tupinamba*\* (Silva & Alves-Silva), and *v-signata*\* (Lutz).

**Distribution.** Atlantic Coastal Forest of eastern Brazil, extending southward to northeastern Argentina and westward into gallery forests in the Brazilian Cerrado.

**Etymology.** The generic name is the Greek word, *ololygon* meaning the croaking of a frog. The gender is feminine.

**Remarks.** Throughout its recent history, *Ololygon* either encompassed the entire “*Hyla rubra*” Group (Fouquette & Delahoussaye 1977) or was considered to be a synonym of *Scinax* (Duellman & Wiens 1992;



Faivovich 2002; Pombal & Gordo 1991). The identity of *Hyla strigilata* Spix, the type species of *Ololygon*, was uncertain until Pimenta *et al.* (2007a) discovered a population of frogs that fits the type description. Almeida and Cardoso (1985) suggested that the “*rubra* group” and “*catharinae* group” of *Ololygon* should be in separate genera. This separation was evident in the cladistics analyses of Faivovich (2002) and Faivovich *et al.* (2005).



**FIGURE 10.** **A.** *Ololygon strigilata*, Fazenda Provisão, Uruçuca, Bahia, Brazil. P. Peloso. **B.** *Ololygon perpusilla*, Estación Ecológica de Boracéia, São Paula, Brazil. M. Teixeira, Jr. **C.** *Julianus uruguayus*, 2 km from the entrance of the CPCN Pró-Mata, 880 m, São Francisco de Paula, Rio Grande do Sul, Brazil. M. Solé. **D.** *Scinax ruber*, KU212178, Ponga Shilcayo, 4 km north-northwest of Tarapoto, 470 m, San Martín, Peru. W. E. Duellman. **E.** *Scinax garbei*, KU 221053, San Jacinto, 175 m, Loreto, Peru. W. E. Duellman. **F.** *Scinax pedromedinae*, KU 215312, Cusco Amazónico, 15 km east Puerto Maldonado, 200 m, Madre de Dios, Peru. W. E. Duellman.

Even though we have molecular data for only 30% of the species of *Scinax* (*sensu lato*), three distinct major clades are evident in the tree (Fig. 4). One of these recognized herein is *Ololygon* that contains the species in the “*catharinae* clade,” as recognized by Faivovich (2002) and updated in Frost (2015). Faivovich (2002) and

Faivovich *et al.* (2005) noted some myological and osteological differences between certain members of the “*catharinae* clade” (= *Ololygon*) and the “*rubra* clade” (= *Scinax*). However, the utility of these characters will be ascertained only after thorough comparisons of many more species in both genera.

Faivovich *et al.* (2005) recognized two groups of species in their “*catharinae* clade.” One of these is the “*perpusilla*” group, first defined by Peixoto (1987). This group contains at least nine small species that breed in terrestrial bromeliads in coastal southeastern Brazil. Our tree contains three of these species that form a distinctive clade separate from the species in the “*catharinae* group,” which breed in streams.

### ***Julianus* new genus**

*Juliana*. Type species: *Hyla uruguayana* Schmidt.

**Definition.** Small frogs with slightly truncate discs on fingers and toes, webbing reduced between fingers and absent between Fingers I and II (Fig. 10C); venter immaculate; eggs deposited in ponds.

**Content.** Two species: *Julianus pinimus*\* (Bokermann & Sazima) and *J. uruguayana* (Schmidt), new combinations.

**Distribution.** Minas Gerais, Brazil, and extreme southern Brazil, Uruguay, and northern Corrientes, Argentina.

**Etymology.** The generic name is a patronym for Julian Faivovich in recognition of his many contributions to our knowledge of South American frogs. The gender is masculine.

**Remarks.** In our phylogenetic tree (Fig. 4), *Julianus uruguayana* is the strongly supported (97%) long branch sister taxon of *Scinax*. *Hyla pinima* of Bokermann and Sazima (1973) has been associated with *J. uruguayana* because of characteristics of the larval oral disc (Kolenc *et al.* 2003). Based on the interpretation of data by Kolenc *et al.* (2003) and Faivovich *et al.* (2005), we place *H. pinima* in the genus *Julianus*.

### ***Scinax* Wagler, 1830**

*Scinax* Wagler, 1830:201. Type species: *Hyla aurata* Wied, 1821, by subsequent designation (Stejneger, 1907:76).  
*Garbeana* Miranda-Ribeiro, 1926:95. Type species: *Garbeana garbei* by monotypy.

**Definition.** Small to medium-sized frogs with slightly truncate discs on fingers and toes, webbing reduced between fingers and absent between Fingers I and II (Fig. 10D); venter immaculate; eggs deposited in ponds.

**Content.** Sixty-three species: *Scinax acuminatus* (Cope), *altae*\* (Dunn), *alter*\* (Lutz), *baumgardneri*\* (Rivero), *blairi*\* (Fouquette & Pyburn), *boesemani* (Goin), *boulengeri* (Cope), *cabralensis*\* Drummon, Baêta & Pires, *caldarum*\* (Lutz), *camposseabrai*\* (Bokermann), *cardosoi*\* (Carvalho-e-Silva & Peixoto), *castroviejei*\* De la Riva, *chiquitanus* (De la Riva), *constrictus*\* Lima, Bantos & Giaretta, *cretatus*\* Nunes & Pombal, *crospedospilus* (Lutz), *cruentommus* (Duellman), *curicica*\* Pugliese, Pombal & Sazima, *cuspidatus*\* (Lutz), *danae*\* (Duellman), ? *dolloi*\* Werner, *duartei* (Lutz), *elaeochrous* (Cope), *eurydice*\* (Bokermann), *exiguus*\* (Duellman), *funereus* (Cope), *fuscomarginatus* (Lutz), *fuscovarius* (Lutz), *garbei* (Miranda-Ribeiro), *granulatus*\* (Peters), *hayii* (Barbour), *ictericus* Duellman & Wiens, *imbegue*\* Nunes, Kwet & Pombal, *iquitorum*\* Moravec, Tuanama, Pérez-Peña & Lehr, *jolyi* Lescure & Marty, *juncae*\* Nunes & Pombal, *karenanneae*\* (Pyburn), *kennedyi*\* (Pyburn), *lindsayi*\* Pyburn, ? *madeirae*\* (Bokermann), *manriquei*\* Barrio-Amorós, Orellana & Chacón-Ortiz, *maracaya*\* (Cardoso & Sazima), *nasicus* (Cope), *nebulosus* (Spix), *oreites* Duellman and Wiens, *pachycrus*\* (Miranda-Ribeiro), *pedromedinae* (Henle), *perereca*\* Pombal, Haddad & Kasahara, *proboscideus* (Brongersma), *quinquefasciatus* (Fowler), *rogerioi*\* Pugliese, Baêta & Pombal, *rostratus* (Peters), *ruber* (Laurenti), *sateremawe*\* Stauro & Peloso, *similis* (Cochran), *squalirostris* (Lutz), *staufferi* (Cope), *sugillatus* (Duellman), *tigrinus*\* Nunes, Carvalho & Pereira, *tymbamirim*\* Nunes, Kwet & Pombal, *villasboasi*\* Brusquetti, Jansen, Barrio-Amorós, Segalla & Haddad, *wandae*\* (Pyburn & Fouquette), and *x-signatus* (Spix).

**Distribution.** Tropical Mexico through Central America to extreme northern Peru west of the Andes; east of the Andes through South America southward to Uruguay and northern Argentina, including Tobago, Trinidad, and Saint Lucia in the Lesser Antilles.



**Etymology.** The generic name is derived from the Greek *skinos* meaning quick or nimble, an appropriate name for these agile frogs. The gender is masculine.

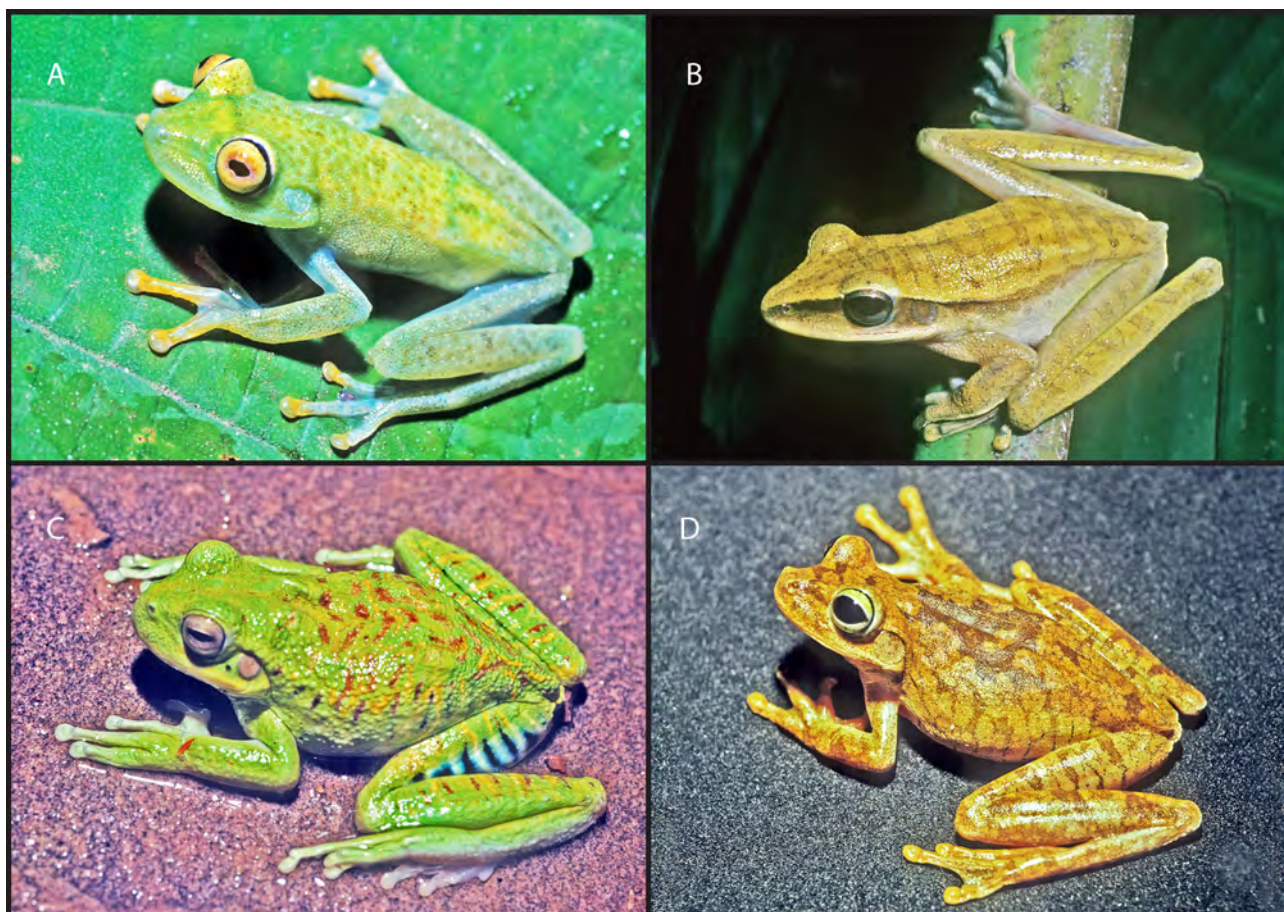
**Remarks.** See preceding Remarks in the account of *Oloolygon*. Only 28 of the 64 species of *Scinax* (44%) are included in our analysis of DNA sequences (Fig. 4). The clade recognized herein as *Scinax* is well supported (94%). Within *Scinax*, one clade with only 71% support contains eight species of the *S. rostratus* Group (Fig. 10E), originally defined by Duellman (1972a). Many of the other poorly supported clades in *Scinax* contain Cis-Andean and eastern Brazilian species. Structurally *S. pedromedinae* (Fig. 10F) is like members of the *S. rostratus* Group, but in our tree (Fig. 4) it is not within that group. Many named taxa are known only from the type localities, whereas the widespread *S. ruber* certainly is a composite of several species as evidenced by differences in color patterns, webbing, and calls (Duellman, 2005).

### Subfamily Cophomantinae Hoffmann, 1878

Cophomantina Hoffmann, 1878:614. Type genus *Cophomantis* Peters, 1870:650, junior synonym of *Hypsiboas*, Wagler, 1830:200 (fide Peters, 1873 “1872”: 772).

**Definition.** Small to large, mostly arboreal frogs lacking casque heads; many have stream-adapted tadpoles. Chromosome complement  $2n = 24$ , except  $2n = 22$  in *Hypsiboas albopunctatus*, and 18, 20, and 22 in some species of *Aplastodiscus*.

**Content.** Seven genera 179 species.



**FIGURE 11.** Representatives of species groups of *Hypsiboas* defined by Faivovich *et al.* 2005. **A.** *H. sibleszi* (*H. benitezi* Group), KU 181099, Km 127, El Dorado–Santa Elena de Uairén Road, 1250 m, Bolívar, Venezuela. **B.** *H. lanciformis* (*H. albopunctatus* Group), KU 221881, San Jacinto, 175 m, Loreto, Peru. **C.** *H. riojanus* (*H. pulchellus* Group), KU 160195, 6 km W Betanzas, 3330 m, Potosí, Bolivia. **D.** *H. crepitans* (*H. faber* Group), KU 166781, 16 km northeast Barrancas, 140 m, Bariñas, Venezuela. All by W. E. Duellman.

**Distribution.** Tropical and subtropical South America northward from Bolivia, Uruguay and northern Argentina to Nicaragua, and the Islands of Tobago and Trinidad.

**Etymology.** The familial name is derived from the Greek *kophos* meaning dull and the Greek *mantis* meaning prophet. Hoffmann's (1878) intention for the meaning of the familial name is unknown. The gender is masculine.

**Remarks.** Our molecular data coupled with morphological data necessitate the recognition of one new genus within *Hyloscirtus*. Enlarged oral discs completely bordered by papillae and bearing large numbers of tooth rows are characteristic of four stream-breeding genera. Two of these genera (*Colomascirtus* and *Hyloscirtus*) are sister taxa in the Andes. The other two genera (*Bokermannohyla* in southeastern Brazil and *Myersiophyla* in the Guiana Highlands) represent independent lineages. The largest known LTRF is 16/21 in *Myersiophyla neblinaria* Faivovich, McDiarmid, and Myers (2013).

Molecular data are available for only 56 of the 90 recognized species of *Hypsiboas* (62%). There are some clades that might be recognized as genera, but each is a progressive stepwise arrangement within *Hypsiboas*. First and foremost among these is the *Hypsiboas benitezi* Group (Fig. 11A), defined by Faivovich *et al.* (2005). Four of the species in this well-supported (98%) clade (Fig. 4) occur in northeastern South America, whereas two others (*H. nympa* Faivovich, Moravec, Cisneros-Heredia and Köhler and *H. microderma* Pyburn exist in the upper Amazon Basin. The *Hypsiboas albopunctatus* (Fig. 11B) and *Hypsiboas pulchellus* (Fig. 11C) groups also are well supported (99%). Likewise, the *Hypsiboas faber* Group (Fig. 11D) of Faivovich *et al.* (2005) is well supported (100%) in our tree, which contains, except for *H. albomarginatus* (Spix), the gladiator frogs that construct nests, as defined by Kluge (1979), not the misuse of the term by Köhler *et al.* (2010). However, *H. boans* (Linnaeus), a nest-building gladiator frog is related to *H. semilineatus* and *H. geographicus* in our tree. Such apparent discrepancies indicate that greater taxon sampling and more thorough molecular refinement is essential to construct a realistic phylogeny of this large group of Neotropical treefrogs.

### ***Colomascirtus* new genus**

*Colomascirtus*. Type species: *Hyla larinopygion* Duellman, 1973.

**Definition.** Large, colorful frogs attaining SVLs of more than 70 mm (Fig. 12A); cloacal region swollen; white parietal peritoneum and mental gland absent; stream-dwelling tadpoles with large oral discs directed ventrally and having one or two complete rows of marginal papillae; LTRF 4–14/6–17. Chromosome complement unknown.

**Content.** Seventeen species: *Colomascirtus antioquia*\* (Rivera-Correa & Faivovich), *armatus* (Boulenger), *caucanus*\* (Ardila-Robayo, Ruiz-Carranza, & Rua-Trujillo), *charazani* (Vellard), *chlorosteus*\* (Reynolds & Foster), *condor*\* (Almendáriz, Brito-M., Batallas-R. & Ron), *criptico* (Coloma, Carvajal-Endara, Dueñas, Paredes-Recalde, Morales-Mite, Almeida-Reinoso, Tapia, Hutter, Toral-Contreras & Guayasamin), *larinopygion* (Duellman), *lindae* (Duellman & Altig), *pacha* (Duellman & Hillis), *pantostictus* (Duellman & Berger), *princecharlesi* (Coloma, Carvajal-Endara, Dueñas, Paredes-Recalde, Morales-Mite, Almeida-Reinoso, Tapia, Hutter, Toral-Contreras & Guayasamin), *psarolaimus* (Duellman & Hillis), *ptychodactylus* (Duellman & Hillis), *staufferorum* (Duellman & Coloma), *tapichalaca* (Kizirian, Coloma & Paredes-Recalde), and *tigrinus* (Mueses-Cisneros, & Anganoy-Criollo), all new combinations.

**Distribution.** Cloud forest and subparamo in the Andes of Colombia and Ecuador, and in southern Peru and Bolivia.

**Etymology.** The generic name is a patronym for Luis A. Coloma in combination with the Greek *scirtao* verb meaning to leap. Coloma has been a principal researcher on, and conservationist of, frogs in the northern Andes. The gender is masculine.

**Remarks.** Members of *Colomascirtus* were first defined as the *Hyla larinopygion* Group by Duellman and Hillis (1990) and subsequently by Duellman *et al.* (1997) and Rivera-Correa & Faivovich (2013). Coloma *et al.* (2012) provided a thorough account of the morphology, osteology, development, calls, and ecology of the species in the genus. A detailed morphological study of the tadpoles by Sánchez (2010) revealed two structures (shelf on upper jaw sheath and crown-like ornamentation around naris) that help define two groups of species that are not concordant with the then recognized *Hyla bogotensis* and *Hyla larinopygion* groups (Coloma *et al.* 2012).





**FIGURE 12.** **A.** *Colomascirtus lindae*, KU 164402, 11 km east-southeast Papallacta, 2660 m, Napo, Ecuador. **B.** *Colomascirtus armatus*, KU 173221, Buenos Aires, 2400 m, Cusco, Peru (note humeral spines and hypertrophied forearm). **C.** *Hyloscirtus bogotensis*, KU 169437, Parque Arqueológico San Agustín, 1750 m, Huila, Colombia. **D.** *Hyloscirtus alytolylax*, KU 207706, 4 km NE Dos Ríos, 1149 m, Pichincha, Ecuador. All by W. E. Duellman.

Two species, *Colomascirtus armatus* and *C. charazani*, have been placed in a group variously recognized as the *Hyla armata* Group (Duellman *et al.* 1997) or the *Hyloscirtus armatus* Group (De la Riva *et al.* 2000; Lötters *et al.* 2005). These two species occur in southern Peru and Bolivia, leaving a gap of more than 2000 km from southern Ecuador to southern Peru. Males of these large frogs have clusters of keratinized spines on the prepollex and on the proximal ventral surface of the humerus (Fig. 12B). The LTRF in tadpoles is 13–14/16–17, notably greater than in other species of *Colomascirtus*, 4–9/6–12 (Sánchez 2010). In our tree (Fig. 4) *C. armatus* and *C. charazani* are in a well-supported (100%) clade that is sister of all other *Colomascirtus*. This same arrangement was shown in molecular phylogenetic trees by Faivovich *et al.* (2005), Wiens *et al.* (2010), Pyron & Wiens (2011), Coloma *et al.* (2012), and Rivera-Correa & Faivovich (2013). In the phylogenetic analysis by Almendáriz *et al.* (2014), a different topology was recovered with *C. armatus* and *C. charazani* as sister taxa of *Hyloscirtus*; however their arrangement had less support and was based on fewer genes than those by Coloma *et al.* (2012) and Rivera-Correa & Faivovich (2013).

### ***Hyloscirtus* Peters, 1882**

*Hyloscirtus* Peters, 1882. Type species: *Hyloscirtus bogotensis* Peters, 1862, by original designation.

**Definition.** Medium-sized frogs (SVL less than 50 mm); dorsum green (Figs. 12C and D); white parietal peritoneum present; mental gland present in males; cloacal region not swollen. Stream-dwelling tadpoles with large oral discs directed ventrally and having one or two complete rows of marginal papillae; LTRF 4–8/5–15. Chromosome complement unknown.

**Content.** Eighteen species: *Hyloscirtus albopunctulatus*\* (Boulenger), *alytolylax* (Duellman), *bogotensis*\* (Peters), *callipeza*\* (Duellman), *colymba* (Dunn), *denticulentus*\* (Duellman), *estevesi*\* (Rivero), *jahni*\* (Rivero), *lascinius* (Rivero), *lynchi*\* (Ruiz-Carranza & Ardila-Robayo), *mashpi*\* Guayasamin, Rivera-Correa, Arteaga-Navarro, Culebras, Bustamente, Pyron, Peñafiel, Morochz & Hutter, *palmeri* (Boulenger), *phyllognathus* (Melin), *piceigularis*\* (Ruiz-Carranza & Lynch), *platydactylus*\* (Boulenger), *sarampiona*\* (Ruiz-Carranza & Lynch), *simmonsii* (Duellman), and *torrenticola*\* (Duellman & Altig).

**Distribution.** Cloud forest and lower montane rainforest from central Costa Rica to central Ecuador on the Pacific slopes of the Andes, western Mérida Andes in Venezuela, southward on Amazonian slopes of the Andes to central Peru.

**Etymology.** The generic name is derived from *Hylas* in Greek mythology and the Greek *scirtao* verb meaning to leap.

**Remarks.** *Hyloscirtus* as recognized here is the *Hyla bogotensis* Group originally defined by Duellman (1972b) and further recognized by Duellman *et al.* (1997) and Faivovich *et al.* (2005). Investigation of tadpole morphology by Sánchez (2010) resulted in defining two groups of species; no molecular data are available for one group (*H. bogotensis*, *callipeza*, *lynchi*, *platydactylus*, and sp. Huila). See remarks under *Colomascirtus*.

## Family Phyllomedusidae Günther, 1859

Phyllomedusidae Günther, “1858” 1859:346. Type genus: *Phyllomedusa* Wagler, 1830, by monotypy.

**Definition.** Iris vertically elliptical; arciferal pectoral girdle, eight procoelous presacral vertebrae, separate calcaneum and astragalus, intercalary cartilages between terminal and penultimate phalanges, claw-shaped terminal phalanges, SVL from 45 mm in *Callimedusa atelopoides* (Duellman *et al.* 1988) to 119 mm in *Phyllomedusa bicolor* (Venâncio & Melo-Sampiro, 2010). Chromosome complement  $2n = 26$ .

**Content.** Eight genera, 59 species.

**Distribution.** Neotropics, from Mexico to northern Argentina.

**Etymology.** The familial name is derived from the Greek *phyll*, meaning leaf, and the Greek *Medousa*. The name alludes to the gelatinous egg masses deposited on leaves of trees.

**Remarks.** Herein we include three genera that have not been recognized recently by previous authors. Two of these names are resurrected from the synonymies of *Agalychnis* and *Phyllomedusa*, whereas the third is new. Our maximum likelihood analysis includes 46 species, 78% of the known members of the family. In the parsimony analysis of 45 species by Faivovich *et al.* (2010), some of the same clades emerge as in our analysis. The principal difference is in the proposed classifications. Our proposal of three additional genera is a reflection on some of the species groups recognized by Faivovich *et al.* (2010). We recovered a major clade of phyllomedusids with 100% support. Within this clade are large frogs, genus *Phyllomedusa* (100% support), with vomerine teeth and another clade with 100% support of smaller frogs lacking vomerine teeth (100% support). Within the latter are two clades with significant support. One clade, *Pithecopus* (100% support), is characterized by having opposable thumbs and no bright flash colors. In the second clade, *Callimedusa* (78% support), the thumb is not opposable, and with one exception, all have bright flash colors.

## *Pithecopus* Cope, 1866

*Pithecopus* Cope, 1866:86. Type species: *Phyllomedusa azurea* Cope, 1862, by original designation.

*Bradymedusa* Miranda-Ribeiro. 1926:104. Type species: *Bradymedusa moschata* Miranda Ribeiro (= *Phyllomedusa rohdei*) by subsequent designation by Funkhouser 1957:18.

**Definition.** Medium-sized species (SVL  $\pm 45$  mm); Toe I much longer than, and opposable to Toe II (Fig. 13A); vomerine teeth absent; tadpoles with moderately small oral disc directed anteroventrally.

**Content.** Nine species: *Pithecopus ayeaye* Lutz, *azureus* (Cope), *centralis* (Bokermann), *hypochondrialis* (Daudin), *megacephalus* (Miranda-Ribeiro), *nordestinus* (Caramaschi), *oreades* (Brandão), *palliatius* (Peters), and *rohdei* (Mertens), all are new combinations.



**Distribution.** Tropical South America east of the Andes from southern Venezuela to northern Argentina

**Etymology.** The generic name is derived from the Greek *pithekodes* meaning ape-like. The gender is masculine.

**Remarks.** Lutz's (1966) resurrection of Cope's genus *Pithecopus* was not accepted by most herpetologists; instead these frogs were designated as the *Phyllomedusa hypochondrialis* Group (e.g., Faivovich *et al.* 2010). The monophyly of *Pithecopus* is strongly supported (100%), as is the monophyly of *Pithecopus* + *Callimedusa* (Fig. 4). The larger frogs in the genus *Phyllomedusa* (Fig. 13B) tend not to be agile branch walkers.

### ***Callimedusa* new genus**

*Callimedusa*. Type species: *Phyllomedusa perinesos* Duellman, 1973.

**Definition.** Small to medium-sized species (SVL of 44 mm in *Callimedusa atelopoides* to 62 mm in *C. tomopterna*); Toe I slightly longer than Toe II, not opposable; vomerine teeth present (except in *C. atelopoides*); flash colors on flanks and hidden surfaces of thighs purple or black; palpebral membrane reticulated or not; tadpoles having moderately small oral discs directed anteroventrally.

**Content.** Six species: *Callimedusa atelopoides* (Duellman, Cadle & Cannatella), *baltea* (Duellman & Toft), *duellmani* (Cannatella), *ecuatoriana* (Cannatella), *perinesos* (Duellman), and *tomopterna* (Cope); all new combinations.

**Distribution.** Amazonian slopes of the Andes from Ecuador to central Peru; upper Amazon Basin from Colombia to Bolivia; Guianan Region.

**Etymology.** The generic name is derived from the Greek *kalos* meaning beautiful and the Greek *Medousa*. The name alludes to the beautiful coloration of the flanks of members of this genus. The gender is feminine.

**Remarks.** The monophyly of this genus is rather well supported (78%), but that of the “*Phyllomedusa perinesos* Group” of Cannatella (1982) within *Callimedusa* is only moderately supported (66%). The four species having allopatric ranges on the Amazon slopes of the Andes in Ecuador and Peru (*C. baltea*, *duellmani*, *ecuatoriana*, and *perinesos*) closely resemble one another (Figs. 14A and B). In our analysis, the sister species is *C. atelopoides* (Fig. 14D), an inhabitant of the upper Amazon Basin. This species differs from all other phyllomedusids by being small, brown, terrestrial; furthermore, it is unlike other *Callimedusa* in lacking vomerine teeth and clavicles in the pectoral girdle (Duellman *et al.* 1988). The analysis places *C. tomopterna* as the sister species to the remaining members of the genus (Fig. 14C). This colorful frog that ranges throughout much of the Amazon Basin is widely allopatric to the Andean species.

### ***Phyllomedusa* Wagler, 1830**

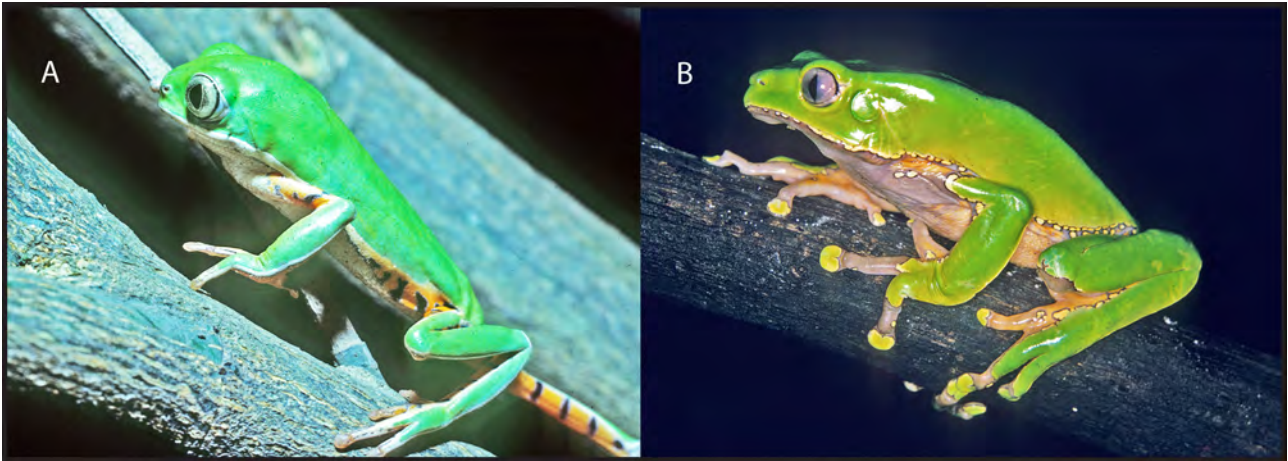
*Phyllomedusa* Wagler, 1830:201. Type species: *Rana bicolor* Boddaert, 1772, by monotypy.

**Definition.** Large frogs (SVL to 130 mm in *Phyllomedusa bicolor*; Fig. 13B), little or no webbing on feet, none on hand; vomerine teeth present; palpebral membrane not reticulated; tadpoles having moderately small oral discs directed anteroventrally.

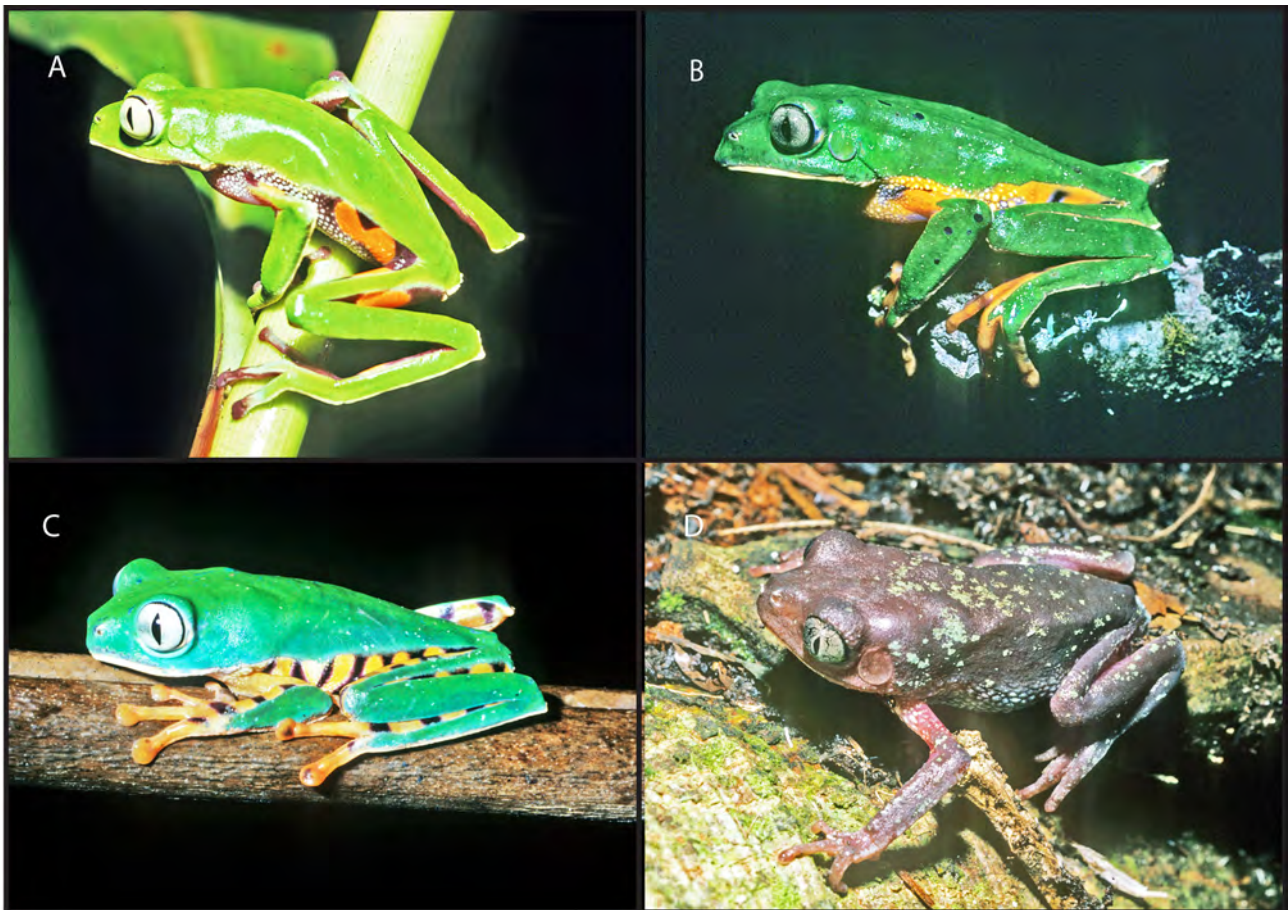
**Content.** Fifteen species: *Phyllomedusa bahiana* Lutz, *bicolor* (Boddaert), *boliviana* Boulenger, *burmeisteri* Boulenger, *camba* De la Riva, *coelestis*\* (Cope), *distincta* Lutz, *iheringii* Boulenger, *neildi* Barrio-Amorós, *sauvagii* Boulenger, *tarsius* (Cope), *tetraploidea* Pombal & Haddad, *trinitatis* Mertens, *vaillantii* Boulenger, and *venusta*\* Duellman & Trueb.

**Distribution.** Amazon Basin, Chacoan Region in Paraguay, eastern Brazil southward to Uruguay and northeastern Argentina, Guianan Region, Trinidad and northern Venezuela, Cordillera Occidental and Magdalena Valley in Colombia, and extreme eastern Panama.

**Etymology.** According to Duellman (2001), the generic name is derived from the Greek *phyll*, meaning leaf, and the Greek *Medousa*. The name alludes to the gelatinous egg masses deposited on leaves of trees. The gender is feminine.



**FIGURE 13.** A. *Pithecopus hypochondrialis*, KU 183441, Okinawa I, 300 m, Santa Cruz, Bolivia. D. C. Cannatella. B. *Phyllomedusa bicolor*, KU 124907, Leticia, 96 m, Amazonas, Colombia. W. E. Duellman.



**FIGURE 14.** Species of *Callimedusa* A. *C. perinesos*, KU 164450, Río Salado, 1 km upstream from Río Coca, 1410 m, Napo, Ecuador. B. *C. duellmani*, KU 181813, 8 km north-northeast Balzapata, 1860 m, Amazonas, Peru. C. *C. tomopterna*, KU 220332, Río Sucusari, Loreto, 210 m, Peru. D. *C. atelopoides*, KU 204764, Cusco Amazónico, 15 km east Puerto Maldonado, 200 m, Madre de Dios, Peru. All by W. E. Duellman.

**Remarks.** Our analysis shows a 100% support for the monophyly of this genus, within which are three strongly supported clades. The first of these contains only *Phyllomedusa bicolor* and *P. vaillantii* that are unique Among phyllomedusids by having osteoderms in the skin on the dorsum (Ruibal & Shoemaker 1984). Although recognition of the *P. burmeisteri* and *P. tarsius* groups, as proposed by Faivovich *et al.* (2010), is strongly supported in our analysis, there are no known morphological features that distinguish the two groups.



Throughout the overlapping parts of their ranges, the diploid *Phyllomedusa distincta* and the tetraploid *P. tetraploidea* hybridize to produce triploids that are sterile or have low fertility (Haddad *et al.* 1994). Hybridization also occurs between *P. bahiana* and *P. burmeisteri*; putative hybrids are fertile (Pombal & Haddad 1992).

### *Hylomantis* Peters, 1873

*Hylomantis* Peters, 1873 “1872:”772, Type species: *Hylomantis asper* Peters, 1873 “1872.” by monotypy.

**Definition.** Small frogs (SVL less than 50 mm); vomerine teeth present; palpebral membrane not reticulated; tadpoles having enlarged oral disc directed anteriorly.

**Content.** Two species: *Hylomantis asperus* Peters and *H. granulosus* (Cruz).

**Distribution.** Atlantic coastal forest in the states of Bahia and Pernambuco, Brazil.

**Etymology.** The generic name is the combination of *Hylas* of Greek mythology and the Greek *mantis* prophet or soothsayer. The gender is masculine.

**Remarks.** The generic placement of these frogs has been chaotic (see Faivovich *et al.* 2010, and Pimenta *et al.* 2007b). The tadpoles are unique among phyllomedusids by having the eyes lateral and visible from below and an enlarged oral disc directed anteriorly (Nascimento & Skuk 2007). Faivovich *et al.* (2010) recognized *Hylomantis* as a genus containing *H. asperus* (Fig. 15A) and *H. granulosus* plus the “*Phyllomedusa buckleyi* Group.” Herein we consider *Hylomantis* to be composed of two species in northeastern Brazil, more than 3000 km away from the “*Phyllomedusa buckleyi* Group” and from members of the genus *Agalychnis* in Central America and northwestern South America.



**FIGURE 15.** A. *Hylomantis asperus*. Belmonte, Bahia, Brazil. M. Teixeira. Jr. B. *Agalychnis buckleyi*, KU 143225, 16.5 km north-northeast Santa Rosa, 1700 m, Napo, Ecuador. W. E. Duellman. C. *Agalychnis hulli*, Universidad Ricardo Palma, 1.5 km north Teniente López, 310 m, Loreto, Peru. W. E. Duellman. D. *Agalychnis lemur*, KU 63940, Tapanti, 1500 m, Cartago, Costa Rica. W. E. Duellman.

## ***Agalychnis* Cope, 1864**

*Agalychnis* Cope. 1864:181. Type species: *Agalychnis callidryas* Cope, 1852, by original designation.

*Pachymedusa* Duellman, 1968. Type species: *Phyllomedusa dacnicolor* Cope, 1864, by original designation.

**Definition.** Medium-sized frogs (maximum SVL 47 mm in *Agalychnis lemur* [Boulenger] to 93 mm in *A. spurrelli* Boulenger); vomerine teeth present; palpebral membrane reticulated or not; tadpoles having moderately small oral discs directed anteroventrally.

**Content.** Thirteen species: *Agalychnis annae* (Duellman), *buckleyi*\* (Boulenger), *callidryas* (Cope), *dacnicolor* (Cope), *danieli*\* (Ruiz-Carranza, Hernández-Camacho & Rueda-Almonacid), *hulli* (Duellman & Mendelson), *lemur* (Boulenger), *medinae*\* (Funkhouser), *moreletii* (Duméril), *psilopygion*\* (Cannatella), *saltator* Taylor, *spurrelli* Boulenger, and *terranoa* Rivera-Correa, Duarte-Cubides, Rueda-Almonacid & Daza.

**Distribution.** Tropical Mexico throughout Central America to western and Amazonian Ecuador and northern Peru.

**Etymology.** According to Duellman (2001), the generic name is derived from the Greek *aga*, an intensive prefix, and the Greek *lychnis*, a plant with scarlet flowers. Presumably the name refers to the red-eyed treefrog, *Agalychnis callidryas*, the type species of the genus. The gender is feminine.

**Remarks.** The inclusion of *Agalychnis hulli* (Fig. 15C) and *A. lemur* (Fig. 15D) in this genus is problematic, even though their respective support values (88% and 75%) are relatively high. *Agalychnis hulli* is an enigma inasmuch as it is a member of the “*Phyllomedusa buckleyi* Group” as defined by Cannatella (1980) and exists in the Amazon Basin (Duellman & Mendelson 1995), whereas other members of the group live in cloud forests on the slopes of the Andes and Central American highlands. *Agalychnis lemur* is the only species in the so-called “*Phyllomedusa buckleyi* Group” in our analysis. Molecular data are needed from *A. buckleyi* (Fig. 15B), *danieli*, *medinae*, and *psilopygion* before the phylogenetic relationships can be clarified for a suitable classification.

## **Family Pelodyadidae Günther, 1859**

Pelodyadidae Günther, “1858” 1859:345, Type genus: *Pelodyas* Günther, 1859 (= *Litoria* Tschudi, 1838), by original designation.

**Definition.** Arciferal pectoral girdle, eight procoelous presacral vertebrae, astragalus and calcaneum not fused, intercalary cartilages between terminal and penultimate phalanges, claw-shaped terminal phalanges, SVL from 18 mm in female *Litoria microbelos* (Anstis 2013) to 135 mm in *Nyctimystes infrafrenatus*; free-living aquatic tadpoles with LTRF of no more than 2/3. Chromosome complement  $2n = 26$  ( $2n = 24$  in *Nyctimystes infrafrenatus*).

**Content.** Two subfamilies, three genera, and 208 species.

**Distribution.** Australia, Tasmania, New Guinea, Solomon Islands, Bismark Archipelago, Vanuatu, and Seram Island and Moluccas Islands in Indonesia. Introduced into New Caledonia and New Zealand.

**Etymology.** The familial name is taken from the generic name *Pelodyas*, which is derived from the Greek *pelo* meaning clay or mud and the Greek *dryos* meaning tree; the implied meaning is unclear.

**Remarks.** The phylogenetic relationships of pelodyadid frogs has been a major problem. As stated by Frost *et al.* (2006:204–205), “The extensive paraphyly of ‘*Litoria*’ with respect to *Cyclorana* and ‘*Nyctimystes*’ remains the elephant in the room for Australian herpetology, and for reasons that escape us this spectacular problem has largely been ignored until recently.” As a result of their parsimony analysis that included three species of *Nyctimystes* and eight of *Litoria* (0.5% of known pelodyadids) Frost *et al.* (2006) considered *Nyctimystes* to be a junior synonym of *Litoria*, because the generic recognition of *Nyctimystes* made *Litoria* paraphyletic. In our analysis, Phyllomedusidae is the sister taxon of Pelodyadidae, and these two families form the sister group to Hylidae (Fig. 2). The results of a maximum likelihood analysis of molecular data from 109 species (52% of known species) reveal three major clades of pelodyadids (Fig. 2). Within Pelodyadidae two major clades of *Litoria*, as currently recognized, make *Litoria* paraphyletic with *Nyctimystes* intervening. Thus, we resurrect *Dryopsophus* for one of the clades of “*Litoria*.” Furthermore, we recognize the subfamily Pelodyadinae to include *Dryopsophus* and *Nyctimystes*, while leaving *Litoria* as the single genus in Pelobiinae. This classification necessitates rearrangement of the generic synonyms of *Litoria* given by Frost (2015).

## Subfamily Pelobiinae Fitzinger, 1843

Pelobii Fitzinger, 1843:31. Type genus: *Pelobius* Fitzinger, 1843, by original designation.

**Definition.** At the present time no morphological characters are known that distinguish this subfamily from Pelodryadinae.

**Content.** One genus and at least 91 species.

**Distribution.** Northern and eastern Australia, New Guinea and associated islands, Solomon Islands, New Britain, Vanuatu, and Moluccas Islands and Seram Island in Indonesia.

**Etymology.** The familial name is based on the generic name *Pelobius* from the Greek *pelos* meaning earth and the Greek suffix *binos* meaning coming from. The type species of *Pelobius* is *Litoria freycineti* Tschudi, 1838.

**Remarks.** Pelobiinae is the sister group to Pelodryadinae.

## *Litoria* Tschudi, 1838

*Litoria* Tschudi, 1838:77. Type species: *Litoria freycineti* Tschudi, 1838, by monotypy.

*Ranoidea* Tschudi, 1838:76. Type species: *Ranoidea jacksoniensis* Tschudi, 1838, by monotypy. Synonym of *Litoria* by International Commission on Zoological Nomenclature (Bulletin of Zoological Nomenclature 48:337–338).

*Leptyhya* Duméril and Bibron, 1841:504. Substitute name for *Litoria* Tschudi, 1838.

*Pelobius* Fitzinger, 1843:31. Type species: *Litoria freycineti* Duméril and Bibron (= *Litoria freycineti* Tschudi, 1838) by original designation.

*Polyphone* Gistel, 1849:xi. Substitute name for *Ranoidea* Tschudi, 1838.

*Hylomantis* Peters, 1880:224. Type species *Hylomantis fallax* Peters, 1880, by monotypy. Preoccupied by *Hylomantis* Peters 1873 (Amphibia: Anura: Phyllomedusidae).

*Dryomantis* Peters, 1882:8 Replacement name for *Hylomantis* Peters, 1880.

*Coggerdonia* Wells and Wellington, 1985:4. Type species: *Hyla adelaidensis* Gray, 1841, by original designation.

*Colleeneremia* Wells and Wellington, 1975:4. Type species: *Hyla rubella* Gray, 1842, by original designation.

*Llewellynura* Wells and Wellington. 1985:5. Type species: *Hyla dorsalis microbelos* Cogger, 1966, by original designation.

*Mahonabatrachus* Wells and Wellington, 1985:5. Type species: *Hyla meiriana* Tyler, 1969, by original designation.

*Pengilleyia* Wells and Wellington, 1985:5. Type species: *Litoria tyleri* Watson, Gartside, Littlejohn, and Loftus-Hills, 1979, by original designation.

*Rawlinsonia* Wells and Wellington, 1985:5. Type species: *Hyla ewingii* Duméril and Bibron, 1841, by original designation.

*Saganura* Wells and Wellington, 1985:6. Type species: *Hyla burrowsi* Scott, 1942, by original designation.

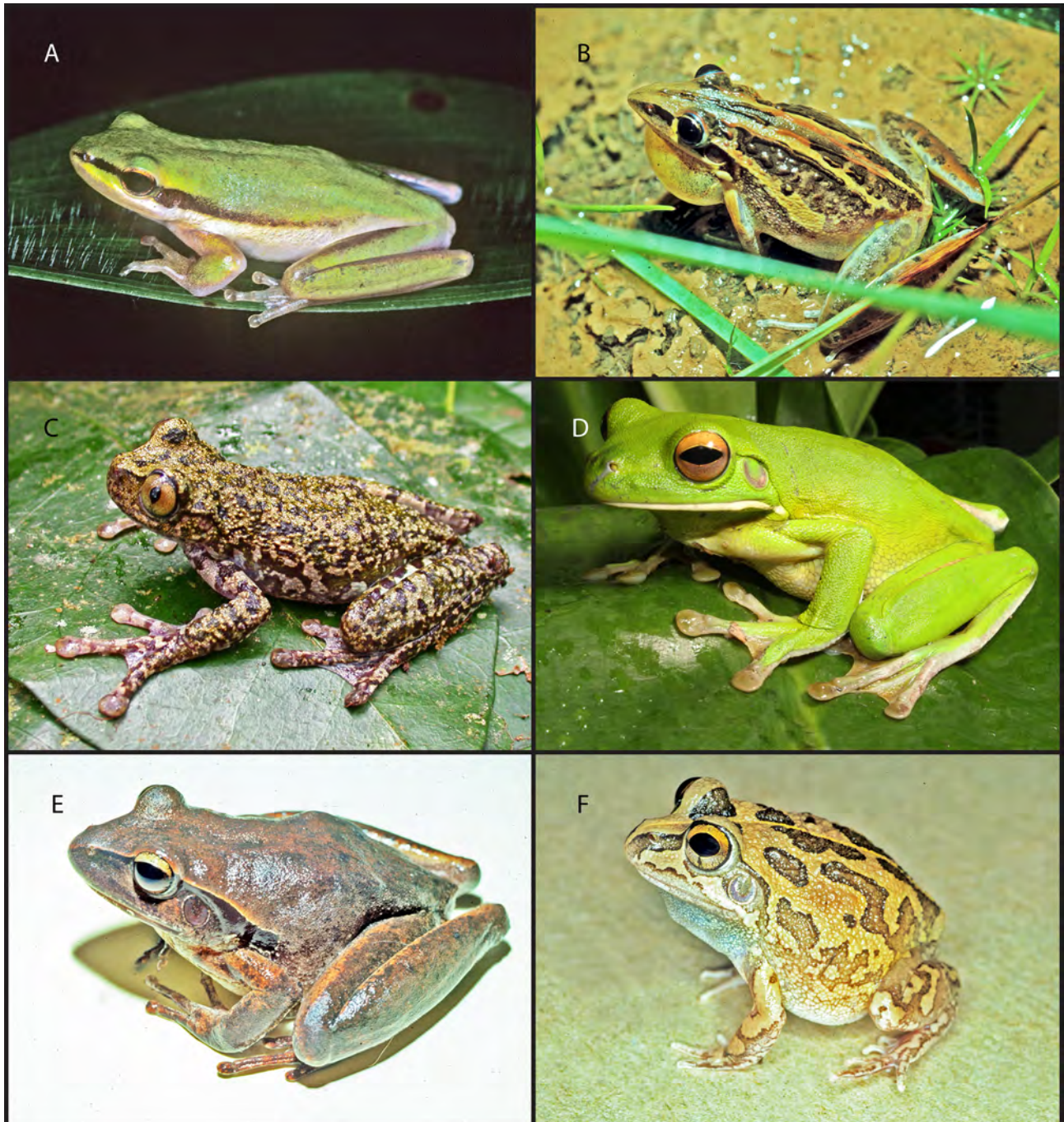
**Definition.** Arboreal frogs with the pupil horizontally elliptical and the palpebral membrane unpigmented (Figs. 16A and B); tadpoles with small anteroventral or enlarged ventral oral discs with a LTRF of 2/3. Chromosome complement  $2n = 26$ .

**Content.** Ninety-one species: *Litoria adelaidensis* (Gray), *albolabris*\* (Wandolleck), *amboinensis* (Horst), *angiana* (Boulenger), *arfakiana* (Peters & Doria), *aurifera*\* Anstis, Tyler, Roberts, Price & Doughty, *axillaris*\* Doughty, *biakensis*\* Günther, *bibonius*\* Kraus and Allison, *bicolor* (Gray), *burrowsi* (Scott), *capitula*\* (Tyler), *chloristona*\* Menzies, Richards & Tyler, *chloronota*\* (Boulenger), *chrisdahli*\* Richards, *christianbergmanni*\* Günther, *congenita* (Peters & Doria), *contrastens*\* (Tyler), *cooloolensis*\* Liem, *coplandi* (Tyler), *corbeni*\* (Wells & Wellington), *darlingtoni* (Loveridge), *dentata* (Keferstein), *dorsalis* Macleay, *electrica* Ingram & Corben, *euryrnastes*\* Menzies, Richards & Tyler, *everetti*\* (Boulenger), *ewingii* (Duméril & Bibron), *fallax* (Peters), *flavescens*\* Kraus & Allison, *freycineti* Tschudi, *gasconi*\* Richards, Oliver, Krey & Tjaturadi, *havina* Menzies, *hilli*\* Hiaso & Richards, *humboldtorum*\* Günther, *inermis* (Peters), *iris* (Tyler), *jervisiensis* (Duméril & Bibron), *latopalmata* (Günther), *leucova* (Tyler), *littlejohni* White, Whitford & Mahony, *lodesdema*\* Menzies, Richards & Tyler, *longicrus*\* (Boulenger), *longirostris* (Tyler & Davies), *lutea*\* (Boulenger), *majikthise* Johnson & Richards, *mareku*\* Günther, *megalops*\* Richards & Iskander, *meiriana* (Tyler), *microbelos* (Cogger), *micromembrana* (Tyler), *modica* (Tyler), *muco*\* Menzies, *multipluca* (Tyler), *mystax*\* (Van Kampen), *nasuta* (Gray), *nigrofrenata* (Günther), *nigropunctata* (Meyer), *oenicolen*\* Menzies & Zweifel, *ollauro*\* Menzies, *olongburensis* Liem & Ingram, *pallida* Davies, Martin & Watson, *paraewingi* Watson, Loftus-Hills & Littlejohn, *peronii* (Tschudi), *personata* Tyler, Davies & Martin, *pronimia* Menzies, *prora* (Menzies), *pygmaea*\* (Meyer), *quadrilineata*\* Tyler & Parker, *revelata* Ingram, Corben & Hosmer, *rothii* (De Vis), *rubella* (Gray), *rubrops*\* Kraus & Allison, *scabra*\*



Günther & Richards, *singadanae*\* Richards, *spartacus* Richards & Oliver, *staccato*\* Doughty & Anstis, *thesaurensis* (Peters), *timida*\* Tyler and Parker, *tornieri* (Nieden), *tyleri* Martin, Watson, Gartside, Littlejohn, & Loftus-Hill, *umarensis*\* Günther, *umbonata*\* Tyler & Davies, *verae*\* Günther, *verreauxii* (Dumeril), *viranula*\* Menzies, Richards & Tyler, *vocivincens*\* Menzies, *wapogaensis*\* Richards & Iskander, *watjulumensis* (Copland), *wisselensis*\* (Tyler), and *wollastoni* (Boulenger).

**Distribution.** Northern and eastern Australia, New Guinea and associated islands: Solomon Islands, New Britain, Vanuatu, and Moluccas Islands and Seram Island in Indonesia.



**FIGURE 16.** **A.** *Litoria bicolor*, KU 179765, AMAX Mining Camp, 300 m, Mitchell Plateau, Western Australia, Australia. W. E. Duellman. **B.** *Litoria nasuta*, KU 179853, AMAX Mining Camp, 300 m, Mitchell Plateau, Western Australia, Australia. W. E. Duellman. **C.** *Nyctimystes papua*, BPBM 16895, East slope Mt. Simpson, 1440 m, Milne Bay Province, Papua New Guinea. F. Kraus. **D.** *Nyctimystes infrafrenatus*, Daintree village area, Queensland, Australia. T. Charlton. **E.** *Dryopsophus lesueurii*, KU 179838, Kilcoy Creek, Queensland, Australia. W. E. Duellman. **F.** *Dryopsophus longipes*, KU 179923, AMAX Mining Camp, 300 m, Mitchell Plateau, Western Australia, Australia. W. E. Duellman.

**Etymology.** The generic name is the Latin noun *litoris* meaning shore. Inasmuch as Tschudi's (1838) description was based on material he observed in Paris that was plundered from a British ship leaving Australia, he may have assumed that the frog lived near the shore. The gender is feminine.

**Remarks.** The following eight species for which molecular data are lacking are regarded as *incertae sedis*: *castanea* (Steindachner), *hunti* Richards, Oliver, Dahl & Tjatiradi, *jeudii* (Werner), *lousiadensis* (Tyler), *multicolor* Günther, *obtusirostris* Meyer, *richardsi* Dennis & Cunningham, and *vagabunda* (Peters & Doria). At the present time they cannot be assigned with certainty to *Litoria* or *Dryopsophus*.

Two-thirds (61) of the species of *Litoria* occur on New Guinea and associated islands. Only three of these (*L. bicolor*, *rothii*, and *rubella*) also occur on Australia.

## Subfamily Pelodyadinae Günther, 1859

Pelodyadidae Günther, "1858" 1859:345, Type genus; *Pelodyas* Günther, 1859 (= *Litoria* Tschudi, 1838), by original designation.

Chiroleptina Mivart, 1869:294. Type genus: *Chiroptes* Günther, 1859, by original designation.

Cycloraninae Parker, 1940:12. Type genus *Cyclorana* Steindachner, 1867, by original designation.

Nyctimystinae Laurent, 1975:283. Type genus *Nyctimystes* Stejneger 1916, by original designation.

**Definition.** Arboreal and terrestrial frogs having free-living aquatic tadpoles. Chromosome complement  $2n = 26$ , except  $2n = 24$  in *Nyctimystes infrafrenatus*.

**Content.** Two genera and 109 species.

**Distribution.** Australia, Tasmania, and New Guinea and associated islands. Introduced in New Caledonia, New Hebrides, and New Zealand.

**Etymology.** Same as family.

**Remarks.** Pelodyadinae is the sister taxon of Pelobiinae.

## *Nyctimystes* Stejneger, 1916

*Nyctimystes* Stejneger, 1916:85. Type species: *Nyctimantis papua* Boulenger, 1897, by monotypy.

*Sandyrana* Wells and Wellington. 1985:6. Type species: *Hyla infrafrenata* Günther, 1867, by original designation.

**Definition.** Pupil vertically elliptical; palpebral membrane reticulated (Fig. 16C). Stream-adapted tadpoles with large, ventral oral discs having a LTRF of 2/3. Chromosome complement  $2n = 26$ . See Remarks for different characteristics of *Nyctimystes infrafrenatus*.

**Content.** Thirty-eight species: *Nyctimystes avocalis*\* Zweifel, *bivocalis*\* Kraus, *brevipalmatus* (Tyler, Martin & Watson) new combination, *calcaratus*\* Menzies, *cheesmani* Tyler, *cryptochrysos*\* Kraus, *daymani*\* Zweifel, *disruptus*\* Tyler, *dux* (Richards & Oliver) new combination, *eucavatus*\* Menzies, *fluviatilis*\* Zweifel, *foricula* Tyler, *granti*\* (Boulenger), *gularis*\* Parker, *humeralis* (Boulenger), *infrafrenatus* (Günther), new combination, *intercastellus*\* Kraus, *kubori* Zweifel, *kuduki*\* Richards, *latratus*\* Menzies, *montanus*\* (Peters & Doria), *myolae*\* Menzies, *narinus* Zweifel, *obsoletus*\* (Lönnberg), *ocreptus*\* Menzies, *papua* (Boulenger), *perimetri*\* Zweifel, *persimilis*\* Zweifel, *pulcher* (Wandolleck), *purpureolatus*\* (Oliver, Richards, Tjaturadi & Iskander) new combination, *rueppelli*\* (Boettger), *sanguinolenta*\* (Van Kampen) new combination, *semipalmatus* Parker, *trachydermis*\* Zweifel, *traunae*\* Menzies, *tyleri*\* Zweifel, and *zweifeli* (Tyler).

**Distribution.** New Guinea and associated islands; eastern Australia from the York Peninsula to New South Wales.

**Etymology.** The generic name is derived from the Greek *nyctos* meaning night and the Greek *myst* meaning mystic; the name alludes to the mysteries of the night. The gender is masculine.

**Remarks.** Frogs of the genus *Nyctimystes* have been treated thoroughly by Zweifel (1958), Tyler and Davies (1979), and Menzies (2006), but the recognition of the genus has been controversial. In our analysis that includes only about one third of the species of *Nyctimystes*, all but three species are in a tight cluster with a support value of 100%. The immediate sister species of that clade is *N. brevipalmatus*, a species widely distributed in eastern Australia. *Nyctimystes dux* and *N. infrafrenatus* (Fig. 16D) form an outlying branch to the rest of the genus.

“*Hyla infrafrenata*” Günther is a highly enigmatic species. Molecular data (99% bootstrap support) clearly place it in *Nyctimystes*, whereas morphologically it is like *Litoria* in having a horizontal pupil and no reticulations on the palpebral membrane (Tyler 1968). Furthermore, unlike species of *Nyctimystes*, it breeds in ponds and has pigmented eggs that hatch into tadpoles with small anteroventral mouths (Anstis 2013). Last, it is the only pelodryadid known to have a chromosome complement of  $2n = 24$  (Menzies & Tippet 1976). The taxonomic position of this species awaits more data and further interpretation to determine if it belongs in *Litoria*, *Nyctimystes*, or in its own genus; if the latter, the generic name *Sandyrana* Wells and Wellington is available.

### **Dryopsophus Fitzinger, 1843**

*Dryopsophus* Fitzinger, 1843:39. Type species: *Hyla citropa* Péron, 1807, by original designation.

*Euscelis* Fitzinger, 1843:31. Type species: *Hyla lesueurii* Duméril and Bibron, 1841, by original designation. Junior synonym of *Euscelis* Brulié, 1832 (Insecta).

*Chiroleptes* Günther 1859:34. Type species *Alytes australis* Gray 1842. Preoccupied by *Chiroleptes* Kirby, 1837 (Insecta).

*Pelodryas* Günther, 1859:119. Type species *Rana caerulea* White, 1790, by monotypy.

*Cyclorana* Steindachner, 1867:29. Type species: *Cyclorana novaehollandiae* Steindachner, 1867, by monotypy.

*Phractops* Peters, 1867:31. Type species *Phractops alutaceus* Peters, 1867 (= *Cyclorana novaehollandiae* Steindachner), by monotypy.

*Chirodrias* Keferstein, 1867:358. Type species: *Chirodrias raniformis* Keferstein, 1867, by monotypy.

*Mitrolysis* Cope, 1889:312. Type species: *Chiroleptes alboguttatus* Günther, 1867, by monotypy.

*Fanchonia* Werner 1893:81. Type species: *Fanchonia elegans* Werner, 1893 (= *Rana aurea* Lesson, 1926), by monotypy.

*Brendanura* Wells and Wellington, 1985:4. Type species: *Chiroleptes alboguttatus* Günther, 1867, by original designation.

*Neophractops* Wells and Wellington, 1985:5. Type species: *Chiroleptes platycephalus* Günther, 1873, by original designation.

*Mosleyia* Wells and Wellington, 1985:5. Type species: *Hyla nannotis* Andersson, 1916, by original designation.

**Definition.** Pupil horizontally elliptical; palpebral membrane unpigmented (Fig. 16E–F); tadpoles with small anteroventral or enlarged ventral oral discs; LTRF 2/3 or 0/0. Chromosome complement  $2n = 26$ .

**Content.** Seventy-one species: *Dryopsophus alboguttatus* (Günther), *andiirrmalin* (McDonald), *aureus* (Lesson), *aruensis*\* (Horst), *auae*\* (Menzies & Tyler), *australis* (Gray), *barringtonensis* (Copland), *becki*\* (Loveridge), *booroolongensis* (Moore), *brevipes* (Peters), *brongersmai*\* (Loveridge), *bulmeri*\* (Tyler), *caeruleus* (White), *callistus*\* (Kraus), *cavernicolus* (Tyler & Davies), *chloris* (Boulenger), *citropus* (Péron), *cryptotis* (Tyler & Martin), *cultripes* (Parker), *cyclorhynchus* (Boulenger), *dahlia* (Boulenger), *daviesae* (Mahony, Knowles, Foster & Donnellan), *dayi* (Günther), *dorsivenuis*\* (Tyler), *elkeae*\* (Günther & Richards), *eschatus*\* (Kraus & Allison), *eucnemis* (Lönnerberg), *exophthalmus* (Tyler, Davies & Aplin), *fuscus*\* (Oliver & Richards), *genimaculatus* (Horst), *gilleni* (Spencer), *gracilentus* (Peters), *graminea*\* (Boulenger), *impurus* (Peters & Doria), *jungguy* (Donnellan & Mahony), *kroombitensis*\* (Hoskin, Hines, Meyer, Clarke & Cunningham), *kumae* (Menzies & Tyler), *lesueurii* (Duméril & Bibron), *longipes* (Tyler & Martin), *loricus*\* (Davies & McDonald), *macki*\* (Richards), *maculosus* (Tyler & Martin), *maini* (Tyler & Martin), *manya* (Van Beurden & McDonald), *moorei* (Copland), *myolus*\* (Hoskin), *nannotis* (Andersson), *napeus*\* (Tyler), *novaehollandiae* (Steindachner), *nudidigitus* (Copland), *nyakalensis* (Liem), *pearsonianus* (Copland), *phyllochrous* (Günther), *piperatus*\* (Tyler & Davies), *platycephalus* (Günther), *pratti*\* (Boulenger), *raniformis* (Keferstein), *rarus*\* (Günther & Richards), *rheocolus* (Liem), *rivicolus*\* (Günther and Richards), *robinsonae*\* (Oliver, Stuart, Fox & Richards), *sauroni*\* (Richards & Oliver), *serratus* (Andersson), *spenceri* (Dubois), *spiniferus*\* (Tyler), *splendidus* (Tyler, Davies & Martin), *subglandulosus* (Tyler & Anstis), *vagitus* (Tyler, Davies & Martin), *verrucosus* (Tyler & Martin), *wilcoxii* (Günther), and *xanthomerus* (Davies, McDonald & Adams); all names are new combinations.

**Distribution.** Australia, Tasmania, and New Guinea. Introduced in New Caledonia, New Hebrides, and New Zealand.

**Etymology.** The generic name is derived from the Greek *dryos* meaning tree and the Greek *psophos* meaning sound or noise. The name obviously refers to the calls from the trees. The gender is masculine.

**Remarks.** Only about one-third of the species of *Dryopsophus* occur in New Guinea, and two of those species (*D. caeruleus* and *D. eucnemis*) are widespread in Australia.

Our analysis of molecular data on 66% of the species of *Dryopsophus* reveals five clades plus outlying species. The first clade has a support value of only 49% and contains eight species in northern and eastern Australia. Within



this group, a well-known species, *Dryopsophus caeruleus*, is the type species of *Pelodryas* Günther. A second clade having a support value of 100% contains four species ranging from Queensland to Victoria in eastern Australia; a member of this group, *D. lesueurii*, is the type species of *Euscelis* Fitzinger. Another clade of four species with a support value of 93% occurs in New Guinea and northern Queensland; no generic name is available for this group. A distinctive clade with a support value of 99% contains four species of stream-breeding frogs in northern Queensland; one of these, *D. nannotis*, is the type species of *Mosleyia* Wells and Wellington. A large group of terrestrial species has been known as *Cyclorana* Steindachner (type species *C. novaehollandiae*). In our analysis, this clade has a support value of only 64%; the clade is widespread in northern Australia and in the interior of the continent. Further, more intense analyses should provide sufficient evidence for the recognition of *Cyclorana*.

The tadpoles of many species in the mountains New Guinea and in Queensland in northern Australia develop in streams and have enlarged ventral mouths with a LTRF of 2/3 (Tyler 1968; Günther & Richards 2005). Two species in Queensland, *Dryopsophus daviesae* and *D. subglandulosus* are unique in not only lacking labial tooth rows but also keratinized beaks (Anstis 2013).

## Biogeography

Herein we provide a brief summary of pertinent aspects of the earth's history. Estimated divergence times of relevant clades of hylid, pelodryadid, and phyllomedusid frogs are compared with the ages of geological events to hypothesize the evolutionary biogeography of these anurans.

**The historical landscape.** When attempting to interpret the temporal aspects of Arborescent biogeography it is necessary to have an understanding of the historical geology and climatology of that part of the world inhabited by these frogs. Examination of the geographical distributions of the families and genera strongly supports a Gondwanan origin. The breakup of Gondwana has been treated by many authors and perhaps best summarized by McLoughlin (2001).

What today are Africa and South America comprised western Gondwana. Sea-floor spreading began in the proto-South Atlantic Ocean in the early Cretaceous about 135–130 Mya. At lower latitudes the separation took place at 119–105 Mya in the Apian Epoch of the Cretaceous. South America remained an isolated continent throughout most of the Cenozoic until its connection with North America via Panama in the late Pliocene (Pittman *et al.* 1993).

The earliest separation between South America and west Antarctica took place in the late Eocene and early Oligocene (35–30.5 Mya) with the subsidence of the Powell Basin. This opened what is now known as the Drake Passage. This seaway permitted the establishment of the South Circumpolar Current (Barker & Burrell 1977; Lawyer & Gahagan 1998). Climatic effects of the circumpolar current resulted in the initiation of the first extensive ice sheets in Antarctica, thereby eliminating a terrestrial biota.

As a result of sea-floor spreading, complete separation of East Antarctica and Australia took place at about the end of the Eocene around 35.5 Mya (Shackleton & Kennett 1975; Veevers *et al.* 1991). Following the separation of Australia from Antarctica, Australia moved northward and collided with island-arc terranes of the Philippines Sea Plate during the Oligocene about 25 Mya (Crowhurst *et al.* 1996). The leading edge of the northward moving Australian plate was formed by a series of volcanic regions. Volcanism began in the early Miocene ( $\pm$  20 Mya) and continues to the present (Davies 2012). New Guinea became separated from Australia in the Pliocene. The continents were last connected at the last glacial maximum only 10,000 years ago.

North America was connected to South America from the late Cretaceous to the mid-late Eocene (84–49 Mya) (Pittman *et al.* 1993). However, there are geophysical data that do not support a contiguous land bridge during the Paleocene (Duque-Caro 1990). Furthermore, according to Haq *et al.* (1987), the drop in sea level between 66 and 68 Mya was of short duration, and the Paleocene was marked by higher sea levels before another drop at the Paleocene-Eocene boundary.

The geology of Central America and the Greater Antilles has been disputed since Donnelly (1985:116) wrote: “The closing of the Central American isthmus is far less dramatic than in other published reconstructions and requires merely that a southerly flap of Central America be gradually swung against Colombia in the early Tertiary. Of course, the final terrestrial emergence is another story; the original speculation that the Panamanian land bridge emerged finally in the late Tertiary is as valid now as it was when Darwin drew the conclusion.” According to

Farris *et al.* (2011) the tectonic collision between Central and South America was initiated 25–23 Mya. Beginning in the mid-Miocene ( $\pm 15$  Mya) the island arc system that was to become the Isthmus of Panama might have made contact with South America. Uplifting of the island-arc system in the late Pliocene and early Pleistocene resulted in the existing continuous land connection between the continents (Coates & Obando 1996). The Middle Miocene connection is supported by uranium-lead geochronology (Montes *et al.* 2015). The suture of the Central American paleopeninsula and South America is along the Río Atrato; thus, that part of Colombia west of the Río Atrato, including the Serranía de Baudó, was part of the Central American paleopeninsula (Galves & Morca 1994).

Today, the Isthmus of Tehuantepec in southern Mexico is a lowland barrier between the Mexican highlands and Nuclear Central American highlands. The central ridges connecting the highlands on either side are only about 250 m above sea level, but they are sufficient to retain most of the rainfall on the Gulf of Mexico lowlands to the north (Duellman 1960). According to Durham *et al.* (1955), sedimentary evidence shows that Nuclear Central America was connected to southern Mexico throughout the Tertiary but that the isthmus had a lower relief and perhaps was only half as wide as present. The highlands of Mexico and Central America mostly were the results of volcanism in the Miocene and Pliocene continuing into the Holocene (Campbell 1999; Schuchert 1935).

In South America the Guianan and Brazilian shields may have been continuous with one another until the late Cretaceous, when both were elevated, and a major embayment of the Atlantic Ocean separated these ancient formations until the late Miocene. Both shields were uplifted farther in the Tertiary (Beurlen 1970; Valetton 1973), and the Brazilian Shield was uplifted further in the Quaternary (Freitas 1951). The Guiana Highlands were uplifted in the early Cretaceous (Gansser 1954). The present table mountains (tepui) are erosional remnants of the Cretaceous uplifts (Haffer 1974).

As the South American plate arced northwestward it encountered the Nazca Plate; the latter's ongoing subduction under the South American Plate is largely responsible for the orogenic events resulting in the rise of the Andes. A major structural deflection of the Andes exists in what is now southern Ecuador and northern Peru. This is the geological Huancabamba Deflection, physiographically referred to as the Huancabamba Depression. There are significant differences in the origins of the mountains to the south of the depression, the central Andes, and those north of the depression, the northern Andes. By the late Cretaceous the Andes were uplifted to elevations probably no higher than 1000 m (Zeil 1979). The central (and southern) Andes were only about half of their present height in the early-mid Miocene (20–10 Mya). The last major uplift of the central Andes was in the Pliocene. Parts of the Cordillera Oriental and the Altiplano were uplifted to their present heights during the last 10 million years (Gregory-Wodzicki 2000); some additional orogenies took place in the Pleistocene (Jaillard *et al.* 2000). The major uplift of the Andes north of the Huancabamba Depression was initiated in the late Miocene and Pliocene and continued into the Quaternary as evidenced by numerous active volcanoes in Colombia and Ecuador. Palynological data show that elevations above 2000 m in the Cordillera Oriental in Colombia were reached in the mid-late Pliocene (van der Hammen 1974). For more detailed discussions of the evolution of the Andes, see Duellman and Lehr (2009) and Lynch and Duellman (1997).

During the Miocene and Pliocene large marine embayments and freshwater lakes existed in what is now the Amazon Basin. Shortly after the elevation of the Andes in the early–mid Miocene, the basin was drained primarily by the precursor of the Río Orinoco that flowed into the Caribbean Sea. In the late Miocene to early Pliocene the present drainage via the Río Amazonas to the Atlantic Ocean was established (Hoorn *et al.* 1995; Hoorn 2006; Latrubesse *et al.* 2010; Mora *et al.* 2010). The present Amazon Basin covers about 8 million km<sup>2</sup>, and the Amazon River is about 6400 km long from its source in the Peruvian Andes to its mouth in northeastern Brazil (Sioli 1984). For a more detailed discussion of the evolution of the South American landscape, see Duellman (2015).

In the early Cretaceous submergence occurred in North America; the continental margins were flooded and a vast interior sea divided North America into two continents (Dunbar 1961). In the middle Cretaceous the Pacific-Cascade-Sierra Nevada mountain system was uplifted, and the Laramide Revolution in the late Cretaceous elevated the Rocky Mountains and the Cordillera Occidental in Mexico. All of these mountains were greatly eroded in the latter part of the Cretaceous and in the Paleocene (King 1958). Plate movements and fluctuating sea levels during the Tertiary resulted in different land connections between North America and Eurasia. McKenna (1975) argued for a land connection between northeastern North America, perhaps via Ellesmere Island and northwestern Europe. This connection, the DeGeer Passage, existed from the Paleocene to the middle Eocene. The Bering connection between Alaska and Siberia existed periodically from the middle Eocene into the Quaternary.

Throughout the Tertiary, high-latitude cooling and climatic deterioration greatly modified the landscape. Wolfe

and Hopkins (1967) contended that a chilling occurred in the middle Oligocene in North America, followed by a relatively mild climate in the late Oligocene that reached a peak in the mid-Miocene. Throughout the Tertiary, but especially beginning in the late Miocene, climate steadily deteriorated partly as a result of the orogeny of the western mountain systems (Duellman & Sweet 1999). These changes resulted in the compression of the Madro-Tertiary forest that previously had occupied much of North America (Axelrod 1958). A broad rain shadow developed east of the rising mountains and forced the deciduous forest eastward of the newly developing grasslands, thereby isolating this forest from its Asiatic component.

The aridification of the Palearctic was caused by the collective formation of the Tibetan Plateau and the Pamir and Tien Shan mountain ranges in the east, and the Iranian Plateau and the Zagros Mountains in the west (Szczerbak 2003; Sindaco & Jeremcenko 2008). These plateaus are responsible for forming the deserts of the Middle East and the Gobi and Talamankan Deserts of Central Asia. These changes pushed the distributions of most amphibians to the edges of the western and eastern Palearctic areas (Ananjeva *et al.* 2006; Aitchison *et al.* 2007).

According to Axelrod (1972), the interior of the large African-American continent was arid prior to the birth of the South Atlantic Ocean, after which maritime and mesic climates developed in eastern South America. In the early Tertiary subtropical mesic climates existed in the southern part of the continent. The orogeny of the Andean mountain chain in the Miocene resulted in a rain shadow in Patagonia. As summarized by Duellman (1999), subsequent to the Eocene, temperate South America gradually became cooler and drier. In the early Tertiary, austral temperate forests dominated by *Nothofagus* extended across Patagonia and northward at least to 30°N latitude (Jeannel 1967). The Miocene witnessed progressive climatic deterioration in Patagonia. Furthermore, the separation of Antarctic from South America resulted in the cold Humboldt Current streaming up the Pacific Coast, which created arid coastal conditions (the Atacama Desert) from 36°S latitude nearly to the Equator.

The onset of aridity in Australia was in the late Eocene; aridification took place again in the mid-Miocene to the Pliocene (Macquenet *et al.* 2010). Final aridification mostly in the Eyrean Province in the central part of the continent was a Pleistocene event (Galloway & Kemp 1981).

**Cretaceous Frogs.** A Gondwanan origin of the archeobatrachian frogs referred to the Pipoidea is shown by the many fossils from South America and Africa, continents now inhabited by living pipid frogs. The fossils range from the early Cretaceous *Thoraciliacus* in Israel (Trueb 1999) to the late Cretaceous *Eoxenopoides* (Estes 1977) and *Vulcanobatrachus* (Trueb *et al.* 2005) from South Africa and *Pachybatrachus* from Niger (Báez & Rage 1998). In South America fossil pipoids are known from various sites in Argentina—*Avitabatrachus* from the middle Cretaceous (Báez *et al.* 2000), *Saltenia* from the Upper Cretaceous (Báez 1981), and the Paleogene *Shelania* (Báez & Trueb 1997).

Three fossil genera of neobatrachians were reported from the upper Aptian-lower Albian deposits (lower Cretaceous Crato Formation) of northeastern Brazil by Báez *et al.* (2009). These authors conducted a phylogenetic analysis of 42 taxa including representatives of neobatrachian families. Two of the species from the lower Cretaceous of northeastern Brazil, *Arariphrynus placidoi* (Leal & Britoi) and *Eurycephalella alcinae* Báez, Moura & Gómez, were nested among hyloid taxa. According to Báez *et al.* (2009) the third species, *Cratia gracilis* Báez, Moura & Gómez, may be a stem neobatrachian or an early branching within crown Neobatrachia. Most importantly, they considered their hyloid taxa to be stem Ranoidea. The age of the upper Aptian-lower Albian deposits (125–112 Mya) place these fossils as probably existing at the very end of the African-South American connection (119–105 Mya).

Two fossils have been described from the Uberata Formation and Maastrichtian Marilla Formation in the Upper Cretaceous (89.3–84.9 Mya) in Minas Gerais, Brazil. One of these, *Baurubatrachus pricei* Báez and Perí originally was considered to be a proto-ceratophryid (Báez & Perí 1989), but our data suggest that *Baurubatrachus* is likely a stem hyloid, not a proto-ceratophryid; this is supported by Báez & Gómez (2014) who suggested that hyperossification concealed relationships. The second species, *Uberobatrachus carvalhoi* Báez, Gómez, Rivero, Martinelli, and Ferraz is regarded as a “nobleobatrachian hyloid” (Báez *et al.* 2012). The ages of these fossils correspond well with ages of genetic diversification that we propose. The most recent common ancestor of all hylids (nobleobatrachians) is <80 Mya (Heinicke *et al.* 2009).

In Madagascar, a large amount of material of the fossil *Beelzebufo ampinga* Asher & Krause reveals great similarities to South America *Ceratophrys* (Evans *et al.* 2014). This species also is from the Maastrichtian epoch of the Upper Cretaceous. Ruane *et al.* (2011) undertook a variety of phylogenetic analyses of *Beelzebufo* and other basal anurans and concluded that *Beelzebufo* was unlikely to represent a crown-group ceratophryine. In a review of

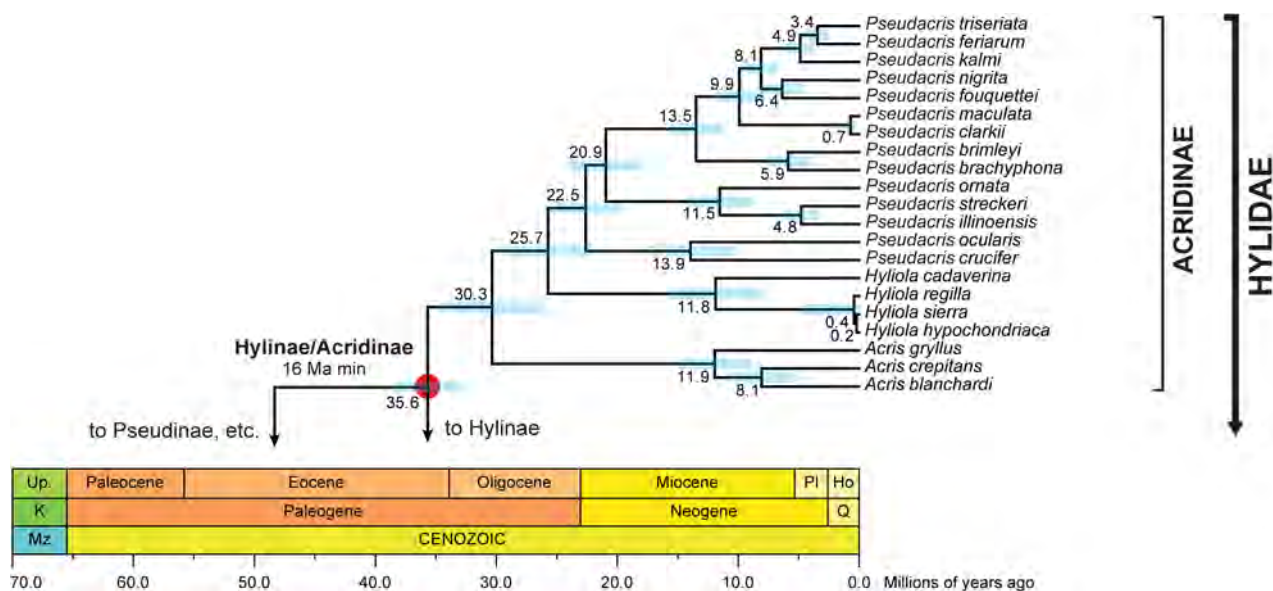
calytocephalellid fossils by Agnolin (2012) the family was defined to contain three genera, *Calytocephalella*, *Beelzebufo* and *Gigantobatrachus*. The fossil neobatrachians from Cretaceous deposits in Argentina, Brazil, and Madagascar indicate that neobatrachians existed in the mid-Cretaceous ( $\pm 120$  Mya) and diversified by the Upper Cretaceous ( $\pm 90$  Mya).

**Tertiary Fossils.** The few Paleogene and Neogene fossils assigned to Hylidae and Pelodyadidae are fragmentary; these are summarized by Sanchiz (1998a). Fossils from the Miocene through the Pleistocene in North America are assigned to *Acris*, *Proacris*, and *Pseudacris*. Fossil *Hyla* are known from the Miocene to the Pleistocene of Europe. Fossils assignable to *Dryophytes* exist from the Miocene, Pliocene, and mostly from the Pleistocene of North America and Japan. Fragmentary material from the Pleistocene has been assigned to *Osteopilus* in the Bahamas, Cuba, and the United States, and similar kinds of material have been assigned to *Pternohyla* in Mexico.

In Australia, fragmentary remains (mostly ilia) reveal the presence of *Dryopsophus* in deposits at the Pliocene-Pleistocene boundary and possibly from the mid-Miocene. Several extant species of *Litoria* are known from Pleistocene deposits. Four taxa from the Miocene that have been assigned to Hylidae cannot at this time be placed in either *Dryopsophus* or *Litoria*. These are *Australobatrachus ilius* Tyler, *Litoria conicula* Tyler, *L. curvata* Tyler, and *L. magna* Tyler. Existing data on these presumed pelodyadids are in Tyler (1976, 1982, 1991, 1994).

Estes and Reig (1973) noted the presence of unstudied bufonid and hylid fossils from the Paleocene of Brazil, but these have yet to be described. Consequently there is a large void in our knowledge of the early evolution of hylid frogs. Our analysis predicts an origin of “hylid” frogs to be 61.8 Mya; this time is approximately 28 million years younger than the hylid frog, *Uberobatrachus carvalhoi*, which may be an ancestor of the modern Neotropical frogs.

**A Timeline for Treefrog Evolution.** According to our dating analysis, crown Arboranae originated 61.8 (57.5–66.1) Mya in the Paleocene (Fig. 17). From its place of origin in South America these treefrogs differentiated and dispersed into the Australo-Papuan Region, Central and North America, the West Indies, and Eurasia. This extensive distribution is exceeded by only two families of anurans, Bufonidae and Ranidae. Herein we attempt to explain the historical events in the evolution of arboranans with respect to time and geography. Temporal events are denoted by calculated times of the nodes in the timetree (Fig. 17). Calculated times are given with their confidence intervals as shown by blue bars on the timetree (Fig. 17).



**FIGURE 17.** Timetree of arboranan frogs estimated with RelTime from DNA sequence data of 19 genes (16,128 aligned sites), based on the ML topology (Fig. 4). Estimated dates of divergence are indicated at each node (in millions of years), with blue bars representing 95% confidence intervals. Calibrated nodes are marked with red dots. The tree is rooted with *Ceuthomantis smaragdinus*, *Dendrobates auratus*, *Haddadus binotatus*, and *Rhinoderma darwinii* (not shown).



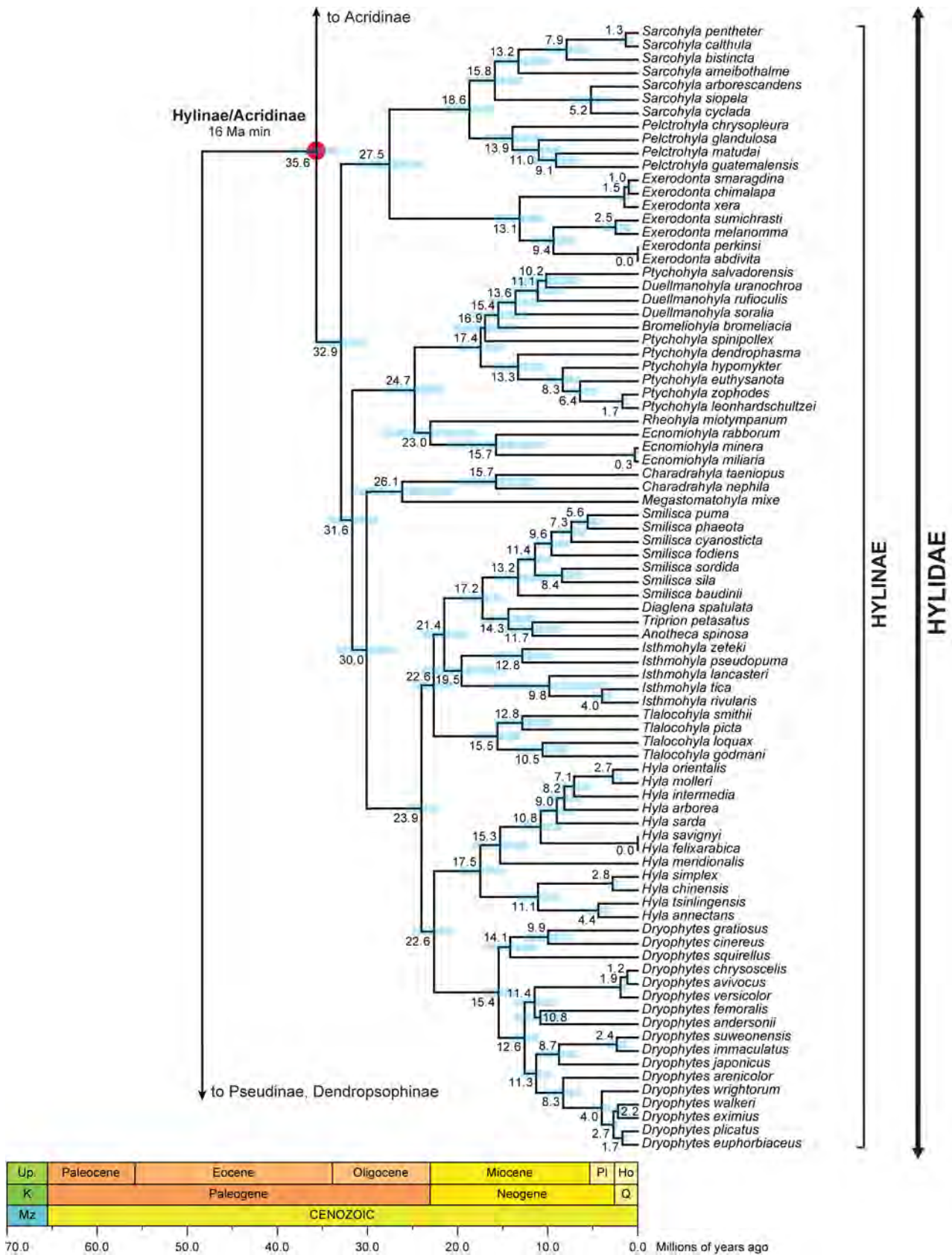


FIGURE 17. (Continued)







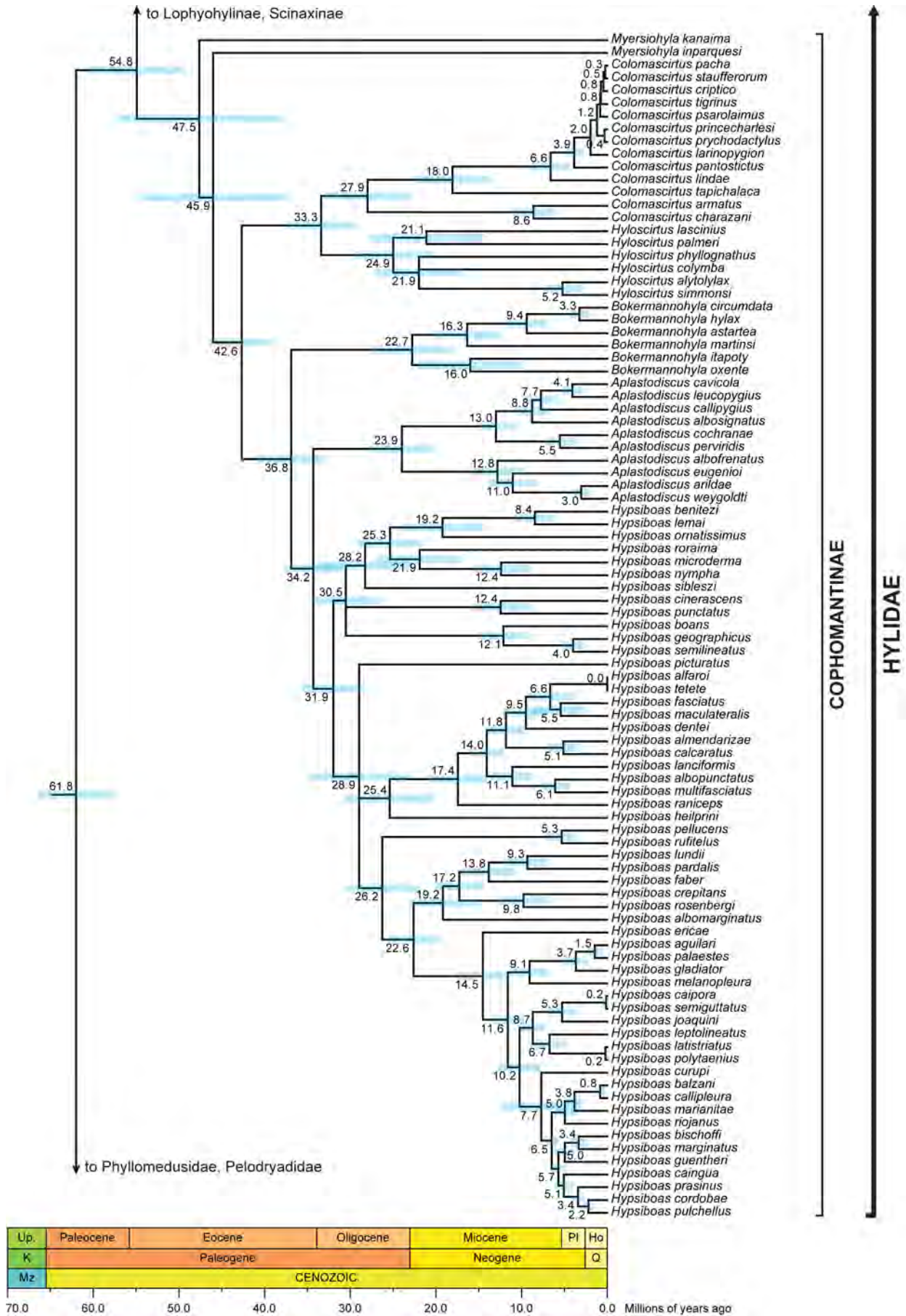


FIGURE 17. (Continued)



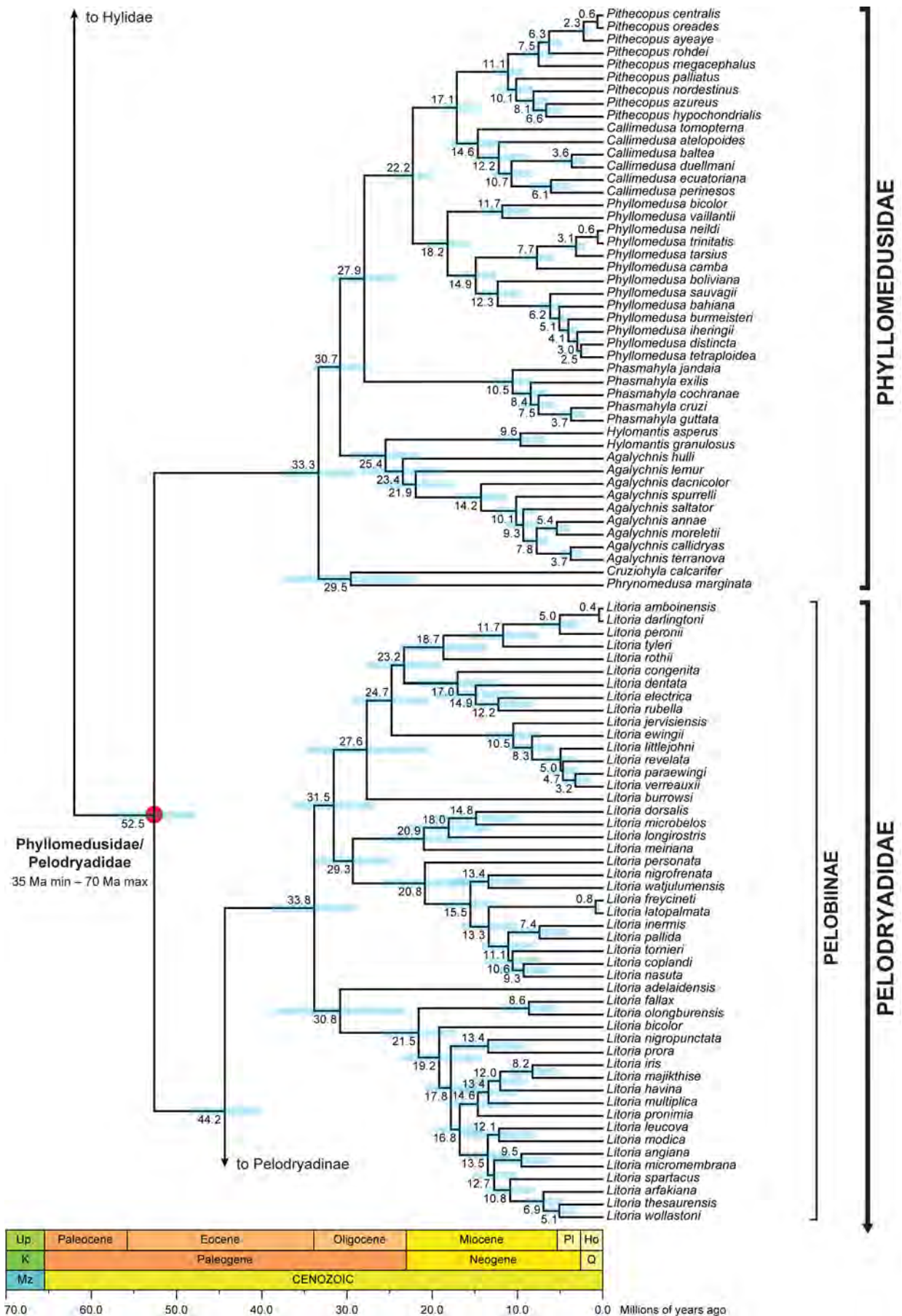


FIGURE 17. (Continued)

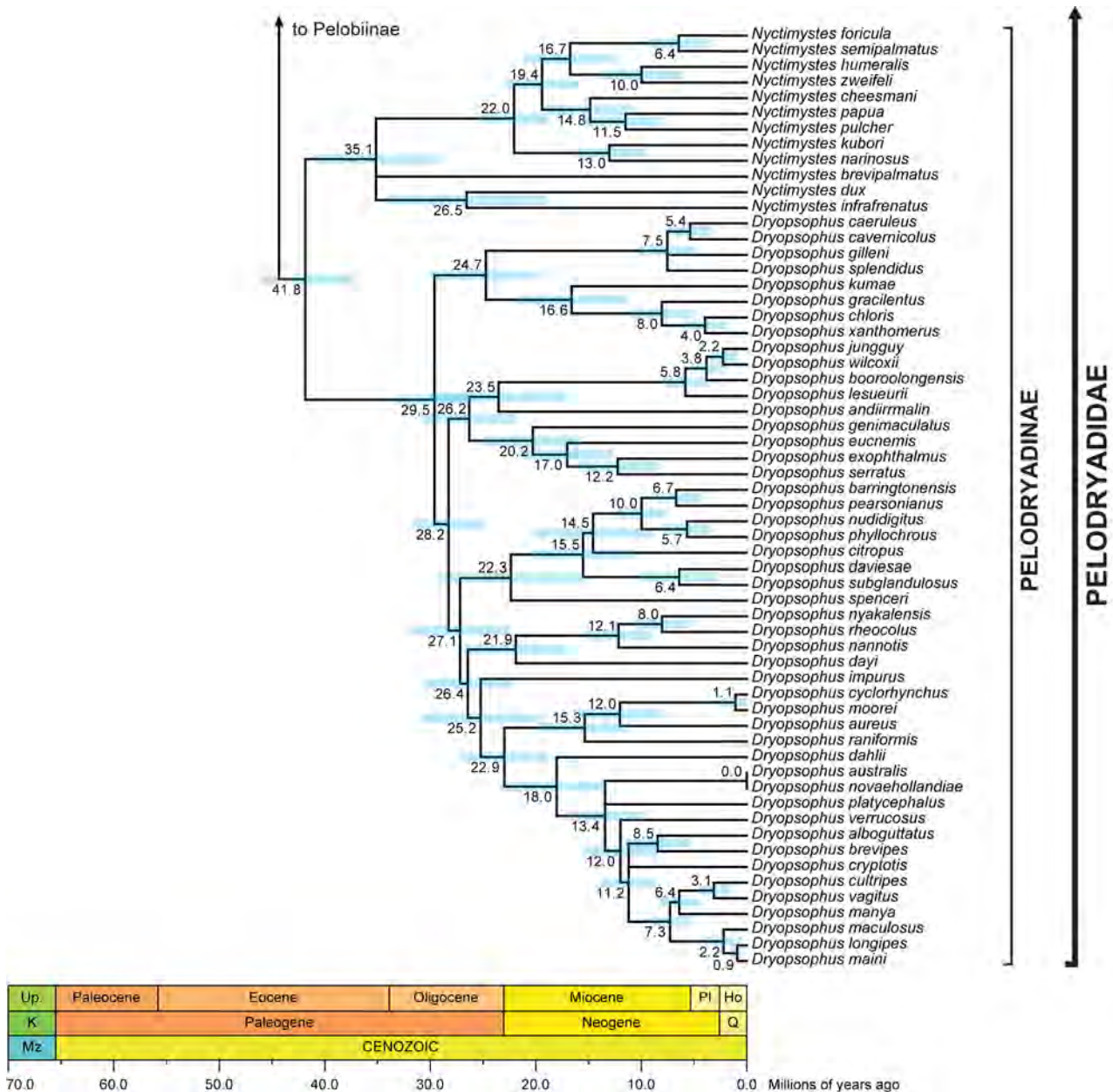


FIGURE 17. (Continued)

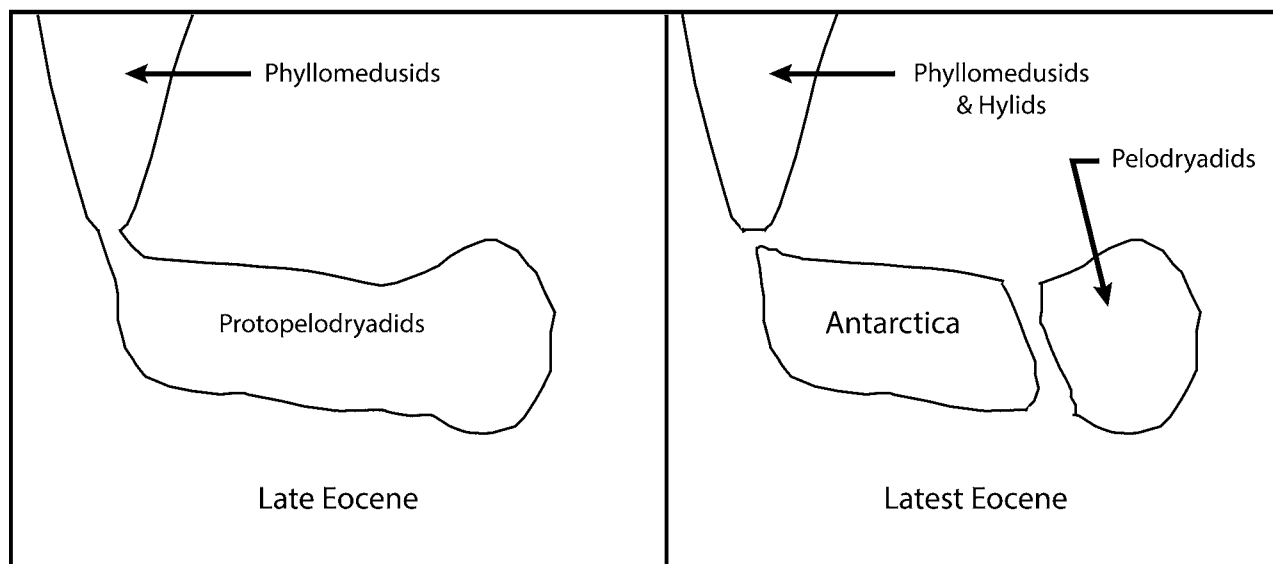
## Pelodryadidae

Tyler (1979:73) eloquently compared faunal relations between Africa and South America and those between that continent and Australia: “South America and Africa may be regarded as lovers who experienced and exploited a large zone of contact and had considerable opportunity for interchange and exchange across it. In contrast, the South American-Australian relationship suffered from being in the form of an arranged engagement of longer duration. The couple never so much as touched one another at any time. The only contact was via a related intermediary named Aunt Arctica, whose presence between them effectively prevented a comparable degree of intimacy, and who is now outwardly cool and distinctly secretive about revealing what took place between them.” So be it.

Although *Hyla meridionalis* now occurs in Mediterranean northwestern Africa, there is no evidence that hylid frogs ever existed in sub-Saharan Africa. These frogs originated in South America and dispersed from there to Australia and to North America. Ancestral Hylidae diverged from the phyllomedusid-pelodryadid clade in the

Paleocene 61.8 (57.5–66.1) Mya. The hylid clade retained the ancestral chromosome complement of  $2n = 24$ , whereas the number changed to  $2n = 26$  in the phyllomedusid-pelodyrid clade. Following the split of pelodyrid and phyllomedusid frogs at 52.5 (47.6–57.4) Mya, the initial divergence (crown node) of pelodyrid frogs occurred in the mid-Eocene 44.2 (40.1–48.3) Mya and that of phyllomedusid frogs was later, 33.3 (29.0–37.6) Mya. When South America separated from Antarctica 35.0–30.5 Mya, ancestral pelodyrid frogs were present on that continent and Australia before the latter separated from Antarctica 35.5 Mya (Fig. 18). Our analysis suggests that the differentiation of what are now Pelodyrinae and Pelobiinae occurred in the mid-Eocene and that the genera of pelodyrids differentiated (crown nodes) in the late Eocene and Oligocene: *Nyctimystes* 35.1 (29.3–40.8), *Litoria* 33.8 (28.9–38.7), *Dryopsophus* 29.5 (26.0–33.1) Mya.

Four major clades of *Litoria* already existed by the early Oligocene (31 Mya). Our limited taxon sampling of New Guinean *Litoria* precludes determination of possible centers of diversification in New Guinea and Australia; likewise, we have no genomic data that might indicate monophyly of the stream-breeding *Litoria* in Queensland. After its diversification from the clade leading to *Dryopsophus*, *Nyctimystes* was restricted to the humid northern part of Australia, which together with the collision of the plates and major uplifts in the Miocene, became New Guinea. Most species of *Nyctimystes* differentiated in the early to mid-Miocene (10–22 Mya). Some major clades of *Dryopsophus* originated in the mid- to late Oligocene (24–26 Mya). The clade containing the terrestrial species of *Dryopsophus* (formerly placed in the genus *Cyclorana*) inhabiting xeric to subhumid regions of Australia diverged in mid-Miocene times—13.4 (8.0–18.8) Mya, the time of major aridification in central and southern Australia.



**FIGURE 18.** Diagrammatic representation of dispersal routes and places of divergence of arboreal frogs in the Eocene.

### Phyllomedusidae

Meanwhile, in South America the first diversification within phyllomedusids took place in the Oligocene 33.3 (29.0–37.6) Mya when the *Cruziophyla-Phrynomedusa* ancestral stock departed from the early branching phyllomedusid ancestor. *Phrynomedusa* differentiated into five species in southeastern Brazil while *Cruziophyla* inhabited the western Amazon Basin and eventually entered Central America. The next major split in the phyllomedusid stock was the divergence of *Agalychnis* (crown node) in the latest Oligocene or earliest Miocene 23.4 Mya (18.6–28.3) Mya. While the major phyllomedusid stock remained in South America, *Agalychnis* differentiated in Central America (see below). Generic differentiation occurred in the Miocene, when *Callimedusa* diverged from *Pithecopus* 17.1 (14.8–19.3) Mya; the former differentiated in the Andes and upper Amazon Basin, whereas the latter evolved into nine species in eastern and northern South America. Ancestral *Phasmahyla* diverged from the *Pithecopus-Callimedusa-Phyllomedusa* stock 27.9 (24.1–31.7) Mya and evolved stream-dwelling tadpoles in southeastern Brazil. *Phyllomedusa* became a distinct lineage 18.2 (15.7–20.6) Mya and

subsequently differentiated into 15 species that collectively inhabit tropical and subtropical South America. Perhaps the most recent generic subdivision was *Hylomantis* in eastern Brazil from *Agalychnis* 25.4 (21.3–29.6) Mya.

## Hylidae

Six major lineages evolved within the Hylidae in the Eocene or earliest Oligocene (crown node times) in South America—Scinaxinae 49.2 (42.0–56.4), Cophomantinae 47.5 (38.0–57.0), Lophohylineae 37.2 (32.3–42.2), Hylinae 32.9 (30.2–35.6), Pseudinae 32.3 (25.8–38.7), and Dendropsophinae 31.9 (25.3–38.5) Mya. All genera except the West Indian *Osteopilus* are endemic to South America except for species that entered Central America.

### Hylidae: Scinaxinae

Our analysis suggests that in the late Eocene (~49 Mya) arboreal *Sphaenorhynchus* diverged from the ancestral scinaxines in the Atlantic Coastal Forest of Brazil. Our limited data suggest that the Brazilian and Amazonian clades of *Sphaenorhynchus* separated in the late Oligocene (~22 Mya). As the climate became drier and seasonal in southern South America in the early Oligocene (~34 Mya), the scinaxine stock diverged into *Julianus* in the southeastern part of the range, *Oolygon* in the Atlantic Coastal Forest, and *Scinax* in the Amazon Basin.

### Hylidae: Cophomantinae

Shortly after the origin of the clade herein referred to as cophomantines, an ancestral stock inhabited the early-uplifted western part of the continent (the proto Andes). This clade representing current *Colomascirtus*, *Hyloscirtus*, and *Myersiophyla* diverged (crown node) in the mid-Eocene 47.5 (38.0–57.0) Mya. These frogs inhabited streams, and their tadpoles developed large suction mouths with many rows of labial teeth as they dispersed through the ever-rising Andes. An early divergence (the crown node) in northern South America restricted *Myersiella* to the Guiana Highlands, whereas in the Andes in the early Oligocene *Colomascirtus* differentiated from *Hyloscirtus* 33.3 (29.3–37.3) Mya. Coloma *et al.* (2012) estimated the minimum divergence time of these events as 61.2 and 40.9 Mya, respectively. The latter inhabited low to moderate elevations, whereas *Colomascirtus* came to inhabit streams at higher elevations.

The other major clade within Cophomantinae subsequently diverged into two lineages in the late Eocene, 36.8 (32.8–40.8) Mya. One clade consisted solely of *Bokermannohyla*, which inhabited the mountains of southeastern Brazil and developed stream-adapted tadpoles. In the other clade, a lowland lineage, *Hypsiboas*, differentiated from a highland group, *Aplastodiscus* with stream-adapted tadpoles, in the late Eocene, 34.2 (30.9–37.5) Mya.

The earliest divergence within *Hypsiboas* occurred in the mid-Oligocene 31.9 (28.4–35.5) Mya when a large group of species (*H. benitezi*–*H. sibleszi*) occupied northeastern South America including the Guiana Highlands. Differentiation of most clades of *Hypsiboas* occurred in the Miocene. For example, the long-legged tree frogs of the *Hypsiboas albopunctatus* Group differentiated about 17.4 (14.0–20.8) Mya in the Amazon Basin and dispersed into coastal Brazil. Likewise, the ancestral large, arboreal frogs in *Hypsiboas albomarginatus* Group diverged about 19.2 (15.4–22.9) Mya. Other species groups are more recent. For example, the clade of Andean species in the *Hypsiboas balzani* Group differentiated in the Pliocene about 5.0 (3.8–6.1) Mya. Similarly, the Pliocene was the time of divergence of the ancestral stock of the *Hypsiboas pulchellus* Group, 5.7 (4.8–6.5) Mya that came to inhabit subtropical highlands from Bolivia to southern Brazil.

### Hylidae: Lophohylineae

Another clade of arboranans now designated Lophohylineae originated (crown node) in the late Eocene, 37.2 (32.3–42.2) Mya. Based on present distributions, lophohylineae originated in the Amazon Basin and subsequently



dispersed into eastern Brazil, the Guianan Region, and the West Indies. An early divergence (the crown node) led to the evolution of *Phyllodytes* in eastern Brazil and *Phytotriades* in Trinidad. A major split in the Lophyohylineae occurred in the late Eocene, 34.6 (30.8–38.4) Mya. The first clade contained ancestral *Trachycephalus*, which became widespread in the American tropics and differentiated into 14 species. The earliest divergence from the ancestral *Trachycephalus* was the differentiation of *Itapotihyla* in the latest Eocene, 33.2 (26.8–39.6) Mya; the single species inhabits the Atlantic Coastal Forest in Brazil. *Itapotihyla* is like some species of *Trachycephalus* in having a casque head. In what is now subhumid regions of northeastern Brazil, the casque-headed, bromeliad-dwelling *Corythomantis* diverged from *Trachycephalus* in the Oligocene, 28.4 (22.6–34.2) Mya. Another clade of casque-headed species diverged (crown node) in the early Miocene, 20.0 (15.4–24.6) Mya; these included the ancestors of *Aparasphenodon* in the upper Orinoco Basin and coastal Brazil, *Argenteohyla* in northeastern Argentina, and *Nyctimantis* in the upper Amazon Basin.

The second major clade of lophyohylineae split into two clades in the early Oligocene, 31.9 (28.2–35.5) Mya. One of these clades became *Osteopilus* (see below). The other divided into three modern genera, diverging 25–28 Mya. This led to *Dryaderces* (single species represented), with two species in the Amazon Basin and on the lower slopes of the adjacent Andes; *Osteocephalus* in the Miocene, 18.2 (15.5–20.9) Mya (crown node) with 23 species in the Amazon Basin, lower slopes of the Andes, and the Guianan Region; and *Tepuihyla* also in the Miocene, 16.5 (12.8–20.3) Mya (crown node) with seven species in the Guiana Highlands.

### Hylid Frogs in the Greater Antilles

The West Indian frogs of the genus *Osteopilus* began differentiating (crown node) in the early Miocene 21.7 (17.3–26.1) Mya. The original colonist or colonists dispersed over-water on flotsam. This timing coincides with the major drainage of the Amazon Basin being to the north into the Caribbean. Our dates are older than the date of 10 Mya sometimes used for the earliest land areas in Jamaica (Donovan 2002), although that date is debated (e.g., Iturralde-Vinent & MacPhee 1999).

The calculated times of speciation of geographic lineages in *Osteopilus* are Miocene events. The earliest divergence was between Cuba and the other Antilles; this divergence of *Osteopilus septentrionalis* (Duméril and Bibron) was at about 21.7 (17.3–26.1) Mya. This was followed by the large Hispaniolan *O. vastus* (Cope) about 20.7 (16.8–24.7) Mya. The Hispaniolan and Jamaican clades differentiated about 18.8 (16.1–21.5). The Hispaniolan clade differentiated into *O. dominicensis* (Tschudi) and *O. pulchrrilineatus* (Cope). The Jamaican clade differentiated into two large species, *O. crucialis* (Harlan) and *O. ocellatus* (Linnaeus), and two small species, *O. marianae* (Dunn) and *O. wilderi* (Dunn).

The existing Antillean hylid fauna contains one other species, *Hypsiboas heilprini* (Noble) that is confined to Hispaniola. We determined that this species diverged from its closest relatives in South America in the late Oligocene, 25.4 (20.2–30.5) Mya, restricting the dispersal event (over-water, on flotsam) to the Caribbean islands, after that time.

### Hylidae: Dendropsophinae

Another major branch of neotropical hylids, the dendropsophines, split from the pseudinines in the Eocene, 44.9 (39.1–50.8) Mya, and began diversifying (crown node) in the early Oligocene, 31.9 (25.3–38.5) Mya. Initially, this group split into a clade containing two small species in the genus *Xenohyla* confined to coastal Brazil and the speciose genus *Dendropsophus*, which occurs throughout tropical South America northward to Mexico and is unique among hylids in having a chromosome complement of  $2n = 30$ .

Several major clades are identifiable within *Dendropsophus*; some of these have defined geographic limits, whereas others are widespread geographically. Among the latter are the *D. marmoratus* Group inhabiting the Amazon Basin, Guiana Region, and the Atlantic Coastal Forest, and the *D. leucophyllatus* Group ranging throughout the Amazon Basin, Guiana Region, and northward to tropical Mexico. These groups evolved in the mid-Miocene; their ages are 17.0 (12.9–21.1) Mya and 18.7 (15.7–21.6) Mya, respectively. Another large group of small species principally inhabiting the Atlantic Coastal Forest but also occurring in the Amazon Basin and Guiana Region is the *D. bipunctatus* Group, which also diverged in the mid-Miocene, 14.9 (10.7–19.1) Mya.

Among the groups with relatively small, defined ranges are the *D. labialis* Group in the northern Andes and the *D. microcephalus* Group in Mexico and Central America. These groups originated later in the Miocene; their ages (crown node times) are 9.6 (6.8–12.3) Mya and 11.2 (8.6–13.7) Mya, respectively.

### **Hylidae: Pseudinae**

In the early Oligocene, 32.3 (25.8–38.7) Mya, the crown node time of this subfamily, a clade of aquatic and semiaquatic frogs with elongate, calcified intercalary elements in the digits gave rise to the semiaquatic *Scarthyla* in the upper Amazon Basin. The major component of the pseudine clade differentiated into the smaller *Lysapsus* and the larger *Pseudis* in the early Miocene about 21.5 (18.4–24.6) Mya. Both genera have broad distributions in the Guiana Region and tropical and subtropical South America east of the Andes.

### **Hylidae: Hylinae**

The divergence of North and Middle American hylid frogs from their relatives in South America was in the early Oligocene, 32.9 (30.2–35.6) Mya. Thus, hylid frogs were in Middle America in the early Miocene. Differentiation (crown node times) of the various genera occurred throughout the Miocene—as early as 26.1 Mya for the origin of *Megastomatohyla* to 13.1 Mya for the origin of *Exerodonta*. A major geographic divergence occurred in the early Miocene, 23.9 (22.3–25.6) Mya, when the clade now known as the Holarctic hylines diverged from the tropical hylines.

The geological uplifts and volcanism in Mexico and Central America began in the late Cretaceous and continues to the present. Only three clades of lowland inhabitants exist in the Middle American tropics; these are in a major clade that also includes *Isthmohyla*, which has stream-adapted tadpoles. The three lowland clades radiated (crown node times) in the mid-Miocene—*Smilisca* 13.2 (10.6–15.9) Mya, *Tlalocohyla* 15.5 (13.0–18.1) Mya, and a casque-headed clade (*Anothea*, *Diaglena*, and *Tripriion*) 14.3 (11.2–17.4) Mya. Slightly later the last clade differentiated into *Diaglena* and *Tripriion* in xeric lowland habitats with tadpoles developing in temporary ponds, and the cloud forest-inhabitant, *Anothea*, with tadpoles developing in tree holes. All species of *Tlalocohyla* range in the lowlands of Mexico; one species extends as far south as Costa Rica. *Smilisca* consists of six species ranging throughout Central America and tropical Mexico.

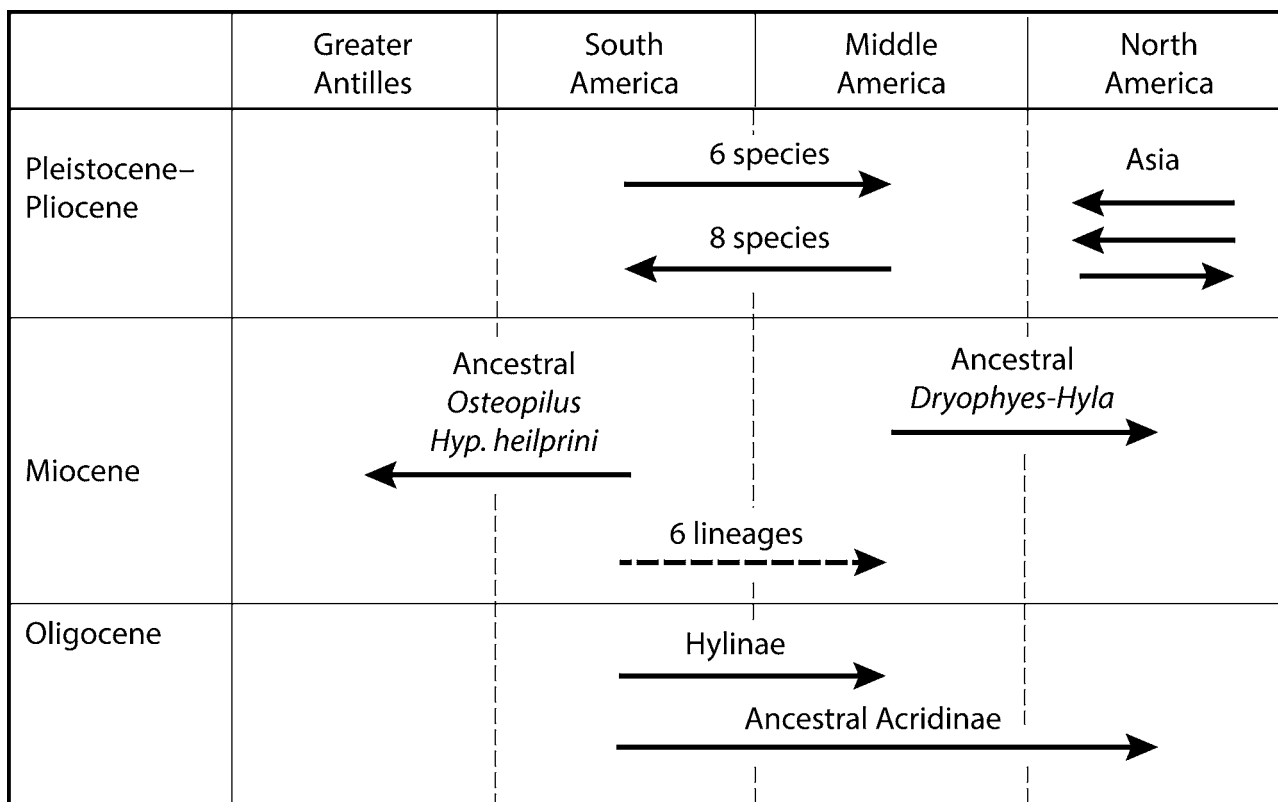
Currently there are 108 species of stream-breeding hylids in nine genera endemic to Middle America. The small stream-breeding *Rheohyla* diverged from the clade that became the large, arboreal hylines in the earliest Miocene, 23.0 (17.8–28.2) Mya. The fringe-limbed tree frogs of the genus *Ecnomiohyla* have disjunct distributions from Oaxaca, Mexico, through Panama, whereas *Rheohyla* occurs only in Mexico west of the Isthmus of Tehuantepec. Nested within the clade of inhabitants of Middle American lowlands is the stream-breeding *Isthmohyla*, which consists of 15 species ranging discontinuously in highlands from Honduras to central Panama. *Isthmohyla* diverged from ancestral *Smilisca* in the early Miocene, 21.4 (18.7–24.1) Mya. All other stream-breeding hylids belong to one major clade. Two of these clades possibly diverged in the late Oligocene. *Megastomatohyla* split with *Charadrahyla* about 26.1 (20.5–31.7) Mya in the Mexican highlands. The crown node time of the clade containing the genera *Bromeliohyla*, *Duellmanohyla*, and *Ptychohyla*, species occurring in the Central American highlands, is about 17.4 (14.9–19.9) Mya. These genera of yet undetermined affinities contain two bromeliad-breeding species in the genus *Bromeliohyla* and *Duellmanohyla* with eight species inhabiting the Central American highlands. That region is also inhabited by *Ptychohyla* with 13 species, some of which occur in southern Mexico.

The Isthmus of Tehuantepec in southern Mexico seems to have played a significant role in the differentiation and distribution of genera of stream-breeding hylines. *Exerodonta* split from the *Plectrohyla-Sarcohyla* lineage in the late Oligocene 27.5 (23.7–31.3) Mya. *Exerodonta*, which radiated (crown node time) in the mid-Miocene 13.1 (10.4–15.8) Mya, inhabits cloud forest and pine-oak forests at elevations of 450–2160 m; nine species occur west of the Isthmus of Tehuantepec and two live east of the isthmus. Likewise in the mid-Miocene, 15.7 (11.5–19.9) Mya, *Charadrohyla* was diversifying in the streams in southern Mexico, where five species live today; one other species occurs in Chiapas to the east of the Isthmus of Tehuantepec. The most striking example of diversification

on opposite sides of the isthmus is *Plectrohyla* (18 species) in the northern Central American highlands to the east of the isthmus and *Sarcohyla* (24 species) in the Mexican highlands to the west of the isthmus. They split in the early mid-Miocene 18.6 (18.6–15.9) Mya. The times of diversification of ancestral stocks on either side of the isthmus coincide with the volcanism in the Miocene that elevated nuclear Central America and southern Mexico.

### The American Interchange

In summarizing the herpetofaunal exchange between North and South America, Estes and Báez (1985:170) lamented: “We are left, then, with relatively little direct evidence from the fossil record of the Cenozoic interchange between North and South America. That such interchange occurred, however, in some cases extensively, has been amply demonstrated by the neontological record.” In the succeeding 30 years the fossil record has revealed little of interest, but the dating of evolutionary events as evidenced by molecular data provides us with a new perspective on the interchange. As noted previously, the timing of the divergence North and Middle American hylid frogs from their relatives in South America took place in the early Oligocene, 32.9 (30.2–35.6) Mya. Thus what are now the Middle American and Holarctic genera of Hylidae originated on the North American landmass while it was separated from South America.



**FIGURE 19.** Geographic dispersal and divergence of arboranan frogs between various land masses in the Tertiary and Quaternary. The six lineages from South America to Middle America are one *Agalychnis*, two *Dendropsophus*, one *Hyloscirtus*, and two *Scinax*.

However, there were other invasions of South American lineages into Central America (Fig. 19). Times of divergence suggest that several lineages had reached Central America prior to the Miocene. The Middle American clade of the *Dendropsophus microcephalus* Group split from its South American relatives in the mid-Miocene 11.2 (8.6–13.8) Mya, somewhat later than the divergence of the Middle American *D. ebraccatus* Cope from its South American relatives—14.3 (11.3–17.3) Mya. In the mid-Miocene the Middle American clade of *Agalychnis* diverged from its South American relatives—10.1 (7.9–12.3) Mya. Also in the mid-Miocene two Middle American species of *Scinax* [*S. elaeochrous* (Cope) and *S. staufferi* (Cope)] split from one another 16.3 (12.0–20.7) Mya. The times of all of these divergences are after the disconnection of the continents in the late Eocene and before the

reconnection of the continents in the Pliocene. Even the maximum times fall short of the Eocene. Unless new geological evidence would show the existence of a land bridge between the continents in the Miocene we are forced to suggest strongly that these five lineages (one *Agalychnis*, two *Dendropsophus*, and two *Scinax*) reached Central America from South America by over-water dispersal.

In addition to the divergence of Middle American species of *Scinax* in the Miocene, three other South American lineages dispersed from South America into Central America in the Miocene. Two of these are species pairs of *Hyloscirtus*, of which the Central American *H. colymba* (Dunn) split from the ancestor to *H. alytolylax* (Duellman) and *H. simmonsii* (Duellman) 21.9 (16.7–27.1) Mya. Also the Panamanian *H. palmeri* (Boulenger) split from the South America *H. lascinius* (Rivero) 21.0 (6.5–35.5) Mya. Four members of the *Dendropsophus microcephalus* Group radiated in Middle America. The major divergence was in the mid-Miocene, 11.2 (8.6–13.8) Mya followed by the split between *D. robertmertensi* (Taylor), and *D. sartori* (Smith) in the Pliocene 4.5 (3.0–6.0) Mya. The largest radiation of a South American group in Central America is that of *Agalychnis*, which also has four species endemic to northwestern South America. Among the Central American taxa, the most morphologically different species diverged from the ancestral lineage first—the small, montane *A. lemur* (Boulenger) in the early Miocene 21.9 (17.4–26.3) Mya and *A. dacnicolor* (Cope) in the mid-Miocene 14.2 (11.3–17.2) Mya. *Agalychnis callidryas* became widely distributed in tropical rainforest from Mexico to Panama, whereas *A. moreletii* and *A. annae* came to be isolated in highlands of nuclear Central America and Costa Rica, respectively.

After the collision of Central America and South America and the formation of the Panamanian Land Bridge between the Chocó and Central America, in the Miocene, the lengthy paleopeninsula extending southward from lower Central America throughout much of the Cenozoic became the trans-Andean Chocoan lowlands of Colombia and northwestern Ecuador. *Scinax boulengeri* (Cope) and its sister-species, *S. sugillatus* (Duellman) in the Pacific lowlands of Ecuador and Colombia, split from other living species of *Scinax* in the mid-Miocene 13.3 (9.0–17.6) Mya. Also, *Hypsiboas pellucens* (Werner) that now exists in Ecuador and southern Colombia split from the Panamanian *H. rufitelus* (Fouquette) in the early Pliocene, 5.3 (3.6–7.1) Mya. This distribution pattern of species in tropical rainforests in lower Central America and Chocoan South America is exhibited by the hylids *Hypsiboas rosenbergi* (Boulenger) and *Smilisca phaeota* (Cope) and phyllomedusids *Agalychnis spurrelli* (Boulenger) and *Cruziohyla calcarifer* (Boulenger), as well as *Dendropsophus ebraccatus*, *Scinax elaeochrous*, *Agalychnis psilopygion*, and *Ecnomiohyla phantasmagoria*, although molecular data are lacking for the latter. The same pattern exists among taxa in other families.

Only three species of Middle American hylid genera entered South America after the Pliocene reconnection of the continents. All are members of the genus *Smilisca*—*S. phaeota*, which, as noted above, has a Chocoan distribution. *Smilisca sila* Duellman and Trueb and *S. sordida* Peters inhabit highlands in Costa

Rica and Panama and northern foothills of the Andes in Colombia; presumably they immigrated to South America during a glacial period in the Pleistocene.

Aside from the earlier invasion of Central America by South American ancestors, many South American taxa have dispersed northward. The greatest distribution is that of *Trachycephalus typhonius* (Linnaeus), which occupies all of tropical Middle America. All others also are inhabitants of tropical lowlands. Two species, *Hypsiboas pugnax* (Schmidt) and *Scinax rostratus* (Peters), inhabit subhumid areas in northern South America and Panama. The Middle American occupancy by four other species consists solely of eastern Panama. Of these, *Hypsiboas boans* (Linnaeus), *H. crepitans* (Wied-Neiwied), and *Scinax ruber* (Linnaeus) have extensive distributions in tropical South America. *Dendropsophus subocularis* (Dunn) inhabits northern Colombia and eastern Panama.

## Holarctic Hylinae

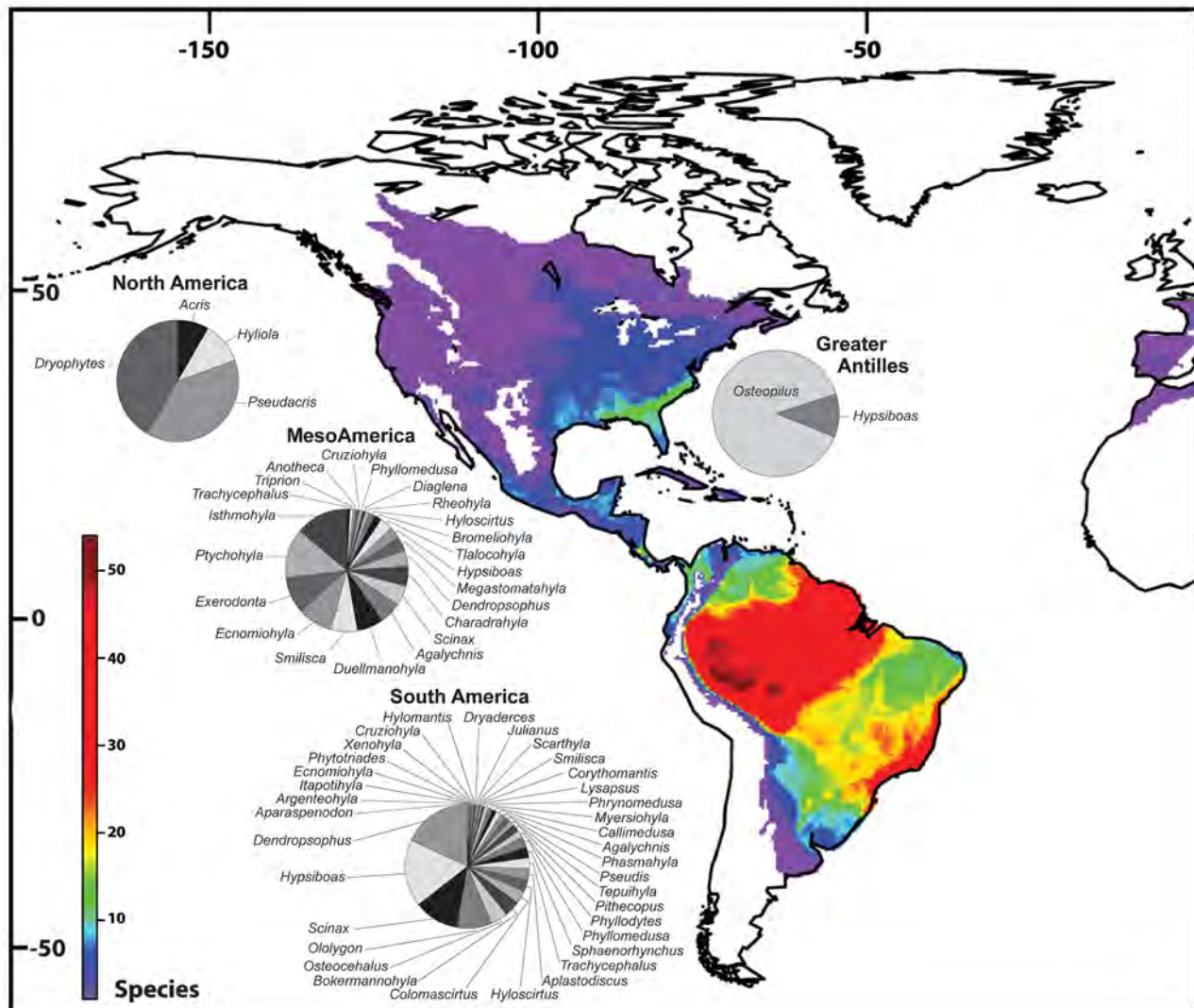
The predominantly Eurasian *Hyla* split from the predominantly North American *Dryophytes* in the Miocene, 22.6 Mya, with the former genus dispersing throughout Eurasia. Subsequent aridification of much of central Asia resulted there in a western clade of eight species of *Hyla* in what is now Europe and southwestern Asia and a far-removed eastern clade in temperate and subtropical southeastern Asia.

Also in the mid-Miocene 15.4 (13.6–17.3) Mya, the clade that remained in North America differentiated genetically, and evolved into what is recognized as *Dryophytes*, which occurs throughout temperate eastern North



America. Our analysis shows that a stock of *Dryophytes* dispersed westward across the Bering Land Bridge to Asia in the late Miocene 8.7 (6.6–10.9) Mya. This stock differentiated into three species in eastern Asia (including Japan), the *Dryophytes immaculatus* Group. The closest relatives of this group, the *Dryophytes eximius* Group, principally inhabited the pine forests from southwestern United States to Guatemala.

Thus there were two dispersals of hylid frogs across the Bering Land Bridge; temporally these are: (1) *Hyla* from east to west, and (2) *Dryophytes* from west to east. In contrast to their Middle American relatives, no lineage of hylines in North America inhabited streams, a habitat that is plentiful in the Appalachian, Rocky, and Sierra Nevada mountain ranges, among others.

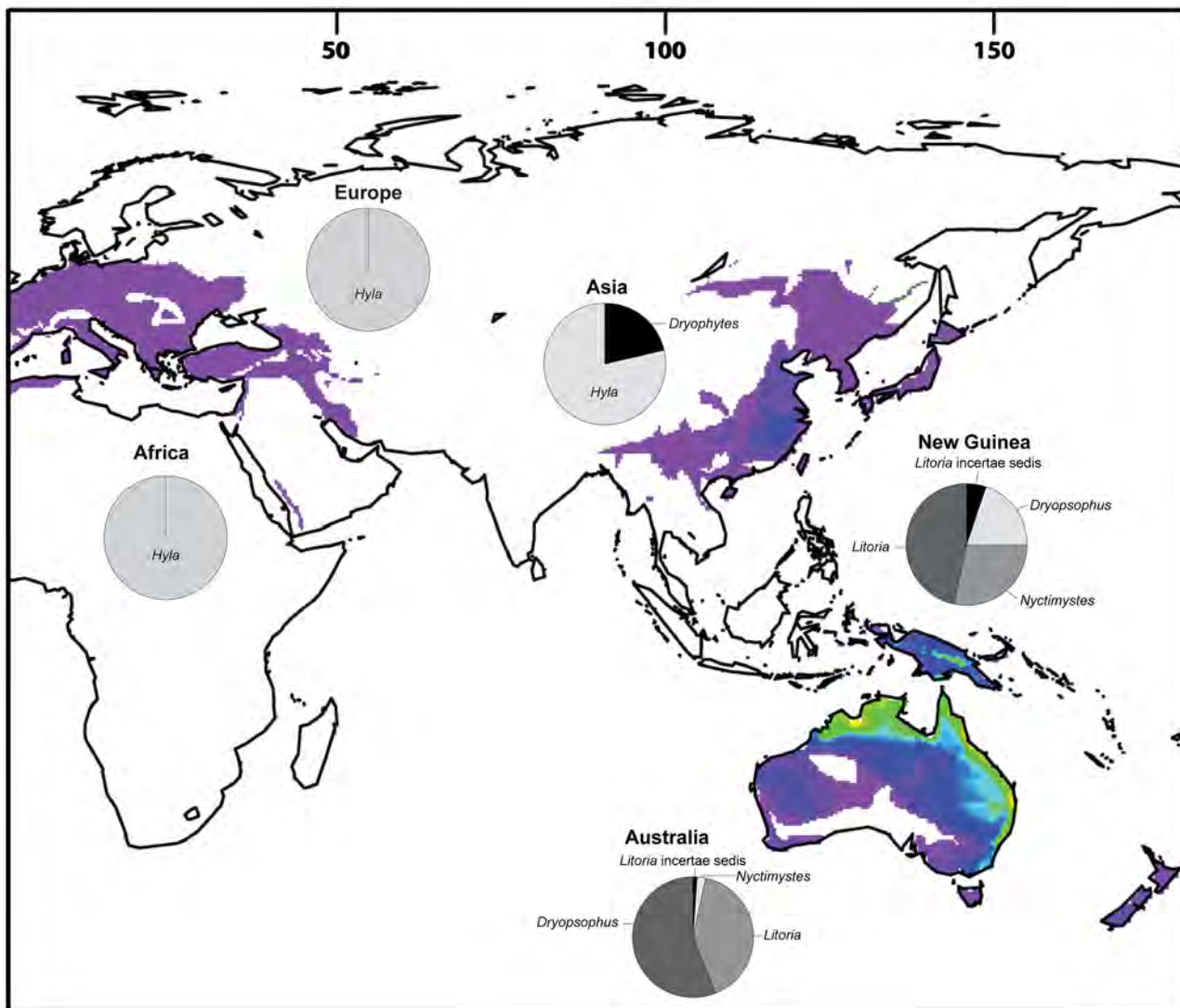


**FIGURE 20.** Map of the New World showing species density of arboranan frogs (color), with white areas representing 0–1 species; range data are from IUCN (2014). Pie diagrams show the proportion of species in each genus, by geographic region. The border between North America and Mesoamerica is the Isthmus of Tehuantepec in southern Mexico.

## Acridinae

The acridines split from the hylines in the late Eocene, 35.6 (32.8–38.4) Mya, followed by radiation in North America beginning in the early Oligocene 30.3 (26.1–34.5) Mya. Thus, there was a second invasion of North America from South America by arboranans. Interestingly, there are no living relatives of North American acridines in Middle America. This North American lineage diverged into two clades in the early Miocene, 30.3 (26.1–34.5) Mya. One of these clades lost a pair of chromosomes to have a complement of  $2n = 22$  and became the semiaquatic *Acris*. The timing is consistent with the Lower Miocene fossil, *Proacris* (Holman, 1961).

The second clade of terrestrial frogs includes *Pseudacris*, which began to radiate (crown node) in the early Miocene, 22.5 (19.6–25.5) Mya. The uplift of the Rocky Mountains and Sierra Nevada Range with the intervening arid Great Basin in the mid-Miocene resulted in vicariance of the *Pseudacris* clade. A closely-related clade west of the mountains, *Hyla*, began to radiate by mid-late Miocene, 11.8 (8.0–15.6) Mya.



**FIGURE 21.** Map of the Old World showing species density of arboranan frogs (color), with white areas representing 0–1 species; range data are from the IUCN (2014). Pie diagrams show the proportion of species in each genus, by geographic region.

### Species Density and Endemism

The evolutionary events of arboranan frogs during the Cenozoic resulted in distribution patterns and geographic regions of high density (Figs. 20–21). The regions having the highest densities in South America are much the same as for all amphibians shown by Duellman (1999). The largest numbers of hylids are in the Amazon Basin and the Atlantic Coastal Forest in Brazil, followed by the mountains in Middle America and those in New Guinea. Many new species are being discovered in the highlands of New Guinea (e.g. Menzies, 2014) and in the Brazilian highlands and the Andes (e.g., Guayasamin *et al* 2015). These discoveries and several studies in process will continue to increase the species density in these humid montane forests, but the number of taxa in the Amazon-Guiana Region also will increase. Molecular studies are revealing that some widespread species in this region actually are composites—e.g., *Hypsiboas* (Caminer & Ron 2014); *Dendropsophus minutus* (Gehara *et al.* 2014).

Likewise, studies of *Osteocephalus* by Jungfer *et al.* (2013) revised the systematics of the genus and revealed nine putative new species. It is doubtful if these “hot spots” will diminish in importance as the number of species (and densities) continues to grow.

The hylid fauna of South America consists of 505 recognized species in 27 genera. There are four large genera—*Dendropsophus* (92 species), *Hypsiboas* (88 species), *Oloolygon* (46 species), and *Scinax* (62 species). These four genera with a total of 288 species make up 56.8% of the hylid fauna in South America. On that continent there are five genera of stream-breeding hylids. Two of these are in the Andes—*Colomascirtus* (17 species) and *Hyloscirtus* (18 species); two in the Atlantic Coastal Forest in Brazil—*Aplastodiscus* (15 species) and *Bokermannohyla* (32 species); and *Myersiohyla* with six species in the Guiana Highlands. These 98 species account for only 19.3% of the hylid fauna in South America. In contrast, the percentage of stream-breeding hylid frogs in South America is much lower than in Mesoamerica and the Mexican portion of North America where 52 of the 87 species (59.8%) and 42 of 56 species (75.0%), respectively, are stream-breeders.

## Biogeographic Summary

- The tree frog (Arboranae) clade diverged from its nobleobatrachian relatives in South America during the latest Cretaceous or early Cenozoic.
- Differentiation of arboranans into the three families (Hylidae, Pelodyadidae, and Phyllomedusidae) occurred in South America during the early Cenozoic.
- Ancestral Hylidae diverged from the phyllomedusid-pelodyadid clade in the late Paleocene.
- Divergence of phyllomedusids and pelodyadids occurred in the mid-Eocene.
- When South America separated from Antarctica 35.0–30.5 Mya, ancestral pelodyadid frogs were present on Antarctica and Australia before they separated about 35.5 Mya.
- In the Australo-Papuan Region the genera of pelodyadids differentiated during the Eocene and Oligocene.
- In tropical South America, the genera of phyllomedusids differentiated in the Miocene and Oligocene.
- In South America differentiation of the major clades (subfamilies) of Hylidae took place in the Eocene to early Oligocene.
- In South America most genera differentiated in the Eocene and Oligocene.
- Middle American hylids diverged from their South American relatives in the early Oligocene.
- Four major lineages of South American arboranans (Phyllomedusidae, Dendropsophinae, Hyliinae, Scinaxinae) invaded Central America in the mid-Cenozoic, before the Pliocene connection of the continents.
- Many South American species entered Central America after the formation of the Panamanian Land Bridge in the mid-Pliocene, but only three species of Middle American origin (*Smilisca*) invaded South America.
- Generic differentiation of hylines in Middle America occurred in the late Oligocene and Miocene.
- Two ancestral clades reached North America. The first became the Acridinae restricted to temperate North America. The second was the hyline stock ancestral to *Dryophytes* in North America and eastern Asia and *Hyla* in Eurasia.
- Regions of highest hylid diversity are the Amazon Basin and the Atlantic Coast Forest in Brazil.

## Discussion

**Phylogenetic Analyses.** Some recent molecular clock analyses of amphibians (Pyron 2014; Pyron & Wiens 2013; Wiens 2011) inferred older divergence times than did this study. Comparison of the ages of key nodes (families, subfamilies, and some genera) from this analysis to comparable nodes in Pyron (2014) revealed, on average, a 28% difference (up to 57% older and 29% younger). In this analysis, we found the base of Arboranae to be 61.8 (57.5–66.1) Mya, whereas other authors obtained older dates of ~67 Mya (Wiens 2011), 71.1 (Pyron and Wiens 2013), and 70.7 (Pyron 2014) for the same node, a modest difference of about 15%.

Inconsistencies in time estimates may result from differences in taxon sampling, phylogeny, sequences used, and timing methodology. Two previous studies (Pyron 2014; Pyron & Wiens 2013) used the phylogeny from Pyron and Wiens (2011), inferred using a 34-partition scheme of stems and loops (for two ribosomal genes) and codon

positions (for each of ten protein-coding genes). Differences in taxon sampling and sequences used by Pyron and Wiens (2011) are detailed above. In the current study, we partitioned by gene only, for a total of 19 data partitions, although like Pyron and Wiens (2011), we performed phylogenetic inference with RAxML and the same model (GTRGAMMA) for all partitions. Wiens (2011) performed phylogenetic inference on a much smaller sample of amphibian taxa (including only 23 arboranans), using only the RAG-1 gene, partitioned by codon position and analyzed with RAxML.

Wiens (2011) estimated dates of divergence using penalized likelihood (r8s). He calibrated 25 nodes throughout his amphibian tree, including the split between Pelodyadidae and Phyllomedusidae (28 Mya min; Sanmartin & Ronquist 2004). From those results, Pyron (2014) and Pyron and Wiens (2013) designed constraints for their penalized likelihood dating analyses. That is, based on the results of Wiens (2011), they placed fixed-age constraints on particular nodes throughout their large amphibian tree, including a constraint of 73.53 Mya on the most recent common ancestor of Arboranae (“Hylidae”), Bufonidae, and other families. In the current study, we used the maximum likelihood method RelTime (Tamura *et al.* 2012) with three nodes calibrated (a total of two minimum and two maximum calibrations). As described above, our results were younger, on average, than those produced in the three studies discussed (Wiens 2011; Pyron & Wiens 2013; Pyron 2014).

In summary, the major difference among published studies of these amphibians, in terms of times of divergence of clades, involves the node at the base of the hyloid radiation, which was an event that almost certainly occurred in South America. Researchers that have estimated that node to be prior to the end-Cretaceous impact event (Wiens 2011; Pyron & Wiens 2013; Pyron 2014) have used assumptions and constraints to obtain the early age whereas researchers that have obtained younger dates (e.g., Roelants *et al.* 2007; Bossuyt & Roelants 2009; Heinicke *et al.* 2009; this study), have not used such constraints, lending support to the younger dates being most likely correct. The significance of such a late date for this major South American expansion of hyloid frogs, compared with the timing of frog radiations on other continents (Roelants *et al.* 2007), is not fully understood, but might be tied to the end-Cretaceous impact event. Tsunamis and local destruction were likely more severe in the New World, close to where the asteroid hit, pruning much of the existing diversity of hyloid frogs.

**Classification.** Few, if any, classifications of large groups of organisms are perfect. Ours is no exception. In the phylogenetic tree some species do not appear where expected. Although incomplete taxon sampling may influence the position of a given taxon on the tree, more likely it is because of insufficient or incorrect genomic data or misidentifications. However the major example in our classification is the placement of *Litoria infrafronata* (*auctororum*) in the genus *Nyctimystes*. This enigmatic species is unique among pelodyadids in having  $2n = 24$  chromosomes (Menzies & Tippet 1976); otherwise, it is like most members of the genera *Dryopsophus* and *Litoria* in having generalized tadpoles developing in lentic water (Anstis 2013). *Litoria infrafronata* lacks the vertical pupil and pigmented reticulations on the lower eyelid that are characteristic of *Nyctimystes*, the tadpoles of which have enlarged sectorial mouths and develop in lotic water (Zweifel 1958). In our analysis, “*Litoria infrafronata*” clearly is categorized as a *Nyctimystes*. The only genes for which all *Nyctimantis* are covered are 12S & 16S; and both of these genes place *N. infrafronatus* with *N. dux*. These two species are outliers of the other species of *Nyctimystes*. Morphologically *N. dux* is most similar to *Litoria graminea* and *L. sauroni* (Richards & Oliver 2006); genetic data are not available for those two species. Obviously this seemingly taxonomic dilemma exists because of lacking genomic data on the presumed relatives of *N. dux* and the absence of data on nuclear genes of all of the species concerned. Additional molecular data may help to clarify the taxonomic placement of *L. infrafronata*.

**Biogeography.** In his major work on biogeography of southern lands, Darlington (1965) maintained the Matthewsian approach of continental stability. But the same year Brundin’s (1965) seminal biogeographic paper based on the phylogeny and distribution of chironomid midges emphasized the significance of Antarctic to Gondwanan biogeography.

Our analysis supports a trans-Antarctic dispersal of arboranans from South America to Australia, resulting in the Pelodyadidae undergoing extensive diversification in the Australo-Papuan Region. There is no evidence to support Pyron’s (2014:793) contention that Pelodyadids arrived in Australia by a “trans-Pacific dispersal event from South America to Australasia approximately 91–52 Ma.” A trans-Antarctic dispersal event is even more evident for two sister taxa (Pyron & Wiens 2011), the South American Calyptocephalellidae and the Australian Myobatrachidae. The fossil record supports Wiens’s (2007) suggestion that these two families diverged in the late Cretaceous. Fossil *Calyptocephalella* are known from the Eocene to the Miocene in Argentina (Muzzoppapa & Báez 2009). Four living genera of myobatrachids are represented in the Australian fossil record: *Lechriodus* in the



Lower Eocene to Upper Miocene, *Limnodynastes* mid- to late Miocene, *Neobatrachus* Upper Miocene to Lower Pliocene, and *Philora* Upper Oligocene to Upper Miocene (Sanchiz 1998b). The earlier calibrated events proposed by Pyron and Wiens (2011) are even more supportive of trans-Antarctic dispersal than are our calibrations. Ancestral pelodyadids and myobatrachids had to have existed on Antarctica for millions of years, during which time they probably diversified in the mild climatic conditions that prevailed in the Cretaceous and Paleogene (Poole & Cantrill 2006).

These two lineages of frogs are not the only taxa that crossed Antarctica. For example, while restricted today to temperate South America, Australia, Tasmania, New Guinea, New Zealand, and New Caledonia, the southern beech trees of the genus *Nothofagus* (Nothofagaceae) underwent their major radiation 55–40 Mya and dispersed across Antarctica (Cook & Crisp 2005). Likewise, ancestral groups of marsupials dispersed from South America, via Antarctica, to Australia in the late Cretaceous or early Paleocene (Beck *et al.* 2008); these authors also suggested that South American microbiothere marsupials are the result of a back dispersal from eastern Gondwana (Antarctica and Australia). Chelid turtles are known from the early Cretaceous to the Recent in Australia and South America (de la Fuente *et al.* 2014); they dispersed via Antarctic from South America to Australia.

The intermittent connections between South America and Central America, the so-called Isthmian Link, have provided the highway for the “Great American Interchange,” an event of monumental significance to the American biota. We have determined that there have been at least six invasions of hylid frogs into Central America from South America prior to the current connection of the continents. Similarly, there have been two invasions of toads of the genus *Bufo* (*sensu lato*) (Pauley *et al.* 2004). The first of these, *Anaxyrus*, is the biogeographic equivalent of the Nearctic hylid genus *Dryophytes*, whereas the second, *Incilius*, is the Middle American equivalent of the numerous genera of hylines in tropical Mexico and Central America. *Rhinella marina* (Linnaeus) apparently is a Plio-Pleistocene invader like the hylid *Trachycephalus typhonius* (Linnaeus); both species are widespread in tropical and subtropical environments throughout Middle America, as well as South America.

In tropical America the largest group of frogs is Terraranae containing nearly 1000 species of direct-developing frogs (Hedges *et al.* 2008). There have been many transgressions of the isthmus by various lineages of Terraranae. The major Middle American group of terraranans is *Craugastor*, a genus containing 113 species ranging throughout Central America, Mexico, and extreme southwestern United States. Based on their molecular clock calibration, Crawford and Smith (2005) estimated that the ancestral stock of *Craugastor* entered Central America from South America in the Paleocene, although Heinicke *et al.* (2007), in a more extensive analysis, estimated that event to be younger, in the Middle Eocene (49–37 Mya). The well-documented molecular analysis of terraranan frogs of the genus *Pristimantis* in Central America and Colombia by Pinto-Sánchez *et al.* (2012) revealed 11 invasions of Central America from South America. Their dates for the dispersals indicated at least eight invasions prior to the mid-Pliocene, the previous estimated creation of the isthmian link.

Once the Panamanian land bridge was established in the Miocene there were many invaders from South America (Bacon *et al.* 2015); among the amphibians were allobatid, dendrobatid, and leptodactylid frogs and caecilians. Santos *et al.* (2009) estimated ten dispersals of dendrobatid frogs from the Chocó Region to Central América in three phases: (1) Two dispersals in the late Miocene, (2) six in the Pliocene, and (3) two in the late Pleistocene. Likewise, Castroviejo *et al.* (2014) provided a molecular-based biogeography of centrolenid frogs that showed two dispersal events from the Chocóan Region into Central America—one in the mid-Miocene and another in the earliest Pliocene. Probably at least one bolitoglossine salamander stock arrived in South America prior to the Pliocene (Hanken & Wake 1982). Otherwise, the relatively few dispersals from Central America to South America were by species that had differentiated from a South American ancestor in Central America, e.g., four species of *Craugastor* (Crawford and Smith, 2005), one species of *Rhinella* (Santos *et al.* 2015), and three species of *Smilisca*. The only Nearctic anuran clade to enter South America is the ranid genus *Lithobates*, represented in South America by three species in the *Lithobates palmipes* Group (Hillis & de Sa 1988).

The origin of the hylid frogs on Caribbean islands parallels that of most other groups of terrestrial vertebrates endemic to the region in being old (but not too old) and having an origin from South America (Hedges 1996; 2001; 2006). Molecular dating of many groups, showing Cenozoic origins (e.g., Heinicke *et al.* 2007) and geologic data showing that continuous land areas did not exist prior to the late Eocene (Iturralde-Vinent & MacPhee 1999) rule out a popular hypothesis that the fauna arose from Proto-Antillean vicariance (Rosen 1975). Overall, the reduced higher-level taxonomic composition of Antillean groups, combined with large radiations of clades present, also supports an origin by overwater dispersal (Hedges 2006). Despite this evidence against proto-Antillean vicariance,

some researchers have continued to support vicariance for Antillean shrews (Solenodon; Roca *et al.* 2004) and Cuban night lizards (*Cricosaura*; Vicario *et al.* 2003), but these two groups are relictual and thus their origin can be explained by dispersal (Hedges 2006). The recent discovery of a bolitoglossine plethodontid salamander in Miocene amber in Hispaniola (Poinar & Wake 2015), a group that is not known to occur today on Caribbean islands, indicates that yet another major group of amphibians dispersed to the islands in the past.

A variant of the vicariance theory was proposed by Iturralde-Vinent and MacPhee (1999) whereby Antillean groups arose through a dry land connection (Aves Ridge) in the mid-Cenozoic. Unfortunately, there is no firm geological evidence for the existence of such a dry land bridge, and in fact geological evidence against it (Ali 2012). Also, there is biological evidence against it in the peculiar taxonomic composition of the biota, which is the same evidence arguing against an earlier land bridge. Therefore, it is not correct to claim support for the Aves Ridge land bridge, as some authors have done (e.g., Alonso *et al.* 2011) simply because they obtained mid-Cenozoic molecular clock dates for their groups. Such clock dates are also consistent with the large body of evidence supporting dispersal, and the dispersal model does not have the geological and taxonomic problems that are associated with the Aves land bridge model. The islands associated with the Aves and Lesser Antilles submarine ridges would have facilitated dispersal, especially at times of low sea level, but would not have provided a dry-land biogeographic corridor for a continental biota as envisioned by Iturralde-Vinent and MacPhee (1999). For these reasons, it is most likely that the arboranan frogs of the Caribbean islands arrived by dispersal on flotsam from South America in the mid-Cenozoic.

Three major patterns exist with respect to Beringian interchanges between Asia and North America. The first of these includes ancient related taxa in eastern Asia and eastern North America; herpetological examples are the primitive salamanders of the genera *Cryptobranchus* in North America and *Megalobatrachus* in eastern Asia (including Japan); these diverged from one another in the Cretaceous (Zhang & Wake 2008), as did *Alligator sinensis* in China and *A. mississippiensis* in North America (Brochu 1999). Both of these examples are remnants of diverse fossils in the Holarctic and the Alligatoridae in the Neotropics as well. Within amphibians a second pattern is like the first but more recent and has Tertiary dispersal from North America to Asia; this includes the plethodontid salamander *Karsenia* in Korea and most relatives in eastern North America (Min *et al.* 2005). This is the pattern observed in the hyline genera *Hyla* in Eurasia and ancestral *Dryophytes* in North America. Within the third pattern there are two examples among anurans that exhibit Neogene migrations from Asia to North America via Beringia—ancestral *Dryophytes eximius* Group and ancestral *Rana boylii* Group (Hillis & Wilcox 2005). Neither of these Groups occurs in eastern North America.

Most dispersal via Beringia is from Asia to North America as has been documented in a variety of organisms, e.g., butterflies (Vila *et al.* 2011) and pikas (Galbreath & Hoberg 2011). Ickert-Bond *et al.* (2009) emphasized that although the Bering Land Bridge had been a major highway for Asian plants into North America it was a barrier to some and a filter for others. Remarkably, North American toads, *Anaxyrus*, did not migrate into Asia where Old World toads, *Bufo*, predominate; neither did acridine hylids. In Middle America many hylid frogs breed in small streams and have stream-adapted tadpoles (see Duellman 2001). This breeding behavior and associated adaptations are absent in North America, where larval salamanders of the plethodontid genera *Desmognathus*, *Eurycea*, *Gyrinophilus*, and *Pseudotriton* are abundant in streams, but these carnivorous larvae would not be in competition with herbivorous tadpoles. Another unsolved mystery!

## Acknowledgments

We are indebted to Manuella Folly and Jorge Soberón for translating the abstract into Portuguese and Spanish, respectively. We are grateful to Luis A. Coloma and two anonymous reviewers for their critical comments on the manuscript, as well as Ana M. Báez for her help with the sections on fossil frogs. Photographs were kindly provided by Tom Charlton, Fred Kraus, Jose P. Pombal Jr., Pedro Peloso, Mirco Solé, and Mauro Teixeira Jr. Julie Marin, Brooke Gattens, and Angela Lu assisted in preparing the species density maps. Duellman is grateful for stimulating discussions on hylid frogs with Ivan Nunes and Linda Trueb. This work was supported by Temple University and by grants to SBH from the U.S. National Science Foundation (1136590 and 1455762).

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APPENDIX 1. GenBank accession numbers.

Species	# of genes	12S	16S	28S	emyc2	emyc3	COI	CXCR4	cytb	H3A	NCXI
# of accessions in alignment		472	457	143	120	98	97	81	278	47	30
<i>Acris blanchardi</i>	3	---	---	---	---	---	---	---	EF988105	---	---
<i>Acris crepitans</i>	17	FJ882758	EF107181	AY844194	AY819194	AY819268	---	EF107468	EF988131	DQ284107	EF107244
<i>Acris gryllus</i>	9	EF566971	---	---	---	---	KJ536151	---	EF988146	---	---
<i>Hyllola cadaverina</i>	10	AY819365	EF472006	AY844334	AY819200	AY819274	---	---	FJ599871	---	---
<i>Hyllola hypochondriaca</i>	2	---	---	---	---	---	KJ536162	---	KJ536199	---	---
<i>Hyllola regilla</i>	11	AY819376	AY291112	---	AY819211	AY819285	KJ536164	---	EU834883	---	---
<i>Hyllola sierra</i>	2	---	---	---	---	---	KJ536166	---	KJ536201	---	---
<i>Pseudacris brachyphona</i>	5	AY326049	---	---	---	---	KJ536184	---	KJ536210	---	---
<i>Pseudacris brimleyi</i>	4	EF472036	AY291094	---	---	---	KJ536183	---	KJ536212	---	---
<i>Pseudacris clarkii</i>	5	AY291093	---	---	---	---	KJ536179	---	KJ536214	---	---
<i>Pseudacris crucifer</i>	14	AY819385	AY843735	DQ283478	AY819220	AY819294	KJ536167	---	EF988160	DQ284114	---
<i>Pseudacris feriarum</i>	5	EF472221	EF472212	---	---	---	KJ536176	---	KJ536221	---	---
<i>Pseudacris fouquettei</i>	5	AY291085	---	---	---	---	KJ536169	---	KJ536226	---	---
<i>Pseudacris illinoensis</i>	5	EF472010	AY291110	---	---	---	KJ536158	---	KJ536209	---	---
<i>Pseudacris kalmi</i>	5	EF472230	AY291087	---	---	---	KJ536172	---	KJ536222	---	---
<i>Pseudacris maculata</i>	7	EF472135	AY291092	---	---	---	KJ536181	---	EF988161	---	---
<i>Pseudacris nigrita</i>	9	EF472231	---	---	AY819221	AY819295	KJ536170	---	AY210862	---	---
<i>Pseudacris ocularis</i>	11	AY291098	---	---	DQ055781	DQ055752	KJ536152	---	AY843982	---	---
<i>Pseudacris ornata</i>	4	AY291106	---	---	---	---	KJ536155	---	GU985379	---	---
<i>Pseudacris streckeri</i>	5	EF472009	AY291108	---	---	---	KJ536156	---	AY210861	---	---
<i>Pseudacris triseriata</i>	9	EF472160	---	AY844335	---	---	KJ536175	---	AY843984	---	---
<i>Aplastodiscus albofrenatus</i>	3	AY819422	AY819539	---	---	---	---	---	---	---	---
<i>Aplastodiscus albosignatus</i>	8	AY843596	---	AY844219	---	---	---	---	AY843817	---	---
<i>Aplastodiscus arildae</i>	8	AY843604	---	AY844223	---	---	---	---	AY843825	---	---
<i>Aplastodiscus callipygius</i>	8	AY843614	---	AY844236	---	---	---	---	AY843840	---	---
<i>Aplastodiscus cavicola</i>	6	AY843617	---	---	---	---	---	---	AY843843	---	---
<i>Aplastodiscus cochranae</i>	8	AY843568	---	AY844200	---	---	---	---	AY843790	---	---

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	cmyc2	cmyc3	COI	CXCR4	cytb	H3A	NCXI
<i>Aplastodiscus eugentoi</i>	7	AY843669						KF751465	AY843913		
<i>Aplastodiscus leucopygius</i>	10	AY843638		AY844261				KF751466	AY843873		
<i>Aplastodiscus perviridis</i>	11	AY843569		AY844201				KF751467	AY843791	DQ284044	
<i>Aplastodiscus weygoldti</i>	6	AY843685							AY843931		
<i>Bokermannohyla astartea</i>	9	AY549322		AY844225	AY819198	AY819272			AY549375		
<i>Bokermannohyla circumdata</i>	10	AY549328		AY844242				KF751468	AY549381		
<i>Bokermannohyla hylax</i>	8	AY549338		AY844254					AY549391		
<i>Bokermannohyla itapoty</i>	2							KF751469			
<i>Bokermannohyla martinsi</i>	7	AY843641		AY844264					AY843878		
<i>Bokermannohyla oxente</i>	1							KF751470			
<i>Colomascirtus armatus</i>	10	AY819423	AY549321	AY844224					AY549374	DQ284070	
<i>Colomascirtus charazani</i>	8	AY843618		AY844239					AY843844		
<i>Colomascirtus criptico</i>	2	JX155814	JX155841								
<i>Colomascirtus larinopygion</i>	2	JX155818	JX155845								
<i>Colomascirtus lindae</i>	2	DQ380361	JX155849								
<i>Colomascirtus pacha</i>	2	AY326057									
<i>Colomascirtus pantostictus</i>	2	AY326052									
<i>Colomascirtus princecharlesi</i>	2	JX155806	JX155833								
<i>Colomascirtus psarolaimus</i>	2	JX155809	JX155836								
<i>Colomascirtus psychodactylus</i>	2	JX155804	JX155831								
<i>Colomascirtus staufferorum</i>	2	JX155816	JX155842								
<i>Colomascirtus tapichalaca</i>	8	AY563625		AY844297					KF751474	AY563627	
<i>Colomascirtus tigrinus</i>	2	JX155810	JX155837								
<i>Hyloscirtus alytolylax</i>	2	JX155798	JX155826								
<i>Hyloscirtus colymba</i>	15	AY843620		AY844243	AY819323	AY819316	FJ766731	KF751472	AY843848		
<i>Hyloscirtus lascinius</i>	1	DQ380359									
<i>Hyloscirtus palmeri</i>	15	AY843650		AY844273	AY819324	AY819317	FJ766733	KF751473	AY843890	DQ284088	
<i>Hyloscirtus phyllonathus</i>	2	DQ380369	JX155827								

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	cmv2	cmv3	COI	CXCR4	cytb	H3A	NCX1
<i>Hyaloscirtus simmonsi</i>	5	DQ380376	---	---	AY819325	AY819318	---	---	---	---	---
<i>Hypsiboas aguilari</i>	8	HM444782	HM444783	KF751464	---	---	---	KF751475	HM444762	---	---
<i>Hypsiboas albomarginatus</i>	10	AY549316	---	AY844218	---	---	---	KF751476	AF549302	---	---
<i>Hypsiboas albopunctatus</i>	9	AY549317	---	---	---	JQ627301	---	---	AY549370	---	---
<i>Hypsiboas alfaroi</i>	5	KF955303	KF955305	---	---	KF955306	---	---	---	---	---
<i>Hypsiboas almeidarizae</i>	2	KF955304	---	---	---	---	---	---	---	---	---
<i>Hypsiboas balzani</i>	7	AY549323	---	AY844226	---	---	---	---	AY549376	---	---
<i>Hypsiboas benitezi</i>	8	AY843606	---	AY844227	---	---	---	KF751477	AY843830	---	---
<i>Hypsiboas bischoffi</i>	5	AY549324	---	---	---	---	---	---	AY549377	---	---
<i>Hypsiboas boans</i>	13	AY843610	---	AY844231	AY819199	AY819273	---	KF751478	AY843835	DQ284086	---
<i>Hypsiboas caingua</i>	9	AY549326	---	AY844234	---	---	---	KF751479	AY549379	---	---
<i>Hypsiboas caipora</i>	1	---	---	---	---	---	---	---	---	---	---
<i>Hypsiboas calcaratus</i>	6	AY326056	---	AY844235	---	---	---	---	AY843839	---	---
<i>Hypsiboas callipleura</i>	3	---	HM480426	---	---	---	---	---	HM535341	---	---
<i>Hypsiboas cinerascens</i>	9	AY549336	---	DQ283466	---	---	---	KF751480	AY549389	DQ284076	---
<i>Hypsiboas cordobae</i>	10	AY549331	---	AY844244	---	---	---	KF751481	AY549384	---	---
<i>Hypsiboas crepitans</i>	7	AY843621	---	---	---	---	---	KF751482	AY843850	---	---
<i>Hypsiboas curupi</i>	1	---	---	---	---	---	---	KF751483	---	---	---
<i>Hypsiboas dentei</i>	3	EF376018	AF467270	---	---	---	---	---	---	---	---
<i>Hypsiboas ericae</i>	7	AY549332	---	---	---	---	---	---	AY549385	---	---
<i>Hypsiboas faber</i>	8	AY549334	AY549333	---	---	JQ627303	---	---	AY549387	---	---
<i>Hypsiboas fasciatus</i>	6	AY819427	EU201109	---	---	---	---	---	AY549388	---	---
<i>Hypsiboas geographicus</i>	4	AY843628	---	---	---	---	---	---	---	---	---
<i>Hypsiboas gladiator</i>	2	---	HM480406	---	---	---	---	---	HM535328	---	---
<i>Hypsiboas guentheri</i>	7	AY843631	AY549337	AY844253	---	---	---	---	AY549390	---	---
<i>Hypsiboas heilprini</i>	8	AY843632	---	---	EU034037	---	---	---	EU034062	---	---
<i>Hypsiboas joaquina</i>	9	AY549340	AY549339	AY844256	---	---	---	KF751484	AY549393	---	---
<i>Hypsiboas lanciformis</i>	9	AY326054	---	AY844258	---	---	---	---	AY843870	---	---

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	cmyc2	cmyc3	COI	CXCR4	cytb	H3A	NCXI
<i>Hypsiboas latistriatus</i>	6	AY549360	---	AY844293	---	---	---	---	AY843921	---	---
<i>Hypsiboas lemai</i>	10	AY843637	---	AY844259	---	---	---	KF751485	AY843871	---	---
<i>Hypsiboas leptolineatus</i>	9	AY549341	---	AY844260	---	---	---	---	AY549394	---	---
<i>Hypsiboas lundii</i>	7	AY843639	---	AY844262	---	---	---	---	AY843874	---	---
<i>Hypsiboas maculateralis</i>	1	---	---	---	---	---	---	---	---	---	---
<i>Hypsiboas marginatus</i>	9	AY549342	---	AY844263	---	---	---	KF751486	AY549395	---	---
<i>Hypsiboas marianitae</i>	7	AY362977	---	---	---	---	---	---	AY549397	---	---
<i>Hypsiboas melanopleura</i>	6	HM444772	HM444778	---	---	---	---	KF751487	HM444756	---	---
<i>Hypsiboas microderma</i>	5	AY843644	---	AY844267	---	---	---	---	AY843881	---	---
<i>Hypsiboas multifasciatus</i>	12	AY843648	---	AY844270	---	---	---	GQ365986	AY843887	---	---
<i>Hypsiboas nympa</i>	9	AY843670	---	AY844289	---	---	---	KF751488	AY843914	---	---
<i>Hypsiboas ornatissimus</i>	3	EF376019	EF376056	---	---	---	---	---	---	---	---
<i>Hypsiboas palcaestes</i>	2	---	HM480414	---	---	---	---	---	HM535351	---	---
<i>Hypsiboas pardalis</i>	7	AY843651	---	---	---	---	---	---	AY843891	---	---
<i>Hypsiboas pellucens</i>	2	AY326058	---	---	---	---	---	---	---	---	---
<i>Hypsiboas picturatus</i>	2	AY326055	---	---	---	---	---	---	---	---	---
<i>Hypsiboas polytaenius</i>	10	AY843655	---	---	AY819209	AY819283	---	---	AY843895	---	---
<i>Hypsiboas prasinus</i>	6	AY549347	---	---	---	---	---	---	AY549400	---	---
<i>Hypsiboas pulchellus</i>	9	AY549352	---	AY844278	---	---	---	---	AY549405	---	---
<i>Hypsiboas punctatus</i>	5	AY549353	---	---	---	---	---	---	AY549406	---	---
<i>Hypsiboas raniceps</i>	12	AY843657	---	---	AY819210	AY819284	---	KF751489	AY843900	---	---
<i>Hypsiboas riojanus</i>	8	AY549356	---	AY844279	---	---	---	---	AY549409	---	---
<i>Hypsiboas roraima</i>	10	AY843660	---	AY844280	---	---	---	KF751490	AY843903	---	---
<i>Hypsiboas rosenbergi</i>	3	AY819438	AY819545	---	---	---	---	---	---	---	---
<i>Hypsiboas rufitellus</i>	9	AY843662	---	AY844282	---	---	F1766740	---	AY843905	---	---
<i>Hypsiboas semiguttatus</i>	8	AY549358	---	AY844285	---	---	---	---	AY549411	---	---
<i>Hypsiboas semilineatus</i>	11	AY843778	AY843779	AY844286	---	---	---	KF751491	AY843909	---	---
<i>Hypsiboas sibleszi</i>	10	AY843667	---	AY844288	---	---	---	KF751492	AY843911	---	---

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APPENDIX I. (Continued)

Species	# of genes	12S	16S	28S	cmv2	cmv3	COI	CXCR4	cytb	H3A	NCXI
<i>Hypsiboas tetete</i>	1	---	---	---	---	---	---	---	---	---	---
<i>Myerstrohyla inparquesi</i>	6	AY843672	---	AY844291	---	---	---	---	---	---	---
<i>Myerstrohyla kanaima</i>	9	AY843634	---	---	---	---	---	GQ365994	AY843868	---	---
<i>Dendropsophus anatalitiasi</i>	1	JX287452	---	---	---	---	---	---	---	---	---
<i>Dendropsophus anceps</i>	8	AY843597	---	AY844220	---	---	---	---	AY843818	---	---
<i>Dendropsophus aperomeus</i>	3	AY819450	AY819549	---	---	---	---	---	---	---	---
<i>Dendropsophus berthelutzae</i>	9	AY843607	---	AY844228	---	---	---	---	AY843831	---	---
<i>Dendropsophus bifurcus</i>	2	AY362975	---	---	---	---	---	---	---	---	---
<i>Dendropsophus bipunctatus</i>	7	AY843608	---	AY844229	---	---	---	---	AY843832	---	---
<i>Dendropsophus branneri</i>	1	---	---	---	---	---	---	---	AF549336	---	---
<i>Dendropsophus brevifrons</i>	8	AY843611	---	AY844232	---	---	---	---	AY843836	---	---
<i>Dendropsophus carnifex</i>	6	AY843616	---	AY844238	---	---	---	---	AY843842	---	---
<i>Dendropsophus coffeus</i>	1	---	JF790050	---	---	---	---	---	---	---	---
<i>Dendropsophus ebraccatus</i>	13	AY843624	FJ542198	AY844247	AY819202	AY819276	---	---	EU034061	---	---
<i>Dendropsophus elegans</i>	4	DQ380355	AF308103	---	---	---	---	---	AF308124	---	---
<i>Dendropsophus elianeae</i>	1	JX287401	---	---	---	---	---	---	---	---	---
<i>Dendropsophus frosti</i>	2	JQ088283	---	---	---	---	---	---	---	---	---
<i>Dendropsophus gaucheri</i>	2	JF973308	JF973298	---	---	---	---	---	---	---	---
<i>Dendropsophus giesleri</i>	7	AY843629	---	AY844251	---	---	---	---	AY843860	---	---
<i>Dendropsophus jimi</i>	1	JX287413	---	---	---	---	---	---	---	---	---
<i>Dendropsophus juliani</i>	1	---	JF790051	---	---	---	---	---	---	---	---
<i>Dendropsophus koechlini</i>	6	AY819369	AY819501	---	AY819204	AY819278	---	---	---	---	---
<i>Dendropsophus labialis</i>	11	AY843635	---	AY844257	JF422634	JF422645	EF653832	---	FJ204208	---	---
<i>Dendropsophus leali</i>	3	AY819451	JF790062	---	---	---	---	---	---	---	---
<i>Dendropsophus leucophyllatus</i>	4	DQ380360	AF308097	---	---	---	---	---	AF308122	---	---
<i>Dendropsophus luddeckei</i>	3	JF422590	JF422594	---	---	---	---	---	---	---	---
<i>Dendropsophus manonegra</i>	2	KF009942	---	---	---	---	---	---	---	---	---
<i>Dendropsophus marmoratus</i>	6	AY843640	---	---	---	---	---	---	AY843877	DQ284085	---

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	cmyc2	cmyc3	COI	CXCR4	cytb	H3A	NCXI
<i>Dendropsophus melanargyreus</i>	2	JF973313	JF790074	---	---	---	---	---	---	---	---
<i>Dendropsophus meridenis</i>	3	JF422585	---	---	---	---	---	---	---	---	---
<i>Dendropsophus microcephalus</i>	11	EF566945	AY844266	AY819206	AY819280	---	---	---	AY843880	---	---
<i>Dendropsophus minusculus</i>	3	DQ380362	EF376061	---	---	---	---	---	---	---	---
<i>Dendropsophus minutus</i>	9	AY549345	---	DQ283456	---	---	EF587819	---	AY549398	DQ284046	---
<i>Dendropsophus miyatai</i>	7	AY843647	---	---	---	---	---	---	AY843886	---	---
<i>Dendropsophus nanus</i>	14	AY549346	AY844271	AY819208	AY819282	---	---	GQ365985	AY549399	DQ284051	---
<i>Dendropsophus parviceps</i>	8	AY843652	---	AY844274	---	---	---	---	AY843892	---	---
<i>Dendropsophus phlebodes</i>	1	---	---	---	---	---	---	---	JX008024	---	---
<i>Dendropsophus reichlei</i>	1	---	JF790108	---	---	---	---	---	---	---	---
<i>Dendropsophus rhodopeplus</i>	5	AY843658	---	---	---	---	---	---	---	---	---
<i>Dendropsophus riveroi</i>	1	DQ380372	---	---	---	---	---	---	---	---	---
<i>Dendropsophus robertmertensi</i>	3	AY819452	AY819551	---	---	---	---	---	---	---	---
<i>Dendropsophus rubicundulus</i>	6	AY843661	---	AY844281	---	---	---	---	AY843904	---	---
<i>Dendropsophus sallii</i>	2	AY362976	---	---	---	---	---	---	---	---	---
<i>Dendropsophus sanborni</i>	8	AY843663	---	AY844283	---	---	---	---	AY843906	---	---
<i>Dendropsophus sarayacuensis</i>	4	AY843664	---	---	---	---	---	---	---	---	---
<i>Dendropsophus sartori</i>	6	AY819453	AY819552	---	AY819322	AY819315	---	---	---	---	---
<i>Dendropsophus schubarti</i>	1	DQ380374	---	---	---	---	---	---	---	---	---
<i>Dendropsophus seniculus</i>	8	AY843666	---	AY844287	---	---	---	---	AY843910	---	---
<i>Dendropsophus timbeba</i>	1	DQ380348	---	---	---	---	---	---	---	---	---
<i>Dendropsophus triangulum</i>	7	AY326053	---	AY844298	---	---	---	---	AY843926	---	---
<i>Dendropsophus tritaeniatius</i>	1	---	JF790114	---	---	---	---	---	---	---	---
<i>Dendropsophus walfordi</i>	5	AY843683	---	---	---	---	---	---	AY843929	---	---
<i>Xenohyla truncata</i>	3	AY843775	---	---	---	---	---	---	AY844018	---	---
<i>Anotheca spinosa</i>	15	AY843566	---	AY844198	AY819195	AY819269	---	---	DQ830847	DQ284101	DQ830860
<i>Bromeliohyala bromeliatica</i>	12	AY843612	---	AY844233	DQ055760	DQ055734	---	---	AY843837	---	---
<i>Charadrahyla nephila</i>	13	AY843649	---	AY844272	DQ388732	DQ388741	---	---	AY843889	DQ284100	---

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	emyc2	emyc3	COI	CXCR4	cytb	H3A	NCX1
<i>Charadriahyla taeniopus</i>	12	AY843679		AY844296	AY819326	AY819319	---	---	AY843924	---	---
<i>Diaglena spatulata</i>	12	DQ830828	DQ830815	---	DQ388739	DQ388748	---	---	DQ830849	---	DQ830857
<i>Dryophytes andersonii</i>	10	EF566956	---	---	DQ055756	DQ055730	---	---	AY831026	---	---
<i>Dryophytes arenicolor</i>	15	DQ347054	F1882776	---	AY819197	AY819271	---	AY364190	AY831027	---	EF107241
<i>Dryophytes avivocus</i>	10	EF566947	---	---	DQ055759	DQ055733	---	---	AY831024	---	---
<i>Dryophytes chrysoceles</i>	6	EF566949	---	---	---	---	HCU66863	---	AY831012	---	---
<i>Dryophytes cinereus</i>	17	AY549327	DQ830810	AY844241	AY819201	AY819275	F1226785	DQ306493	F1226874	DQ284057	DQ830874
<i>Dryophytes euphorbiaceus</i>	11	EF566961	---	AY844248	DQ055763	DQ055736	---	---	AY843855	---	---
<i>Dryophytes eximius</i>	9	EF566957	---	AY844249	---	---	---	---	AY843856	---	---
<i>Dryophytes femoralis</i>	13	DQ055838	EF566964	AY844250	DQ055764	DQ055737	F1226786	---	F1226875	---	---
<i>Dryophytes gratusus</i>	12	EF566966	---	AY844252	GQ374907	GQ374911	---	---	AY843862	---	---
<i>Dryophytes immaculatus</i>	14	GQ374900	GQ374904	---	GQ374908	GQ374912	---	---	---	---	---
<i>Dryophytes japonicus</i>	6	DQ055840	EF566952	AY844255	DQ055766	DQ055739	NC_010232	---	AB303949	---	---
<i>Dryophytes plicatus</i>	13	DQ055842	EF566962	---	DQ055771	DQ055744	---	---	---	---	---
<i>Dryophytes squirellus</i>	4	EF566965	---	AY844295	AY819213	AY819287	F1226851	---	F1226942	---	---
<i>Dryophytes suweonensis</i>	12	AF218709	JQ815328	---	---	---	JQ844538	---	KF564855	---	---
<i>Dryophytes versicolor</i>	6	EF566951	EF566950	---	DQ055778	DQ055749	EF525820	---	AY830973	---	---
<i>Dryophytes walkeri</i>	8	GQ374902	EF566963	---	GQ374910	GQ374914	---	---	---	---	---
<i>Dryophytes wrightorum</i>	13	AY819368	GU989079	---	AY819203	AY819277	---	---	---	---	---
<i>Duellmanohyla rufioculis</i>	11	AY843583	---	AY844212	DQ388725	DQ388740	---	---	AY549368	DQ284059	---
<i>Duellmanohyla soralia</i>	5	AY843584	---	---	AY819196	AY819270	---	---	AY843806	---	---
<i>Duellmanohyla uranochroa</i>	13	---	DQ388750	---	DQ388726	DQ394284	---	---	---	---	---
<i>Ecnomiophyla militaria</i>	3	DQ055841	AY843777	AY844268	DQ055769	DQ055742	F1766699	---	AY843882	DQ284115	---
<i>Ecnomiophyla minera</i>	1	DQ388690	---	---	DQ388731	---	---	---	---	---	---
<i>Ecnomiophyla rabborum</i>	5	---	KC014807	---	---	---	---	---	---	---	---
<i>Exerodonta abdivita</i>	13	DQ388685	DQ388751	---	DQ388727	---	---	---	---	---	---
<i>Exerodonta chimalapa</i>	12	AY843619	---	AY844240	DQ388728	DQ388742	---	---	AY843845	DQ284099	---
<i>Exerodonta melanomma</i>	11	AY843642	---	AY844265	DQ055768	DQ055741	---	---	AY843879	---	---

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	cmcy2	cmcy3	COI	CXCR4	cytb	H3A	NCX1
<i>Exerodonta perkinsi</i>	5	AY843653		AY844275	DQ388733	---	---	---	AY843893	---	---
<i>Exerodonta smaragdina</i>	3	DQ388694	DQ388759	---	DQ388735	---	---	---	---	---	---
<i>Exerodonta sumichrasti</i>	11	AY819454	---	---	DQ055776	---	---	---	---	---	---
<i>Exerodonta xera</i>	12	AY843686	---	AY844300	DQ388736	DQ388745	---	---	AY843932	---	---
<i>Hyla annectans</i>	12	AY843600	---	---	DQ055757	DQ055731	JN700883	---	FJ226919	---	---
<i>Hyla arborea</i>	11	AY843601	---	AY844221	DQ055758	DQ055732	JN801021	---	FJ226865	---	---
<i>Hyla chinensis</i>	4	AY458593	---	---	DQ055761	---	NC_006403	---	AY458593	HM1998949	HM1998954
<i>Hyla felixarabica</i>	3	GQ916739	GQ916782	---	---	---	---	---	---	---	---
<i>Hyla intermedia</i>	15	---	---	---	---	---	FJ226788	---	FJ226880	---	---
<i>Hyla meridionalis</i>	4	EF566953	FJ882757	---	AY819205	AY819279	DQ996400	AY523687	FJ226925	---	AY523710
<i>Hyla molleri</i>	8	---	JN800771	---	---	---	JN800967	---	FJ226918	---	---
<i>Hyla orientalis</i>	4	GQ916752	GQ916809	---	---	---	FJ226769	---	FJ226916	JF499573	---
<i>Hyla sarda</i>	13	---	---	---	---	---	FJ226811	---	FJ226927	---	---
<i>Hyla savignyi</i>	1	EF566954	---	AY844284	DQ055774	DQ055747	JN801023	---	FJ226930	JF499593	---
<i>Hyla simplex</i>	8	---	---	---	DQ055775	---	---	---	---	---	---
<i>Hyla tsinlingensis</i>	1	GQ374901	GQ374905	---	GQ374909	GQ374913	JN700882	---	JX870435	---	---
<i>Isthmohyla lancasteri</i>	14	---	---	---	---	DQ394285	---	---	---	---	---
<i>Isthmohyla pseudopuma</i>	9	AY843656	---	AY844277	DQ055772	DQ055745	---	---	FJ226899	---	DQ830868
<i>Isthmohyla rivularis</i>	11	AY843659	---	---	DQ055773	DQ055746	---	---	AY843902	DQ284058	---
<i>Isthmohyla tica</i>	11	AY819440	DQ830818	---	DQ055777	DQ055748	---	---	---	---	DQ830870
<i>Isthmohyla zeteki</i>	8	EF566968	---	---	DQ055779	DQ055750	---	---	---	---	DQ830869
<i>Megastomatohyla mixe</i>	6	AY843646	---	AY844269	---	---	---	---	AY843885	---	---
<i>Plectrohyla chrysopleura</i>	11	AY819384	AY819516	---	AY819219	AY819293	---	---	---	---	---
<i>Plectrohyla glandulosa</i>	12	AY843730	---	---	DQ388737	---	---	---	AY843976	---	---
<i>Plectrohyla guatemalensis</i>	8	AY843731	---	AY844332	DQ055780	DQ055751	---	---	AY843977	---	---
<i>Plectrohyla mattudai</i>	12	AY843732	---	AY844333	---	---	---	---	AY843978	---	---
<i>Psychohyla dendrophasma</i>	8	AY843623	---	AY844246	DQ055762	DQ055735	---	---	AY843852	---	---
<i>Psychohyla euthysanota</i>	8	AY843744	---	AY844340	---	---	---	---	AY843990	---	---

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	emyc2	emyc3	COI	CXCR4	cytb	H3A	NCXI
<i>Psychohyla hypomykter</i>	8	AY843745	---	---	DQ055782	DQ055753	---	---	AY843991	---	---
<i>Psychohyla leonhardschultzei</i>	5	AY843746	AY819547	AY844341	---	---	---	---	AY843992	---	---
<i>Psychohyla salvadorensis</i>	12	---	AY819547	---	DQ055783	DQ055754	---	---	---	---	---
<i>Psychohyla spinipollex</i>	11	AY843748	---	AY844343	AY819223	AY819297	---	---	AY843994	---	---
<i>Psychohyla zophodes</i>	11	AY843749	---	AY844344	---	DQ388746	---	---	AY843995	---	---
<i>Rheohyla mitoympanum</i>	3	AY843645	---	---	AY819207	AY819281	---	---	AY843884	---	---
<i>Sarcophyla ameibothalame</i>	8	DQ388686	DQ388752	---	---	---	---	---	---	---	---
<i>Sarcophyla arborescandens</i>	7	AY843602	---	AY844222	---	---	---	---	AY843823	---	---
<i>Sarcophyla bistincta</i>	7	AY843609	---	AY844230	---	---	---	---	AY843834	---	---
<i>Sarcophyla calthula</i>	12	AY843615	---	AY844237	---	---	---	---	AY843841	---	---
<i>Sarcophyla cyclada</i>	6	AY843622	---	AY844245	DQ388729	DQ388743	---	---	AY843851	---	---
<i>Sarcophyla peniteter</i>	2	EF566972	---	---	DQ055770	DQ055743	---	---	---	---	---
<i>Sarcophyla siopela</i>	12	---	---	---	DQ388734	---	---	---	---	---	---
<i>Smilisca baudinii</i>	14	EF566967	---	---	DQ388738	DQ388747	---	---	AY549419	---	DQ830862
<i>Smilisca cyanostricta</i>	14	AY843763	---	AY844350	AY819228	AY819302	---	---	AY844008	---	DQ830864
<i>Smilisca fodiens</i>	16	AY843743	---	AY844339	AY819222	AY819296	---	---	DQ830850	---	DQ830863
<i>Smilisca phaeota</i>	13	AY326040	---	AY844351	DQ055784	DQ055755	FJ766834	---	DQ830852	DQ284083	DQ830865
<i>Smilisca puma</i>	9	AY843765	---	---	DQ830823	DQ830829	---	---	DQ830853	---	DQ830866
<i>Smilisca sila</i>	9	DQ388700	DQ830822	---	DQ830824	DQ830830	FJ766836	---	DQ830854	---	---
<i>Smilisca sordida</i>	11	DQ388701	---	---	DQ830825	DQ830831	---	---	---	---	DQ830867
<i>Tlalocohyla godmani</i>	6	DQ388689	DQ830811	---	DQ388730	DQ388744	---	---	---	---	DQ830872
<i>Tlalocohyla loquax</i>	13	AY819431	DQ055822	---	DQ055767	DQ055740	---	---	---	---	---
<i>Tlalocohyla picta</i>	13	AY843654	---	AY844276	---	---	---	---	DQ830855	DQ284121	DQ830871
<i>Tlalocohyla smithii</i>	15	AY843668	---	---	AY819212	AY819286	---	---	DQ830856	---	DQ830873
<i>Triprion petasatus</i>	9	AY843774	---	AY844357	AY819231	AY819305	---	---	DQ830848	DQ284082	DQ830861
<i>Aparasphenodon brunoi</i>	9	AY843567	---	AY844199	---	---	---	---	AY843789	---	---
<i>Argenteohyla siemersi</i>	9	AY843570	---	AY844202	---	---	---	---	AY843792	DQ284064	---
<i>Corythomantis greeningi</i>	5	AY843578	---	AY844209	---	---	---	---	AY843800	---	---

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	cmyc2	cmyc3	COI	CXCR4	cytb	H3A	NCXI
<i>Dryaderces pearsoni</i>	13	KF002006					KF001884		KF001949		
<i>Itapotihyla langsdorffii</i>	4	AY843706	AY844311	AY819214	AY819288	KF001942			AY843951		
<i>Nycimantis rugiceps</i>	8	EU034032	AY843781						AY843945		
<i>Osteocephalus alboguttatus</i>	9	DQ380347	JQ868516						EU034063		
<i>Osteocephalus buckleyi</i>	11	DQ380378	KF002019		EU034038		JX875831		EU034064		
<i>Osteocephalus cabrerai</i>	4	AY843705	AY844310				JX875827		AY843950		
<i>Osteocephalus cannatellai</i>	1	KF002032	KF002031				JX875823				
<i>Osteocephalus carri</i>	4	KF002033									
<i>Osteocephalus castaneicola</i>	6	KF002034					KF001889				
<i>Osteocephalus deridens</i>	4	KF002037	KF002036				JX875817		KF001959		
<i>Osteocephalus festae</i>	6	JX847064					JX875803				
<i>Osteocephalus fuscifacies</i>	6	KF002038					JX875818		KF001960		
<i>Osteocephalus helenae</i>	2	KF002053	KF002040				KF001892		KF001961		
<i>Osteocephalus heyeri</i>	5	KF002054									
<i>Osteocephalus leoniae</i>	11	KF002056	KF002058				KF001893		KF001965		
<i>Osteocephalus lepreurii</i>	5	AY843707	AY844312				KF001900		AY549414		
<i>Osteocephalus mimeticus</i>	7	KF002079					KF001901		KF001969		
<i>Osteocephalus mutabor</i>	8	DQ380379	KF002080		EU034039		JX875824		KF001972		
<i>Osteocephalus oophagus</i>	9	AY843708					KF001902		AY843953		
<i>Osteocephalus planiceps</i>	3	DQ380380	KF002086		EU034040		JX875819				
<i>Osteocephalus subtilis</i>	16	KF002092					KF001906				
<i>Osteocephalus taurinus</i>	9	AY326041	AY844313	AY819215	AY819289	JX564881			JX564881	DQ284075	
<i>Osteocephalus verruciger</i>	6	DQ380381	KF002170		EU034041		JX875842		EU034066		
<i>Osteocephalus yasuni</i>	9	KF002177	KF002171				JX875828		KF001996		
<i>Osteopilus crucialis</i>	12	AY843710		AY844314			EU034052		AY843955		
<i>Osteopilus dominicensis</i>	9	AY843711		AY844315			EU034053		EU034068		
<i>Osteopilus marianae</i>	10	DQ380383	EU034086		EU034043		EU034054		HQ831741		
<i>Osteopilus ocellatus</i>	9	DQ380382	EU034083		EU034042		EU034051		HQ831744		

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	cmv2	cmv3	COI	CXCR4	cytb	H3A	NCXI
<i>Osteopilus pulchrlilineatus</i>	15	AY819436	---	---	EU034044	---	EU034055	---	EU034070	---	---
<i>Osteopilus septentrionalis</i>	12	AY843712	---	AY844316	AY819216	AY819290	KF001943	---	HQ831679	DQ284049	---
<i>Osteopilus vastus</i>	9	AY843713	---	AY844317	EU034046	---	EU034057	---	HQ831742	---	---
<i>Osteopilus wilderi</i>	10	DQ380385	EU034092	---	EU034047	---	EU034058	---	---	---	---
<i>Phyllodytes luteolus</i>	9	AY843721	---	AY844324	---	---	---	---	AY843966	---	---
<i>Phytotriades auratus</i>	3	DQ403726	DQ403730	---	AY819218	AY819292	---	---	EU034078	---	---
<i>Tepuihyla aecii</i>	4	JQ868533	---	---	---	---	---	---	---	---	---
<i>Tepuihyla edelcae</i>	6	AY843770	---	---	---	---	---	---	---	---	---
<i>Tepuihyla exophthalma</i>	6	KF002179	KF002178	---	---	---	KF001939	---	KF001998	---	---
<i>Tepuihyla rodriguezi</i>	4	KF002183	---	---	---	---	KF001941	---	KF002000	---	---
<i>Tepuihyla warreni</i>	10	KF002185	---	---	---	---	---	---	KF002001	---	---
<i>Trachycephalus coriaceus</i>	7	DQ380386	EF376068	---	EU034048	---	---	---	EU034076	---	---
<i>Trachycephalus hadroceps</i>	2	AY843717	---	AY844319	---	---	---	---	AY843962	---	---
<i>Trachycephalus imitatrix</i>	16	EU034036	---	---	---	---	---	---	---	---	---
<i>Trachycephalus jordani</i>	8	AY326042	---	AY844356	AY819230	AY819304	EU034060	---	EU034079	DQ284097	---
<i>Trachycephalus mesophaeus</i>	5	AY843718	---	AY844320	---	---	---	---	AY843963	---	---
<i>Trachycephalus nigromaculatus</i>	9	AY843772	---	---	---	---	---	---	AY844016	---	---
<i>Trachycephalus resinifictrix</i>	2	AY843719	---	AY844321	---	---	---	---	AY843964	---	---
<i>Trachycephalus typhonius</i>	17	JX847093	---	---	---	---	---	---	---	---	---
<i>Trachycephalus venulosus</i>	1	DQ347027	FJ882779	AY844322	AY819217	AY819291	---	GQ366030	EU034077	---	AY948824
<i>Lysapsus bolivianus</i>	2	---	JF789938	---	---	---	---	---	---	---	---
<i>Lysapsus caraya</i>	9	EF152999	---	---	---	---	---	---	---	---	---
<i>Lysapsus laevis</i>	6	EF152998	---	AY844305	---	---	---	---	AY843941	DQ284110	---
<i>Lysapsus limellum</i>	2	EF153002	---	---	---	---	---	---	AY843942	---	---
<i>Pseudeis bolbodactyla</i>	2	EF153007	---	---	---	---	---	---	---	---	---
<i>Pseudeis cardosoi</i>	2	EF152997	---	---	---	---	---	---	---	---	---
<i>Pseudeis fusca</i>	9	EF153003	---	---	---	---	---	---	---	---	---
<i>Pseudeis minuta</i>	12	EF152996	---	AY844336	---	---	---	GQ366028	JX456354	---	---

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	cmyc2	cmyc3	COI	CXCR4	cytb	H3A	NCXI
<i>Pseudis paradoxa</i>	2	AY326032	EF153012	AY844337	AY819187	AY819264	---	---	AY549417	DQ284128	---
<i>Pseudis tocantins</i>	10	EF153004	---	---	---	---	---	---	---	---	---
<i>Scaphyla goinorum</i>	7	AY843752	---	---	AY819224	AY819298	---	---	AY843997	---	---
<i>Julianus uruguayus</i>	6	AY843681	---	AY844299	---	---	---	---	AY843927	---	---
<i>Ololygon berthae</i>	11	AY843754	---	AY844345	---	---	---	---	AY843999	---	---
<i>Ololygon catharinae</i>	2	AY843756	---	AY844346	AY819225	AY819299	---	---	AY844001	---	---
<i>Ololygon faivovitchi</i>	1	---	JN100002	---	---	---	---	---	---	---	---
<i>Ololygon obtriangulata</i>	2	GQ896259	---	---	---	---	---	---	---	---	---
<i>Ololygon peixotoi</i>	2	---	JN100004	---	---	---	---	---	---	---	---
<i>Ololygon perpusilla</i>	7	---	JN099988	---	---	---	---	---	---	---	---
<i>Scinax acuminatus</i>	3	AY843753	---	---	---	---	---	---	AY843998	---	---
<i>Scinax boesemani</i>	6	EF217460	EF217498	---	---	---	---	---	---	---	---
<i>Scinax boulengeri</i>	2	AY843755	---	---	---	---	---	---	AY844000	---	---
<i>Scinax chiquitanus</i>	6	GQ896253	JF789945	---	---	---	---	---	---	---	---
<i>Scinax crosopedospilus</i>	4	AY819391	AY819523	---	AY819226	AY819300	---	---	---	---	---
<i>Scinax cruentommus</i>	1	EF217465	EF217508	---	---	---	---	---	EF364252	---	---
<i>Scinax duartei</i>	7	GQ896255	---	---	---	---	---	---	---	---	---
<i>Scinax elaeochrous</i>	1	AY843757	---	---	---	---	---	---	AY844002	---	---
<i>Scinax funereus</i>	1	GQ896256	---	---	---	---	---	---	---	---	---
<i>Scinax fuscomarginatus</i>	9	---	JF789985	---	---	---	---	---	---	---	---
<i>Scinax fuscovarius</i>	7	AY843758	---	AY844347	---	---	JQ627315	---	AY844003	---	---
<i>Scinax garbei</i>	1	AY326033	---	DQ283457	---	---	---	---	---	DQ284047	---
<i>Scinax hayii</i>	1	GQ896257	---	---	---	---	---	---	---	---	---
<i>Scinax ictericus</i>	3	GQ896258	---	---	---	---	---	---	---	---	---
<i>Scinax jolyi</i>	7	EF376036	AF467261	---	---	---	---	---	---	---	---
<i>Scinax nasicus</i>	4	AY843759	---	AY844348	---	---	---	---	AY844004	---	---
<i>Scinax nebulosus</i>	1	EF217471	EU201096	---	---	---	---	---	AF549386	---	---
<i>Scinax oreites</i>	1	GQ896260	---	---	---	---	---	---	---	---	---

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	emyc2	emyc3	COI	CXCR4	cytb	H3A	NCX1
<i>Scinax pedromedinae</i>	3	GQ896261	---	---	---	---	---	---	---	---	---
<i>Scinax proboscideus</i>	1	EF217468	EF217511	---	---	---	---	---	---	---	---
<i>Scinax quinquefasciatus</i>	3	GQ896262	---	---	---	---	---	---	---	---	---
<i>Scinax rostratus</i>	8	EF376039	EF376071	---	---	---	---	---	---	---	---
<i>Scinax ruber</i>	1	AY326034	---	---	---	---	---	---	EF364235	DQ284045	---
<i>Scinax similis</i>	7	GQ896263	---	---	---	---	---	---	---	---	---
<i>Scinax squatirostris</i>	9	AY843760	---	AY844349	---	---	---	---	---	---	---
<i>Scinax staufferi</i>	6	AY843761	---	---	---	---	---	GQ366029	AY844006	---	---
<i>Scinax sugillatus</i>	4	AY819392	AY819524	---	AY819227	AY819301	---	---	---	---	---
<i>Scinax x-signatus</i>	6	EF217437	EF217480	---	---	---	---	---	EF364246	---	---
<i>Sphaenorhynchus dorisae</i>	12	AY843766	---	---	---	---	---	---	AY844011	---	---
<i>Sphaenorhynchus lacteus</i>	1	AY819394	AY549367	AY844352	AY819229	AY819303	---	---	AY549420	DQ284048	---
<i>Sphaenorhynchus orophilus</i>	2	DQ380388	---	---	---	---	---	---	---	---	---
<i>Litoria adelaidensis</i>	2	FJ965862	FJ945365	---	---	---	---	---	---	---	---
<i>Litoria amboinensis</i>	2	FJ965863	FJ945366	---	---	---	---	---	---	---	---
<i>Litoria angiana</i>	2	FJ965865	FJ945368	---	---	---	---	---	---	---	---
<i>Litoria arfakiana</i>	2	AY326039	---	---	---	---	---	---	---	---	---
<i>Litoria bicolor</i>	2	DQ116835	DQ116859	---	---	---	---	---	---	---	---
<i>Litoria burrowsi</i>	2	FJ965870	FJ945373	---	---	---	---	---	---	---	---
<i>Litoria congenita</i>	2	FJ965872	FJ945375	---	---	---	---	---	---	---	---
<i>Litoria coplandi</i>	2	DQ116841	DQ116865	---	---	---	---	---	---	---	---
<i>Litoria darlingtoni</i>	2	FJ965875	FJ945378	---	---	---	---	---	---	---	---
<i>Litoria dentata</i>	2	FJ965877	FJ945379	---	---	---	---	---	---	---	---
<i>Litoria dorsalis</i>	2	FJ965878	FJ945380	---	---	---	---	---	---	---	---
<i>Litoria electrica</i>	3	FJ965880	FJ945382	---	---	---	---	---	---	---	---
<i>Litoria ewingii</i>	3	FJ965884	FJ945386	---	---	---	---	---	---	---	---
<i>Litoria fallax</i>	8	DQ116836	DQ116860	---	---	---	AF198298	---	---	---	---
<i>Litoria freycineti</i>	2	AY843693	---	---	---	---	---	GQ365989	AY843939	DQ284122	---

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	cmyc2	cmyc3	COI	CXCR4	cytb	H3A	NCXI
<i>Litoria havina</i>	4	FJ965890	FJ945392	---	---	---	---	---	---	---	---
<i>Litoria inermis</i>	2	DQ283211	---	---	---	---	---	---	---	DQ284243	---
<i>Litoria iris</i>	2	FJ965893	FJ945395	---	---	---	---	---	---	---	---
<i>Litoria jervisiensis</i>	2	FJ965895	FJ945397	---	---	---	---	---	---	---	---
<i>Litoria latopalmaria</i>	2	FJ965898	FJ945400	---	---	---	---	---	---	---	---
<i>Litoria leucova</i>	2	FJ965900	FJ945402	---	---	---	---	---	---	---	---
<i>Litoria littlejohni</i>	2	FJ965901	FJ945403	---	---	---	---	---	---	---	---
<i>Litoria longirostris</i>	2	FJ965902	FJ945404	---	---	---	---	---	---	---	---
<i>Litoria majikihise</i>	8	FJ965903	FJ945405	---	---	---	---	---	---	---	---
<i>Litoria meiriana</i>	2	AY843695	---	---	---	---	---	---	---	DQ284125	---
<i>Litoria microbelos</i>	2	DQ116831	DQ116855	---	---	---	---	---	---	---	---
<i>Litoria micromembrana</i>	2	FJ965904	AF136336	---	---	---	---	---	---	---	---
<i>Litoria modica</i>	2	FJ965906	FJ945407	---	---	---	---	---	---	---	---
<i>Litoria multiplicata</i>	2	FJ965910	FJ945412	---	---	---	---	---	---	---	---
<i>Litoria nasuta</i>	2	DQ116838	DQ116862	---	---	---	---	---	---	---	---
<i>Litoria nigrofrenata</i>	2	FJ965912	FJ945414	---	---	---	---	---	---	---	---
<i>Litoria nigropunctata</i>	2	FJ965913	FJ945415	---	---	---	---	---	---	---	---
<i>Litoria olongburensis</i>	2	FJ965916	FJ945418	---	---	---	---	---	---	---	---
<i>Litoria pallida</i>	2	DQ116840	DQ116864	---	---	---	---	---	---	---	---
<i>Litoria paraewingi</i>	2	FJ965917	FJ945419	---	---	---	---	---	---	---	---
<i>Litoria peronii</i>	2	AY819408	DQ116857	---	---	---	---	---	---	---	---
<i>Litoria personata</i>	2	FJ965919	FJ945421	---	---	---	---	---	---	---	---
<i>Litoria pronimia</i>	2	FJ965922	FJ945424	---	---	---	---	---	---	---	---
<i>Litoria prora</i>	2	FJ965923	FJ945425	---	---	---	---	---	---	---	---
<i>Litoria revelata</i>	2	FJ965925	FJ945427	---	---	---	---	---	---	---	---
<i>Litoria rothii</i>	3	DQ116834	DQ116858	---	---	---	---	---	---	---	---
<i>Litoria rubella</i>	2	DQ116832	DQ116856	---	---	---	---	---	---	---	---
<i>Litoria spartacus</i>	2	FJ965930	FJ945432	---	---	---	---	---	---	---	---

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	cmyc2	cmyc3	COI	CXCR4	cytb	H3A	NCXI
<i>Litoria thesaurensis</i>	2	GQ896273	AF136318	---	---	---	---	---	---	---	---
<i>Litoria tornieri</i>	2	DQ116837	DQ116861	---	---	---	---	---	---	---	---
<i>Litoria tylei</i>	2	FJ965934	FJ945436	---	---	---	---	---	---	---	---
<i>Litoria verreauxii</i>	2	FJ965935	FJ945437	---	---	---	---	---	---	---	---
<i>Litoria watjulumensis</i>	2	DQ116842	DQ116866	---	---	---	---	---	---	---	---
<i>Litoria wollastoni</i>	3	FJ965937	FJ945439	---	---	---	---	---	---	---	---
<i>Dryopsophus alboguttatus</i>	2	DQ116846	DQ116870	---	---	---	---	---	---	---	---
<i>Dryopsophus andiirrmalin</i>	14	FJ965864	FJ945367	---	---	---	---	---	---	---	---
<i>Dryopsophus aureus</i>	8	DQ116845	DQ116869	---	AY819233	AY819307	EU043187	---	AY843937	DQ284098	---
<i>Dryopsophus australis</i>	2	AY843580	---	---	---	---	---	GQ365987	AY843802	DQ284124	---
<i>Dryopsophus barringtonensis</i>	2	FJ965867	FJ945370	---	---	---	---	---	---	---	---
<i>Dryopsophus booroolongensis</i>	3	FJ965868	FJ945371	---	---	---	---	---	---	---	---
<i>Dryopsophus brevipes</i>	16	AY819411	FJ945355	---	---	---	---	---	---	---	---
<i>Dryopsophus caeruleus</i>	2	AY326038	AF136316	---	AY819234	AY819308	AY883980	GQ365988	AY843938	---	AY948821
<i>Dryopsophus cavernicolus</i>	2	FJ965871	FJ945374	---	---	---	---	---	---	---	---
<i>Dryopsophus chloris</i>	1	DQ116851	DQ116874	---	---	---	---	---	---	---	---
<i>Dryopsophus citropus</i>	2	---	AF282611	---	---	---	---	---	---	---	---
<i>Dryopsophus cryptotis</i>	2	FJ965852	FJ945356	---	---	---	---	---	---	---	---
<i>Dryopsophus cultripes</i>	2	FJ965853	FJ945357	---	---	---	---	---	---	---	---
<i>Dryopsophus cyclorhynchus</i>	2	FJ965874	FJ945377	---	---	---	---	---	---	---	---
<i>Dryopsophus dahlit</i>	1	DQ116844	DQ116868	---	---	---	---	---	---	---	---
<i>Dryopsophus daviesae</i>	6	FJ965876	---	---	---	---	---	---	---	---	---
<i>Dryopsophus dayi</i>	3	FJ965939	DQ283220	---	---	---	AF304266	---	---	DQ284250	---
<i>Dryopsophus eucnemis</i>	2	FJ965882	AF136315	---	---	---	AF304232	---	---	---	---
<i>Dryopsophus exophthalmus</i>	7	FJ965885	AF136314	---	---	---	---	---	---	---	---
<i>Dryopsophus genimaculatus</i>	2	DQ283222	---	DQ283592	---	---	AF304231	---	---	DQ284252	---
<i>Dryopsophus gilleni</i>	2	DQ116849	DQ116872	---	---	---	---	---	---	---	---
<i>Dryopsophus gracilentus</i>	2	DQ116853	DQ116876	---	---	---	---	---	---	---	---

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	cmyc2	cmyc3	COI	CXCR4	cytb	H3A	NCXI
<i>Dryopsophus timpurus</i>	2	FJ965891	FJ945393	---	---	---	---	---	---	---	---
<i>Dryopsophus jungguy</i>	2	FJ965896	FJ945398	---	---	---	---	---	---	---	---
<i>Dryopsophus kumae</i>	5	FJ965897	FJ945399	---	---	---	---	---	---	---	---
<i>Dryopsophus lesueurii</i>	2	FJ965899	DQ283204	---	---	---	---	---	---	DQ284236	---
<i>Dryopsophus longipes</i>	2	FJ965854	DQ116867	---	---	---	---	---	---	---	---
<i>Dryopsophus maculosus</i>	8	FJ965855	FJ945359	---	---	---	---	---	---	---	---
<i>Dryopsophus maini</i>	9	FJ882737	FJ945360	---	---	---	---	EF107475	---	---	EF107252
<i>Dryopsophus manya</i>	2	FJ965857	FJ945361	---	AY819232	AY819306	---	---	EF125030	---	---
<i>Dryopsophus moorei</i>	6	FJ965909	FJ945411	---	---	---	---	---	---	---	---
<i>Dryopsophus nannois</i>	2	FJ965911	DQ283218	---	---	---	AF304249	---	---	DQ284248	---
<i>Dryopsophus novaehollandiae</i>	2	FJ965858	FJ945362	---	---	---	---	---	---	---	---
<i>Dryopsophus nudidigitus</i>	2	FJ965914	FJ945416	---	---	---	---	---	---	---	---
<i>Dryopsophus nyakalensis</i>	2	FJ965915	FJ945417	---	---	---	---	---	---	---	---
<i>Dryopsophus pearsonianus</i>	2	FJ965918	FJ945420	---	---	---	---	---	---	---	---
<i>Dryopsophus phyllochrous</i>	1	FJ965920	FJ945422	---	---	---	---	---	---	---	---
<i>Dryopsophus platycephalus</i>	3	FJ965859	---	---	---	---	---	---	---	---	---
<i>Dryopsophus raniformis</i>	3	FJ965924	FJ945426	---	---	---	EU043205	---	---	---	---
<i>Dryopsophus rheocolus</i>	3	FJ965926	AF136327	---	---	---	AF304291	---	---	---	---
<i>Dryopsophus serratus</i>	2	GU323597	FJ945390	---	---	---	AF304215	---	---	---	---
<i>Dryopsophus spenceri</i>	2	FJ965932	FJ945434	---	---	---	---	---	---	---	---
<i>Dryopsophus splendidus</i>	2	DQ116850	DQ116873	---	---	---	---	---	---	---	---
<i>Dryopsophus subglandulosus</i>	2	FJ965933	FJ945435	---	---	---	---	---	---	---	---
<i>Dryopsophus vagitus</i>	2	FJ965860	FJ945363	---	---	---	---	---	---	---	---
<i>Dryopsophus verrucosus</i>	2	FJ965861	FJ945364	---	---	---	---	---	---	---	---
<i>Dryopsophus wilcoxi</i>	2	FJ965936	FJ945438	---	---	---	---	---	---	---	---
<i>Dryopsophus xanthomerus</i>	2	DQ116852	DQ116875	---	---	---	---	---	---	---	---
<i>Nyctimystes brevipalmatus</i>	2	FJ965869	FJ945372	---	---	---	---	---	---	---	---
<i>Nyctimystes cheesmani</i>	2	FJ965938	FJ945440	---	---	---	---	---	---	---	---
<i>Nyctimystes dux</i>	5	FJ965879	FJ945381	---	---	---	---	---	---	---	---

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	cmyc2	cmyc3	COI	CXCR4	cytb	H3A	NCX1
<i>Nyctimystes forficula</i>	2	FJ965941	FJ945443	---	AY819235	AY819309	---	---	---	---	---
<i>Nyctimystes humeralis</i>	9	FJ965942	FJ945444	---	---	---	---	---	---	---	---
<i>Nyctimystes infrafronatus</i>	9	AY843694	AY844304	---	---	---	FJ952304	GQ365990	AY843940	---	---
<i>Nyctimystes kubori</i>	8	AY326037	---	---	---	---	JX564879	GQ365991	JX564879	---	---
<i>Nyctimystes narinosus</i>	2	AY843703	AY844308	---	---	---	---	GQ365992	AY843948	---	---
<i>Nyctimystes papua</i>	12	FJ965943	FJ945445	---	---	---	---	---	---	---	---
<i>Nyctimystes pulcher</i>	2	FJ965944	FJ945446	---	---	---	---	GQ365993	AY843946	DQ284126	AY948843
<i>Nyctimystes semipalmatus</i>	2	FJ965945	FJ945447	---	---	---	---	---	---	---	---
<i>Nyctimystes zweifeli</i>	10	FJ965949	FJ945451	---	---	---	---	---	---	---	---
<i>Agalychnis amae</i>	15	GQ366221	---	---	EF174320	---	---	GQ365977	GQ365913	---	---
<i>Agalychnis callidryas</i>	14	EF566944	GQ366223	---	EF174321	---	AB612053	AB612054	EF125028	DQ284401	AB612055
<i>Agalychnis daenicolor</i>	7	AY326047	AY844318	AY819237	AY819311	---	---	GQ365995	EF125036	---	---
<i>Agalychnis hulli</i>	14	GQ366226	---	---	---	---	---	GQ365980	---	---	---
<i>Agalychnis lemur</i>	10	AY843725	---	---	AY819238	AY819312	FJ766721	GQ365981	EF125035	---	---
<i>Agalychnis moreletii</i>	8	GQ366227	---	---	EF174323	---	---	GQ365982	GQ365916	---	---
<i>Agalychnis saltator</i>	9	AY326044	---	---	---	---	---	GQ365983	GQ365917	---	---
<i>Agalychnis spurrelli</i>	1	AY819401	AY326043	---	AY819236	AY819310	---	---	EF125033	---	---
<i>Agalychnis terranova</i>	1	---	KC589394	---	---	---	---	---	---	---	---
<i>Callimedusa atelopoides</i>	7	AY819413	---	---	---	---	---	---	---	---	---
<i>Callimedusa baltea</i>	1	GQ366252	---	---	---	---	---	GQ366008	GQ365941	---	---
<i>Callimedusa duellmani</i>	2	AY819414	---	---	---	---	---	---	---	---	---
<i>Callimedusa ecuatoriana</i>	1	KF756940	---	---	---	---	---	---	---	---	---
<i>Callimedusa perinesos</i>	16	GQ896278	---	---	---	---	---	---	---	---	---
<i>Callimedusa tompierna</i>	13	AY326045	AY844328	AY819239	AY819313	JX564887	---	GQ366024	JX564887	---	---
<i>Cruziolyha calcarifer</i>	4	AY843562	AY844196	EF174324	---	---	FJ766565	GQ365984	EF125034	---	---
<i>Hylomantis asperus</i>	11	GQ366222	---	---	---	---	---	GQ365978	---	---	---
<i>Hylomantis granulosus</i>	8	AY843687	AY844301	---	---	---	---	GQ365979	GQ365914	---	---
<i>Phasmahyla cochranae</i>	3	AY843715	---	---	---	---	---	GQ365996	AY843960	---	---
<i>Phasmahyla cruzi</i>	8	---	---	---	---	---	---	GQ365998	---	---	---

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APPENDIX 1. (Continued)

Species	# of genes	12S	16S	28S	cmcy2	cmcy3	COI	CXCR4	cytb	H3A	NCXI
<i>Phasmahyla exilis</i>	8	GQ366231						GQ365997	GQ365920		
<i>Phasmahyla guttata</i>	7	AY843716							GQ365921		
<i>Phasmahyla jandaia</i>	7	GQ366233						GQ365999	GQ365922		
<i>Phrynomedusa marginata</i>	7	AY819417	GQ366234						GQ365923		
<i>Phyllomedusa bahiana</i>	9	GQ366251							GQ365940		
<i>Phyllomedusa bicolor</i>	10	AY843723						GQ366009	AY843968		
<i>Phyllomedusa boliviana</i>	10	GQ896277	GQ366254					GQ366010	GQ365942		
<i>Phyllomedusa burmeisteri</i>	5	GQ366257						GQ366011	GQ365945		
<i>Phyllomedusa camba</i>	9	GQ366259									
<i>Phyllomedusa distincta</i>	7	GQ366263						GQ366013	GQ365951		
<i>Phyllomedusa iheringii</i>	7	GQ366264							GQ365952		
<i>Phyllomedusa neildi</i>	9	GQ366270						GQ366015	GQ365958		
<i>Phyllomedusa sauvaigi</i>	9	GQ366283						GQ366018	GQ365971		
<i>Phyllomedusa tarsius</i>	12	AY843726		AY844326				GQ366020	AY843971		
<i>Phyllomedusa tetraploidea</i>	7	AY843727		AY844327				GQ366021	GQ365973		
<i>Phyllomedusa trinitatis</i>	10	GQ896279	GQ366287					GQ366026	GQ365975		
<i>Phyllomedusa vaillanti</i>	9	AY549363		AY844329				GQ366027	AY549416		
<i>Pithecopus ayeaye</i>	8	GQ366245						GQ366003	GQ365935		
<i>Pithecopus azureus</i>	3	GQ896276	GQ366247					GQ366005	GQ365936		
<i>Pithecopus centralis</i>	12	GQ366261							GQ365948		
<i>Pithecopus hypochondrialis</i>	7	FJ882741	AY948748					GQ366014	AY843969	GQ345210	AY948826
<i>Pithecopus megacephalus</i>	9	GQ366269							GQ365957		
<i>Pithecopus nordestinus</i>	5	GQ366272						GQ366016	GQ365961		
<i>Pithecopus oreades</i>	6	GQ366279							GQ365966		
<i>Pithecopus palliatus</i>	9	AY326046						GQ366017	GQ365968		
<i>Pithecopus rohdei</i>	14	GQ366240						GQ366000	GQ365929		
<i>Ceuthomantis smaragdinus</i>	15	GQ345133		GQ345141	GQ345154	GQ345169		GQ345190	GQ345208		GQ345238
<i>Dendrobates auratus</i>	16	DQ347026	AY364565	AY844211		JX564862		AY364184	AY843803	DQ284072	AY948823
<i>Haddadus binotatus</i>	14	EF493361		DQ283493	GQ345147	GQ345165		GQ345183	GQ345198	DQ284142	GQ345231
<i>Rhinoderma darwini</i>	3	AY364357	AY364378	DQ283654		JX564891		AY364192	DQ502589	DQ284320	AY523733

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APPENDIX I. (Continued)

Species	NDI	ND2	POMC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
# of accessions in alignment	222	54	169	215	232	166	12	45	190
<i>Acris blanchardi</i>	---	---	EF988255	---	---	---	---	---	EF988317
<i>Acris crepitans</i>	FJ882759	FJ882759	GQ366031	EF107304	AY844533	AY844762	EF107403	---	AY844019
<i>Acris gryllus</i>	---	---	EF988267	AY844359	AY844534	AY844763	---	---	AY844020
<i>Hylliola cadaverina</i>	AY819497	---	AY819115	---	AY844722	---	---	---	AY844162
<i>Hylliola hypochondriaca</i>	---	---	---	---	---	---	---	---	---
<i>Hylliola regilla</i>	AY819508	---	AY819126	DQ679268	AY844725	---	---	---	AY844165
<i>Hylliola sierra</i>	---	---	---	---	---	---	---	---	---
<i>Pseudacris brachyphona</i>	---	KJ536245	---	---	---	---	---	---	---
<i>Pseudacris brimleyi</i>	---	---	---	---	---	---	---	---	---
<i>Pseudacris clarkii</i>	---	KJ536246	---	---	---	---	---	---	---
<i>Pseudacris crucifer</i>	AY819517	KJ536232	EF988269	---	AY844723	AY844927	---	---	AY844163
<i>Pseudacris feriarum</i>	---	KJ536237	---	---	---	---	---	---	---
<i>Pseudacris fouquettei</i>	---	KJ536249	---	---	---	---	---	---	---
<i>Pseudacris illinoensis</i>	---	KJ536235	---	---	---	---	---	---	---
<i>Pseudacris kalmi</i>	---	KJ536240	---	---	---	---	---	---	---
<i>Pseudacris maculata</i>	---	KJ536247	EF988270	---	---	---	---	---	EF988332
<i>Pseudacris nigrata</i>	AY819518	KJ536251	AY819136	---	---	---	---	---	---
<i>Pseudacris ocularis</i>	DQ055834	KJ536230	DQ055808	---	AY844724	---	---	---	AY844164
<i>Pseudacris omata</i>	---	---	---	---	---	---	---	---	---
<i>Pseudacris streckeri</i>	---	KJ536234	---	---	---	---	---	---	---
<i>Pseudacris triseriata</i>	---	KJ536242	---	---	AY844726	AY844928	---	---	AY844166
<i>Aplastodiscus albofrenatus</i>	AY819539	---	---	---	---	---	---	---	---
<i>Aplastodiscus albovignatus</i>	---	---	---	AY844385	AY844570	AY844796	---	---	AY844042
<i>Aplastodiscus arildae</i>	---	---	---	AY844392	AY844578	AY844803	---	---	AY844049
<i>Aplastodiscus callipygius</i>	---	---	---	AY844402	AY844592	AY844813	---	---	AY844058
<i>Aplastodiscus cavicola</i>	---	---	---	AY844405	AY844594	AY844814	---	---	---
<i>Aplastodiscus cochranae</i>	---	---	---	AY844365	AY844542	AY844770	---	---	AY844024

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APPENDIX 1. (Continued)

Species	NDI	ND2	POMC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
<i>Aplastodiscus eugenioi</i>	---	---	---	AY844456	AY844660	AY844875	---	---	---
<i>Aplastodiscus leucopygius</i>	KF794106	---	---	AY844425	AY844622	AY844840	---	---	AY844084
<i>Aplastodiscus perrivids</i>	KF794107	---	---	AY844366	AY844543	AY844771	---	---	AY844025
<i>Aplastodiscus weygoldti</i>	---	---	---	AY844467	AY844678	AY844887	---	---	---
<i>Bokermannohyla astarteae</i>	AY819495	---	AY819113	---	AY844580	---	---	---	---
<i>Bokermannohyla circumdata</i>	KF794108	---	---	AY844409	AY844598	AY844817	---	---	AY844064
<i>Bokermannohyla hylax</i>	---	---	---	AY844419	AY844614	AY844832	---	---	AY844077
<i>Bokermannohyla itapoty</i>	KF794109	---	---	---	---	---	---	---	---
<i>Bokermannohyla maritinsi</i>	---	---	---	---	AY844626	AY844844	---	---	AY844086
<i>Bokermannohyla oxente</i>	---	---	---	---	---	---	---	---	---
<i>Colomascirtus armatus</i>	KF794111	---	---	AY844393	AY844579	AY844804	---	---	AY844050
<i>Colomascirtus charazani</i>	KF794112	---	---	AY844406	AY844595	---	---	---	AY844061
<i>Colomascirtus criptico</i>	---	---	---	---	---	---	---	---	---
<i>Colomascirtus larinopygion</i>	---	---	---	---	---	---	---	---	---
<i>Colomascirtus lindae</i>	---	---	---	---	---	---	---	---	---
<i>Colomascirtus pacha</i>	---	---	---	---	---	---	---	---	---
<i>Colomascirtus pantostictus</i>	---	---	---	---	---	---	---	---	---
<i>Colomascirtus princecharlesi</i>	---	---	---	---	---	---	---	---	---
<i>Colomascirtus psarolaimus</i>	---	---	---	---	---	---	---	---	---
<i>Colomascirtus psychodactylus</i>	---	---	---	---	---	---	---	---	---
<i>Colomascirtus staufferorum</i>	---	---	---	---	---	---	---	---	---
<i>Colomascirtus tapichalaca</i>	KF794114	---	---	---	AY844672	---	---	---	AY844121
<i>Colomascirtus tigrinus</i>	---	---	---	---	---	---	---	---	---
<i>Hyloscirtus alytolylax</i>	---	---	---	---	---	---	---	---	---
<i>Hyloscirtus colymba</i>	KF794113	EU034095	AY819157	AY844410	AY844599	AY844818	---	---	AY844065
<i>Hyloscirtus lascinius</i>	---	---	---	---	---	---	---	---	---
<i>Hyloscirtus palmeri</i>	AY819554	---	AY819158	AY844439	AY844636	AY844854	---	---	AY844095
<i>Hyloscirtus phyllognathus</i>	---	---	---	---	---	---	---	---	---
<i>Hyloscirtus simmonsii</i>	AY819555	---	AY819159	---	---	---	---	---	---

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APPENDIX 1. (Continued)

Species	NDI	ND2	POMC	RAGI	Rho	SIA	SILC8A3	TNS3	TYR
<i>Hypsiboas aguilari</i>	KF794115	---	---	HM444764	HM444769	---	---	---	---
<i>Hypsiboas albonarginatus</i>	KF794116	FJ502641	---	AY844384	AY844568	AY844794	---	---	---
<i>Hypsiboas albopunctatus</i>	JN898847	JQ023191	---	---	JQ023434	AY844795	---	---	AY844041
<i>Hypsiboas alfaroi</i>	---	---	KF955307	KF955322	---	---	---	---	---
<i>Hypsiboas almandarizae</i>	---	---	---	KF955311	---	---	---	---	---
<i>Hypsiboas balzani</i>	---	---	---	AY844395	AY844582	AY844806	---	---	---
<i>Hypsiboas benitezii</i>	KF794117	---	---	AY844396	AY844583	---	---	---	---
<i>Hypsiboas bischoffi</i>	---	---	---	AY844398	AY844586	---	---	---	---
<i>Hypsiboas boans</i>	KF794118	---	AY819114	---	AY844588	AY844809	---	---	AY844055
<i>Hypsiboas caingua</i>	KF794119	---	---	---	AY844591	AY844812	---	---	AY844057
<i>Hypsiboas caipora</i>	KF794120	---	---	---	---	---	---	---	---
<i>Hypsiboas calcaratus</i>	---	---	---	KF955314	---	---	---	---	EF376134
<i>Hypsiboas callipleura</i>	KF794121	---	---	---	---	---	---	---	---
<i>Hypsiboas cinerascens</i>	AY819542	---	---	---	AY844610	AY844828	---	---	---
<i>Hypsiboas cordobae</i>	KF794122	---	---	AY844411	AY844600	AY844819	---	---	AY844066
<i>Hypsiboas crepitans</i>	---	---	---	AY844412	AY844601	---	---	---	AY844067
<i>Hypsiboas curupi</i>	---	---	---	---	---	---	---	---	---
<i>Hypsiboas dentei</i>	---	---	---	---	---	---	---	---	EF376124
<i>Hypsiboas ericae</i>	KF794123	---	---	AY844416	AY844605	---	---	---	AY844071
<i>Hypsiboas faber</i>	KF794124	FJ502710	---	---	AY844607	AY844825	---	---	---
<i>Hypsiboas fasciatus</i>	---	---	---	KF955309	AY844608	---	---	---	EF376135
<i>Hypsiboas geographicus</i>	AY819541	---	---	---	---	---	---	---	EF376122
<i>Hypsiboas gladiator</i>	---	---	---	---	---	---	---	---	---
<i>Hypsiboas guentheri</i>	KF794125	---	---	---	AY844612	AY844830	---	---	---
<i>Hypsiboas heilprini</i>	KF794126	---	EU034114	---	AY844613	AY844831	---	---	---
<i>Hypsiboas joaquina</i>	KF794127	---	---	AY844421	AY844616	AY844834	---	---	---
<i>Hypsiboas lanciformis</i>	AY819543	---	---	KF955325	AY844619	AY844837	---	---	AY844081
<i>Hypsiboas latistratus</i>	KF794128	---	---	---	AY844668	---	---	---	---
<i>Hypsiboas lemai</i>	KF794129	---	---	AY844423	AY844620	AY844838	---	---	AY844082

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APPENDIX 1. (Continued)

Species	ND1	ND2	POMC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
<i>Hypsiboas leptolineatus</i>	KF794130	---	---	AY844424	AY844621	AY844839	---	---	AY844083
<i>Hypsiboas lundii</i>	---	---	---	---	AY844623	AY844841	---	---	AY844085
<i>Hypsiboas maculateralis</i>	---	---	---	KF955317	---	---	---	---	---
<i>Hypsiboas marginatus</i>	KF794131	---	---	AY844426	AY844624	AY844842	---	---	---
<i>Hypsiboas marianitae</i>	KF794132	---	---	AY844427	AY844625	AY844843	---	---	---
<i>Hypsiboas melanopleura</i>	KF794133	---	---	---	HM444766	---	---	---	---
<i>Hypsiboas microderma</i>	KF794134	---	---	---	---	---	---	---	---
<i>Hypsiboas multifasciatus</i>	GQ366299	JQ023295	GQ366036	AY844436	AY844633	AY844851	---	---	AY844093
<i>Hypsiboas nympha</i>	KF794135	---	---	AY844457	AY844661	---	---	---	AY844112
<i>Hypsiboas ornativittatus</i>	---	---	---	---	---	---	---	---	EF376125
<i>Hypsiboas palaestes</i>	---	---	---	---	---	---	---	---	---
<i>Hypsiboas pardalis</i>	KF794136	---	---	---	AY844637	AY844855	---	---	AY844096
<i>Hypsiboas pellucens</i>	---	---	---	---	---	---	---	---	---
<i>Hypsiboas picturatus</i>	---	---	---	---	---	---	---	---	---
<i>Hypsiboas polytaenius</i>	KF794137	---	AY819124	AY844443	AY844641	AY844859	---	---	---
<i>Hypsiboas prasinus</i>	---	---	---	---	AY844642	AY844860	---	---	AY844100
<i>Hypsiboas pulchellus</i>	KF794138	---	---	AY844445	AY844644	AY844862	---	---	AY844102
<i>Hypsiboas punctatus</i>	KF794139	---	---	---	AY844645	---	---	---	---
<i>Hypsiboas raniceps</i>	JQ023173	JQ023296	AY819125	---	JQ023459	AY844863	---	---	AY844103
<i>Hypsiboas riojanus</i>	KF794141	---	---	AY844447	AY844648	AY844865	---	---	---
<i>Hypsiboas roraima</i>	KF794143	---	---	AY844448	AY844650	AY844866	---	---	AY844104
<i>Hypsiboas rosenbergi</i>	KF794142	---	---	---	---	---	---	---	---
<i>Hypsiboas ruffitatus</i>	KF794144	---	---	---	AY844652	AY844867	---	---	AY844105
<i>Hypsiboas semiguttatus</i>	KF794145	---	---	AY844452	AY844655	AY844870	---	---	---
<i>Hypsiboas semilineatus</i>	KF794146	FJ502780	---	AY844453	AY844656	AY844871	---	---	AY844108
<i>Hypsiboas sibleszi</i>	KF794147	---	---	AY844455	AY844658	AY844873	---	---	AY844110
<i>Hypsiboas tetete</i>	---	---	---	KF955323	---	---	---	---	---
<i>Myersiolyta inparquesi</i>	---	---	---	---	AY844663	AY844876	---	---	AY844114
<i>Myersiolyta kanaima</i>	GQ366307	---	---	AY844422	AY844617	AY844835	---	---	AY844079

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APPENDIX 1. (Continued)

Species	NDI	ND2	POMC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
<i>Dendropsophus anataliasiasi</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus anceps</i>	---	---	---	AY844386	AY844571	AY844797	---	---	AY844043
<i>Dendropsophus aperomeus</i>	AY819549	---	---	---	---	---	---	---	---
<i>Dendropsophus berthaltutzae</i>	---	JQ410480	---	AY844397	AY844584	AY844807	---	---	AY844052
<i>Dendropsophus bifurcus</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus bipunctatus</i>	---	---	---	---	AY844585	AY844808	---	---	AY844053
<i>Dendropsophus branneri</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus brevifrons</i>	---	---	---	AY844400	AY844589	AY844810	---	---	EF376128
<i>Dendropsophus carnifex</i>	---	---	---	AY844404	---	---	---	---	AY844060
<i>Dendropsophus coffeus</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus ebraecatus</i>	FJ542150	EU034096	AY819117	AY844415	AY844604	AY844822	---	---	AY844070
<i>Dendropsophus elegans</i>	---	JQ410654	---	---	---	---	---	---	---
<i>Dendropsophus elianae</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus frosti</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus gaucheri</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus giesleri</i>	---	---	---	AY844417	---	AY844827	---	---	AY844075
<i>Dendropsophus jimi</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus juliani</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus koechlini</i>	AY819501	---	AY819119	---	---	---	---	---	---
<i>Dendropsophus labialis</i>	---	---	JF422463	---	AY844618	AY844836	---	---	AY844080
<i>Dendropsophus leali</i>	AY819550	---	---	---	---	---	---	---	---
<i>Dendropsophus leucophyllatus</i>	---	---	---	---	---	---	---	---	JN692124
<i>Dendropsophus luddeckei</i>	---	---	JF422610	---	---	---	---	---	---
<i>Dendropsophus manonegra</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus marmoratus</i>	---	---	---	AY844428	DQ283782	---	---	---	---
<i>Dendropsophus melanargyreus</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus meridensis</i>	---	---	JF422622	---	---	---	---	---	---
<i>Dendropsophus microcephalus</i>	AY819503	---	AY819121	AY844430	AY844628	AY844846	---	---	---
<i>Dendropsophus minusculus</i>	---	---	---	---	---	---	---	---	EF376131

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APPENDIX 1. (Continued)

Species	NDI	ND2	POMIC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
<i>Dendropsophus minutus</i>	---	---	---	AY844432	DQ283758	---	---	---	AY844089
<i>Dendropsophus miyatai</i>	---	---	---	AY844435	AY844632	AY844850	---	---	AY844092
<i>Dendropsophus nanus</i>	GQ366298	---	AY819123	AY844437	AY844634	AY844852	---	---	EF376132
<i>Dendropsophus parviceps</i>	---	---	---	AY844440	AY844638	AY844856	---	---	AY844097
<i>Dendropsophus phlebodes</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus reichlei</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus rhodopeplus</i>	---	---	---	AY844446	AY844647	AY844864	---	---	---
<i>Dendropsophus riveroi</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus robertmertensi</i>	AY819551	---	---	---	---	---	---	---	---
<i>Dendropsophus rubicundulus</i>	---	---	---	AY844449	AY844651	---	---	---	---
<i>Dendropsophus salli</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus sanborni</i>	---	---	---	AY844450	AY844653	AY844868	---	---	AY844106
<i>Dendropsophus sarayacuensis</i>	---	---	---	AY844451	---	AY844869	---	---	---
<i>Dendropsophus sartori</i>	AY819552	---	AY819156	---	---	---	---	---	---
<i>Dendropsophus schubarti</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus seniculus</i>	---	---	---	AY844454	AY844657	AY844872	---	---	AY844109
<i>Dendropsophus timbeba</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus triangulum</i>	---	---	---	AY844464	AY844673	---	---	---	AY844122
<i>Dendropsophus tritaeniatius</i>	---	---	---	---	---	---	---	---	---
<i>Dendropsophus walfordi</i>	---	---	---	---	AY844676	AY844886	---	---	---
<i>Xenohyla truncata</i>	---	---	---	---	---	---	---	---	---
<i>Anotheca spinosa</i>	AY819492	---	AY819110	DQ830928	DQ830913	AY844768	---	DQ830950	AY844022
<i>Bromeliohyla bromeliacia</i>	DQ055816	---	DQ055788	AY844401	AY844590	AY844811	---	---	AY844056
<i>Charadrahyla nephila</i>	DQ388756	---	DQ388712	AY844438	AY844635	AY844853	---	---	AY844094
<i>Charadrahyla taenitopus</i>	AY819556	---	DQ055803	AY844463	AY844671	AY844883	---	---	AY844120
<i>Diaglena spatulata</i>	DQ388763	---	DQ838733	DQ830930	DQ838736	DQ830963	---	DQ830946	---
<i>Dryophytes andersonii</i>	DQ055812	---	DQ055785	---	AY844572	AY844798	---	---	AY844044
<i>Dryophytes arenicolor</i>	FJ882776	FJ882776	AY819112	AY364220	AY364401	AY844802	EF107393	---	DQ347187
<i>Dryophytes avivocus</i>	DQ055815	---	---	GU989062	AY844581	AY844805	---	---	AY844051

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APPENDIX 1. (Continued)

Species	ND1	ND2	POMC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
<i>Dryophytes chrysoceles</i>	---	---	---	GU989054	GU944712	---	---	---	---
<i>Dryophytes cinereus</i>	KF794110	---	AY819116	AY323766	AY323749	AY844816	---	DQ830949	AY844063
<i>Dryophytes euphorbiaceus</i>	DQ055818	---	HMI152406	---	AY844606	AY844823	---	---	AY844072
<i>Dryophytes eximius</i>	---	---	HMI152416	GU989060	GU944718	AY844824	---	---	AY844073
<i>Dryophytes femoralis</i>	DQ055819	---	DQ055792	FJ227060	AY844609	AY844826	---	---	AY844074
<i>Dryophytes gratus</i>	DQ055820	---	DQ055793	AY844418	AY844611	AY844829	---	---	AY844076
<i>Dryophytes immaculatus</i>	GQ374904	---	GQ374916	---	---	---	---	---	---
<i>Dryophytes japonicus</i>	AB303949	AB303949	DQ055794	FJ227068	AY844615	AY844833	---	---	AY844078
<i>Dryophytes plicatus</i>	DQ055826	---	HMI152405	---	---	---	---	---	---
<i>Dryophytes squirrelus</i>	AY819510	---	AY819128	FJ227074	AY844670	AY844882	---	---	AY844119
<i>Dryophytes suaveonensis</i>	---	---	---	---	---	---	---	---	---
<i>Dryophytes versicolor</i>	DQ055831	---	HMI152404	AY844465	AY844675	AY844885	---	---	AY844124
<i>Dryophytes walkeri</i>	GQ374906	---	GQ374918	---	---	---	---	---	---
<i>Dryophytes wrightorum</i>	AY819500	---	HMI152407	GU989051	GU944709	---	---	---	---
<i>Duellmanohyla rufioculis</i>	DQ388749	---	DQ388705	AY844377	AY844556	AY844782	---	---	AY844033
<i>Duellmanohyla soralia</i>	AY819493	---	AY819111	AY844378	AY844557	AY844783	---	---	AY844034
<i>Duellmanohyla uranochroa</i>	DQ388750	---	DQ388706	---	---	---	---	---	---
<i>Ecnomiophyla miliaria</i>	---	---	DQ055797	AY844431	AY844629	AY844847	---	---	AY844088
<i>Ecnomiophyla minera</i>	---	---	DQ388711	---	---	---	---	---	---
<i>Ecnomiophyla rabborum</i>	---	---	---	---	---	---	---	---	---
<i>Exerodonta abdivita</i>	DQ388751	---	DQ388707	---	---	---	---	---	---
<i>Exerodonta chimalapa</i>	DQ388753	---	DQ388708	AY844407	AY844596	AY844815	---	---	AY844062
<i>Exerodonta melanomma</i>	DQ055823	---	DQ055796	AY844429	AY844627	AY844845	---	---	AY844087
<i>Exerodonta perkinsi</i>	DQ388757	---	DQ388713	AY844441	AY844639	AY844857	---	---	AY844098
<i>Exerodonta smaragdina</i>	DQ388759	---	DQ388716	---	---	---	---	---	---
<i>Exerodonta sumichrasti</i>	---	---	DQ055802	---	---	---	---	---	---
<i>Exerodonta xera</i>	---	---	DQ388717	AY844468	AY844679	AY844888	---	---	AY844126
<i>Hyla annectans</i>	DQ055813	---	DQ055786	AY844388	AY844574	AY844800	---	---	AY844045
<i>Hyla arborea</i>	DQ055814	---	DQ055787	FJ227042	AY844575	---	---	---	AY844046

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APPENDIX 1. (Continued)

Species	NDI	ND2	POMC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
<i>Hyla chinensis</i>	NC_006403	AY458593	DQ055789	HM998976	---	---	---	---	---
<i>Hyla felixarabica</i>	---	---	---	---	GQ916814	---	---	---	GQ916706
<i>Hyla intermedia</i>	---	---	---	FJ227093	---	---	---	---	---
<i>Hyla meridionalis</i>	AY523763	DQ902277	AY819120	AY571662	GQ916820	---	AY948860	---	GQ916722
<i>Hyla molleri</i>	---	---	---	FJ227101	---	---	---	---	---
<i>Hyla orientalis</i>	---	---	---	FJ227102	GQ916819	---	---	---	GQ916721
<i>Hyla sarda</i>	JN788041	---	---	FJ227092	---	---	---	---	---
<i>Hyla savignyi</i>	DQ055829	---	DQ055801	FJ227052	AY844654	---	---	---	AY844107
<i>Hyla simplex</i>	---	---	---	---	---	---	---	---	---
<i>Hyla tsinlingensis</i>	GQ374905	---	GQ374917	---	---	---	---	---	---
<i>Isthmohyla lancasteri</i>	---	---	---	---	---	---	---	---	---
<i>Isthmohyla pseudopuma</i>	DQ055827	---	DQ055799	FJ227075	DQ830922	DQ830971	---	DQ830960	AY844101
<i>Isthmohyla rivularis</i>	DQ055828	---	DQ055800	---	AY844649	---	---	---	---
<i>Isthmohyla tica</i>	DQ055830	---	DQ055804	DQ830938	DQ830923	DQ830972	---	DQ830953	---
<i>Isthmohyla zeteki</i>	DQ830875	---	DQ055806	DQ830939	DQ830924	DQ830973	---	DQ830959	---
<i>Megastomatohyla mixe</i>	---	---	---	AY844434	AY844631	AY844849	---	---	AY844091
<i>Plectrohyla chrysopleura</i>	AY819516	---	AY819134	---	---	---	---	---	---
<i>Plectrohyla glandulosa</i>	DQ388760	---	DQ388718	AY844500	AY844718	AY844923	---	---	AY844159
<i>Plectrohyla guatemalensis</i>	DQ055833	---	DQ055807	AY844501	AY844719	AY844924	---	---	AY844160
<i>Plectrohyla natudai</i>	---	---	---	AY844502	AY844720	AY844925	---	---	AY844161
<i>Psychohyla dendrophasma</i>	AY819540	---	DQ055790	AY844414	AY844603	AY844821	---	---	AY844069
<i>Psychohyla euthysanota</i>	---	---	---	AY844509	AY844731	AY844933	---	---	AY844170
<i>Psychohyla hypomykter</i>	DQ055832	---	DQ055809	---	AY844732	---	---	---	---
<i>Psychohyla leonhardschultzei</i>	---	---	---	AY844510	AY844733	AY844934	---	---	AY844171
<i>Psychohyla salvadorensis</i>	AY819547	---	DQ055810	---	---	---	---	---	---
<i>Psychohyla spinipollex</i>	AY819520	---	AY819138	AY844512	AY844735	AY844936	---	---	AY844173
<i>Psychohyla zophodes</i>	DQ388761	---	DQ388719	AY844513	AY844736	AY844937	---	---	AY844174
<i>Rheohyla miotympanum</i>	AY819504	---	AY819122	AY844433	AY844630	AY844848	---	---	AY844090
<i>Sarcohyla amethohtalame</i>	DQ388752	---	---	---	---	---	---	---	---

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APPENDIX 1. (Continued)

Species	ND1	ND2	POMC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
<i>Sarcophyla arborescandens</i>	---	---	---	AY844390	AY844576	AY844801	---	---	AY844047
<i>Sarcophyla bisinicta</i>	---	---	---	AY844399	AY844587	---	---	---	AY844054
<i>Sarcophyla calthula</i>	---	---	---	AY844403	AY844593	---	---	---	AY844059
<i>Sarcophyla cyclada</i>	DQ388754	---	DQ388709	AY844413	AY844602	AY844820	---	---	AY844068
<i>Sarcophyla pentheter</i>	DQ055825	---	DQ055798	---	---	---	---	---	---
<i>Sarcophyla siopela</i>	---	---	DQ388715	---	---	---	---	---	---
<i>Smitisca baudinii</i>	DQ388762	---	DQ388720	DQ830932	DQ830917	AY844946	---	DQ830956	---
<i>Smitisca cyanosticta</i>	AY819525	---	AY819143	DQ830933	DQ830918	AY844947	---	DQ830957	AY844184
<i>Smitisca fodiens</i>	AY819519	---	AY819137	DQ830931	DQ830916	AY844932	---	DQ830944	AY844169
<i>Smitisca phaeota</i>	AY819548	---	DQ055811	DQ830934	AY844751	AY844948	---	DQ830947	AY844185
<i>Smitisca puma</i>	DQ830876	---	DQ388721	DQ830935	AY844752	AY844949	---	DQ830952	AY844186
<i>Smitisca sila</i>	---	---	DQ388722	---	DQ830921	DQ830969	---	---	---
<i>Smitisca sordida</i>	---	---	DQ388723	DQ830936	DQ388703	DQ830970	---	DQ830951	---
<i>Tlalocohyla godmani</i>	DQ388755	---	DQ388710	DQ830942	DQ830927	DQ830976	---	DQ830945	---
<i>Tlalocohyla loquax</i>	DQ055822	---	DQ055795	---	---	---	---	---	---
<i>Tlalocohyla picta</i>	DQ388758	---	DQ388714	DQ830940	DQ830925	AY844858	---	DQ830948	AY844099
<i>Tlalocohyla smithii</i>	AY819509	---	AY819127	DQ830941	DQ830926	AY844874	---	DQ830958	AY844111
<i>Triprion petasatus</i>	AY819528	---	AY819146	DQ830929	DQ830914	AY844955	---	DQ830943	AY844193
<i>Aparasphenodon brunoi</i>	KF002246	---	---	AY844364	AY844541	AY844769	---	---	AY844023
<i>Argenteohyla siemersi</i>	---	---	---	AY844367	AY844544	AY844772	---	---	AY844026
<i>Corythomantis greeningi</i>	KF002247	---	---	AY844374	AY844551	AY844779	---	---	AY844030
<i>Dryaderces pearsoni</i>	KF002189	---	---	---	---	---	---	---	---
<i>Itapotihyla langsdorffii</i>	AY819511	---	KF002003	AY844482	AY844697	AY844903	---	---	AY844137
<i>Nyctimantis rugiceps</i>	---	EU034098	---	---	---	---	---	---	---
<i>Osteocephalus alboguttatus</i>	KF002192	EU034097	JX875744	EU034132	---	---	---	EU034151	---
<i>Osteocephalus buckleyi</i>	EU034082	---	JX875730	EU034133	---	---	---	EU034152	---
<i>Osteocephalus cabrerai</i>	KF002199	---	JX875762	AY844481	AY844696	AY844902	---	---	AY844136
<i>Osteocephalus cannatellai</i>	---	---	JX875755	---	---	---	---	---	---
<i>Osteocephalus carri</i>	---	---	---	---	---	---	---	---	---

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APPENDIX 1. (Continued)

Species	NDI	ND2	POMC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
<i>Osteocephalus castaneicola</i>	KF002200	---	---	---	---	---	---	---	---
<i>Osteocephalus deridens</i>	KF002202	---	JQ868484	---	---	---	---	---	---
<i>Osteocephalus festae</i>	HQ600613	---	JX875728	---	---	---	---	---	---
<i>Osteocephalus fuscifacies</i>	KF002203	---	JX875750	---	---	---	---	---	---
<i>Osteocephalus helena</i>	KF002205	---	JX875739	---	---	---	---	---	---
<i>Osteocephalus heyeri</i>	---	---	---	---	---	---	---	---	---
<i>Osteocephalus leoniae</i>	KF002206	---	---	---	---	---	---	---	---
<i>Osteocephalus lepteurii</i>	KF002214	---	JQ868498	AY844483	AY844698	AY844904	---	---	AY844138
<i>Osteocephalus mimeticus</i>	KF002215	---	---	---	---	---	---	---	---
<i>Osteocephalus mutabor</i>	HQ600609	---	JX875756	---	---	---	---	---	---
<i>Osteocephalus oophagus</i>	KF002219	---	---	AY844484	AY844699	---	---	---	AY844139
<i>Osteocephalus planiceps</i>	KF002221	EU034099	EU034118	EU034134	---	---	---	EU034153	---
<i>Osteocephalus subtilis</i>	---	---	---	---	---	---	---	---	---
<i>Osteocephalus taurinus</i>	JX564881	JX564881	AY819130	EU034135	AY844700	AY844905	---	EU034154	AY844140
<i>Osteocephalus verruciger</i>	KF002241	EU034101	JX875743	---	---	---	---	EU034155	---
<i>Osteocephalus yasuni</i>	KF002242	---	JX875759	---	---	---	---	---	---
<i>Osteopilus crucialis</i>	EU034084	EU034103	EU034121	---	---	---	---	EU034157	---
<i>Osteopilus dominicensis</i>	EU034085	EU034104	EU034122	HQ831912	AY844701	---	---	EU034158	AY844141
<i>Osteopilus marianae</i>	EU034086	---	EU034123	EU034138	---	---	---	EU034159	---
<i>Osteopilus ocellatus</i>	EU034083	EU034102	EU034120	EU034136	---	---	---	EU034156	---
<i>Osteopilus pulchritineatus</i>	EU034087	EU034105	EU034124	EU034139	---	---	---	EU034160	---
<i>Osteopilus septentrionalis</i>	EU034090	EU034108	KF002004	EU034142	---	AY844906	---	EU034161	AY844142
<i>Osteopilus vastus</i>	EU034091	---	EU034128	EU034144	---	AY844907	---	EU034162	AY844143
<i>Osteopilus wilderi</i>	EU034092	EU034110	EU034129	EU034145	---	---	---	EU034163	---
<i>Phyllodytes luteolus</i>	GQ366314	---	GQ366043	AY844494	AY844708	AY844913	---	---	AY844150
<i>Phyllotriades auratus</i>	AY819515	---	AY819133	EU034148	---	---	---	EU034166	---
<i>Tepuihyala aecii</i>	---	---	JQ868478	---	---	---	---	---	---
<i>Tepuihyala edelcaae</i>	---	---	JQ868475	AY844530	---	---	---	---	---
<i>Tepuihyala exophthalma</i>	KF002244	---	JQ868483	---	---	---	---	---	---

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APPENDIX 1. (Continued)

Species	ND1	ND2	POMC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
<i>Tepuithyla rodriguezi</i>	JQ742387	---	JQ868474	---	---	---	---	---	---
<i>Tepuithyla warreni</i>	JQ742403	---	---	---	---	---	---	---	---
<i>Trachycephalus coriaceus</i>	EU034093	EU034111	EU034130	EU034146	---	---	---	EU034164	EF376139
<i>Trachycephalus hadroceps</i>	---	---	---	AY844490	AY844704	---	---	---	AY844146
<i>Trachycephalus imitatrix</i>	---	EU034112	---	---	---	---	---	---	---
<i>Trachycephalus jordani</i>	KF002248	EU034113	JX875777	EU034150	AY844758	AY844953	---	EU034167	AY844190
<i>Trachycephalus mesophaeus</i>	---	---	---	AY844491	AY844705	AY844910	---	---	AY844147
<i>Trachycephalus nigromaculatus</i>	---	---	---	---	AY844759	---	---	---	AY844191
<i>Trachycephalus resinifictrix</i>	---	---	JQ868481	AY844492	AY844706	AY844911	---	---	AY844148
<i>Trachycephalus typhonius</i>	---	---	JX875780	---	---	---	---	---	---
<i>Trachycephalus venulosus</i>	GQ366341	FJ882779	GQ366072	EU034147	AY364396	AY844912	AY948880	EU034165	DQ347161
<i>Lysapsus bolivianus</i>	---	---	---	---	---	---	---	---	---
<i>Lysapsus caraya</i>	---	---	---	---	---	---	---	---	---
<i>Lysapsus laevis</i>	---	---	---	AY844476	AY844689	AY844896	---	---	AY844133
<i>Lysapsus limellum</i>	---	---	---	AY844477	AY844690	AY844897	---	---	---
<i>Pseudis bolbodactyla</i>	---	---	---	---	---	---	---	---	---
<i>Pseudis cardosoi</i>	---	---	---	---	---	---	---	---	---
<i>Pseudis fusca</i>	---	---	---	---	---	---	---	---	---
<i>Pseudis minuta</i>	GQ366339	---	GQ366070	AY844505	---	AY844929	---	---	---
<i>Pseudis paradoxa</i>	AY819483	---	AY819102	AY323773	AY323748	---	---	---	AY844167
<i>Pseudis tocanins</i>	---	---	---	---	---	---	---	---	---
<i>Scarothyla goinorum</i>	AY819521	---	AY819139	AY844514	AY844738	AY844938	---	---	---
<i>Julianus uruguayus</i>	---	---	---	---	AY844674	AY844884	---	---	AY844123
<i>Ololygon berthae</i>	---	---	---	---	AY844740	AY844940	---	---	---
<i>Ololygon catharinae</i>	AY819522	---	AY819140	AY844517	AY844742	AY844941	---	---	---
<i>Ololygon faivovitchi</i>	JN100003	---	---	---	---	---	---	---	---
<i>Ololygon obtriangulata</i>	---	---	---	---	---	---	---	---	---
<i>Ololygon peixotoi</i>	JN100004	---	---	---	---	---	---	---	---
<i>Ololygon perpusilla</i>	JN099994	---	---	---	---	---	---	---	---

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APPENDIX 1. (Continued)

Species	NDI	ND2	POMC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
<i>Scinax acuminatus</i>	---	---	---	AY844515	AY844739	AY844939	---	---	AY844176
<i>Scinax boesemani</i>	---	---	---	---	---	---	---	---	JN692123
<i>Scinax boulengeri</i>	---	---	---	AY844516	AY844741	---	---	---	AY844177
<i>Scinax chiquitanus</i>	---	---	---	---	---	---	---	---	---
<i>Scinax crosopedospilus</i>	AY819523	---	AY819141	---	---	---	---	---	---
<i>Scinax cruentommus</i>	---	---	---	---	---	---	---	---	EF376149
<i>Scinax duartei</i>	---	---	---	---	---	---	---	---	---
<i>Scinax elaeochrous</i>	---	---	---	AY844518	AY844743	AY844942	---	---	AY844178
<i>Scinax funereus</i>	---	---	---	---	---	---	---	---	---
<i>Scinax fuscomaginnatus</i>	---	---	---	---	---	---	---	---	---
<i>Scinax fuscovarius</i>	---	---	---	AY844519	AY844744	AY844943	---	---	AY844179
<i>Scinax garbei</i>	---	---	---	---	DQ283759	DQ282650	---	---	DQ282898
<i>Scinax hayii</i>	---	---	---	---	---	---	---	---	---
<i>Scinax ictericus</i>	---	---	---	---	---	---	---	---	---
<i>Scinax jolyi</i>	---	---	---	---	---	---	---	---	EF376141
<i>Scinax nasicus</i>	---	---	---	AY844520	AY844745	---	---	---	AY844180
<i>Scinax nebulosus</i>	---	---	---	---	---	---	---	---	EF376144
<i>Scinax oreites</i>	---	---	---	---	---	---	---	---	---
<i>Scinax pedromedinae</i>	---	---	---	---	---	---	---	---	---
<i>Scinax proboscideus</i>	---	---	---	---	---	---	---	---	EF376143
<i>Scinax quinquefasciatus</i>	---	---	---	---	---	---	---	---	---
<i>Scinax rostratus</i>	---	---	---	---	---	---	---	---	EF376145
<i>Scinax ruber</i>	---	---	---	AY844521	AY844746	AY844944	---	---	JN692122
<i>Scinax similis</i>	---	---	---	---	---	---	---	---	---
<i>Scinax squalirostris</i>	---	---	---	AY844522	AY844747	AY844945	---	---	AY844182
<i>Scinax staufferi</i>	GQ366340	---	GQ366071	AY844523	AY844748	---	---	---	AY844183
<i>Scinax stugillatus</i>	AY819524	---	AY819142	---	---	---	---	---	---
<i>Scinax x-signatus</i>	---	---	---	---	---	---	---	---	EF364144
<i>Sphaenorhynchus dorisae</i>	---	---	---	AY844526	AY844753	---	---	---	AY844187

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APPENDIX 1. (Continued)

Species	ND1	ND2	POMC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
<i>Sphaenorhynchus lacteus</i>	AY819526	---	AY819144	AY844527	AY844754	---	---	---	AY844188
<i>Sphaenorhynchus orophilus</i>	---	---	---	---	---	---	---	---	---
<i>Litoria adelaidensis</i>	---	---	---	---	---	---	---	---	---
<i>Litoria amboinensis</i>	---	---	---	---	---	---	---	---	---
<i>Litoria angiana</i>	---	---	---	---	---	---	---	---	---
<i>Litoria arfakiana</i>	---	---	---	---	---	---	---	---	---
<i>Litoria bicolor</i>	---	---	---	---	---	---	---	---	---
<i>Litoria burrowsi</i>	---	---	---	---	---	---	---	---	---
<i>Litoria congenita</i>	---	---	---	---	---	---	---	---	---
<i>Litoria coplandi</i>	---	---	---	---	---	---	---	---	---
<i>Litoria darlingtoni</i>	---	---	---	---	---	---	---	---	---
<i>Litoria dentata</i>	---	---	---	---	---	---	---	---	---
<i>Litoria dorsalis</i>	---	---	---	---	---	---	---	---	---
<i>Litoria electrica</i>	---	---	---	---	---	---	---	---	---
<i>Litoria ewingii</i>	---	---	---	EF551562	---	---	---	---	---
<i>Litoria fallax</i>	---	---	---	---	---	---	---	---	---
<i>Litoria freycineti</i>	---	---	---	AY844473	AY844686	AY844894	---	---	---
<i>Litoria havina</i>	---	---	---	---	---	---	---	---	---
<i>Litoria inermis</i>	---	---	---	---	DQ283892	---	---	---	---
<i>Litoria iris</i>	---	---	---	---	---	---	---	---	---
<i>Litoria jervisiensis</i>	---	---	---	---	---	---	---	---	---
<i>Litoria latopalmata</i>	---	---	---	---	---	---	---	---	---
<i>Litoria leucova</i>	---	---	---	---	---	---	---	---	---
<i>Litoria littlejohni</i>	---	---	---	---	---	---	---	---	---
<i>Litoria longirostris</i>	---	---	---	---	---	---	---	---	---
<i>Litoria majikihise</i>	---	---	---	---	---	---	---	---	---
<i>Litoria meiriana</i>	GQ366304	---	---	AY844475	AY844688	AY844895	---	---	AY844132
<i>Litoria microbelos</i>	---	---	---	---	---	---	---	---	---
<i>Litoria micromembrana</i>	---	---	---	---	---	---	---	---	---

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APPENDIX 1. (Continued)

Species	NDI	ND2	POMC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
<i>Litoria modica</i>	---	---	---	---	---	---	---	---	---
<i>Litoria multiplicata</i>	---	---	---	---	---	---	---	---	---
<i>Litoria nasuta</i>	---	---	---	---	---	---	---	---	---
<i>Litoria nigrofrenata</i>	---	---	---	---	---	---	---	---	---
<i>Litoria nigropunctata</i>	---	---	---	---	---	---	---	---	---
<i>Litoria olongburensis</i>	---	---	---	---	---	---	---	---	---
<i>Litoria pallida</i>	---	---	---	---	---	---	---	---	---
<i>Litoria paraeewingi</i>	---	---	---	---	---	---	---	---	---
<i>Litoria peronii</i>	---	---	---	---	---	---	---	---	---
<i>Litoria personata</i>	---	---	---	---	---	---	---	---	---
<i>Litoria pronimita</i>	---	---	---	---	---	---	---	---	---
<i>Litoria prora</i>	---	---	---	---	---	---	---	---	---
<i>Litoria revelata</i>	---	---	---	---	---	---	---	---	---
<i>Litoria rothii</i>	---	---	---	---	---	---	---	---	---
<i>Litoria rubella</i>	AY819536	---	---	---	---	---	---	---	---
<i>Litoria spartacus</i>	---	---	---	---	---	---	---	---	---
<i>Litoria thesaurensis</i>	---	---	---	---	---	---	---	---	---
<i>Litoria tomeri</i>	---	---	---	---	---	---	---	---	---
<i>Litoria tyleri</i>	---	---	---	---	---	---	---	---	---
<i>Litoria verreauxii</i>	---	---	---	---	---	---	---	---	---
<i>Litoria watjulumensis</i>	---	---	---	---	---	---	---	---	---
<i>Litoria wollastoni</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus alboguttatus</i>	EF080969	---	---	---	---	---	---	---	---
<i>Dryopsophus andirimalin</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus aureus</i>	AY819530	---	GQ366037	EF174309	AY844684	AY844892	---	EF179205	AY844130
<i>Dryopsophus australis</i>	GQ366300	---	---	AY844376	AY844553	---	---	---	---
<i>Dryopsophus barringtonensis</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus booroolongensis</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus brevipes</i>	AY819537	---	---	---	---	---	---	---	---

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APPENDIX 1. (Continued)

Species	ND1	ND2	POMC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
<i>Dryopsophus caeruleus</i>	GQ366301	---	AY819149	AY323767	AY323751	AY844893	AY948877	EF179206	AY844131
<i>Dryopsophus cavernicolus</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus chloris</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus citropus</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus cryptotis</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus cultripes</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus cyclorhynchus</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus dahlii</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus daviesae</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus dayi</i>	---	---	---	---	DQ283897	DQ282757	---	---	---
<i>Dryopsophus eucnemis</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus exophthalmus</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus genimaculatus</i>	---	---	---	---	DQ283899	DQ282759	---	---	---
<i>Dryopsophus gilleni</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus gracilentus</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus impurus</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus jungguy</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus kumae</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus lesueurii</i>	---	---	---	---	DQ283887	DQ282747	---	---	---
<i>Dryopsophus longipes</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus maculosus</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus maini</i>	FJ882738	FJ882738	---	EF107311	---	---	EF107411	---	---
<i>Dryopsophus manya</i>	AY819529	---	AY819147	EF174308	---	---	---	EF179204	---
<i>Dryopsophus moorei</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus nannotis</i>	---	---	---	---	DQ283896	DQ282756	---	---	---
<i>Dryopsophus novaehollandiae</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus nudidigitus</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus nyakalensis</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus pearsonianus</i>	---	---	---	---	---	---	---	---	---

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APPENDIX 1. (Continued)

Species	ND1	ND2	POMC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
<i>Dryopsophus phyllochrous</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus platycephalus</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus raniformis</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus rheocolus</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus serratus</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus spenceri</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus splendidus</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus subglanulosus</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus vagitus</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus verrucosus</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus wilcoxii</i>	---	---	---	---	---	---	---	---	---
<i>Dryopsophus xanthomerus</i>	---	---	---	---	---	---	---	---	---
<i>Nyctimystes brevipalmatus</i>	---	---	---	---	---	---	---	---	---
<i>Nyctimystes chee-smani</i>	---	---	---	---	---	---	---	---	---
<i>Nyctimystes dix</i>	---	---	---	---	---	---	---	---	---
<i>Nyctimystes fornicula</i>	---	---	AY819150	---	---	---	---	---	---
<i>Nyctimystes humeralis</i>	---	---	---	---	---	---	---	---	---
<i>Nyctimystes infrafronatus</i>	GQ366302	---	---	AY844474	AY844687	---	---	---	---
<i>Nyctimystes kubori</i>	GQ366303	JX564879	---	AY844479	AY844693	---	---	---	---
<i>Nyctimystes narinosus</i>	GQ366305	---	---	---	AY844694	---	---	---	AY844135
<i>Nyctimystes papua</i>	---	---	---	---	---	---	---	---	---
<i>Nyctimystes pulcher</i>	GQ366306	FJ882740	---	AY948941	AY844692	---	AY948907	---	AY844134
<i>Nyctimystes semipalmatus</i>	---	---	---	---	---	---	---	---	---
<i>Nyctimystes zweifelti</i>	---	---	---	---	---	---	---	---	---
<i>Agalychnis annae</i>	GQ366291	---	EF158394	EF174311	---	---	---	EF179207	GQ366198
<i>Agalychnis callidryas</i>	FJ489260	---	EF158395	AY323765	AY323750	DQ282880	---	EF179208	DQ283018
<i>Agalychnis dactylos</i>	GQ366308	---	AY819152	AY844488	AY844702	AY844908	---	EF179216	AY844144
<i>Agalychnis hulli</i>	GQ366293	---	GQ366033	GQ366073	GQ366101	---	---	---	---
<i>Agalychnis temur</i>	GQ366294	---	GQ366034	EF174318	AY844712	AY844917	---	EF179214	AY844154

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APPENDIX 1. (Continued)

Species	NDI	ND2	POMC	RAG1	Rho	SIA	SLC8A3	TNS3	TYR
<i>Agalychnis moreletii</i>	GQ366295	---	EF158397	EF174314	GQ366102	---	---	EF179210	---
<i>Agalychnis saltator</i>	GQ366296	---	EF158398	EF174315	---	---	---	EF179211	---
<i>Agalychnis spurrelli</i>	EF396332	---	AY819151	EF174313	---	---	---	EF179212	---
<i>Agalychnis terranova</i>	---	---	---	---	---	---	---	---	---
<i>Callimedusa atelopoides</i>	---	---	---	---	---	---	---	---	---
<i>Callimedusa baltea</i>	GQ366321	---	---	GQ366085	GQ366127	---	---	---	---
<i>Callimedusa dhellmani</i>	---	---	---	---	---	---	---	---	---
<i>Callimedusa ecuatoriana</i>	KF756942	---	---	---	---	---	---	---	---
<i>Callimedusa perinesos</i>	---	---	---	---	---	---	---	---	---
<i>Callimedusa tomopterna</i>	GQ366337	JX564887	GQ366068	EF174319	GQ366157	AY844920	---	EF179215	GQ366219
<i>Cruziohyla calcarifer</i>	GQ366297	---	GQ366035	EF174317	GQ366103	---	---	EF179213	DQ282950
<i>Hylomanis asperus</i>	---	---	---	---	GQ366098	---	---	---	---
<i>Hylomanis granulatus</i>	GQ366292	---	GQ366032	AY844469	GQ366099	AY844889	---	---	AY844127
<i>Phasmahyla cochranae</i>	GQ366309	---	GQ366038	GQ366076	GQ366105	---	---	---	---
<i>Phasmahyla cruzi</i>	GQ366311	---	GQ366041	---	---	---	---	---	---
<i>Phasmahyla exilis</i>	GQ366310	---	GQ366039	GQ366077	GQ366106	---	---	---	---
<i>Phasmahyla guttata</i>	---	---	GQ366040	AY844489	GQ366107	AY844909	---	---	AY844145
<i>Phasmahyla jandaia</i>	GQ366312	---	GQ366042	---	GQ366108	---	---	---	---
<i>Phrynomedusa marginata</i>	GQ366313	---	---	GQ366078	GQ366109	---	---	---	GQ366199
<i>Phyllomedusa bahiana</i>	---	HQ262457	GQ366050	---	GQ366126	---	---	---	GQ366205
<i>Phyllomedusa bicolor</i>	GQ366322	---	---	AY844495	AY844710	AY844915	---	---	AY844152
<i>Phyllomedusa boliviana</i>	GQ366323	HQ262456	GQ366051	GQ366086	GQ366128	---	---	---	GQ366206
<i>Phyllomedusa burmeisteri</i>	GQ366324	HQ262466	GQ366052	GQ366087	GQ366130	---	---	---	GQ366208
<i>Phyllomedusa camba</i>	---	---	GQ366054	GQ366088	GQ366134	---	---	---	---
<i>Phyllomedusa distincta</i>	GQ366326	HQ262477	GQ366055	---	GQ366135	---	---	---	GQ366210
<i>Phyllomedusa iheringii</i>	GQ366328	HQ262488	GQ366057	---	GQ366136	---	---	---	---
<i>Phyllomedusa neildi</i>	GQ366329	---	---	---	GQ366142	---	---	---	GQ366214
<i>Phyllomedusa sauvaigi</i>	GQ366332	---	GQ366065	GQ366094	GQ366152	---	---	---	GQ366216
<i>Phyllomedusa tarsius</i>	---	---	---	GQ366095	AY844713	AY844918	---	---	AY844155

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APPENDIX 1. (Continued)

Species	ND1	ND2	POMC	RAG1	Rh0	SIA	SLC8A3	TNS3	TYR
<i>Phyllomedusa tetraploidea</i>	GQ366334	HQ262487	GQ366066	GQ366096	GQ366156	AY844919	---	---	AY844156
<i>Phyllomedusa trinitatis</i>	---	---	---	GQ366097	GQ366158	---	---	---	GQ366220
<i>Phyllomedusa vaillanti</i>	GQ366338	---	---	AY844498	AY844716	AY844921	---	---	AY844158
<i>Pithecopus ayeaye</i>	GQ366318	---	GQ366046	GQ366083	GQ366119	---	---	---	GQ366202
<i>Pithecopus azureus</i>	GQ366320	---	---	GQ366084	GQ366122	---	---	---	GQ366204
<i>Pithecopus centralis</i>	---	---	---	---	---	---	---	---	---
<i>Pithecopus hypochondrials</i>	GQ366327	---	---	AY948929	AY844711	AY844916	AY948882	---	AY844153
<i>Pithecopus megacephalus</i>	---	---	GQ366058	GQ366090	GQ366139	---	---	---	GQ366213
<i>Pithecopus nordesinus</i>	GQ366330	---	GQ366059	GQ366091	GQ366143	---	---	---	GQ366215
<i>Pithecopus oreades</i>	---	---	GQ366062	---	GQ366146	---	---	---	---
<i>Pithecopus palliatus</i>	GQ366331	---	---	GQ366092	---	---	---	---	---
<i>Pithecopus rohdei</i>	GQ366315	---	GQ366044	GQ366082	GQ366111	---	---	---	GQ366200
<i>Ceuthomantis smaragdinus</i>	GQ345251	---	GQ345267	GQ345287	GQ345305	GQ345317	GQ345338	---	---
<i>Dendrobates auratus</i>	JX564862	HQ290980	---	EU325909	AY364395	AY844781	AY948879	---	DQ347160
<i>Haddadus binotatus</i>	---	---	GQ345259	GQ345278	DQ283807	GQ345309	GQ345329	---	DQ282918
<i>Rhinoderma darwini</i>	FJ882755	JX564891	---	AY364222	AY364403	DQ282813	AY948895	---	---