SYSTEMATIC REVIEW OF THE FROG FAMILY HYLIDAE, WITH SPECIAL REFERENCE TO HYLINAE: PHYLOGENETIC ANALYSIS AND TAXONOMIC REVISION

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SYSTEMATIC REVIEW OF THE FROG FAMILY HYLIDAE, WITH SPECIAL REFERENCE TO HYLINAE: PHYLOGENETIC ANALYSIS AND TAXONOMIC REVISION

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ABSTRACT

Hylidae is a large family of American, Australopapuan, and temperate Eurasian treefrogs of approximately 870 known species, divided among four subfamilies. Although some groups of Hylidae have been addressed phylogenetically, a comprehensive phylogenetic analysis has never been presented.

The first goal of this paper is to review the current state of hylid systematics. We focus on the very large subfamily Hylinae (590 species), evaluate the monophyly of named taxa, and examine the evidential basis of the existing taxonomy. The second objective is to perform a phylogenetic analysis using mostly DNA sequence data in order to (1) test the monophyly of the Hylidae; (2) determine its constituent taxa, with special attention to the genera and species groups which form the subfamily Hylinae, and c) propose a new, monophyletic taxonomy consistent with the hypothesized relationships.

We present a phylogenetic analysis of hylid frogs based on 276 terminals, including 228 hylids and 48 outgroup taxa. Included are exemplars of all but 1 of the 41 genera of Hylidae (of all four nominal subfamilies) and 39 of the 41 currently recognized species groups of the species-rich genus *Hyla*. The included taxa allowed us to test the monophyly of 24 of the 35 nonmonotypic genera and 25 species groups of *Hyla*. The phylogenetic analysis includes approximately 5100 base pairs from four mitochondrial (12S, tRNA valine, 16S, and cytochrome *b*) and five nuclear genes (rhodopsin, tyrosinase, RAG-1, seventh in absentia, and 28S), and a small data set from foot musculature.

Concurring with previous studies, the present analysis indicates that Hemiphractinae are not related to the other three hylid subfamilies. It is therefore removed from the family and tentatively considered a subfamily of the paraphyletic Leptodactylidae. Hylidae is now restricted to Hylinae, Pelodryadinae, and Phyllomedusinae. Our results support a sister-group relationship between Pelodryadinae and Phyllomedusinae, which together form the sister taxon of Hylinae. *Agalychnis*, *Phyllomedusa*, *Litoria*, *Hyla*, *Osteocephalus*, *Phrynohyas*, *Ptychohyla*, *Scinax*, *Smilisca*, and *Trachycephalus* are not monophyletic. Within *Hyla*, the *H. albomarginata*, *H. albopunctata*, *H. arborea*, *H. boans*, *H. cinerea*, *H. eximia*, *H. geographica*, *H. granosa*, *H. microcephala*, *H. miotympanum*, *H. tuberculosa*, and *H. versicolor* groups are also demonstrably nonmonophyletic. Hylinae is composed of four major clades. The first of these includes the Andean stream-breeding *Hyla*, *Aplastodiscus*, all Gladiator Frogs, and a Tepuian clade. The second clade is composed of the 30-chromosome *Hyla*, *Lysapsus*, *Pseudis*, *Scarthyla*, *Scinax* (including the *H. uruguaya* group), *Sphaenorhynchus*, and *Xenohyla*. The third major clade is composed of *Nyctimantis*, *Phrynohyas*, *Phyllodytes*, and all South American/West Indian casque-headed frogs: *Aparasphenodon*, *Argenteohyla*, *Corythomantis*, *Osteocephalus*, *Osteopilus*, *Tepuihyla*, and *Trachycephalus*. The fourth major clade is composed of most of the Middle American/Holarctic species groups of *Hyla* and the genera *Acris*, *Anotheca*, *Duellmanohyla*, *Plectrohyla*, *Pseudacris*, *Ptychohyla*, *Pternohyla*, *Smilisca*, and *Triprion*. A new monophyletic taxonomy mirroring these results is presented where Hylinae is divided into four tribes. Of the species currently in ‘‘*Hyla*’’, 297 of the 353 species are placed in 15 genera; of these, 4 are currently recognized, 4 are resurrected names, and 7 are new. *Hyla* is restricted to *H. femoralis* and the *H. arborea*, *H. cinerea*, *H. eximia*, and *H. versicolor* groups, whose contents are redefined. *Phrynohyas* is placed in the synonymy of *Trachycephalus*, and *Pternohyla* is placed in the synonymy of *Smilisca*. The genus *Dendropsophus* is resurrected to include all former species of *Hyla* known or suspected to have 30 chromosomes. *Exerodonta* is resurrected to include the former *Hyla sumichrasti* group and some members of the former *H. miotympanum* group. *Hyloscirtus* is resurrected for the former *Hyla armata*, *H. bogotensis*, and *H. larinopygion* groups. *Hypsiboas* is resurrected to include several species groups—many of them redefined here—of Gladiator Frogs. The former *Hyla albofrenata* and *H. albosignata* complexes of the *H. albomarginata* group are included in *Aplastodiscus*.

New generic names are erected for (1) *Agalychnis calcarifer* and *A. craspedopus*; (2) *Osteocephalus langsdorffii*; the (3) *Hyla aromatica*, (4) *H. bromeliacia*, (5) *H. godmani*, (6) *H. mixomaculata*, (7) *H. taeniopus*, (8) and *H. tuberculosa groups*; (9) the clade composed of the *H. pictipes* and *H. pseudopuma* groups; and (10) a clade composed of the *H. circumdata*, *H. claresignata*, *H. martinsi*, and *H. pseudopseudis* groups.

RESUMO

A família Hylidae é constituída por aproximadamente 870 espécies, agrupadas em quatro subfamílias e com distribuição nas Américas, Austrália/Papua-Nova Guiné e Eurásia. Apesar de alguns grupos de Hylidae terem sido estudados separadamente, uma hipótese filogenética compreensiva para a família nunca foi proposta.

O objetivo inicial desse estudo é rever o atual estado sistemático da família Hylidae. Atenção especial é dada à subfamília Hylinae (590 especies), para a qual nós avaliamos o monofiletismo dos taxa atualmente reconhecidos e examinamos as bases do arranjo taxonômico aceito no presente. O segundo objetivo é realizar uma análise filogenética usando caracteres obtidos, em sua maioria, a partir de seqüências de ADN, a fim de (1) testar o monofiletismo da família Hylidae;(2) determinar sua constituição taxonômica, dando ênfase aos gêneros e grupos de espécies incluídos na subfamília Hylinae; e (3) propor uma nova taxonomia baseada em grupos monofiléticos e consistente com a hipótese filogenética aqui apresentada.

Neste trabalho apresentamos, juntamente com uma revisão sistemática dos hilídeos, uma análise filogenética baseada em 275 terminais, sendo 227 de hilídeos, mais 48 taxas representando grupos externos. Na análise filogenética estão representados 40 dos 41 gêneros de Hylidae das quatro subfamílias reconhecidas e 39 dos 41 grupos atualmente reconhecidos para o grande gênero *Hyla*. Os táxons incluídos permitem testar a monofilia de 24 dos gêneros não monotípicos e 25 grupos de espécies de *Hyla*. A análise filogenética inclui aproximadamente 5100 pares de bases de quatro genes mitocondriais (12S, tval, 16S, citocromo *b*) e cinco genes nucleares (rodopsina, tirosinase, RAG-1, seventh in absentia e 28s), além de um pequeno conjunto de dados sobre a musculatura do pé.

De forma similar ao que tem sido observado em outros estudos, a presente análise indica que os Hemiphractinae não são relacionados às outras três subfamílias de hilídeos, portanto, sendo removidos desta família e tentativamente considerados como uma subfamília dos parafiléticos Leptodactylidae. Hylidae é agora restrita a Hylinae, Pelodryadinae e Phyllomedusinae. Nossos resultados corroboram uma relação de grupos irmãos entre estas duas últimas subfamílias, que juntas correspondem ao táxon irmão de Hylinae. *Phyllomedusa*, *Agalychnis*, *Litoria*, *Hyla*, *Osteocephalus*, *Phrynohyas*, *Pseudis*, *Ptychohyla*, *Scinax*, *Smilisca* e *Trachycephalus* não são monofiléticos. Dentro do gênero *Hyla*, os grupos de *H. albomarginata*, *H. albopunctata*, *H. arborea*, *H. boans*, *H. cinerea*, *H. eximia*, *H. geographica*, *H. granosa*, *H. microcephala*, *H. miotympanum*, *H. tuberculosa* e *H. versicolor* não são monofiléticos.

Em nossa análise, Hylinae aparece composta por quatro grandes clados. O primeiro deles incluindo todas as rãs-gladiadoras, as espécies andinas de *Hyla* que se reproduzem em riachos e um clado dos Tepuis. O segundo grande clado é composto por *Scinax*, *Sphaenorhynchus*, ‘‘pseudídeos’’, *Scarthyla* e as espécies de *Hyla* com 30 cromossomos. O terceiro grande clado é composto por *Phyllodytes*, *Phrynohyas*, *Nyctimantis* e todas as seguintes pererecas-de-capacete da América do Sul e Índias Ocidentais: *Argenteohyla*, *Aparasphenodon*, *Corythomantis*, *Osteocephalus*, *Osteopilus*, *Tepuihyla* e *Trachycephalus*. O quarto e último grande clado é composto pela maioria dos grupos de espécies de *Hyla* centro-americanos/holárticos e pelos gêneros *Acris*, *Anotheca*, *Duellmanohyla*, *Plectrohyla*, *Pseudacris*, *Ptychohyla*, *Pternohyla*, *Smilisca* e *Triprion*. É apresentada uma nova taxonomia monofilética, espelhando estes resultados, onde Hylinae é dividida em quatro tribos. Das espécies correntemente incluídas em *Hyla*, 297 de 353 são alocadas em 15 gêneros, dos quais quatro são correntemente reconhecidos, quatro são nomes revalidados e seis são novas descrições. O gênero *Hyla* fica restrito aos grupos de *H. arborea*, *H. cinerea*, *H. eximia*, *H. femoralis* e *H. versicolor*, sendo o conteúdo de alguns destes grupos redefinido. *Phrynohyas* é sinonimizada a *Trachycephalus*, *Pternohyla* é sinonimizada a *Smilisca* e *Duellmanohyla* é sinonimizada a *Ptychohyla*. O gênero *Dendropsophus* é revalidado para as espécies de *Hyla* com, ou presumivelmente tendo, 30 cromossomos. *Exerodonta* é revalidado, passando a incluir os grupos de *Hyla sumichrasti* e *H. pinorum*. *Hyloscirtus* é revalidado para acomodar os grupos de *Hyla armata*, *H. bogotensis* e *H. larinopygion*. *Hypsiboas* é revalidada para acomodar diversos grupos de espécies—muitos deles aqui redefinidos—de rãs-gladiadoras. Os complexos de *Hyla albofrenata* e *H. albosignata*, do grupo de *H. albomarginata*, são incluídos no gênero *Aplastodiscus*.

Nomes genéricos novos são apresentados para (1) *Agalychnis calcarifer* e *A. craspedopus*, (2) *Osteocephalus langsdorffii* e para os grupos de espécies de (3) *Hyla aromatica*, (4) *H.*

bromeliacia, (5) *H. godmani*, (6) *H. mixomaculata*, (7) *H. taeniopus*, (8) *H. tuberculosa*, e para o clado compostos pelos grupos de espécies de (9) *H. pictipes* e *H. pseudopuma* e para o clado composto pelos grupos de espécies de (10) *H. circumdata*, *H. claresignata*, *H. martinsi* e *H. pseudopseudis*.

RESUMEN

Hylidae es una familia muy grande (aproximadamente 870 especies conocidas) de ranas arboricolas de America, Australia y Papua, y Eurasia, y esta dividida en cuatro subfamilias. Aunque existen algunos estudios que analizan las relaciones filogeneticas de algunos grupos aislados de Hylidae, no existe ningun analisis filogenetico de toda la familia.

Los objetivos de este trabajo son, primero, revisar el estado actual de la sistematica de la familia, haciendo enfasis en la subfamilia Hylinae, que es la mas grande (590 especies), y evaluando la evidencia existente para la monofilia de los distintos agrupamientos taxonomicos. El segundo objetivo es realizar un analisis filogenetico basado principalmente en secuencias de ADN, con el proposito de a) testear la monofilia de la familia Hylidae, b) determinar que taxa la constituyen, con especial atencion en los generos y grupos de especies de la subfamilia Hylinae, c) proponer una nueva taxonomia monofiletica, consistente con nuestra hipotesis filogenetica.

Se presenta una revision completa del estado de conocimiento de la sistematica de la familia Hylidae, junto con un analisis filogenetico de 276 terminales, incluyendo 228 Hylidae y 48 grupos externos. Se incluyen representantes de 40 de los 41 generos de de las cuatro subfamilias de Hylidae, y de 39 de los 41 grupos de especies del genero *Hyla*. Asimismo, los taxa incluidos permitieron testear la monofilia de 24 de los 35 generos no monotipicos, y 25 grupos de especies de *Hyla*. El analisis filogenetico incluye aproximadamente 5100 pares de bases de cuatro genes mitocondriales (12S, tRNA valina, 16S, cytocromo *b*) y cinco genes nucleares (rhodopsina, RAG-1, seventh in absentia, tyrosinasa y 28S), y una matriz de 38 characteres de musculatura del pie.

En coincidencia con estudios anteriores, los resultados del analisis indican que los Hemiphractinae no pertenecen a Hylidae, y por lo tanto se los excluye de la familia, que hora es restringida a Hylinae, Pelodryadinae, y Phyllomedusinae. Nuestros resultados soportan la monofilia de estas dos ultimas subfamilias, que a su vez son el taxon hermano de Hylinae. *Phyllomedusa*, *Agalychnis*, *Litoria*, *Hyla*, *Osteocephalus*, *Phrynohyas*, *Trachycephalus*, *Smilisca*, *Ptychohyla*, y *Scinax* no son monofleticos. Ademas, dentro de *Hyla*, los grupos de *H. albomarginata*, *H. albopunctata*, *H. arborea*, *H. boans*, *H. cinerea*, *H. eximia*, *H. geographica*, *H. granosa*, *H. microcephala*, *H. miotympanum*, *H. tuberculosa*, y *H. versicolor* tampoco son monofileticos. Hylinae resulta estar compuesto por cuatro clados principales. El primero de estos incluye a *Aplastodiscus* y todos los grupos de especies de *Hyla* incluidos en las ranas gladiadoras, las *Hyla* que se reproducen en arroyos de los Andes, y un clado de los Tepuies Guayaneses. El segundo clado principal esta compuesto por *Scarthyla*, *Scinax*, *Sphaenorhynchus*, ‘‘pseudidos’’, y las *Hyla* de 30 cromosomas. El tercer clado principal esta compuesto por *Nyctimantis*, *Phyllodytes*, *Phrynohyas*, y todas las ranas ‘‘cabeza de casco’’ sudamericanas y de las Indias Occidentales: *Argenteohyla*, *Aparasphenodon*, *Corythomantis*, *Osteopilus*, *Osteocephalus*, *Trachycephalus*, y *Tepuihyla*. El cuarto clado principal esta compuesto por la mayoria de los grupos de especies de *Hyla* Centro Americanos y holarticos y los generos *Acris*, *Anotheca*, *Duellmanohyla*, *Plectrohyla*, *Pseudacris*, *Ptychohyla*, *Pternohyla*, *Smilisca*, y *Triprion*.

Con base en estos resultados, se presenta una nueva taxonomia monofiletica, adonde Hylinae es dividida en cuatro tribus. Ademas, 297 de las 353 especies hasta ahora incluidas en *Hyla* son divididas en 15 generos, cuatro de los cuales son generos que ya estaban en uso, cuatro son nombres resucitados de la sinonimia de *Hyla*, y siete son nuevos. *Hyla* es restringido a *H. femoralis* y los grupos de *H. arborea*, *H. cinera*, *H. eximia*, e *H. versicolor*, cuyos contenidos son en algunos casos redefinidos. Asi mismo, *Phrynohyas* es incluido en la sinonimia de *Trachycephalus*, y *Pternohyla* en la sinonimia de *Smilisca*. *Dendropsophus* es revalidado para incluir todas las especies previamente incluidas en los grupos de especies de 30 cromosomas, o sospechadas de tener 30 cromosomas. *Exerodonta* es revalidado para incluir el grupo de *Hyla sumichrasti*, y un fragmento de especies incluidas en el grupo de *H. miotympanum*.

Hyloscirtus es revalidado para incluir los grupos de *H. armata*, *H. bogotensis*, e *H. larinopygion*. *Hypsiboas* es revalidado para incluir muchos grupos de especies—varios de ellos aqui redefinidos—de ranas gladiadoras. Los complejos de *Hyla albofrenata* e *H. albosignata* del grupo de *H. albomarginata* son incluidos en *Aplastodiscus*.

Nuevos nombres genericos son propuestos para (1) *Agalychnis calcarifer* y *A. craspedopus*, (2) *Osteocephalus langsdorffii*, los grupos de (3) *Hyla aromatica*, (4) *H. bromeliacia*, (5) *H. godmani*, (6) *H. mixomaculata*,(7) *H. taeniopus*, (8) *H. tuberculosa*, y para los clados compuestos por los grupos de (9) *H. pictipes* y *H. pseudopuma*, y por los grupos de (10) *H. circumdata, H. claresignata, H. martinsi*, e *H. pseudopseudis*.

INTRODUCTION

Hylidae is a large family of American, Australopapuan, and temperate Eurasian treefrogs of approximately 870 known species, composed of four subfamilies (Duellman, 2001; Darst and Cannatella, 2004; Frost, 2004). Although some groups of Hylidae have been addressed phylogenetically (e.g., Campbell and Smith, 1992; Duellman and Campbell, 1992; Mendelson et al., 2000; Faivovich, 2002; Haas, 2003; Moriarty and Cannatella, 2004; Faivovich et al., 2004), a comprehensive phylogenetic analysis has never been presented.

The first goal of this paper is to review the state of hylid systematics. We focus on the very large subfamily Hylinae, evaluate the monophyly of named taxa, and examine the evidential basis of the existing taxonomy. The second objective is to perform a phylogenetic analysis using four mitochondrial and five nuclear genes in order to (1) test the monophyly of the family Hylidae; (2) determine its constituent taxa, with special attention to the genera and species groups which form the subfamily Hylinae; and (3) propose a new, monophyletic taxonomy consistent with the hypothesized relationships.

MATERIALS AND METHODS

In most revisionary studies involving major taxonomic rearrangements and phylogenetic analyses it is normal to have a section on the history of taxonomic changes. The scale of this particular study makes that goal impractical. A discussion of the state of the taxonomy of hylid frogs is dealt with simultaneously with discussions of the taxa chosen for the purpose of phylogenetic analysis.

TAXON SAMPLING

Any phylogenetic analysis has an important component of experimental design associated with the selection of the terminal taxa. In an ideal phylogenetic study, all terminal descendants of a given hypothetical ancestor should to be included in order to avoid ‘‘problems’’ due to taxon sampling. This ideal condition is unattainable, and all notions of relationships among organisms are affected to an unknown degree by incomplete taxon sampling. Because there is no way of ever knowing all the hylid species that have become extinct, we concentrate on the diversity that we do know. Furthermore, due to the unavailability of samples we cannot include sequences of all of the nearly 860 currently described species of Hylidae. What, therefore, is the best taxon sampling for this study? Because our primary goal is to test the monophyly of all available genera and species groups of Hylidae, the most appropriate terminals to include are those that provide the strongest test of previously hypothesized relations. By considering morphological divergence as a rough guide to DNA sequence diversity, maximally diverse taxa within a given group are likely to pose a stronger test of its monophyly than do morphologically similar taxa (Prendini, 2001). Groups for which no apparent synapomorphies are known are a priori more likely to be nonmonophyletic, and therefore good representations of the morphological diversity of these groups are especially appropriate. Our success varied in securing multiple representatives of these groups.

The following discussion deals in part with the state of knowledge of frog phylogenetics. Included within the discussion is a list of terminals used in this analysis along with a justification and explanation for our choices. A summary of the species included is presented in table 1. To conserve space, species authorships are not mentioned in the

TABLE 1

Species Included in this Analysis and Species Groups or Genera They Represent

Species	Genus or species group
Acris crepitans	*Acris*
Acris gryllus	*Acris*
Anotheca spinosa	*Anotheca*
Aparasphenodon brunoi	*Aparasphenodon*
Aplastodiscus cochranae	*Aplastodiscus*
Aplastodiscus perviridis	*Aplastodiscus*
Argenteohyla siemersi	*Argenteohyla*
Corythomantis greeningi	*Corythomantis*
Duellmanohyla rufioculis	*Duellmanohyla*
Duellmanohyla soralia	*Duellmanohyla*
Hyla sp. 1 (aff. *H. ehrhardti*)	*H. albofrenata* complex[a]
Hyla arildae	*H. albofrenata* complex
Hyla weygoldti	*H. albofrenata* complex
Hyla albomarginata	*H. albomarginata* complex
Hyla pellucens	*H. albomarginata* complex
Hyla rufitela	*H. albomarginata* complex
Hyla albosignata	*H. albosignata* complex
Hyla callipygia	*H. albosignata* complex
Hyla cavicola	*H. albosignata* complex
Hyla leucopygia	*H. albosignata* complex
Hyla albopunctata	*H. albopunctata* group
Hyla lanciformis	*H. albopunctata* group
Hyla multifasciata	*H. albopunctata* group
Hyla raniceps	*H. albopunctata* group
Hyla annectans	*H. arborea* group
Hyla arborea	*H. arborea* group
Hyla japonica	*H. arborea* group
Hyla savignyi	*H. arborea* group
Hyla armata	*H. armata* group
Hyla charazani	*H. armata* group
Hyla inparquesi	*H. aromatica* group
Hyla bistincta	*H. bistincta* group
Hyla calthula	*H. bistincta* group
Hyla boans	*H. boans* group
Hyla crepitans	*H. boans* group
Hyla faber	*H. boans* group
Hyla lundii	*H. boans* group
Hyla pardalis	*H. boans* group
Hyla colymba	*H. bogotensis* group
Hyla palmeri	*H. bogotensis* group
Hyla bromeliacia	*H. bromeliacia* group
Hyla cinerea	*H. cinerea* group
Hyla femoralis	*H. cinerea* group
Hyla gratiosa	*H. cinerea* group
Hyla squirella	*H. cinerea* group
Hyla astartea	*H. circumdata* group
Hyla circumdata	*H. circumdata* group
Hyla hylax	*H. circumdata* group
Hyla sp. 3	*H. circumdata* group
Hyla sp. 4	*H. circumdata* group
Hyla carnifex	*H. columbiana* group
Hyla berthalutzae	*H. decipiens* group
Hyla arenicolor	*H. eximia* group
Hyla euphorbiacea	*H. eximia* group
Hyla eximia	*H. eximia* group
Hyla walkeri	*H. eximia* group
Hyla calcarata	*H. geographica* group
Hyla fasciata	*H. geographica* group
Hyla geographica	*H. geographica* group
Hyla kanaima	*H. geographica* group
Hyla microderma	*H. geographica* group
Hyla picturata	*H. geographica* group
Hyla roraima	*H. geographica* group
Hyla semilineata	*H. geographica* group
Hyla picta	*H. godmani* group
Hyla smithii	*H. godmani* group
Hyla granosa	*H. granosa* group
Hyla sibleszi	*H. granosa* group
Hyla labialis	*H. labialis* group
Hyla pacha[b]	*H. larinopygion* group
Hyla pantosticta	*H. larinopygion* group
Hyla tapichalaca	*H. larinopygion* group
Hyla ebraccata	*H. leucophyllata* group
Hyla sarayacuensis	*H. leucophyllata* group
Hyla triangulum	*H. leucophyllata* group
Hyla martinsi	*H. martinsi* group
Hyla marmorata	*H. marmorata* group
Hyla senicula	*H. marmorata* group
Hyla bipunctata	*H. microcephala* group
Hyla microcephala	*H. microcephala* group
Hyla nana	*H. microcephala* group
Hyla rhodopepla	*H. microcephala* group
Hyla sanborni	*H. microcephala* group
Hyla walfordi	*H. microcephala* group
Hyla miyatai	*H. minima* group
Hyla minuta	*H. minuta* group
Hyla arborescandens	*H. miotympanum* group
Hyla cyclada	*H. miotympanum* group
Hyla melanomma	*H. miotympanum* group
Hyla miotympanum	*H. miotympanum* group
Hyla perkinsi	*H. miotympanum* group
Hyla mixe	*H. mixomaculata* group
Hyla brevifrons	*H. parviceps* group
Hyla giesleri	*H. parviceps* group
Hyla parviceps	*H. parviceps* group
Hyla rivularis	*H. pictipes* group
Hyla sp. 5 (aff. *H. thorectes*)	*H. pictipes* group
Hyla sp. 6 (aff. *H. pseudopseudis*)	*H. pseudopseudis* group
Hyla pseudopuma	*H. pseudopuma* group
Hyla andina	*H. pulchella* group
Hyla balzani	*H. pulchella* group
Hyla bischoffi	*H. pulchella* group
Hyla caingua	*H. pulchella* group
Hyla cordobae	*H. pulchella* group
Hyla sp. 7 (aff. *H. semiguttata*)	*H. pulchella* group
Hyla ericae	*H. pulchella* group
Hyla guentheri	*H. pulchella* group

TABLE 1
(*Continued*)

Species	Genus or species group
Hyla joaquini	*H. pulchella* group
Hyla latistriata	*H. pulchella* group, *H. polytaenia* clade
Hyla leptolineata	*H. pulchella* group, *H. polytaenia* clade
Hyla marginata	*H. pulchella* group
Hyla marianitae	*H. pulchella* group
Hyla polytaenia	*H. pulchella* group, *H. polytaenia* clade
Hyla prasina	*H. pulchella* group
Hyla pulchella	*H. pulchella* group
Hyla riojana	*H. pulchella* group
Hyla semiguttata	*H. pulchella* group
Hyla punctata	*H. punctata* group
Hyla rubicundula	*H. rubicundula* group
Hyla chimalapa	*H. sumichrasti* group
Hyla xera	*H. sumichrasti* group
Hyla nephila	*H. taeniopus* group
Hyla taeniopus	*H. taeniopus* group
Hyla dendrophasma	*H. tuberculosa* group
Hyla miliaria	*H. tuberculosa* group
Hyla uruguaya	*H. uruguaya* group
Hyla andersonii	*H. versicolor* group
Hyla avivoca	*H. versicolor* group
Hyla versicolor	*H. versicolor* group
Hyla anceps	Unassigned
Hyla benitezi	Unassigned
Hyla heilprini	Unassigned
Hyla lemai	Unassigned
Hyla sp. 2[c]	Unassigned
Hyla sp. 8[d]	Unassigned
Hyla sp. 9 (aff. *H. alvarengai*)	Unassigned
Lysapsus laevis	*Lysapsus*
Lysapsus limellum	*Lysapsus*
Nyctimantis rugiceps	*Nyctimantis*
Osteocephalus cabrerai	*Osteocephalus*
Osteocephalus langsdorffii	*Osteocephalus*
Osteocephalus leprieurii	*Osteocephalus*
Osteocephalus oophagus	*Osteocephalus*
Osteocephalus taurinus	*Osteocephalus*
Osteopilus crucialis	*Osteopilus*
Osteopilus dominicensis	*Osteopilus*
Osteopilus septentrionalis	*Osteopilus*
Osteopilus vastus	*Osteopilus*
Phrynohyas hadroceps	*Phrynohyas*
Phrynohyas mesophaea	*Phrynohyas*
Phrynohyas resinifrictix	*Phrynohyas*
Phrynohyas venulosa	*Phrynohyas*
Phyllodytes luteolus	*Phyllodytes*
Phyllodytes sp.	*Phyllodytes*
Plectrohyla glandulosa	*Plectrohyla*
Plectrohyla guatemalensis	*Plectrohyla*
Plectrohyla matudai	*Plectrohyla*
Pseudacris cadaverina	*Pseudacris*
Pseudacris crucifer	*Pseudacris*
Pseudacris ocularis	*Pseudacris*
Pseudacris regilla	*Pseudacris*
Pseudacris triseriata	*Pseudacris*
Pseudis minuta	*Pseudis*
Pseudis paradoxa	*Pseudis*
Pternohyla fodiens	*Pternohyla*
Ptychohyla euthysanota	*Ptychohyla*
Ptychohyla hypomykter	*Ptychohyla*
Ptychohyla leonhardschultzei	*Ptychohyla*
Ptychohyla spinipollex	*Ptychohyla*
Ptychohyla zophodes	*Ptychohyla*
Ptychohyla sp.	*Ptychohyla*
Scarthyla goinorum	*Scarthyla*
Scinax acuminatus	*S. ruber* clade
Scinax berthae	*S. catharinae* clade
Scinax boulengeri	*S. ruber* clade
Scinax catharinae	*S. catharinae* clade
Scinax elaeochrous	*S. ruber* clade
Scinax fuscovarius	*S. ruber* clade
Scinax nasicus	*S. ruber* clade
Scinax ruber	*S. ruber* clade
Scinax squalirostris	*S. ruber* clade
Scinax staufferi	*S. ruber* clade
Smilisca baudinii	*Smilisca*
Smilisca cyanosticta	*Smilisca*
Smilisca phaeota	*Smilisca*
Smilisca puma	*Smilisca*
Sphaenorhynchus dorisae	*Sphaenorhynchus*
Sphaenorhynchus lacteus	*Sphaenorhynchus*
Tepuihyla edelcae	*Tepuihyla*
Trachycephalus jordani	*Trachycephalus*
Trachycephalus nigromaculatus	*Trachycephalus*
Triprion petasatus	*Triprion*
Xenohyla truncata	*Xenohyla*
Hylidae, Hemiphractinae	
Cryptobatrachus sp.	*Cryptobatrachus*
Flectonotus sp.	*Flectonotus*
Gastrotheca cornuta	*ovifera* group
Gastrotheca fissipes	*ovifera* group
Gastrotheca cf. *marsupiata*	*marsupiata* group
Gastrotheca pseustes	*marsupiata* group
Hemiphractus johnsoni	*Hemiphractus*
Stefania evansi	*S. evansi* group
Stefania schuberti	*S. ginesi* group
Hylidae, Phyllomedusinae	
Agalychnis calcarifer	*Agalychnis*
Agalychnis callidryas	*Agalychnis*
Agalychnis litodryas	*Agalychnis*
Agalychnis saltator	*Agalychnis*
Hylomantis granulosa	*Hylomantis*
Pachymedusa dacnicolor	*Pachymedusa*

TABLE 1
(*Continued*)

Species	Genus or species group
Phyllomedusinae	
Phasmahyla cochranae	*Phasmahyla*
Phasmahyla guttata	*Phasmahyla*
Phyllomedusa bicolor	Unassigned
Phyllomedusa hypochondrialis	*P. hypochondrialis* group
Phyllomedusa lemur	*P. buckleyi* group
Phyllomedusa palliata	Unassigned
Phyllomedusa tarsius	*P. tarsius* group
Phyllomedusa tetraploidea	*P. burmeisteri* group
Phyllomedusa tomopterna	*P. tarsius* group
Phyllomedusa vaillanti	Unassigned
Hylidae, Pelodryadinae	
Cyclorana australis	*Cyclorana australis* group
Litoria arfakiana	*Litoria arfakiana* group
Litoria aurea	*Litoria aurea* group
Litoria caerulea	*Litoria caerulea* group
Litoria freycineti	*Litoria freycineti* group
Litoria infrafrenata	*Litoria infrafrenata* group
Litoria meiriana	*Litoria meiriana* group
Nyctimystes kubori	Unassigned
Nyctimystes narinosus	Unassigned
Nyctimystes pulcher	Unassigned
OUTGROUPS	
Allophrynidae	
Allophryne ruthveni	*Allophryne*
Astylosternidae	
Trichobatrachus robustus	*Trichobatrachus*
Brachycephalidae	
Brachycephalus ephippium	*Brachycephalus*
Bufonidae	
Atelopus varius	*Atelopus*
Bufo arenarum	*Bufo*
Dendrophryniscus minutus	*Dendrophryniscus*
Dydinamipus sjoestedti	*Dydinamipus*
Melanophryniscus klappenbachi	*Melanophryniscus*
Osornophryne guacamayo	*Osornophryne*
Pedostibes hossi	*Pedostibes*
Schismaderma carens	*Schismaderma*
Centrolenidae	
Centrolene prosoblepon	*Centrolene*
Cochranella bejaranoi	*Cochranella*
Hyalinobatrachium eurygnathum	*Hyalinobatrachium*
Dendrobatidae	
Colostethus talamancae	*Colostethus*
Dendrobates auratus	*Dendrobates*
Phyllobates bicolor	*Phyllobates*
Heleophrynidae	
Heleophryne purcelli	*Heleophryne*
Hemisotidae	
Hemisus marmoratus	*Hemisus*
Leptodactylidae, Ceratophryinae	
Ceratophrys cranwelli	*Ceratophrys*
Odontophrynus americanus	*Odontophrynus*
Leptodactylidae, Cycloramphinae	
Crossodactylus schmidti	*Crossodactylus*
Leptodactylidae, Eleutherodactylinae	
Eleutherodactylus pluvicanorus	*Eleutherodactylus* (*Craugastor*)
Eleutherodactylus thymelensis	*Eleutherodactylus* (*Eleutherodactylus*)
Phrynopus sp.	*Phrynopus*
Leptodactylidae, Leptodactylinae	
Adenomera sp.	*Adenomera*
Edalorhina perezi	*Edalorhina perezi*
Leptodactylus ocellatus	*Leptodactylus*
Limnomedusa macroglossa	*Limnomedusa*
Lithodytes lineatus	*Lithodytes*
Physalaemus cuvieri	*Physalaemus*
Pleurodema brachyops	*Pleurodema*
Pseudopaludicola falcipes	*Pseudopaludicola*
Leptodactylidae, Telmatobiinae	
Alsodes gargola	*Alsodes*
Atelognathus patagonicus	*Atelognathus*
Batrachyla leptopus	*Batrachyla*
Eupsophus calcaratus	*Eupsophus*
Telmatobius sp.	*Telmatobius*
Mantellidae	
Mantidactylus femoralis	*Mantidactylus*
Microhylidae	
Scaphiophryne marmorata	*Scaphiophryne*
Kaloula conjuncta	*Kaloula*
Myobatrachidae, Limnodynastinae	
Limnodynastes salmini	*Limnodynastes*
Neobatrachus sudelli	*Neobatrachus*
Myobatrachidae, Myobatrachinae	
Pseudophryne bibroni	*Pseudophryne*
Ranidae	
Fejervarya limnocharis	*Fejervarya*
Platymantis sp.	*Platymantis*
Rana temporaria	*Rana*
Rhacophoridae	
Rhacophorus bipunctatus	*Rhacophorus*

[a] Refers to the three complexes of the *Hyla albomarginata* group recognized by Cruz and Peixoto ("1985" [1987]).

[b] This species was included by Darst and Cannatella (2004) as *Hyla* sp., and its sequences were deposited in GenBank as "*Hyla* sp. KU 202760". Its collection number reveals that it is a paratype of *Hyla pacha* (see Duellman and Hillis, 1990).

[c] Faivovich, Moravec, Cisneros, and Köhler are currently describing this new species from the western Amazon Basin.

[d] Myers and Donnelly are currently describing this new species from the Guayana highlands.

text but are given in the section ‘‘Taxonomic Conclusions: A New Taxonomy of Hylinae and Phyllomedusinae’’ and in appendix 1. For museum abbreviations used throughout this paper see appendix 2.

OUTGROUP SELECTION

Recent studies (Haas, 2003; Darst and Cannatella, 2004) have suggested that the Hylidae as traditionally understood is not monophyletic, with the Hemiphractinae displaced phylogenetically from the Hylinae, Phyllomedusinae, and Pelodryadinae. The aforementioned studies did not provide extensive outgroup comparisons. In order to avail ourselves of a strong test of hylid monophyly, we included 48 nonhylid outgroup taxa representing 14 neobatrachian families.

Basal Neobatrachians

Heleophrynidae, Sooglossidae, Limnodynastinae and Myobatrachinae[1] have been related to each other by several authors (Lynch, 1973; Duellman and Trueb, 1986; Ford and Cannatella, 1993; Hay et al., 1995; Ruvinsky and Maxson, 1996; Biju and Bossuyt, 2003; Darst and Cannatella, 2004). While in the past they were considered part of Hyloidea, they were recently excluded by Darst and Cannatella (2004). The evidence indicates that they are basal neobatrachians distantly related to the apparently monophyletic Hyloidea; however, their exact positions and interrelationships are still unclear (Darst and Cannatella, 2004; Haas, 2003). We include one heleophrynid (*Heleophryne purcelli*), one myobatrachine (*Pseudophryne bibroni*), and two limnodynastines (*Limnodynastes salmini* and *Neobatrachus sudelli*) in our study. Furthermore, because some members of the Australopapuan hylids have been posited to be related to the Myobatrachidae (Lynch, 1971; Savage, 1973), their inclusion provides a strong test of hylid monophyly.

Ranoidea

Recent papers dealing with ranoid groups (Emerson et al., 2000; Vences et al., 2003a) or at least ranoid exemplars (Biju and Bossuyt, 2003; Darst and Cannatella, 2004) have suggested the existence of three major clades, although this remains to be elucidated. The three major clades are composed of (1) Arthroleptidae, Astylosternidae, Hemisotidae, and Hyperoliidae; (2) Microhylidae; and (3) the remaining ranoids (including Petropedetidae, Mantellidae, Rhacophoridae, and the paraphyletic Ranidae). We include exemplars of Astylosternidae, Hyperoliidae, Hemisotidae, Microhylidae, Ranidae, Mantellidae, and Rhacophoridae.

Hyloidea

The Hylidae has long been considered to be embedded within a poorly defined major group of neobatrachians (Nicholls, 1916; Noble, 1922; Lynch, 1971, 1973; Ford and Cannatella, 1993) for which no morphological evidence of monophyly exists, although molecular evidence (Hay et al., 1995; Ruvinsky and Maxson, 1996; Darst and Cannatella, 2004) does support its monophyly. As redefined by Darst and Cannatella (2004) Hyloidea includes the nonmonophyletic Leptodactylidae (Ford and Cannatella, 1993; Haas, 2003), Dendrobatidae, Hylidae, Bufonidae, Brachycephalidae, Centrolenidae, Rhinodermatidae, and the monotypic Allophrynidae. In order to have a strong test of the monophyly of hylids, we include representatives of most of the nonhylid hyloid families.

The monophyly of Dendrobatidae is not controversial (see Grant et al., 1997), although recent phylogenetic analyses using ribosomal mitochondrial sequences (Vences et al., 2000; Santos et al., 2003; Vences et al., 2003b) show that there is a serious need to redefine most of the currently recognized genera. According to the results of Vences et al. (2003b), there are two major clades of dendrobatids: (1) one composed of *Dendrobates*, *Phyllobates*, *Cryptophyllobates*, *Epipedobates* (paraphyletic), *Minyobates*, and several groups of the rampantly polyphyletic *Colostethus*; and (2) another clade composed of *Mannophryne*, *Nephelobates*, *Allobates*, and two separate clades of *Colostethus* (none

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[1] We are referring to these two myobatrachid subfamilies separately; we are not aware of any putative synapomorphy supporting the monophyly of Myobatrachidae.

of the aforementioned analyses included the apparently primitive genus *Aromobates*; see Myers et al. 1991). We include as exemplars of the first major clade *Dendrobates auratus* and *Phyllobates bicolor*, and as exemplar of the second clade, *Colostethus talamancae*.

Bufonidae is a monophyletic group (for a list of morphological synapomorphies, see Ford and Cannatella, 1993; Haas, 2003) for which no study addressing comprehensively its internal relationships has been published. Partial studies (Graybeal, 1997; Darst and Cannatella, 2004; Haas, 2003) support the idea that *Melanophryniscus* is one of its most basal clades in the family. As a rough sample of bufonid diversity we include representatives of *Melanophryniscus*, *Dendropryniscus*, *Atelopus*, *Didynamipus*, *Schismaderma*, *Bufo*, *Pedostibes*, and *Osornophryne*.

The notion that the presumably monophyletic Centrolenidae (Ruiz-Carranza and Lynch, 1991) is closely related to hylids (Lynch, 1973; Duellman and Trueb, 1986; Ford and Cannatella, 1993) was recently challenged by the phylogenetic analyses of Haas (2003), who used larval morphology, and Darst and Cannatella (2004), who used mitochondrial ribosomal genes. Austin et al. (2002) recently provided molecular evidence supporting a relationship between Centrolenidae and the monotypic Allophrynidae. The internal relationships of Centrolenidae remain virtually unstudied. As a rough representation of centrolenid diversity, in this study we include *Centrolene prosoblepon*, *Cochranella bejaranoi*, and *Hyalinobatrachium eurygnathum*. We also include *Allophryne ruthveni*.

Leptodactylid nonmonophyly has been accepted for some time (Lynch, 1971) and was confirmed in an explicit cladistic framework by analyses using morphology (Haas, 2003) and DNA sequences (Ruvinsky and Maxson, 1996; Darst and Cannatella, 2004; Vences et al., 2003b). In the analysis by Darst and Cannatella (2004), Leptodactylidae is rampantly paraphyletic because all the other hyloid exemplars are nested within it.

From the five currently recognized subfamilies of leptodactylids (Laurent, 1986) there is more or less convincing evidence of monophyly for two of them: Eleutherodactylinae (direct development, eggs relatively large, few in number; Lynch, 1971[2]) and Leptodactylinae (presence of a bony element in the sternum; Lynch, 1971). The analysis of Darst and Cannatella (2004) corroborated the monophyly of these two groups, albeit with limited taxon sampling. In the analysis by Haas (2003), the exemplars of Leptodactylinae were not monophyletic. No demonstrable synapomorphies are known for Ceratophryinae, Cycloramphinae or Telmatobiinae. Considering this situation, we include several leptodactylid exemplars (see table 1); our poorest sampling is within Cycloramphinae, where we only have representation for one genus, *Crossodactylus*.

The single representative of Brachycephalidae included by Darst and Cannatella (2004) in their analysis was nested within the exemplars of the leptodactylid subfamily Eleutherodactylinae, as suggested earlier by Izecksohn (1988). We include *Brachycephalus ephippium* in our analysis.

Of the hyloid families, only Rhinodermatidae is not represented in our analysis. This group was suggested to be nested in the subfamily Telmatobiinae by Barrio and Rinaldi de Chieri (1971) based on a similar karyotype and by Manzano and Lavilla (1995a) based on the presence of the m. pelvocutaneus in *Rhinoderma* and *Eupsophus*. In the DNA sequences analyses by Ruvinsky and Maxson (1996) and Biju and Bossuyt (2003) *Rhinoderma* appears in different positions within Hyloidea.

THE INGROUP: HYLIDAE

Inasmuch as the hylids are the primary focus of this study, our sampling is most dense for this taxon and requires substantially more detailed discussion than does our outgroup selection.

Duellman (1970) arranged the family in four subfamilies: Amphignathodontinae, Hemiphractinae, Hylinae (including both the Australian and American groups), and Phyllomedusinae. Trueb (1974) subsequently synonymized the Amphignathodontinae and Hemiphractinae. On the basis of evidence

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[2] Note that Lynch (1971) presented an extensive definition of the group; it is unclear if any of the other character states he mentioned could be considered synapomorphic.

presented by Tyler (1971), Duellman (1977) placed the Australian hylids in their own subfamily, Pelodryadinae, although Savage (1973) had previously regarded it as a different family and suggested that it was derived from Myobatrachidae.

Duellman (2001), based mostly on da Silva's results (1998), presented a phylogenetic analysis where hylids, including the subfamily Pseudinae, were considered to be monophyletic. Synapomorphies suggested by Duellman (2001) as being common to his three most parsimonious trees are the possession of claw-shaped terminal phalanges and the three articular surfaces on metacarpal III. The possibility of hylid polyphyly has not been seriously considered by most frog systematists, even after Ruvinsky and Maxson's (1996) results (which showed their single Hemiphractinae exemplar not closely related with the other hylid exemplars), until the idea was suggested on morphological grounds by Haas (2003), followed by Darst and Cannatella (2004) on the basis of molecular evidence. These authors found no evidence of a relationship between Hemiphractinae and the other hylid subfamilies, which were thought to form a monophyletic group. Beyond this result, Haas (2003) presented evidence from larval morphology that suggested that Pelodryadinae is paraphyletic with respect to Hylinae (Hylinae not being demonstrably monophyletic), with Pseudinae and Phyllomedusinae possibly being imbedded within it.[3]

Hemiphractinae

Mendelson et al. (2000) and Duellman (2001) presented brief taxonomic histories of this taxon. The monophyly of Hemiphractinae is supported by the presence of bell-shaped gills in larvae and by female transport of eggs in a specialized depression or sac in the dorsum (Noble, 1927). Burton (2004) added the broad m. abductor brevis plantae hallucis. In Duellman's (2001) cladogram, Hemiphractinae is considered to be the sister group of Phyllomedusinae, with the evidence of this relationship being the proximal head of metacarpal II not between prepollex and distal prepollex, and the larval spiracle sinistral and ventrolateral.

Haas's (2003) exemplar[4] of the Hemiphractinae was *Gastrotheca riobambae*. His results suggested that Hemiphractinae are unrelated to other hylids, although the position of Hemiphractinae within Neobatrachia is still unresolved. A similar result regarding Hemiphractinae as being unrelated to hylids was advanced by Ruvinsky and Maxson (1996) and corroborated by Darst and Cannatella (2004). These authors also did not recover the exemplars of Hemiphractinae that they used (*Gastrotheca pseustes* and *Cryptobatrachus* sp.) as forming a monophyletic group.[5]

Hemiphractinae includes five genera: *Cryptobatrachus, Flectonotus, Gastrotheca, Hemiphractus,* and *Stefania*. Mendelson et al. (2000) studied the relationships among these genera, performing a phylogenetic analysis using morphological and life-history characters, arriving at the topology (*Cryptobatrachus Flectonotus* (*Stefania* (''*Gastrotheca*'' + *Hemiphractus*))). This analysis included five outgroups, all of which were representatives of the other hylid subfamilies. The results suggested that *Cryptobatrachus* and *Flectonotus* are each monophyletic, and that *Gastrotheca* is paraphyletic with *Hemiphractus* nested within it. As Hass (2003)

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[3] Burton (2004) presented a study of hylid foot myology, a valuable collection of observations on many species, including the definition of numerous characters, and a phylogenetic analysis of the hylid subfamilies combining his characters with those employed by Duellman (2001). The list of synapomorphies provided (Burton 2004: 228) is the result of optimizing the data set on his strict consensus tree. When only unambiguous synapomorphies common to all the most parsimonious trees are considered, the list is reduced considerably, and there are no unambiguous transformations from foot musculature that support relationships among the subfamilies (these are supported solely by the characters from Duellman, 2001). Instead, some foot muscle character states are autapomorphic for Allophrynidae, Hemiphractinae, Phyllomedusinae, and Pseudinae (Burton's paper was submitted before Darst and Cannatella's paper was published). Throughout the present paper, all the synapomorphies reported from Burton's (2004) study are only those that occur in all equally parsimonious trees.

[4] Haas (2003) noted that the larval morphology of several species of *Gastrotheca* is quite similar, so presumably his selection of *G. riobambae* as an exemplar would have little effect on the analysis.

[5] However, a reanalysis of their data using parsimony and considering insertions/deletions as a fifth state did recover a monophyletic Hemiphractinae (Faivovich, personal obs.).

noted, however, Mendelson et al.'s (2000) outgroup structure could not test the proposition of hylid diphyly.

Cryptobatrachus: In the analysis performed by Mendelson et al. (2000), the monophyly of the two representatives of *Cryptobatrachus* is supported by several osteological characters, among them the presence of an anteromedial process in the neopalatine.[6] In their analysis, the relationship between *Cryptobatrachus* and the other Hemiphractinae is unresolved. This genus comprises three described species; in this study we include sequences of an unidentified species available from GenBank.

Gastrotheca: Mendelson et al. (2000) suggested that *Hemiphractus* is nested within *Gastrotheca*, a result that contrasts with the opinions of previous workers (Noble, 1927; Trueb, 1974; Duellman and Hoogmoed, 1984) who considered *Hemiphractus* basal among marsupial frogs because they lack a brooding pouch. However, Mendelson et al. (2000) continued to recognize *Hemiphractus* (the older of both names) and *Gastrotheca* pending a more complete phylogenetic study. Synapomorphies of the clade composed of these two genera are: cultriform process becoming distinctly narrow anteriorly; anterior process of vomer articulating only with maxilla; pre- and postchoanal process bifurcating at the level of the dentigerous process; nature of occipital artery pathway (a groove); brooding pouch with posterior opening; and bell-shaped gills fused distally.

Most of the 49 currently recognized species of *Gastrotheca* are placed in four species groups, the *G. marsupiata*, *G. nicefori*, *G. plumbea*, and *G. ovifera* groups (Duellman et al., 1988a). These groups are generally defined on the basis of overall similarity. The only character-based test of their monophyly, the analysis of Mendelson et al. (2000), included 17 exemplars and suggested that none of the three nonmonotypic groups is monophyletic.

Dubois (1987) placed the species within three subgenera: *Gastrotheca*, *Duellmania* (part of the *G. plumbea* group), and *Opisthodelphys* (*G. ovifera* as well as parts of the *G. marsupiata* and *G. plumbea* groups). *Duellmania* and *Opisthodelphys* were shown to be paraphyletic by Mendelson et al. (2000), although they did not test the monophyly of the subgenus *Gastrotheca*. In this study we include two species of the *Gastrotheca marsupiata* group (*G.* cf. *marsupiata* and *G. pseustes*) and two of the *G. ovifera* group (*G. cornuta* and *G. fissipes*).

Hemiphractus: Relationships of this genus were recently reviewed by Sheil et al. (2001), who provided a number of unambiguous synapomorphies to support its monophyly (such as the cultriform process of the parasphenoid that becomes distinctly narrow anteriorly, the presence of a zygomatic ridge, and the presence of a supraorbital ridge). *Hemiphractus* has six described species; we include *Hemiphractus helioi* in our study.

Stefania: Duellman and Hoogmoed (1984), Señaris et al. (''1996'' [1997]), and MacCulloch and Lathrop (2002) reviewed this genus. Señaris et al. (''1996'' [1997]) suggested that the zygomatic ramus of the squamosal being close to or in contact with the maxilla was a diagnostic character state of *Stefania*, ''at least for the Venezuelan species'' (translated from the Spanish). Mendelson et al. (2000) did not test the monophyly of *Stefania* since they included only one exemplar (*S. evansi*). It is unclear if any of the autapomorphies of *S. evansi* in that study are actually synapomorphies of *Stefania*.

Stefania was divided by Rivero (1970) into two species groups based on head shape (''as broad as long or longer than broad'' in the *S. evansi* group; ''much broader than long'' in the *S. ginesi* group). The only test of the monophyly of these two groups is the phylogenetic analysis of the seven species then known, performed by Duellman and Hoogmoed (1984). In that analysis, the *S. ginesi* group was monophyletic and nested within the paraphyletic *S. evansi* group. Although Señaris et al. (''1996'' [1997]) suggested the origin of the *S. ginesi* group from the *S. evansi* group, they continued to recognize of both groups.

Since the revision of Duellman and Hoogmoed (1984), another 11 species assigned to both species groups of *Stefania* have been

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[6] For the synapomorphy list, we copied the data set from the. pdf file of Mendelson et al. (2000) and evaluated character distribution in TNT (Goloboff et al., 2000).

named (see Barrio Amorós and Fuentes, 2003; MacCullogh and Lathrop, 2002). In our analysis we include one exemplar of the *Stefania evansi* group (*S. evansi*) and one of the *S. ginesi* group (*S. schuberti*).

Flectonotus: Duellman and Gray (1983) reviewed these frogs as two genera, *Flectonotus* and *Fritziana*, even though their phylogenetic analysis indicated that *Flectonotus* was paraphyletic with respect to *Fritziana*. Subsequently, Weygoldt and Carvalho e Silva (1991) placed *Fritziana* in the synonymy of *Flectonotus* to render a monophyletic taxonomy. *Flectonotus* is composed of five described species.

In the analysis by Mendelson et al. (2000), the position of *Flectonotus* remained unresolved with respect to *Cryptobatrachus* and the clade composed of *Stefania* plus *Gastrotheca*. Synapomorphies of *Flectonotus* in that analysis are: quadratojugal that does not articulate with maxilla; brooding pouch formed by dorsolateral folds of skin; overlap between m. intermandibularis and m. submentalis; and absence of supplementary elements of m. intermandibularis. Because of very limited availability of species of *Flectonotus*, in this study we include only *Flectonotus* sp., an unidentified species from southeastern Brazil, whose female has a brooding pouch with a middorsal slit.

Pelodryadinae

The monophyly of this Australopapuan group is supported by a single possible synapomorphy: presence of supplementary apical elements of m. intermandibularis (Tyler, 1971). Although relationships between Australian and New World hylids were recognized very early (most species of *Litoria* were named as *Hyla*), hypotheses regarding the relationships of Pelodryadinae with other groups have been rarely advanced. Trewavas (1933), Duellman (1970), and Bagnara and Ferris (1975) suggested a relationship between Pelodryadinae with Phyllomedusinae. Trewavas (1933) observed similarities in laryngeal structures in the limited data set at her disposal (only three pelodryadines and two phyllomedusines). Duellman (1970) referred to ‘‘similarities in vertebral characters’’ without further details and to identical number of chromosomes. Bagnara and Ferris (1975) noticed the presence in some species of *Litoria* of large melanosomes containing the red pigment rhodomelanochrome (later identified as pterorhodin; Misuraca et al., 1977), a character state previously known only for some species of Phyllomedusinae. Specifically, Bagnara and Ferris (1975) suggested that some species of *Litoria* could be related to the Phyllomedusinae, an implicit suggestion of Pelodryadinae paraphyly. This idea was discussed by Tyler and Davies (1978a), who rejected the possibility of pelodryadine paraphyly but did not address a possible sister-taxon relationship of Pelodryadinae and Phyllomedusinae. This alternative was suggested again, based on chromosome morphology, by Kuramoto and Allison (1991). In the phylogenetic analyses presented by Duellman (2001), Pelodryadinae was placed as the sister of a clade composed of the remaining subfamilies, which are united in having a distally bifid tendo superficialis. In this same cladogram, the only synapomorphy of Pelodryadinae is the anterior differentiation of the m. intermandibularis, although the monophyly of Pelodryadinae was assumed and not tested in that analysis.

The phylogenetic analysis performed by Haas (2003) presents the most extensive test of Pelodryadinae monophyly so far published; his Pelodryadinae exemplars form a paraphyletic series with respect to his Neotropical hylid exemplars. More recently, Darst and Cannatella (2004) and Hoegg et al. (2004) presented evidence from the ribosomal mitochondrial and nuclear genes supporting the monophyly of their Pelodryadinae sample and the monophyly of Pelodryadinae + Phyllomedusinae.

Litoria: The diagnosis and contents of *Litoria* were reviewed by Tyler and Davies (1978b). It is unclear whether any of the character states included in their extensive diagnosis are synapomorphic. However, considering subsequent comments by several authors (King et al., 1979; Tyler, 1979; Tyler and Davies, 1979; Maxson et al., 1985; Haas and Richards, 1998), the available evidence suggests that *Litoria* is paraphyletic with respect to the other genera of Pelodryadinae, *Nyctimystes* and *Cyclorana*, with the latter being the sister taxon of the *L. aurea* group.

The 132 currently recognized species (updated from Frost, 2004) placed in 37 species groups (Tyler and Davies, 1978b) make an exhaustive sampling of the group a goal beyond the present analysis.[7] Relationships among some species groups of *Litoria* were addressed by means of albumin immunological distances as determined through microcomplement fixation (Maxson et al., 1982; Hutchinson and Maxson, 1986, 1987). From a character-based (as opposed to a distance-based) perspective, relationships among the species groups of *Litoria* remain unknown, and the monophyly of most of those groups with more than single species remains untested.

Tyler and Davies (1978b) tentatively divided the 37 species groups into three ''Categories'', A (8 species groups), B (14 species groups), and C (7 species groups). Tyler (1982) added a fourth category (D), where he included the *Litoria nannotis* group. These groupings were criticized by King (1980) on karyotypic grounds. Besides, the monophyly of these four categories remain largely untested, with the only possible exception being the work by Cunningham (2002) on the *L. nannotis* group; however, his lack of sufficient outgroup sampling precluded a rigorous test.

In our analyses we include representatives of two species groups of category A, *Litoria aurea* (the *L. aurea* group) and *L. freycineti* (the *L. freycineti* group); three representatives of category B, *L. caerulea* (the *L. caerulea* group), *L. infrafrenata* (the *L. infrafrenata* group), and *L. meiriana* (the *L. meiriana* group); and one representative of category C, *L. arfakiana* (the *L. arfakiana* group).

Nyctimystes: This genus was rediagnosed by Tyler and Davies (1979). Among the list of characters provided by them, the synapomorphies of *Nyctimystes* seem to be the vertical pupil and the presence of palpebral venation. Tyler and Davies (1979) suggested that *Nyctimystes* was most closely related to some species groups of *Litoria* from New Guinea, implying that *Nyctimystes* is nested within *Litoria*. Specifically, they referred to the *L. angiana*, *L. arfakiana*, *L. becki*, *L. dorsivena*, *L. eucnemis*, and *L. infrafrenata* groups as the most likely to be related to *Nyctimystes*, because they share with *Nyctimystes* similarities in cranial structure (the *L. infrafrenata* and *L. eucnemis* groups) or the presence of large unpigmented ova and lotic tadpoles bearing large, ventral, suctorial mouths (the other groups). *Nyctimystes* currently comprises 24 described species, 5 of which (*N. disruptus*, *N. oktediensis*, *N. trachydermis*, *N. tyleri*, and *N. papua*) were included in the *N. papua* species group by Zweifel (1983) and Richards and Johnston (1993). We could not locate tissues of any members of the *N. papua* group, so we cannot test its monophyly. Nevertheless, we include the available species *N. kubori*, *N. narinosus*, and *N. pulcher*.

Cyclorana: This genus was thought to be related to the Australian leptodactylids (now Myobatrachidae) by Parker (1940), and was considered as such by Lynch (1971). Tyler (1972) first proposed its relationship to Australian hylids on the basis of the presence of a differentiated apical element of the m. intermandibularis. Subsequently, Tyler (1978) transferred *Cyclorana* to Hylidae. Tyler (1979), King et al. (1979), and Tyler et al. (1981) considered it to be related to the *Litoria aurea* group, a result that was coincident with the analyses of albumin immunological distances generated by microcomplement fixation (Hutchinson and Maxson, 1987). Burton (1996) suggested that having the m. palmaris longus divided into two segments (as opposed to three) is a synapomorphy supporting the monophyly of *Cyclorana*, *L. dahlii*, and *L. alboguttata* (two species of the *L. aurea* group). Based on sperm morphology, Meyer et al. (1997) transferred *L. alboguttata* to *Cyclorana*. The only morphological synapomorphy suggested for *Cyclorana* is the anterior ossification of the sphenethmoid to incorporate a portion of the tectum nasi (Tyler and Davies, 1993).

The 13 species of *Cyclorana* have been separated into different groups based on karyotypes, sperm morphology, and immuno-

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[7] A detailed analysis of Pelodryadinae is currently being carried out by S. Donnellan. Taxon sampling here is provided to optimize characters effectively to the base of the Pelodryadinae and not to reevaluate the taxonomy of *Litoria* and its generic satellites.

logical distances (King et al., 1979; Maxson et al., 1982; Maxson et al., 1985; Meyer et al., 1997). These are the *C. brevipes*, *C. australis*, and *C. platicephala* ‘‘lineages’’. In the present study, we include only *C. australis*.

Phyllomedusinae

Cruz (1990) and Duellman (2001) provided taxonomic histories of this group, mostly at the generic level. The monophyly of Phyllomedusinae has not been controversial; several character states have been advanced to support it. Some of the muscular character states include the supplementary posterolateral elements of the m. intermandibularis (Tyler, 1971); tendo superficialis pro digiti II (pes) arising from a deep, triangular muscle, which originates on the distal tarsal 2–3; tendo superficialis pro digiti III arising entirely from the aponeurosis plantaris; and m. extensor brevis superficialis digiti IV with a single slip (Burton, 2004). There are also several larval character states that support the monophyly of this group; for example, the arcus subocularis of larval chondrocranium with distinct lateral processes (Fabrezi and Lavilla; 1992, Haas, 2003); ultralow suspensorium (Haas, 2003); secondary fenestrae parietales (Haas, 2003); and absence of a passage between ceratohyal and ceratobranchial I (Haas, 2003).

The subfamily is comprised of six nominal genera: *Agalychnis* (8 species), *Hylomantis* (2 species), *Pachymedusa* (1 species), *Phasmahyla* (4 species), *Phrynomedusa* (5 species), and *Phyllomedusa* (32 species). Cruz (1990) discussed the taxonomic distribution of several character states shared by subsets of these genera. A cladistic analysis testing the monophyly of each of these and their interrelationships remains to be completed.

Agalychnis: Duellman (2001) presented a phylogenetic analysis of *Agalychnis* and *Pachymedusa*, using a vector of character states present in the *Phyllomedusa buckleyi* group as an outgroup (data taken from Cannatella, 1980). His analysis suggested no synapomorphies for *Agalychnis*. In our analysis we include all species available to us: *A. calcarifer*, *A. callidryas*, *A. litodryas*, and *A. saltator* (species not included are *A. annae*, *A. craspedopus*, *A. moreletii*, and *A. spurrelli*).

Hylomantis: This genus was resurrected by Cruz (1990) for the species formerly placed in the *Phyllomedusa aspera* group (Cruz, ‘‘1988’’ [1989]). From the extensive diagnosis presented by Cruz (1990), the only apparent synapomorphy of *Hylomantis* seems to be the lanceolate discs of fingers and toes. Cruz (1990: 725), however, considered likely that *Hylomantis* was paraphyletic with respect to *Phasmahyla*. *Hylomantis* has two described species, *H. aspera* and *H. granulosa*. Only *H. granulosa* was available for this study.

Pachymedusa: This monotypic genus was recognized by Duellman (1968a) to reflect his view that a remnant of the ancestral stock gave rise to the other Phyllomedusinae. However, Duellman (2001) found no evidence supporting the monophyly of *Agalychnis* independent of *Pachymedusa*. The single species *Pachymedusa dacnicolor* is included in our analysis.

Phasmahyla: This genus was erected by Cruz (1990) for the species formerly contained in the *Phyllomedusa guttata* group (Bokermann and Sazima, 1978; Cruz, 1982). Cruz (1990) provided an extensive definition of the genus based on adult and larval morphology. Probable synapomorphies of *Phasmahyla* are the lack of a vocal sac in adult males and larval modifications presumably associated with surface film feeding, such as the anterodorsal position of the oral disc, reduction in number and size of labial tooth rows, distribution and shape of submarginal papillae, and the upper jaw sheath with a medial projection (see Cruz, 1982, 1990). The genus is composed of four species, *P. cochranae*, *P. exilis*, *P. guttata*, and *P. jandaia*. We include *Phasmahyla cochranae* and *P. guttata* in our study.

Phrynomedusa: This genus was resurrected by Cruz (1990) for the species formerly placed in the *Phyllomedusa fimbriata* group (Izecksohn and Cruz, 1976; Cruz, 1982). From the extensive definition provided by Cruz (1990), possible synapomorphies of *Phrynomedusa* appear to be the presence of a bicolored iris and the complete marginal papillae in the oral disc of the larva. *Phrynomedusa* contains five described species; unfortunately, we could not secure any representatives of this taxon for the present study.

Phyllomedusa: No synapomorphies are known to support the monophyly of the 32 species of *Phyllomedusa*. This genus includes simply those species that are not included in the other five genera of Phyllomedusinae. There are currently five species groups recognized within *Phyllomedusa*: the *P. buckleyi* group (Cannatella, 1980), *P. burmeisteri* group (Lutz, 1950; Pombal and Haddad, 1992), *P. hypochondrialis* group (Bokermann, 1965a), *P. perinesos* group (Cannatella, 1982), and *P. tarsius* group (De la Riva, 1999). The monophyly of these groups had not been tested, and relationships among them remain unstudied. Furthermore, several species (e.g., *P. bicolor*, *P. palliata*, *P. tomopterna*, and *P. vaillanti*) have not been assigned to any species group. Some authors (Funkhouser, 1957; Duellman, 1968a, 1969; Cannatella, 1980; Jungfer and Weygoldt, 1994) have suggested that the *Phyllomedusa buckleyi* group deserves generic recognition.

Duellman et al. (1988b) posited the existence of a clade composed of most species of *Phyllomedusa* (excluding the *P. buckleyi* group and the *P. guttata* group, now *Phasmahyla*, but see below), implicitly including the species now placed in *Hylomantis*. Apparent synapomorphies of this clade are the well-developed parotoid glands; the presence of the slip of the m. depressor mandibulae that originates from the dorsal fascia at the level of the m. dorsalis scapulae; first toe longer than second; and the eggs wrapped in leaves. Duellman et al. (1988b) explicitly excluded the species then included in the *P. guttata* group (now *Phasmahyla*) from this apparent clade. However, Lutz (1954), Bokermann and Sazima (1978), Weygoldt (1984), and Haddad (personal obs.) reported *P. guttata*, *P. jandaia*, *P. exilis*, and *P. cochranae*, respectively, to oviposit in folded leaves, and Cruz (1990) reported in *Hylomantis* the presence of the slip of the m. depressor mandibulae that originates from the dorsal fascia at the level of the m. dorsalis scapulae. In this study we include representatives of the *Phyllomedusa buckleyi* group (*P. lemur*), *P. burmeisteri* group (*P. tetraploidea*), *P. hypochondrialis* group (*P. hypochondrialis*), and *P. tarsius* group (*P. tarsius*). We include also *P. bicolor*, *P. palliata*, *P. tomopterna*, and *P. vaillanti*, four species unassigned to groups.

Hylinae

This taxon is the primary focus of this study. Hyline monophyly is supported by two synapomorphies: the tendo superficialis digiti V with an additional tendon that arises ventrally from m. palmaris longus (da Silva, 1998, as cited by Duellman, 2001), and karyotype with 24 (or more) chromosomes (Duellman, 2001). The published molecular evidence is ambiguous regarding the issue.[8]

No comprehensive study of hyline systematics has been published, although the results of one unpublished dissertation (da Silva, 1998) have been widely circulated (e.g., Duellman, 2001). Although the problems of hylid systematics have been recognized for some time, almost all work has been done at the level of satellite genera (e.g., *Duellmanohyla*, *Plectrohyla*, *Ptychohyla*, *Scinax*) or species groups of *Hyla*.

For the purpose of our analysis we included representatives of all 27 genera of Hylinae. Within the genus *Hyla*, we included exemplars of 39 of the 41 species groups that had been recognized (we lack exemplars for the *H. claresignata* and *H. garagoensis* groups). We are not recognizing monotypic species group because (1) they do not represent testable hypothesis, and (2) they are

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[8] In the analysis of Darst and Cannatella (2004), Hylinae (including pseudids) is monophyletic only in their maximum likelihood analysis, not in their parsimony analysis. If, unlike Darst and Cannatella (2004), insertion/deletion events are considered as informative variations, their results still show a paraphyletic Hylinae, having *Leptodactylus pentadactylus* + *Lithodytes lineatus* nested within Hylinae. In the same analysis Hemiphractinae is monophyletic. We do not think that these differences in results reflect relative merits of the different approaches but instead represent problems in the taxon sampling of the analysis of Darst and Cannatella (2003) (which was not designed to test the monophyly of Hylinae). Salducci et al. (2002) presented a molecular phylogenetic analysis using a fragment of 16S of a sampling restricted to sequences available in GenBank and Hylidae of French Guyana. *Rana palmipes* and *Hyalinobatrachium taylori* were the only outgroups. Considering the restricted taxon sampling and the minimal number of outgroups, their results are difficult to interpret or to compare with other studies.

not a rank in the Linnean taxonomy and therefore are not required for consistency and stability purposes.

Hyla is the most species-rich genus of hylid frogs. It is currently placed in 41 species groups, plus other species that had not been associated with any group. In turn, major clades composed of several of these species groups have been suggested. Because no study has ever suggested *Hyla* to be monophyletic and several have suggested that it is paraphyletic with respect to other hyline genera (Duellman and Campbell, 1992; Cocroft, 1994; Faivovich, 2002; Haas, 2003; Darst and Cannatella, 2004; Faivovich et al., 2004), we refer further discussion to the headings for the various genera and species groups. Comments about apparent major clades and proposed relationships among species groups are mostly reserved for the discussion section of this paper.

Gladiator Frogs

Kluge (1979: 1) referred to the frogs then placed in the *Hyla boans* group as ''gladiator frogs'' ''in view of their extremely pugnacious behavior and the well developed prepollical spines that they use when fighting.'' Following Duellman (1970, 1977), Kluge (1979) included in the group *H. boans*, *H. circumdata*, *H. crepitans*, *H. faber*, *H. pardalis*, and *H. pugnax*. Nevertheless, a prepollical spine has been reported for several species groups. Furthermore, territorial fighting has been reported or suspected to occur in several of these species.[9] Because of this, and due to the lack of a better term, we prefer to use the term ''Gladiator Frogs'' to refer collectively to all the mostly South American species having a prepollical spine, as was done by Faivovich et al. (2004), instead of restricting its use to the *H. boans* group. The species groups that are currently referred to the Gladiator Frog clade are the *H. albomarginata*, *H. albopunctata*, *H. boans*, *H. circumdata*, *H. claresignata*, *H. geographica*, *H. granosa*, *H. martinsi*, *H. pseudopseudis*, *H. pulchella*, and *H. punctata*[10] groups (Bokermann, 1972, Hoogmoed, 1979, Duellman et al., 1997, Eterovick and Brandão, 2001, Duellman, 2001, Faivovich et al., 2004).

Hyla albomarginata Group: The *H. albomarginata* group was first recognized formally by Cochran (1955) for a group of species (*H. albomarginata*, *H. albosignata*, *H. albofrenata*, *H. musica*) that Lutz (''1948'' [1949]) referred to as the green species of *Hyla* of southeastern Brazil. Cochran (1955) included *H. prasina* (latter included in the *H. pulchella* group by Lutz, 1973) in this group. Duellman (1970) presented a definition of the group and included, besides the species considered by Cochran (1955), *H. rufitela*, *H. pellucens*, *H. albopunctulata* (now considered a member of the *H. bogotensis* group; see below), and *H. albolineata* (now considered a species of *Gastrotheca*; see Sachsse et al., 1999).

Cruz and Peixoto (''1985'' [1987]) divided the *Hyla albomarginata* group into three ''complexes'': the *H. albomarginata* complex, containing *H. albomarginata* and *H. rufitela*; the *H. albofrenata* complex, containing *H. albofrenata*, *H. arildae*, *H. ehrhardti* (as *H. arianae*; see Faivovich et al., 2002), *H. musica*, and *H. weygoldti*; and the *H. albosignata* complex, containing *H. albosignata*, *H. callipygia*, *H. cavicola*, *H. fluminea*, and *H. leucopygia*. *Hyla pellucens* should also be included in the *albomarginata* complex, because this species was included by Duellman (1970) but was overlooked by Cruz and Peixoto (''1985'' [1987]); very likely the same applies for *H. rubracyla*, a species that was resurrected from the synonymy of *H. pellucens* by Duellman (1974) and included in the *H. albomarginata* group

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[9] It remains to be studied if these territorial behaviors are homologous. Species of this putative clade, other than some members of the *H. boans* group, where combat was observed or are suspected to occur, are *Hyla circumdata* (Haddad, personal obs.), *H. cordobae* (Faivovich, personal obs.), *H. goiana* (Menin et al., 2004), *H. joaquini* (Garcia et al., 2003), *H. marginata* (Garcia et al., 2001b), *H. marianitae* (Duellman et al., 1997), *H. prasina* (Haddad, personal obs.), *H. melanopleura* (Lehr and May, 2004), *H. pulchella* (Gallardo, 1970; Langone, ''1994'' [1995]), *H. punctata* (Sehinkman and Faivovich, personal obs.), *H. raniceps* (Guimarães et al., 2001), *H. riojana* (Blotto and Baldo, personal commun.), and *H. semilineata* (Haddad, personal obs.).

[10] Faivovich et al. (2004) mentioned that Duellman et al. (1997) did not include the *Hyla punctata* group within a putative clade of gladiator frogs, but overlooked the fact that Duellman (2001: 776) stated that ''members of the . . . *H. punctata* group might be included'' in this clade.

by Duellman in Frost (1985). The only possible synapomorphies that were proposed for these complexes were the red coloration of the webbing in the two species of the *H. albomarginata* complex studied by the authors, and presence of cloacal ornamentation in the *H. albosignata* complex (several instances of homoplasy within hylids). Haddad and Sawaya (2000) and Hartmann et al. (2004) further suggested that the *H. albofrenata* and *H. albosignata* complexes share a reproductive mode where the male constructs a subterranean nest in the muddy side of streams and pools that is completely concealed after spawning, a nest where larvae spend early stages of development; subsequent to flooding, the exotrophic larvae live in ponds or streams.

Cruz et al. (2003) added *Hyla ibirapitanga* and *H. sibilata* to the *H. albosignata* complex. Note that species included in both the *H. albofrenata* and *H. albosignata* complexes do not posses a prepollical spine, as do species in the *H. albomarginata* complex. On recent occasions, some authors (Haddad and Sawaya, 2000; Garcia et al., 2001a) referred directly to the *H. albofrenata* and *H. albosignata* groups without further comment. We include in the present analysis representatives of the three complexes: *H. albosignata*, *H. callipygia*, *H. cavicola*, and *H. leucopygia* as representatives of the *H. albosignata* complex; *H. arildae*, *H. weygoldti*, and a *Hyla* sp. 1, a new species similar to *H. ehrhardti*, as representatives of the *H. albofrenata* complex; and *H. albomarginata*, *H. pellucens*, and *H. rufitela* as exemplars of the *H. albomarginata* complex.

Hyla albopunctata Group: Cochran (1955) recognized the *H. albopunctata* group on the basis of the ‘‘more streamlined body shape, by lacking an outer metatarsal tubercle, and by having the fingers webbed only at the base . . . ’’. She included in the group *H. albopunctata*, *H. raniceps*, and several species from southeastern Brazil that are now in the *H. claresignata* and *H. pulchella* groups. Cochran and Goin (1970) recognized a *H. lanciformis* group (on the basis of large size, a white margin on the upper lip, pointed heads, and reduced webbing between the fingers) in which they included *H. lanciformis*, *H. multifasciata*, and *H. boans* (name applied incorrectly to *H. albopunctata*; see Duellman, 1971a). Duellman (1971a) implicitly united these two groups and considered the larger *H. albopunctata* group to be composed of *H. albopunctata*, *H. lanciformis*, *H. multifasciata*, and *H. raniceps*. De Sá (1995, 1996) stated that there was no evidence supporting the monophyly of the group. Caramaschi and Niemeyer (2003) added *H. leucocheila* to the group and suggested that it was monophyletic, but they presented no evidence to this effect. We include all species except *H. leucocheila* in our analysis.

Hyla boans Group: The constitution of the *H. boans* group as well as the definition of the group present a rather confusing history. Affinities between species of what is currently called the *H. boans* group were first recognized by Cochran (1955), who included in what she called the *H. faber* group the species *H. crepitans*, *H. faber*, *H. langsdorffii* (now a species of *Osteocephalus*, see Duellman, 1974), and *H. pardalis*. Some of the diagnostic characters of this group were large size and the presence of what she called a prominent spurlike prepollex in males. Cochran and Goin (1970) included *H. faber*, *H. pardalis*, *H. rosenbergi*, and *H. maxima* (now a junior synonym of *H. boans*; see Duellman, 1971a) in the *H. maxima* group, and they excluded *H. crepitans*, placing it in its own group. Duellman (1970) presented a formal definition of the *H. boans* group, in which he included *H. boans*, *H. circumdata* (now in the *H. circumdata* group), *H. crepitans*, *H. faber*, *H. langsdorffii*, *H. pardalis*, and *H. rosenbergi*. Lutz (1973) included the species in three different groups,[11] in one of which she also included several species now included in the *H. circumdata*, *H. pseudopseudis*, and *H. martinsi* groups (the ‘‘species with long, sharp pollex rudiment’’). Kluge (1979) resurrected *H. pugnax* from the synonymy of *H. crepitans*, including it also in the *H. boans* group. Martins and Haddad (1988) included in the group *H. lundii* (using the name *H. biobeba*, a junior synonym, see Caramaschi and Napoli, 2004), based on ob-

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[11] The ‘‘species with long, sharp pollex rudiment’’, the ‘‘species with undulated glandular outline’’, and the ‘‘species with pattern on the transparent part of the lower eyelid’’.

servations of nest construction done by Jim (1980). Implicitly, they also removed *H. circumdata* from the group. Hoogmoed (1990) resurrected *H. wavrini* from the synonymy of *H. boans* and retained it in the group. Duellman (2001) omitted *H. lundii* from the group without comment. Caramaschi and Rodrigues (2003) added *H. exastis*, suggesting that it was related to *H. lundii* and *H. pardalis* on the basis of its lichenous color pattern and the rugose skin texture. Caramaschi and Napoli (2004) presented a formal definition of the group. In summary, and following Caramaschi and Napoli (2004), we regard the *H. boans* group to be composed of *H. boans*, *H. crepitans*, *H. exastis*, *H. faber*, *H. lundii*, *H. pardalis*, *H. pugnax*, *H. rosenbergi*, and *H. wavrini*. The only synapomorphy that has ever been proposed for this group is the nest-building behavior of males, which has been observed in most species (see Martins and Moreira, 1991 for a review). Early reports of *H. crepitans* indicated that males do not construct nests; this was shown to be facultative by Caldwell (1992). This behavior is still unknown in *H. pugnax*. From this group we include in our analysis *H. boans*, *H. crepitans*, *H. faber*, *H. lundii*, and *H. pardalis*.

Hyla circumdata Group: This group was first mentioned by Bokermann (1967a, 1972), without providing any diagnosis. Heyer (1985) provided the first formal definition, diagnosing the group by the combination of a well-developed prepollex and the posterior face of the thigh having dark vertical stripes. The group was further discussed and expanded by Caramaschi and Feio (1990), Pombal and Haddad (1993), Napoli (2000), Caramaschi et al. (2001), and Napoli and Pimenta (2003). Three other species groups, the *H. claresignata*, *H. martinsi*, and *H. pseudopseudis* groups, as well as *H. alvarengai*, historically had been satellites of the *H. circumdata* group, with these species being alternatively included or excluded from the group. These groups and *H. alvarengai* are treated separately. With the recognition of these three groups being separate from the *H. circumdata* group, it is unclear which synapomorphies support its monophyly as currently defined.

Duellman et al. (1997) suggested that all species of the *Hyla circumdata* group should be transferred to the *H. pulchella* group. Faivovich et al. (2004) demonstrated by using DNA sequences from four mitochondrial genes that the two groups are not closely related. In the analysis of Faivovich et al. (2004), the three exemplars of the *H. circumdata* group then available (*H. astartea*, *H. circumdata*, and *H. hylax*) formed a monophyletic group that is the sister taxon of the remaining Gladiator Frogs they included in their analysis. Napoli and Pimenta (2003), Napoli and Caramaschi (2004), and Napoli (2005) recognized 15 species in the group: *H. ahenea*, *H. astartea*, *H. caramaschii*, *H. carvalhoi*, *H. circumdata*, *H. feioi*, *H. gouveai*, *H. hylax*, *H. ibitipoca*, *H. izecksohni*, *H. lucianae*, *H. luctuosa*, *H. nanuzae*, *H. ravida*, and *H. sazimai*. We include five species in our analysis: *H. astartea*, *H. circumdata*, *H. hylax*, as well as *Hyla* sp. 3 and *Hyla* sp. 4, two undescribed species from littoral areas of northern São Paulo (state) and southrn Rio de Janeiro (state), Brazil, respectively.

Hyla claresignata Group: A close relationship between *H. clepsydra* and *H. claresignata* was suggested by Bokermann (1972), who noticed striking similarities in larval and adult morphology. Bokermann (1972) suggested a possible relationship of these species with the *H. circumdata* group; following him, Jim and Caramaschi (1979) included *H. clepsydra* and *H. claresignata* in the *H. circumdata* group. However, subsequent workers (Caramaschi and Feio, 1990; Pombal and Haddad, 1993) who referred to the *H. circumdata* group did not include them in the group. The *H. claresignata* group was recognized in the restricted form by Duellman et al. (1997). Possible synapomorphies of the *H. claresignata* group are character states associated with the torrent-dwelling larvae of these species: oral disc completely surrounded by marginal papillae, and 7/12–8/13 labial tooth rows. We were not able to secure samples of either of the two species of this group.

Hyla geographica Group: This group was delimited by Cochran (1955: 180) as being characterized by its ‘‘extremely attenuate limbs’’. Cochran and Goin (1970) characterized the species of this group as ‘‘moderate-sized tree frogs with elongate dermal appendages on the heels and reduced webbing between the fingers.'' Duellman (1973a) presented an extensive characterization of the group (including vomers large with angular dentigerous processes, each bearing as many as 20 teeth; nuptial excrescences present in breeding males; projecting prepollices absent in both sexes; calcars present; palpebral membrane clear or reticulated). However, it is unclear from his account if any of these character states could be considered synapomorphic of the group.

Duellman (1973a) included in this group *Hyla calcarata*, *H. fasciata*, and *H. geographica*. Later, Pyburn (1977, 1984) added *H. microderma* and *H. hutchinsi*. Goin and Woodley (1969) considered *H. kanaima* related to the *H. geographica* group, and Pyburn (1984) included *H. kanaima* in the group. Lutz (1963, 1973) and Bokermann (1966a) stressed similarities between *H. secedens* and *H. semilineata* (as *H. geographica*), but Caramaschi et al. (2004a) suggested that actually this species is closer to *H. bischoffi* (of the *H. pulchella* group). Duellman (*in* Frost, 1985) and Duellman and Hoogmoed (1992), respectively, included *H. picturata* and *H. roraima* in the *H. geographica* group. D'Heursel and de Sá (1999) argued for the recognition of *H. semilineata*, a species that had previously been placed in the synonymy of *H. geographica*. Lescure and Marty (2000) included *H. dentei*, a species that Bokermann (1967b) considered to have character states of both *H. raniceps* (*H. albopunctata* group) and the *H. geographica* group. Caramaschi et al. (2004a) added *H. pombali* to the group. In summary, the *H. geographica* group is currently composed of 11 species: *H. calcarata*, *H. dentei*, *H. fasciata*, *H. geographica*, *H. hutchinsi*, *H. kanaima*, *H. microderma*, *H. picturata*, *H. pombali*, *H. roraima*, and *H. semilineata*. We include *H. fasciata*, *H. calcarata*, *H. kanaima*, *H. microderma*, *H. picturata*, *H. roraima*, and *H. semilineata* in our study.

Hyla granosa Group: This group was first defined by Cochran and Goin (1970) as green frogs that share the vomerine teeth being in rather heavy, arched series, and with males having a ''protruding spine in the prepollex''. These authors included *H. granosa*, *H. rubracyla* (now in the *H. albomarginata* complex of the *H. albomarginata* group, see above), and *H. guibei* (now a junior synonym of *H. pellucens*; see Duellman, 1974). Previously, Rivero (1964) stated that *H. alemani* was allied with *H. granosa*. Rivero (''1971'' [1972]) considered *H. sibleszi* to be related to *H. granosa*. Hoogmoed (1979) mentioned, without any diagnosis, the *H. granosa* group in the Guayanas, in which he included *H. ornatissima*. Mijares-Urrutia (1992a) considered *H. alemani*, *H. granosa*, *H. ornatissima*, and *H. sibleszi* to be the members of this group, and he provided a characterization based on larval features. We are not aware of any synapomorphies for this group. In this analysis we include *H. granosa* and *H. sibleszi*.

Hyla martinsi Group: This group was recognized by Bokermann (1965b) for two species, *H. langei* and *H. martinsi*, characterized by the presence of an extensive hooklike humeral crest and by a bifid prepollex. Bokermann (1964a) noticed ''superficial similarities'' of *H. martinsi* with *H. circumdata*. Caramaschi and Feio (1990) and Cardoso (1983) included *H. martinsi* in the *H. circumdata* group for having the diagnostic characters established by Heyer (1985). However, based on the presence of bifid prepollex and a humeral spine, Caramaschi et al. (2001) preferred to keep it as a separate species group. As a representative of this group we include *H. martinsi* in the analysis.

Hyla pseudopseudis Group: This group was recognized by Pombal and Caramaschi (1995) as closely related to the *H. circumdata* group, from which it was differentiated mostly by its color pattern. Eterovick and Brandão (2001) further differentiated both groups based on the presence of short, lateral irregular tooth rows and for having additional posterior tooth rows (6–8 rows) in the oral discs of the larvae of the *H. pseudopseudis* group (a maximum of 5 posterior rows in the *H. circumdata* group). Caramaschi et al. (2001) transferred *H. ibitiguara* from the *H. circumdata* group to the *H. pseudopseudis* group on the basis of its similar external morphology, color pattern, and habits. The group currently comprises three species, *H. ibitiguara*, *H. pseudopseudis* and *H. saxicola*, plus *Hyla* sp. 6 (aff. *H. pseudopseudis*), a new species from Bahia, Brazil, that is being described by Lugli and Haddad (in prep.). Only tissues of this new species were available for this study.

Hyla pulchella Group: The history of this group was recently reviewed by Faivovich et al. (2004). These authors also presented a phylogenetic analysis based on mitochondrial DNA sequences of four genes, and included 10 of the then 14 species included in the group, plus exemplars of the former *H. polytaenia* group and several outgroups. Their results indicate that the *H. polytaenia* group, as defined by Cruz and Caramaschi (1998), is nested within the *H. pulchella* group. Consequently, species included in the *H. polytaenia* group were transferred to the *H. pulchella* group, where they are recognized as the *polytaenia* clade. Considering this action and the species status given to *H. cordobae* and *H. riojana*, Faivovich et al. (2004) raised the number of species included in the *H. pulchella* group to 25. Carnaval and Peixoto (2004) recently added *H. freicanecae* to the group. Caramaschi et al. (2004a) suggested that *H. secedens* is related to *H. bischoffi*, therefore adding implicitly the species to the *H. pulchella* group. Caramaschi and Cruz (2004) added *H. beckeri* and *H. latistriata* to the *H. polytaenia* clade, adding two more species to the *H. pulchella* group. Faivovich et al. (2004) had doubts regarding the recognition of *H. callipleura*. Duellman et al. (1997) included this name as a junior synonym of *H. balzani*, but Köhler (2000) resurrected it using the combination *H.* cf. *callipleura* for some populations in Bolivia. We tentatively recognize *H. callipleura* as valid, but stress the necessity of further studies to clarify its status.

While the monophyly of this redefined *Hyla pulchella* group is supported by molecular evidence, no morphological synapomorphies have been proposed so far (see also comments for the *H. circumdata* and *H. larinopygion* groups). In summary, there are 30 species included in this group: *H. albonigra*; *H. andina*; *H. balzani*; *H. beckeri*; *H. bischoffi*; *H. buriti*; *H. caingua*; *H. callipleura*; *H. cipoensis*; *H. cordobae*; *H. cymbalum*; *H. ericae*; *H. freicanecae*; *H. goiana*; *H. guentheri*; *H. joaquini*; *H. latistriata*; *H. leptolineata*; *H. marginata*; *H. marianitae*; *H. melanopleura*; *H. palaestes*; *H. phaeopleura*; *H. polytaenia*; *H. prasina*; *H. pulchella*; *H. riojana*; *H. secedens*; *H. semiguttata*; and *H. stenocephala*. In this analysis we include the same species that were available to Faivovich et al. (2004) (*H. andina*; *H. balzani*; *H. bischoffi*; *H. caingua*; *H. cordobae*; *H. ericae*; *H. guentheri*; *H. joaquini*; *H. leptolineata*; *H. marginata*; *H. marianitae*; *H. prasina*; *H. pulchella*; *H. riojana*; *H. semiguttata*, and an undescribed species), plus *H. polytaenia*. The species that Faivovich et al. (2004) called *Hyla* sp. 2 corresponds to what Caramaschi and Cruz (2004) recently described as *H. latistriata*, and so is included under that name.

Hyla punctata Group: This group was first recognized by Cochran and Goin (1970), who included *H. punctata*, *H. rhodoporus*, and *H. rubeola* (these last two were subsequently considered to be synonyms of *H. punctata* by Duellman, 1974). They characterized the group as ‘‘moderately small green tree frogs with small vomerine tooth patches, reduced webbing between the fingers, without spines on the pollex, and without ulnar or tarsal ridges.’’ Hoogmoed (1979) mentioned this group without defining it. No synapomorphies have been proposed for this group. Besides *H. punctata*, two other species could be included on this poorly defined group: *H. hobbsi*, a species resurrected from the synonymy of *H. punctata* by Pyburn (1978), and *H. atlantica*, a name recently applied by Caramaschi and Velosa (1996) for the populations on eastern Brazil previously considered as *H. punctata*. In this analysis we include *H. punctata*.

Species of Probable Gladiator Frogs Unassigned to Species Group: *Hyla alvarengai*: This bizarre species was said by Bokermann (1964a) to share some character states with *H. martinsi* and *H. saxicola* (now placed in the *H. martinsi* and *H. pseudopseudis* groups, respectively), such as the notable development of the prepollex and the shape of the sacral diapophyses. Lutz (1973) included it in the group of the ‘‘species with long, sharp pollex rudiment’’, together with *H. crepitans*, *H. faber*, and species now included in the *H. circumdata* and *H. martinsi* groups. She referred to it as *Hyla* (*Plectrohyla*?) *alvarengai* and stated that it was ‘‘devoid of affinities with the very large species of *Hyla*’’, suggesting instead a possible relationship with *Plectrohyla*. A similar opinion was presented by Sazima and Bokermann (1977), who noticed ‘‘superficial similarities’’ with *Plectrohyla*, but they argued that they differed in larval morphology, spawn, and vocalizations. Duellman et al. (1997) included *H. alvarengai* in the *H. circumdata* group, presumably because it shares the diagnostic characters of the group. Eterovick and Brandão (2001) and Caramaschi et al. (2001) did not consider it as a member of the *H. circumdata* group. Unfortunately, we could not secure this species for our analysis, although we include a new species similar to *H. alvarengai* that is in the process of being described by Lugli and Haddad (in prep.).

Hyla fuentei: This species was described by Goin and Goin (1968) based on a single adult female from Surinam. Hoogmoed (1979) mentioned the existence of two additional specimens collected close to the type locality. Since then, no author has referred to this species. From the original description, there are few characters that allow the association of this species with any other group of *Hyla*. The angulate dentigerous process of the vomer suggests that this species could be associated with certain Gladiator Frogs, as some species currently placed in the *H. albopunctata*, *H. boans*, and *H. geographica* groups have this character state. A study of the holotype and discovery of male specimens should clarify the matter.

Hyla heilprini: This West Indian hylid was associated with the *H. albomarginata* group by Duellman (1970) based on the presence of a ‘‘green’’ peritoneum (actually it is white parietal peritoneum, like in species of the *H. albomarginata*, *H. bogotensis*, *H. granosa*, and *H. punctata* groups; Lynch and Ruiz-Carranza [1991: 4]; Faivovich, personal obs.) and external pigmentation. This was followed by Trueb and Tyler (1974), who noticed that its morphology was ‘‘highly reminiscent’’ of those from that species group. While it seems clear that *H. heilprini* is a Gladiator Frog, we are not aware of any synapomorphy relating it to the *H. albomarginata* group. This species was included in the analysis.

Three species of *Hyla* from the Venezuelan Tepuis: There are three species of *Hyla* from the Venezuelan Tepuis that have not been posited to be related to any other species or group of species: *H. benitezi*, *H. lemai*, and *H. rhythmicus*. The presence of a prepollical spine (Rivero, ‘‘1971’’ [1972]; Donnelly and Myers, 1991; Señaris and Ayarzagüena, 2002) associates these species with Gladiator Frogs. *Hyla benitezi* and *H. lemai* were included in the analysis.

Hyla varelae: Carrizo (1992) described this species based on a single adult male. It was suggested to be related to *H. raniceps* in the description. No additional specimens have been collected since the description, and it was not included in this analysis.

Andean Stream-Breeding *Hyla*

Duellman et al. (1997) presented a phylogenetic analysis restricted to wholly or partially Andean species groups of *Hyla*. On their most parsimonious tree, the *H. armata*, *H. bogotensis*, and *H. larinopygion* groups together form a monophyletic group supported by three transformations in larval morphology: the enlarged, ventrally oriented oral disc; the complete marginal papillae; and labial tooth rows formula 4/6 or more.

Hyla armata Group: The *H. armata* group was first recognized by Duellman et al. (1997) for its single species, *H. armata*. Köhler (2000) and De la Riva et al. (2000) subsequently reported that *H. charazani* was a second member of the *H. armata* group. Duellman et al. (1997) described four synapomorphies for the *H. armata* group: the presence in males of keratin-covered bony spines on the proximal ventral surface of the humerus, on the expanded distal element of the prepollex, and on the first metacarpal; tadpole tail long with low fins and bluntly rounded tip; forearms hypertrophied; and the presence of a ‘‘shelf’’ on the larval upper jaw sheath. We include both species in our analysis.

Hyla bogotensis Group: This group was reviewed by Duellman (1970, 1972b, 1989) and Duellman et al. (1997). The only synapomorphy that has been suggested for this group is the presence in males of a mental gland.[12] *Hyla albopunctulata* was redescribed

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[12] See Duellman (2001) and La Marca (1985) for comments on taxonomic distribution and morphological variation of this gland, and Romero de Perez and Ruiz-Carranza (1996) for its histological structure.

by Duellman and Mendelson (1995), who rejected a possible relationship with the *H. bogotensis* group, as suggested by Goin *in* Rivero (1969) and Duellman (*in* Frost, 1985), and they simply stated that its relationships were unclear. Faivovich et al. (in prep.) studied two male syntypes (BMNH 1880.12. 5159 and 1880.12.5160), which posses a noticeable mental gland. For this reason, we associate this species with the *H. bogotensis* group. The *Hyla bogotensis* group is then composed of 15 species: *H. albopunctulata*, *H. alytolylax*, *H. bogotensis*, *H. callipeza*, *H. colymba*, *H. denticulenta*, *H. jahni*, *H. lascinia*, *H. lynchi*, *H. palmeri*, *H. phyllognata*, *H. piceigularis*, *H. platydactyla*, *H. simmonsi*, and *H. torrenticola*. In this analysis we were able to include only *H. colymba* and *H. palmeri*.

Hyla larinopygion Group: Duellman and Hillis (1990) and Duellman and Coloma (1993) reviewed this group, and Duellman and Hillis (1990) and Duellman et al. (1997) provided a formal definition, although it is unclear whether any of the morphological character states employed in these characterizations is synapomorphic for the group. Duellman and Hillis (1990) performed a phylogenetic analysis using isozymes of five species of the group. In the phylogenetic analysis of Duellman et al. (1997), the authors did not identify any synapomorphy for the *H. larinopygion* group; it merely lacks the apparent synapomorphies of the *H. armata* and *H. bogotensis* groups. Because of problems with the limits of the *H. larinopygion* group, Kizirian et al. (2003) were uncertain about the placement of *H. tapichalaca*, a species that they considered most similar to the *H. larinopygion*, *H. armata*, and *H. pulchella* groups.[13] Faivovich et al. (2004) showed that *H. tapichalaca* and *H. armata* (the only exemplars of Andean stream-breeding *Hyla* they included) were sister taxa, and only very distantly related to the *H. pulchella* group. The *H. larinopygion* group currently comprises nine species: *H. caucana*, *H. larinopygion*, *H. lindae*, *H. pacha*, *H. pantosticta*, *H. psarolaima*, *H. ptychodactyla*, *H. sarampiona*, and *H. staufferorum*. In this analysis, we include *H. pacha*, *H. pantosticta*, and *H. tapichalaca*.

The 30-Chromosome *Hyla*

Only the species of the *Hyla microcephala* group were initially reported to have 30 chromosomes (Duellman and Cole, 1965; Duellman, 1967). However, as species of other groups were reported to have 30 chromosomes (Duellman, 1970; Bogart, 1973), it became evident that this was a characteristic of several species groups. Currently, the *H. columbiana*, *H. decipiens*, *H. garagoensis*, *H. labialis*, *H. leucophyllata*, *H. marmorata*, *H. microcephala*, *H. minima*, *H. minuta*, *H. parviceps*, and *H. rubicundula* groups, plus several species unassigned to any group are believed to conform to a monophyletic group supported by this character state (Duellman, 1970; Duellman and Trueb; 1983; Duellman et al., 1997; Napoli and Caramaschi, 1998; Carvalho e Silva et al., 2003).

Hyla columbiana Group: This group was first proposed by Duellman and Trueb (1983) for three species: *H. carnifex*, *H. columbiana*, and *H. praestans*. Kaplan (1991, 1999) found no evidence of monophyly for the group. Kaplan (1997) resurrected *H. bogerti* from the synonymy of *H. carnifex*, adding a fourth species to the group. Kaplan (1999) suggested that ‘‘the presence of two close, triangular lateral spaces between the cricoid and arytenoids at the posterior part of the larynx’’ is a synapomorphy of the *H. columbiana* group excluding *H. praestans*, which he considered to be closely related to the *H. garagoensis* group. The group therefore is composed of *H. bogerti*, *H. carnifex*, and *H. columbiana*. In the present analysis, we include *H. carnifex*.

Hyla decipiens Group: While describing the tadpoles of *H. oliveirai* and *H. decipiens*, Pugliese et al. (2000) noticed that they have marginal papillae (unlike other known larvae of the *H. microcephala* group), and they pointed out that they may not be members of the *H. microcephala* group as considered by Bastos and Pombal (1996). Pugliese et al. (2000) noticed similarities in tadpole morphology with *H. berthalutzae*, with which

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[13] The only character state that led Kizirian et al. (2003) to consider *Hyla tapichalaca* similar to the *H. pulchella* group is the presence of an enlarged, pointed, recurved prepollex.

these two species also share oviposition on leaves outside the water. Pugliese et al. (2000) also associated *H. haddadi* with these three species based on external similarity.

Carvalho e Silva et al. (2003) suggested the recognition of the *Hyla decipiens* group for these species. The group was defined by larval features that include one row of marginal papillae, an ovoid body in lateral view, eyes in the anterior third of the body, dorsal fin arising at the end of the body, tail with transverse dark stripes on a light background, and pointed tip without a flagellum. It is unclear which of these character states could be considered to be possible synapomorphies. Perhaps one apparent synapomorphy of the group, not mentioned by the authors, could be the oviposition on leaves outside the water. The group is composed of *H. berthalutzae*, *H. decipiens*, *H. haddadi*, and *H. oliveirai*. In our analysis, we include *H. berthalutzae*.

Hyla garagoensis Group: This species group was first recognized by Kaplan and Ruiz-Carranza (1997), who diagnosed it by the presence of alternated pigmented and unpigmented longitudinal stripes on the hindlimbs of larvae. The *H. garagoensis* group is currently composed of three species, *H. garagoensis*, *H. padreluna*, and *H. virolinensis*. Unfortunately, no species of this group was available for our analysis.

Hyla labialis Group: This group was first recognized by Cochran and Goin (1970) for *H. labialis* (including what is now *H. platydactyla*, a species of the *H. bogotensis* group). They characterized the group by the vomerine teeth being in two rounded patches and by the presence of a well-developed axillary membrane (referred to as a patagium) that is bright blue in life. Duellman (1989) presented a more extensive definition of the group, noting that the axillary membrane was absent, a point with which we agree. A similar definition was presented by Duellman et al. (1997). No synapomorphies were suggested for this species group. The group currently comprises three species, *H. labialis*, *H. meridensis*, and *H. pelidna*. In this study we include *H. labialis*.

Hyla leucophyllata Group: This group was defined and later partly reviewed by Duellman (1970, 1974). From Duellman's (1970) extensive definition, the only possible synapomorphy seems to be the presence of two glandular patches in the pectoral region (this character state, however, was ignored in every subsequent paper dealing with phylogenetic relationships of 30-chromosome *Hyla*). In the phylogenetic analysis presented by Duellman and Trueb (1983), the only synapomorphy they proposed for the group was violin larval body shape. This character state seems problematic in that it is present in larvae of some species associated with the *H. microcephala* and *H. rubicundula* groups (see Lavilla, 1990; Pugliese et al., 2001), and therefore the level of inclusiveness of the clade that is supported by this transformation is unclear. From the perspective of adult morphology, we suggest that glandular patches in the pectoral region is a synapomorphy of the *H. leucophyllata* group; we observed it clearly on specimens of both sexes in all species of the group. Another character state that is either a likely synapomorphy of the *H. leucophyllata* group or of a more inclusive clade is the oviposition on leaves hanging over water (this oviposition mode occurs also in other 30-chromosome species; see comments in the *H. microcephala* and *H. parviceps* groups).

The *Hyla leucophyllata* group is composed of seven species: *H. bifurca*, *H. ebraccata*, *H. elegans*, *H. leucophyllata*, *H. triangulum*, *H. rossalleni*, and *H. sarayacuensis*. In our analysis, we include *H. ebraccata*, *H. sarayacuensis*, and *H. triangulum*.

Hyla marmorata Group: This group was recognized by Cochran (1955) for *H. marmorata*, *H. microps*, and *H. giesleri* based on the presence of an axillary membrane, warty skin around the margin of the lower lip, short snout, crenulated margin of limbs, short hindlimbs, developed finger and toe webbing, dorsal marbled pattern, and orange coloration in thighs and webbings. Bokermann (1964b) further diagnosed the group by its possession of a very large vocal sac. Several of these character states are possible synapomorphies for the group (such as the warty skin around the margin of the lower lip, the crenulated margin of limbs, the dorsal marbled pattern). Duellman and Trueb (1983) suggested that this group could be diagnosed by the presence of a row of small marginal papillae in the larval oral disc.

Bokermann (1964b), like Cochran (1955), included in the *Hyla marmorata* group other species as well: *H. parviceps*, *H. microps*, *H. schubarti*, and *H. moraviensis* (now considered a synonym of *H. lancasteri*; see Duellman, 1966). Subsequent authors transferred these species to other groups. This group is now composed of eight species: *H. acreana*, *H. dutrai*, *H. marmorata*, *H. melanargyrea*, *H. nahdereri*, *H. novaisi*, *H. senicula*, and *H. soaresi*. In our analysis we include *H. marmorata* and *H. senicula*.

Hyla microcephala Group: This group was defined by Duellman and Fouquette (1968) and Duellman (1970). Despite their extensive characterization, the only character state mentioned by these authors that subsequently has been considered a possible synapomorphy of this group is the lack of marginal papillae in the oral disc. Later, Duellman and Trueb (1983) added the depressed body shape of the larvae, another likely synapomorphy.

While the study of Duellman and Fouquette (1968) was focused on Middle American species, Duellman (1970) referred a number of South American species to the *Hyla microcephala* group. Overall, he included in the group *H. elongata* (a junior synonym of *H. rubicundula*; see Napoli and Caramaschi, 1999), *H. microcephala*, *H. minuta*, *H. nana*, *H. phlebodes*, *H. robertmertensi*, *H. sartori*, and *H. werneri*. Duellman (1972a) also included *H. mathiassoni* and *H. rhodopepla* in the group, and he excluded *H. minuta*. Cochran and Goin (1970) also had excluded *H. minuta* by placing it in their *H. minuta* group. Duellman (1973b) included *H. gryllata*, and Langone and Basso (1987) added *H. minuscula*, *H. sanborni*, and *H. walfordi*.

Cruz and Dias (1991) placed *Hyla bipunctata* in the group on the basis of larval characters.[14] Márquez et al. (1993) included *H. leali* in the *H. microcephala* group, without mentioning that it was included by Duellman (1982) in the *H. minima* group. Furthermore, Márquez et al. (1993) noticed that *H. leali* and *H. rhodopepla* share vocalizations with short, pulsatile notes with extremely low dominant frequencies. Because of these similarities in vocalizations of *H. leali* with a species of the *H. microcephala* group, in the absence of other evidence we prefer to keep *H. leali* in this group.

Bastos and Pombal (1996) suggested that *Hyla branneri*, *H. decipiens*, *H. haddadi*, and *H. oliveirai* were closely related species that could be tentatively associated with the *H. microcephala* group based on overall similarity of adult morphology, but this was questioned by Pugliese et al. (2000) and Carvalho e Silva et al. (2003), who excluded these species from the group (see comments for the *H. decipiens* group). Pombal and Bastos (1998) also added *H. berthalutzae*, *H. cruzi*, and *H. meridiana*. Cruz et al. (2000) added *H. pseudomeridiana*. Köhler and Lötters (2001a) tentatively included *H. joannae*, based on its similarities in vocalization and adult morphology with *H. leali* (but see comments regarding *H. leali* above). Carvalho e Silva et al. (2003) added *H. studerae* and excluded *H. berthalutzae* (see comments for the *H. decipiens* group).

Of the 20 species currently included in the *Hyla microcephala* group, tadpoles are only known for 9 species: *H. bipunctata*, *H. meridiana*, *H. microcephala*, *H. nana*, *H. phlebodes*, *H. pseudomeridiana*, *H. rhodopepla*, *H. sanborni*, and *H. studerae* (Bokermann, 1963, Duellman, 1970, 1972a, Lavilla, 1990, Cruz and Dias, 1991, Cruz et al., 2000, Pugliese et al., 2000, Carvalho e Silva et al., 2003). All of these species have the two apparent synapomorphies of the *H. microcephala* group (see comments for the *H. rubicundula* group).

The 20 species currently included in the *Hyla microcephala* group are *H. bipunctata*, *H. branneri*, *H. cruzi*, *H. gryllata*, *H. joannae*, *H. leali*, *H. mathiassoni*, *H. meridiana*, *H. microcephala*, *H. minuscula*, *H. nana*, *H. phlebodes*, *H. pseudomeridiana*, *H. rhodopepla*, *H. robertmertensi*, *H. sanborni*, *H. sartori*, *H. studerae*, *H. walfordi*, and *H. werneri*. In this analysis we include *H. bipunctata*, *H. microcephala*, *H. nana*, *H. rhodopepla*, *H. sanborni*, and *H. walfordi*.

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[14] Duellman (2001) stated that the relationships of *Hyla bipunctata* were uncertain. Presumably he was not aware of the description of its tadpole by Cruz and Dias (1991).

Hyla minima Group: Duellman (1982) tentatively grouped together five species from the Upper and Middle Amazon Basin and eastern Andes for which data on larval morphology, vocalizations, and osteology were mostly absent. He based the grouping of these species on small body size and distribution. The species he included were *H. aperomea*, *H. leali*, *H. minima*, *H. riveroi*, and *H. rossalleni*. The group as such was not named until Duellman *in* Frost (1985) referred to it as the *H. minima* group. Vigle and Goberdhan-Vigle (1990) added *H. miyatai* to this group; Márquez et al. (1993) implicitly transferred *H. leali* to the *H. microcephala* group (see comments for the *H. microcephala* group above); De la Riva and Duellman (1997) redescribed *H. rossalleni* and placed it in the *H. leucophyllata* group.

Small size is a difficult criterion to apply for the *Hyla minima* group, considering that its constituent species are not smaller than several species of the *H. microcephala* group. Duellman (2001) suggested that the *H. minima* group should be associated with the *H. parviceps* group. Unfortunately, this does not improve the systematics of these frogs, because no synapomorphies are known for either of these two groups (see the *H. parviceps* group for more comments). In the present analysis, we could include only *H. miyatai*.

Hyla minuta Group: This group was first defined by Cochran (1955); most of the species then included subsequently were transferred by several authors to the *H. leucophyllata*, *H. microcephala*, or *H. rubicundula* groups. The character state Cochran (1955) used to distinguish the *H. minuta* group was the immaculate anterior and posterior surfaces of the thigh, a character state that is shared by several 30-chromosome *Hyla*.

Martins and Cardoso (1987) described *Hyla xapuriensis* and referred it to the *H. minuta* group without providing any definition. Köhler and Lötters (2001b) described *H. delarivai* and tentatively suggested that it is close to *H. minuta*. Duellman and Trueb (1983) stated that the *H. minuta* group contained two species, but they did not state which one was the second species, and they provided no evidence for its monophyly. The group is currently composed of *H. minuta* and *H. xapuriensis*, and, following Köhler and Lötters (2001b), we tentatively include *H. delarivai*. For the purpose of our analysis, only *H. minuta* was available.

Hyla parviceps Group: This group was first defined by Duellman (1970), and by Duellman and Crump (1974), who also reviewed it. According to Duellman and Crump (1974), the species in the *H. parviceps* group differ from other 30-chromosome *Hyla* species by having: (1) a pronounced sexual dimorphism in size; (2) shorter snout; (3) tympanic ring indistinct or absent; (5) small (or reduced) axillary membrane; (9) sexual dimorphism in width of dorsolateral stripes; (10) suborbital bars; (11) thighs marked with spots; (13) iris pale gray with red ring around pupil; (15) more perichondral ossification in the tectum nasi and solum nasi; and (17) squamosal articulating with prootics. Duellman and Crump (1974) characterized the tadpoles as having ovoid bodies and xiphicercal tails with moderately deep fins not extending into body; anteroventral oral disc, large marginal papillae, robust serrated jaw sheaths, and no more than one row of labial teeth. It is unclear which of these character states could be synapomorphies of the group. Duellman and Trueb (1983) did not provide any synapomorphy for the group.

Duellman and Crump (1974) included in the *Hyla parviceps* group *H. bokermanni*, *H. brevifrons*, *H. luteoocellata*, *H. microps*, *H. parviceps*, and *H. subocularis*. Heyer (1977) added *H. pauiniensis*. Heyer (1980) resurrected *H. giesleri* from the synonymy of *H. microps*. Weygoldt and Peixoto (1987) tentatively included *H. ruschii* in the group. Martins and Cardoso (1987) added *H. timbeba*. Duellman and Trueb (1989) added *H. allenorum* and *H. koechlini*. Duellman (2001) added *H. grandisonae* and *H. schubarti*. Lescure and Marty (2000) referred *H. luteoocellata* to a separate group, the *H. luteoocellata* group, which they characterized by the presence of a cream-colored suborbital stripe. Because they did not discuss differences with the *H. parviceps* group, we still consider *H. luteoocellata* a member of the *H. parviceps* group. However, the species they described, *H. gaucheri*, does not seem to have this stripe.

The *Hyla parviceps* group is currently

composed of 15 species: *H. allenorum*, *H. bokermanni*, *H. brevifrons*, *H. gaucheri*, *H. giesleri*, *H. grandisonae*, *H. koechlini*, *H. luteoocellata*, *H. microps*, *H. parviceps*, *H. pauiniensis*, *H. ruschii*, *H. schubarti*, *H. subocularis*, and *H. timbeba*. In our analysis we include *H. brevifrons*, *H. giesleri*, and *H. parviceps*.

Hyla rubicundula Group: This group was recently defined by Napoli and Caramaschi (1998) and was diagnosed by small body size, patternless thighs, and green dorsum in life that changes to pinkish or violet when preserved. Bogart (1970), Rabello (1970) and Gruber (2002) reported a 30-chromosome karyotype in *H. rubicundula* and *H. elianeae*. Historically, species of this group were associated with species now placed in the *H. microcephala* group, such as *H. nana* and *H. sanborni* (Lutz, 1973). The group is currently composed of *H. anataliasiasi*, *H. araguaya*, *H. cachimbo*, *H. cerradensis*, *H. elianeae*, *H. jimi*, *H. rhea*, *H. rubicundula*, and *H. tritaeniata*. In our analysis, we include *H. rubicundula*.

Species Known or Presumed to Have 30 Chromosomes Not Assigned to Any Group: *Hyla anceps*: Lutz (1948, 1973) associated *H. anceps* with *H. leucophyllata* based on it having an axillary membrane, tadpoles with xiphicercal tail, and vivid flash colors. Cochran (1955) considered this species to have no known close relatives and placed it on its own species group. Bogart (1973) reported a 30-chromosome karyotype for this species, and he tentatively associated it with *H. microcephala*, *H. bipunctata*, *H. elongata* (a junior synonym of *H. rubicundula*), and *H. rhodopepla* for sharing a single pair of telocentric chromosomes. Regardless of having been reported to have 30 chromosomes, *Hyla anceps* has been ignored in all subsequent literature dealing with phylogenetic relations of 30-chromosome species of *Hyla*. Wogel et al. (2000) redescribed the tadpole of *H. anceps* and stated that its morphology supported the idea of this species belonging to its own species group, without giving further details. We include this species in the analysis.

Hyla amicorum: This species was considered to be similar to *H. battersbyi* and *H. minuta* (Mijares-Urrutia, 1998). On this basis we consider it a 30-chromosome species. We could not include this species in the analysis.

Hyla battersbyi: Since its original description (Rivero, 1961) this species has been scarcely mentioned in the literature. We consider it tentatively as a 30-chromosome species based on the association made by Mijares-Urrutia (1998) of this species with *H. minuta* based on overall similarity. We could not include this species in the analysis.

Hyla haraldschultzi: Bokermann (1962) stated that the relationships of this species were uncertain. Lutz (1973), while treating the ‘‘small to minute forms’’, where she included most of the 30-chromosome *Hyla*, considered *H. haraldschultzi* to be insufficiently known. We could not include this species in the analysis.

Hyla limai: In the original description, Bokermann (1962) associated this species with *H. minuta* and *H. werneri*. Apart from a brief comment by Lutz (1973), it has not been referred to again in the literature. Haddad (unpubl. data), based on morphological variation in populations of *H. minuta*, finds that *H. limai* could be a junior synonym of this species. We could not include this nominal species in the analysis.

Hyla praestans: Duellman and Trueb (1983) originally placed this species in the *H. columbiana* group. Kaplan (1999), based on the presence of a small medial depression in the internal surface of each arytenoid, suggested that *H. praestans* was related to the *H. garagoensis* group and possibly its sister taxon. We could not secure samples for the analysis.

Hyla stingi: This species, externally similar to *H. minuta*, has been suggested to be the sister group of a clade composed of the *H. minuta*, *H. marmorata*, *H. parviceps*, *H. leucophyllata*, and *H. microcephala* groups (this being supported by the reduction in the labial tooth row formula from 1/2 to 0/1; Kaplan, 1994). The apparent synapomorphy uniting *H. stingi* with this clade is the anterior position of the oral disc. This species could not be included in the analysis.

Hyla tintinnabulum: This species was associated with *H. branneri* and *H. rubicundula* by Lutz (1973). This fact and our study of one of the syntypes (NHMG 473; adult male) suggest that it is a 30-chromosome

Hyla. We could not include this species in the analysis.

Hyla yaracuyana: This species was associated with the 30-chromosome *Hyla* by Mijares-Urrutia and Rivero (2000), but it was not included in any species group. We could not include this species in the analysis.

Middle American/Holarctic Clade

The monophyly of most Middle American and Holarctic Hylinae was suggested by Duellman (1970, 2001) based on biogeographic grounds. This clade would include most Middle American and Holarctic species groups of *Hyla* plus the genera *Acris*, *Anotheca*, *Duellmanohyla*, *Plectrohyla*, *Pseudacris*, *Pternohyla*, *Ptychohyla*, *Smilisca*, and *Triprion*.

Acris: This very distinctive taxon was reviewed by Duellman (1970) and was included in several studies of Holarctic hylids (Gaudin, 1974; Hedges, 1986; Cocroft, 1994; da Silva, 1997). In the strict consensus of the analysis by Cocroft (1994), the position of *Acris* was unresolved with respect of the other Holarctic hylids. In the reanalysis done by da Silva (1997), it is sister to a clade composed of the species of the *Hyla cinerea* and *H. versicolor* groups. The two species *A. crepitans* and *A. gryllus* are included in our analysis.

Anotheca: This monotypic genus was reviewed by Duellman (1970, 2001). Autapomorphies of this taxon include the unique skull ornamentation composed of sharp, dorsally pointed spines in the margins of frontoparietal, maxilla, nasal (including canthal ridge), and squamosal, and character states that result in its reproductive mode, including the female feeding tadpoles with trophic eggs (see Jungfer, 1996). We include the single species *Anotheca spinosa* in this analysis.

Duellmanohyla: This genus was reviewed by Duellman (2001). *Duellmanohyla* was proposed by Campbell and Smith (1992), based on four suggested synapomorphies involving larval morphology: a greatly enlarged, pendant oral disc (referred to as funnel-shaped mouth by Duellman, 2001); long and pointed serrations on the jaw sheaths; upper jaw sheath lacking lateral processes; and greatly shortened tooth rows. Duellman (2001) added the bright red iris and the labial stripe expanded below the orbit. *Duellmanohyla* contains the following eight species: *D. chamulae, D. ignicolor, D. lythrodes, D. rufioculis, D. salvavida, D. schmidtorum, D. soralia*, and *D. uranochroa*. In our analysis, we include *D. rufioculis* and *D. soralia*.

Hyla arborea Group: All of the species of *Hyla* of Europe, North Africa, and Asia have long been recognized as composing a single species group (Stejneger, 1907; Pope, 1931). Probably because species of this group have generally been discussed in isolation of other hylids, we are not aware of any author having provided a diagnosis of this group that could differentiate them, at least phenotypically, from the Nearctic species placed in the *H. cinerea* and *H. eximia* groups. No synapomorphy has ever been suggested; the monophyly of the group has apparently been assumed based on geography and the external similarity of most species (9 of the 16 currently recognized species have been considered at some point of it taxonomic history to be subspecies or varieties of *H. arborea*).

Various authors considered the *Hyla arborea* group to be closely related with some North American species. Based on similarities in advertisement calls, Kuramoto (1980) suggested that the *H. arborea* group is closely related to the *H. eximia* group of temperate Mexico and southwestern United States.

The assumed monophyly of the *Hyla arborea* group was challenged by Anderson (1991) on karyotypic grounds, and this was supported by Borkin (1999). These authors suggested the presence of at least two lineages resulting from two independent invasions to Eurasia. According to Anderson (1991), at least *H. japonica* and *H. suweonensis* (she did not include other eastern Asian species) share the presence of a NOR in chromosome 6 with the representatives she studied of the *H. eximia* group (*H. arenicolor*, *H. euphorbiacea*, *H. eximia*), some of the *H. versicolor* group (*H. avivoca*, *H. chrysoscelis*, *H. versicolor*; *H. femoralis*), and with *H. andersonii*. *Hyla arborea*, *H. chinensis*, *H. meridionalis*, and *H. savignyi* share with most Nearctic species of *Hyla*, as well as several of the outgroups that Anderson (1991) included, the NOR located in chromosomes 10/11 (she considered the chromosome pairs to be homologous in these species, with the shift in NOR position presumably corresponding to modulation of heterochromatin material and not to a translocation event; Anderson 1991: 323).

The *Hyla arborea* group as currently understood is composed of the following 16 species: *H. annectans*, *H. arborea*, *H. chinensis*, *H. hallowellii*, *H. immaculata*, *H. intermedia*, *H. japonica*, *H. meridionalis*, *H. sanchiangensis*, *H. sarda*, *H. savignyi*, *H. simplex*, *H. suweonensis*, *H. tsinlingensis*, *H. ussuriensis*, and *H. zhaopingensis*. In this analysis we include *H. arborea*, *H. annectans*, *H. japonica*, and *H. savignyi*.

Hyla bistincta Group: This group was reviewed by Duellman (2001). The lack of evidence supporting the monophyly of the *H. bistincta* group, together with the possibility that *Plectrohyla* is nested within it, has been repeatedly noted (Duellman and Campbell: 1992; Toal, 1994; Wilson et al., 1994a; Mendelson and Toal, 1995; Ustach et al., 2000; Canseco-Márquez et al., 2002).

Duellman (2001) presented a cladistic analysis of the *Hyla bistincta* group that included the 17 species known at that time, using a vector of character states of *Plectrohyla* and *H. miotympanum* as the root. He reported that the analysis resulted in 89 most parsimonious trees, from which he chose one that is presented in his figure 400 (Duellman 2001: 952). In this tree, the *H. bistincta* group is monophyletic, being supported by a single transformation, the loss of vocal slits. A reanalysis of his data set[15] indicates that *Plectrohyla* is nested within the *H. bistincta* group on several of the most parsimonious trees, and that the strict consensus tree is almost entirely collapsed. Therefore, Duellman's analysis provides no evidence for the monophyly of the *H. bistincta* group.

The *Hyla bistincta* group currently comprises the following 18 described species: *H. ameibothalame*, *H. bistincta*, *H*, *calthula*, *H. calvicollina*, *H. celata*, *H. cembra*, *H. charadricola*, *H. chryses*, *H. crassa*, *H. cyanomma*, *H. labedactyla*, *H. mykter*, *H. pachyderma*, *H. pentheter*, *H. psarosema*, *H. robertsorum*, *H. sabrina*, and *H. siopela*. In this analysis we include *H. bistincta* and *H. calthula*.

Hyla bromeliacia Group: The taxonomy, composition, and history of this group were reviewed by Duellman (1970, 2001). Possible synapomorphies suggested by Duellman (2001) are those modifications of the phytotelmic larvae, mostly the depressed body and the elongated tail. The other characters he used to separate this group from the bromeliad-dwelling species of the *H. pictipes* group are likely plesiomorphic, such as the lack of massive temporal musculature (present only in *H. zeteki* and *H. picadoi*), the presence of more than one tooth row (only one in *H. picadoi* and *H. zeteki*), and the oral disc not entirely bordered by a single row of papillae (as in *H. zeteki* and *H. picadoi*). The group comprises two species, *H. bromeliacia* and *H. dendroscarta*. In this study we include only *H. bromeliacia*.

Hyla cinerea Group: This group was first recognized by Blair (1958) based on advertisement call structure. For a review of its history see Anderson (1991). The group is currently composed of four species, *H. cinerea*, *H. femoralis*, *H. gratiosa*, and *H. squirella*, and the group is monophyletic in the analyses of Hedges (1986), Cocroft (1994), and da Silva (1998), being supported by allozyme data (taken in the last two studies from Hedges, 1986). We included all four species of the group in the present analysis.

Hyla eximia Group: The taxonomy, composition, and history of this group were thoroughly reviewed by Duellman (1970, 2001). Duellman (2001) presented an extensive definition; however, it is unclear which of the character states could be taken as evidence of monophyly of the group. Hedges (1986) and Cocroft (1994) included two species, *H. arenicolor* and *H. eximia*, in their analyses. While in Hedges's (1986) results these two species form a monophyletic group, on the strict consensus of Cocroft's (1994) most parsimonious trees, both species are not monophyletic and form a basal polytomy with several other species of *Hyla*. da Silva's (1997) reanalysis of Cocroft's (1994) data set

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[15] This reanalysis, like that attempted by Canseco-Márquez et al. (2002), could not reproduce the results presented by Duellman (2001). The present discussion is based on the results that were obtained using the additivities specified by Duellman. It resulted in 45 most parsimonious trees of 56 steps, with CI = 0.57 and RI = 0.52.

yielded on its strict consensus *H. arenicolor* and *H. eximia* as a monophyletic group, which appears to be supported by the allozyme data of Hedges (1986). Besides the seven species included by Duellman (2001) in the group, Eliosa León (2002) resurrected *H. arboricola* from the synonymy of *H. eximia*, adding an eigth species to the group. See the *H. arborea* group for additional comments. The *H. eximia* group is currently composed of eight species: *Hyla arboricola*, *H. arenicolor*, *H. bocourti*, *H. euphorbiacea*, *H. eximia*, *H. plicata*, *H. walkeri*, and *H. wrightorum*. In this analysis we include *H. arenicolor*, *H. euphorbiacea*, *H. eximia*, and *H. walkeri*.

Hyla godmani Group: The taxonomy, composition, and history of this group were reviewed by Duellman (1970, 2001). Duellman (2001) included in this group the only lowland pond-breeders from Middle America that do not have 30 chromosomes. He suggested as tentative evidence of monophyly the weakly ossified skulls and the presence of an axillary membrane. This group currently comprises four species: *H. godmani*, *H. loquax*, *H. picta*, and *H. smithii*. We include *H. picta* and *H. smithii* in our analysis.

Hyla miotympanum Group: The taxonomy, composition, and history of this group were thoroughly reviewed by Duellman (1970, 2001). Duellman (2001), using a hypothetical outgroup, suggested eight synapomorphies for the group[16]: abbreviated axillary membrane; indistinct fold on wrist; fingers less than one-half webbed; tarsal fold present through the entire length of the tarsus; cloacal opening directed posteroventrally; nuptial excrescences present; medial ramus of pterygoid short, not in contact with prootic; and larval oral disc in ventral position. It seems unlikely that any of these character transformations will hold as synapomorphies of the group in the context of a more inclusive analysis. The group currently contains 11 species: *H. abdivita*, *H. arborescandens*, *H. bivocata*, *H. catracha*, *H. cyclada*, *H. hazelae*, *H. juanitae*, *H. melanomma*, *H. miotympanum*, *H. perkinsi*, and *H. pinorum*. Our analysis includes *H. arborescandens*, *H. cyclada*, *H. melanomma*, *H. miotympanum*, and *H. perkinsi*.

Hyla mixomaculata Group: Duellman (1970) reviewed the group and listed several character states that define it. Some of these are probably synapomorphies, such as (known) larvae with an enlarged oral disc with 7/10 or 11 labial tooth rows (the largest number of posterior tooth rows known for a Middle American hylid group); the taxonomic distribution of other character states indicate that they are likely synapomorphies of a more inclusive clade, such as the large frontoparietal fontanelle and the absence (or reduction, unclear on fig. 211 of Duellman, 1970) of the quadratojugal. The group is currently composed of four species, *H. mixe*, *H. mixomaculata*, *H. nubicola*, and *H. pellita*. Only *H. mixe* was available for this analysis.

Hyla pictipes Group: The taxonomy, composition, and history of this group were reviewed by Duellman (1970, 2001). Duellman (2001) provided a phylogenetic analysis[17] of the montane species of *Hyla* of lower Central America, where he included the *H. pseudopuma* and *H. pictipes* groups.

Duellman (2001) suggested six synapomorphies for the group: slender nasals in adults; tadpoles with stream-dwelling habits; oral disc ventral; complete marginal papillae; only one row of marginal papillae; and presence of submarginal papillae. Note that with the possible exception of slender nasals in adults, the other three character states as defined by Duellman (2001) are also present in several other groups of Middle American stream-breeding frogs (i.e., the *Hyla bistincta* group, *H. mixomaculata* group, *H. sumichrasti* group, and *Plectrohyla*).

The *Hyla pictipes* group includes 11 species: *H. calypsa*, *H. debilis*, *H. insolita*, *H. lancasteri*, *H. picadoi*, *H. pictipes*, *H. rivu-*

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[16] Note that in ''the preferred'' cladogram, there is a character 27 as one of the synapomorpies of the *Hyla miotympanum* group; presumably this is an error for 17, since the data set has 22 characters, and character 17 is inclusive of the ingroup.

[17] We could not reproduce the results of Duellman (2001) using his data matrix under the same additivities. This is most probably due to an editorial problem with the data matrix; the scores for *Hyla debilis* are all 0. Evidently the data set as printed is different from that used to choose the trees shown, where *H. debilis* is the sister species of *H. rivularis*. Because of this situation, we discuss the synapomorphies shown in the book, not those from our reanalysis.

laris, *H. thorectes*, *H. tica*, *H. xanthosticta*, and *H. zeteki*. Considering the uncertainties regarding the monophyly of this group, an appropriate taxon sampling should ideally include representatives of the four former species groups currently combined into the *H. pictipes* group. Unfortunately, the only representatives available are *H. rivularis* and *Hyla* sp. 5 (aff. *H. thorectes*), an undescribed species from Mexico similar to *H. thorectes*.

Hyla pseudopuma Group: The taxonomy, composition, and history of this group were reviewed by Duellman (1970, 2001), who could not provide a synapomorphy for it. In his phylogenetic analysis of the *H. pseudopuma* and *H. pictipes* groups, the *H. pseudopuma* group appears as a basal unresolved grade, although this is a consequence of constraining the nonmonophyly of the *H. pseudopuma* group by using *H. angustilineata* as the root. The *H. pseudopuma* group includes four species: *H. angustilineata*, *H. graceae*, *H. infucata*, and *H. pseudopuma*. In this study we include only *H. pseudopuma*.

Hyla sumichrasti Group: The taxonomy, composition, and history of this group were reviewed by Duellman (1970, 2001). Possible synapomorphies for the group (Duellman, 2001) are the presence of massive nasals, and tadpoles with immense oral discs, with 3/6 to 3/7 labial tooth rows instead of the 2/3 to 2/6 of the *H. miotympanum* group. The group currently includes four species: *H. chimalapa*, *H. smaragdina*, *H. sumichrasti*, and *H. xera*. In this study we include *H. chimalapa* and *H. xera*.

Hyla taeniopus Group: This group was reviewed by Duellman (1970, 2001), who defined it as having well-ossified quadratojugals in contact with maxillaries, and tadpoles that have ventral mouths with two or three anterior rows of teeth and three or four posterior rows. While the presence of enlarged testes is a possible synapomorphy of a subgroup composed of *H. altipotens*, *H. trux*, and *H. taeniopus*, there is no evidence for the monophyly of the entire group (Mendelson and Campbell, 1999; Duellman, 2001). Five species are currently included in this group: *H. altipotens*, *H. chaneque*, *H. nephila*, *H. taeniopus*, and *H. trux*. In this analysis, we include *H. nephila* and *H. taeniopus*.

Hyla tuberculosa Group: Affinities among species of fringe-limbed treefrogs were first suggested by Dunn (1943) and by Taylor (1948, 1952) based on their overall appearance. Firschein and Smith (1956) suggested that the presence of a ''prepollex'' (presumably referring to an enlarged prepollex) and similarity of external habitus, size, skin texture, and fringed limbs were indicative of a common origin. Duellman (1970, 2001) presented a formal definition of the group, asserting that these frogs be placed in the same group based on their large size, presence of dermal fringes on the limbs (although absent in *H. dendrophasma*), extensive webbing on hand and feet, and modified prepollices. (Importantly, note that apparently the modified prepollices involve three different morphologies: modification into a projecting spine *or* a spadelike blade *or* a clump of spines; Duellman, 1970.) Duellman (2001) added that there is no compelling evidence that the group is monophyletic, an opinion that we share. Furthermore, he tentatively suggested that this group could be related with the Gladiator Frogs rather than with the Middle American/ Holarctic clade. The *Hyla tuberculosa* group has been referred to as the *H. miliaria* group (Campbell et al., 2000; Duellman, 1970, 2001; Savage and Heyer, ''1968'' [1969]) and is composed of *H. dendrophasma*, *H. echinata*, *H. fimbrimembra*, *H. miliaria*, *H. minera*, *H. phantasmagoria*, *H. salvaje*, *H. thysanota*, *H. tuberculosa*, and *H. valancifer*. In this analysis, we include *H. dendrophasma* and *H. miliaria*.

Hyla versicolor Group: This group was first recognized by Blair (1958) on the basis of advertisement call structure. See Duellman (1970) and Anderson (1991) for a brief taxonomic history. Both Blair (1958) and Duellman (1970) included *H. arenicolor* in the group until Hedges (1986), Cocroft (1994), and da Silva (1997) showed on successive analyses that this species was more closely related to *H. eximia* (see the *H. eximia* group for further comments), always on the basis of the allozyme data collected by Hedges (1986).

Although placed originally in the *Hyla cinerea* group by Blair (1958), *H. andersonii* was transferred to the *H. versicolor* group by Wiley (1982), with this being supported by Hedges (1986), Cocroft (1994), and da Silva

(1997) on the basis of the allozyme data collected by Hedges (1986). Similarly, *H. femoralis* was considered a member of the *H. versicolor* group until Hedges (1986) transferred it to the *H. cinerea* group, an assignment also corroborated by da Silva (1997). The group currently comprises four species: *H. andersonii*, *Hyla avivoca*, *H. chrysoscelis*, and *H. versicolor*. In this study we include all but *H. chrysoscelis*.

Pseudacris: The phylogenetic relationships of this genus were reviewed by Hedges (1986), Cocroft (1994), da Silva (1997), and Moriarty and Cannatella (2004). Hedges (1986) presented an electrophoretic analysis of 33 presumed genetic loci, where all species of *Pseudacris* were monophyletic, and which provided evidence to include the former *Hyla cadaverina*, *H. crucifer*, and *H. regilla* in *Pseudacris*. Cocroft (1994) performed a phylogenetic analysis of *Pseudacris*, including several Holarctic hylids as outgroups, with characters from various sources (osteology, vocalizations, karyotypes, allozymes, sperm morphology) and previous analyses (Hedges, 1986). The strict consensus of his most parsimonious trees shows *P. crucifer* as the sister taxon of the remaining species of *Pseudacris*; the two classically recognized species groups (the *P. ornata* and the *P. nigrita* groups) each being monophyletic; and *P. ocularis* being the sister taxon of the *P. nigrita* group. However, Hedges (1986) found no evidence supporting the inclusion of *P. cadaverina* and *P. regilla* in *Pseudacris*, and for this reason he treated them as *Hyla*. Furthermore, the relationships of the remaining, monophyletic species of *Pseudacris* with the other Holarctic hyline are unresolved. In the modified reanalysis performed by da Silva (1997), the strict consensus shows that the clade composed of *H. regilla* and *H. cadaverina* is sister to *Pseudacris* and is supported apparently by allozyme data. Because of this, these two species are considered again to be within *Pseudacris* (da Silva, 1997).

Moriarty and Cannatella (2004) presented a phylogenetic analysis of the mitochondrial ribosomal genes 12S, tRNA valine, and 16S that included all species of *Pseudacris* and three outgroups, *Hyla andersonii*, *H. chrysoscelis*, and *H. eximia*. The analysis identified four major clades: (1) the *P. regilla* clade (*P. cadaverina* and *P. regilla*; Moriarty and Cannatella referred to it as the West Coast clade); (2) the *Pseudacris ornata* clade (*P. ornata*, *P. streckeri*, and *P. illinoiensis*; Moriarty and Cannatella called it fat frogs clade); (3) the *P. crucifer* clade (*P. crucifer* and *P. ocularis*); and (4) the *P. nigrita* clade (including *P. brimleyi*, *P. brachyphona*, *P. clarkii*, *P. feriarum*, *P. maculata*, and *P. triseriata*; Moriarty and Cannatella called it Trilling Frogs clade). In our study we include *Pseudacris cadaverina*, *P. crucifer*, *P. ocularis*, *P. regilla*, and *P. triseriata*.

Pternohyla: This Mexican casque-headed frog genus was reviewed by Trueb (1969) and Duellman (1970, 2001). In Duellman's (2001) phylogenetic analysis of *Pternohyla*, *Smilisca*, and *Triprion*, the monophyly of *Pternohyla* is supported by four synapomorphies: small discs on fingers; supernumerary tubercles diffuse or absent; large inner metatarsal tubercle[18]; and large marginal papillae in the larval oral disc. Unfortunately, small discs on fingers are a synapomorphy only under an accelerated optimization (ACCTRAN), and therefore they have no evidential value for the clade.

In Duellman's (2001) analysis, *Triprion* plus *Pternohyla* forms a monophyletic group nested within *Smilisca*. The synapomorphies supporting *Triprion* plus *Pternohyla* are[19]: nasals with broad medial contact; median ramus of pterygoid not in contact with prootic; maxilla moderately expanded laterally; cranial-integumentary co-ossification present; webbing between fingers absent; and inner metatarsal tubercle small. *Pternohyla* is composed of two similar species, *P. dentata*, and

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[18] For the character ‘‘inner metatarsal tubercle’’, Duellman (2001) defined four character states: moderate (0), small (1), large (2), and spadelike (3). He stated that he considered this character as additive in the order 0→1→2→3; unless there is an editorial mistake, this seems a rather peculiar and unjustified ordering.

[19] Duellman maps on his preferred tree character states 4.1, 7.2, 8.1, 9.1, 13.1, 16.1, and 19.1. However, an examination of the character list and matrix shows that there is no state 2 defined for character 7, and that character 13 is actually an autapomorphy of *Triprion spatulatus*; it is very likely that 13 is a typographical error for character 14, which according to the data set is a synapomorphy for the group; in the synapomorphy list given above, we assume that these problems were fixed, and so we ignore character state 7.2.

P. fodiens. In this analysis we include *P. fodiens*.

Plectrohyla: This genus was reviewed by Duellman (2001) and discussed by McCranie and Wilson (2002). Its phylogenetic relationships were addressed by Duellman and Campbell (1992), Wilson et al. (1994a), and Duellman (2001). The monophyly of *Plectrohyla* does not appear to be controversial. Duellman and Campbell (1992) listed six synapomorphies: bifurcated alary process of premaxilla; sphenethmoid ossified anteriorly, incorporating the septum nasi and projecting forward to the leading margins of the nasals; frontoparietals abutting broadly anteriorly and posteriorly, exposing a small area of the frontoparietal fontanelle; hypertrophied forearms; and absence of lateral folds in the oral disc. Wilson et al. (1994a) added ‘‘prepollex enlarged, elongated, ossified, flat, terminally blunt.’’ Duellman (2001) interpreted that this definition corresponded to more than one character, and so he divided it into two characters, the derived state of the first one being ‘‘enlarged and ossified prepollex in both sexes’’, and the derived state of the second one being ‘‘enlarged and truncate prepollex.’’ See comments under the *Hyla bistincta* group.

Plectrohyla currently contains 18 species: *P. acanthodes*, *P. avia*, *P. chrysopleura*, *P. dasypus*, *P. exquisitia*, *P. glandulosa*, *P. guatemalensis*, *P. hartwegi*, *P. ixil*, *P. lacertosa*, *P. matudai*, *P. pokomchi*, *P. psiloderma*, *P. pycnochila*, *P. quecchi*, *P. sagorum*, *P. tecunumani*, and *P. teuchestes*. In this analysis we include *P. guatemalensis*, *P. glandulosa*, and *P. matudai*.

Ptychohyla: This group was reviewed by Duellman (2001). Campbell and Smith (1992) suggested three synapomorphies for *Ptychohyla*: the presence of two rows of marginal papillae, an increased number of tooth rows in larvae (from 3/5 to 6/9), and a strongly developed lingual flange of the pars palatina of the premaxilla. Duellman (2001) also suggested as synapomorphies the presence of ventrolateral glands in breeding males, and the coalescence of tubercles to form a distinct ridge on the ventrolateral edge of the forearm. The increase in the number of tooth rows could actually be a synapomorphy not of *Ptychohyla* but for a more inclusive clade containing *Ptychohyla* plus other species of stream-breeding hylids that also have a tooth row formula larger than 2/3. Similarly, ventrolateral glands are present also in some species of *Duellmanohyla* (Campbell and Smith, 1992; Duellman, 2001).

For an unstated reason, Savage (2002a) excluded *Ptychohyla legleri* and *P. salvadorensis* from *Ptychohyla*, placing them back in *Hyla*. These two species were originally in *Hyla* (former *H. salvadorensis* group; see Duellman, 1970) until Campbell and Smith (1992) transferred them to *Ptychohyla*. Because we are not aware of any evidence supporting Savage's action, we consider them to be members of *Ptychohyla*.

Ptychohyla is composed of 12 species: *P. acrochorda*, *P. erythromma*, *P. euthysanota*, *P. hypomykter*, *P. legleri*, *P. leonhardschultzei*, *P. macrotympanum*, *P. panchoi*, *P. salvadorensis*, *P. sanctaecrucis*, *P. spinipollex*, and *P. zophodes*. In this analysis we include *P. euthysanota*, *P. hypomykter*, *P. leonhardschultzei*, *P. spinipollex*, *P. zophodes*, and *Ptychohyla* sp., an undescribed species from Oaxaca, Mexico.

Smilisca: This genus was reviewed by Duellman and Trueb (1966) and Duellman (1970, 2001). Duellman (2001) could advance no evidence for the monophyly of *Smilisca*. He presented a phylogenetic analysis rooted with a hypothetical ancestor, whose strict consensus showed *Pternohyla* plus *Triprion* nested within *Smilisca*, being more closely related to *S. baudinii* and *S. phaeota*. The synapomorphies supporting *Pternohyla* + *Triprion* + ‘‘*Smilisca*’’ are the presence of lateral flanges on the frontoparietals, and the unexposed frontoparietal fontanelle. The species of *Smilisca* have been divided (Duellman and Trueb, 1966) into the *S. sordida* group (*S. puma* and *S. sordida*), the *S. baudinii* group (*S. baudinii*, *S. cyanosticta*, and *S. phaeota*), and *S. sila*, a form considered intermediate between these two groups. In Duellman's (2001) phylogenetic analysis, *S. sila* plus the *S. sordida* group is monophyletic, with its synapomorphy being the short maxillary process of the nasal. *Smilisca* contains six species: *S. baudinii*, *S. cyanosticta*, *S. phaeota*, *S. puma*, *S. sila*, and *S. sordida*. In this analysis we include the three species in the *S. baudinii* group, *S. bau-*

dinii, *S. cyanosticta*, *S. phaeota*, and one species of the *S. sordida* group, *S. puma*.

Triprion: This genus was reviewed by Trueb (1969) and Duellman (1970, 2001). In Duellman's (2001) phylogenetic analysis of *Pternohyla*, *Smilisca*, and *Triprion*, the monophyly of *Triprion* is supported by three synapomorphies[20]: maxilla greatly expanded laterally, prenasal bone present, and presence of parasphenoid odontoids. See comments for *Smilisca* and *Pternohyla*. *Triprion* is composed of two species, *T. petasatus* and *T. spatulatus*. In the analysis we include *T. petasatus*.

Casque-Headed Frogs and Related Genera

Duellman's (2001) suggestion of Middle American/Holarctic frogs being monophyletic clearly separates the Middle American casque-headed frogs (*Triprion*, *Pternohyla*) from the South American and West Indian casque-headed frogs. This is not surprising considering that traditionally the group known as the casque-headed frogs was considered to be nonmonophyletic (Trueb, 1970a, 1970b). However, the position of the South American and West Indian casque-headed frogs remains controversial, and no author has presented evidence indicating whether they form a monophyletic group.

Aparasphenodon: This genus of casque-headed frogs was reviewed and characterized by Trueb (1970a) and Pombal (1993). The presence of a prenasal bone is a likely synapomorphy of *Aparasphenodon* (with a known homoplastic occurrence in *Triprion*, as reported by Trueb, 1970a). This genus currently comprises three species, *A. bokermanni*, *A. brunoi*, and *A. venezolanus*. We include *A. brunoi* in the analysis.

Argenteohyla: This monotypic genus was described and reviewed by Trueb (1970b), who segregated it from *Trachycephalus*, where it had been placed by Klappenbach (1961). Motives for this segregation were the absence in *Argenteohyla* of several character states of *Trachycephalus* as redefined by Trueb (1970a), such as the dermal sphenethmoid, the poorer development of ossification and cranial sculpturing, and vocal sacs that when inflated protrude posteroventrally to the angles of the jaw. Possible autapomorphies of this taxon include the fusion of the zygomatic ramus of the squamosal with the pars facialis of the maxilla. The genus comprises a single species, *A. siemersi*, for which a northern subspecies, *A. s. pederseni*, was described by Williams and Bosso (1994). In this analysis we included a specimen that corresponds to the northern form.

Corythomantis: This monotypic genus was reviewed by Trueb (1970a). Autapomorphies of this genus include the absence of palatines, and nasals that conceal the allary processes of premaxillaries (Trueb, 1970a). We include the single species *Corythomantis greeningi* in this analysis.

Osteocephalus: This genus was diagnosed by Goin (1961) and Trueb (1970a) and studied in detail by Trueb and Duellman (1971). These authors recognized five species: *Osteocephalus verruciger*, *O. taurinus*, *O. buckleyi*, *O. leprieurii*, and *O. pearsoni*. In the last 20 years, several new species were described, adding to a total of 18 currently recognized species (see Jungfer and Hödl, 2002; Lynch, 2002). Trueb and Duellman (1971) employed 20 character states to characterize *Osteocephalus*. Jungfer and Hödl (2002) modified some of these characters to take into account subsequently discovered species. As stated by Ron and Pramuk (1999), referring to the diagnostic states employed earlier by Trueb and Duellman (1971), it is unclear which, if any, of the character states are synapomorphic for the genus. Trueb (1970a) and Trueb and Duellman (1971) suggested, based on the presence of paired lateral vocal sacs in the five species then recognized, that *Osteocephalus* was related to a group composed of *Argenteohyla*, *Trachycephalus*, and *Phrynohyas*.

Martins and Cardoso (1987) described *Ostecephalus subtilis* that, unlike the other species known at that time, is characterized by a single, subgular vocal sac that expands laterally; a similar morphology was described by Smith and Noonan (2001) in *O. exophthalmus*. Jungfer and Schiesari (1995) described *O. oophagus*, a species with a single, median vocal sac, a reproductive mode in-

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[20] On his preferred tree (his fig. 410), one of the character transformations is numbered 18; this is a typographical error for 12, the only other character that supports this clade but not shown in the tree.

volving oviposition in bromeliads, and phytotelmous oophagous larvae. Jungfer et al. (2000), Jungfer and Lehr (2001), and Lynch (2002) described four species, *O. deridens, O. fuscifacies, O. leoniae,* and *O. heyeri,* which also have a single, median vocal sac. According to Lynch (2002), *O. cabrerai* also shares this characteristic. Reproductive modes are unknown for *O. cabrerai, O. exophthalmus*, *O. heyeri*, *O. leoniae,* and *O. subtilis*; spawning in bromeliads is suspected for *O. deridens* and *O. fuscifacie*s (Jungfer et al., 2000). Note that Lynch (2002) doubted a possible relationship between *O. heyeri* and what he called the ''presumed clade of oophagous species'' (where he included *O. deridens, O. fuscifacies,* and *O. oophagus*), suggesting instead that it could be related to what he called *O. rodriguezi* (at that time already transferred to the new genus *Tepuihyla* by Ayarzagüena et al., ''1992'' [1993b]). While the species known or suspected to spawn in bromeliads could be monophyletic, we are not aware of any synapomorphy supporting the monophyly of all remaining species of *Osteocephalus*.

The species currently included in *Osteocephalus* are *O. buckleyi*, *O. cabrerai*, *O. deridens*, *O. elkejungingerae*, *O. exophthalmus, O. fuscifacies*, *O. heyeri*, *O. langsdorffii*, *O. leoniae*, *O. leprieurii*, *O. mutabor*, *O. oophagus*, *O. pearsoni*, *O. planiceps*, *O. subtilis*, *O. taurinus*, *O. verruciger*, and *O. yasuni*. Considering the uncertainties regarding *Osteocephalus,* we attempted to include representatives of the morphological and reproductive diversity within the genus: *O. cabrerai*, *O. langsdorffii*, *O. leprieurii*, *O. oophagus*, and *O. taurinus*.

Osteopilus: The genus *Osteopilus* was resurrected by Trueb and Tyler (1974) for three apparently related species that were often referred to collectively as the *Hyla septentrionalis* group (see Dunn, 1926; Trueb, 1970a). Trueb and Tyler (1974) provided a diagnostic definition of the genus; a possible synapomorphy is the differentiation of the m. intermandibularis to form supplementary apical elements. Trueb and Tyler (1974) also maintained, due to the impressive morphological divergence, that *Osteopilus,* the other Antillean groups then considered to be in *Hyla* (*H. heilprini*, *H. marianae, H. pulchrilineata*, *H. vasta*, *H. wilderi*), and the new genus they erected, *Calyptahyla,* represented several independent invasions from the mainland.

Maxson (1992) and Hass et al. (2001), using albumin immunological distances, suggested that *Osteopilus* is paraphyletic with respect to most other West Indian hylids (with the exception of *Hyla heilprini*, a Gladiator Frog). Hedges (1996) mentioned that unpublished DNA sequence data confirmed these findings. Anderson (1996) presented a karyological study of the three species of *Osteopilus,* indicating that her data were compatible with a monophyletic *Osteopilus*. Based on the comments by Hedges (1996), and immunological results of Hass et al. (2001), Franz (2003), Powell and Henderson (2003a, 2003b), and Stewart (2003) transferred *Calyptahyla crucialis, H. marianae*, *H. pulchrilineata*, *H. vasta,* and *H. wilderi* to *Osteopilus* that now includes eight species. *Osteopilus* is grouped together only on the basis of the immunological distance results, as no discrete character data set supporting its monophyly has yet been published. The species of *Osteopilus* available for our study were *O. crucialis*, *O. dominicensis*, *O. septentrionalis*, and *O. vastus*.

Phrynohyas: This genus was reviewed by Duellman (1971b). Although very distinctive externally, the only seeming synapomorphy in the diagnostic definition of *Phrynohyas* provided by Duellman (1971b) is the extensively developed parotoid glands in the occipital and scapular regions. Likely related to this character state, the viscous, milky secretions of the species of this genus could also be considered synapomorphic. Lescure and Marty (2000) transferred *Hyla hadroceps* to this genus; this was confirmed in a phylogenetic analysis using the mitochondrial ribosomal gene 12S by Guillaume et al. (2001). Pombal et al. (2003) described *P. lepida*. See *Osteocephalus* for further comments. *Phrynohyas* currently contains seven species: *P. coriacea*, *P. hadroceps*, *P. imitatrix*, *P. lepida*, *P. mesophaea*, *P. resinifictrix*, and *P. venulosa*. In our analysis we include *P. hadroceps*, *P. mesophaea*, *P. resinifictrix,* and *P. venulosa*.

Tepuihyla: This genus was defined by Ayarzagüena et al. (''1992'' [1993b]) for five species of *Osteocephalus* previously considered to constitute the *O. rodriguezi* species group (Duellman and Hoogmoed, 1992; Ayarzagüena et al., ''1992'' [1993a]). Ayarzagüena et al. (''1992'' [1993b]) differentiated *Tepuihyla* from *Osteocephalus* using the following character states present in *Tepuihyla*: subgular vocal sac, absence or extreme reduction of hand webbing, more reduced toe webbing, smaller size, absence of cranial coossification, large frontoparietal fontanelle, shorter nasals, and shorter frontoparietals. It is unclear which, if any, of these character states are apparent synapomorphies of *Tepuihyla*. There are eight species currently included in this genus: *T. aecii*, *T. celsae*, *T. edelcae*, *T. galani*, *T. luteolabris*, *T. rimarum*, *T. talbergae*, and *T. rodriguezi*. In this analysis we include only *T. edelcae*.

Trachycephalus: The relationships of this casque-headed taxon were discussed by Trueb (1970a) and Trueb and Duellman (1971). They diagnosed *Trachycephalus* from *Argenteohyla*, *Osteocephalus*, and *Phrynohyas* for having heavily casqued and co-ossified skulls, a medial ramus of pterygoid that does not articulate with the prootic, and a parasphenoid having odontoids. A likely synapomorphy of *Trachycephalus* is the presence of exostosis on the alary process of the premaxillae (Trueb, 1970a). *Trachycephalus* contains three species: *T. atlas*, *T. jordani*, and *T. nigromaculatus*. In this analysis we include *T. jordani* and *T. nigromaculatus*.

Species and Species Groups of *Hyla* Not Associated with Any Major Clade

Hyla aromatica Group: This group was proposed by Ayarzagüena and Señaris (''1993'' [1994]) for two species from the Venezuelan Tepuis, *H. aromatica* and *H. inparquesi*, which they could not associate with any of the species groups known from the Guayanas. Ayarzagüena and Señaris (''1993'' [1994]) noticed that the *H. aromatica* group shares some characters with the *H. larinopygion* group; however, they preferred to retain it as a separate group. They justified this decision based on the smaller size of members of the *H. aromatica* group, different coloration pattern, supraorbital cartilaginous process, vomerine odontophores smoothly S-shaped and with more odontophores, small nasals, and large prepollex. They included as well other character states, that actually, like some of these just mentioned, are either shared with several neotropical groups (supraorbital cartilaginous process; Faivovich, personal obs.), or some species of the *H. larinopygion* group (vomerine odontophores smoothly S-shaped; Duellman and Hillis, 1990: 5), or with the *H. armata* group (labial tooth row formula; see Cadle and Altig, 1991), or they support the monophyly of the *H. aromatica* group (adults with strong odor). Considering the lack of evidence of monophyly for the *H. larinopygion* group, Ayarzagüena and Señaris (''1993'' [1994]) cannot be questioned for recognizing a separate species group.

Ongoing research by Faivovich and McDiarmid suggests that *Hyla loveridgei* should also be considered part of the *H. aromatica* group. For this analysis, we include *H. inparquesi*.

Hyla uruguaya Group: This group has never been mentioned as such in the literature. However, clear similarities had been shown by Langone (1990) between *H. uruguaya* and *H. pinima* (these species being almost undistinguishable). Possible synapomorphies of the *H. uruguaya* group are the bicolored iris (also shared with *Aplastodiscus;* see Garcia et al., 2001a), the presence in tadpoles of two small, keratinized plates below the lower jaw sheath, and a reduction in the size of the marginal papillae of the posterior margin of the oral disc relative to the other papillae (Kolenc et al., ''2003'' [2004]). From this apparent clade we include *H. uruguaya* in our analysis.

Hyla chlorostea: Duellman at al. (1997) proposed the recognition of a species group to include the enigmatic *Hyla chlorostea*, a species known only from its holotype (a subadult male), which could not be associated with any known group of *Hyla* after its description (Reynolds and Foster, 1992). Unfortunately, we were unable to include this taxon in our analysis.

Hyla vigilans: Different perspectives concerning this enigmatic species were summarized by Suarez-Mayorga and Lynch (2001a). These authors rejected the possibility of a relationship with *Scinax* (as suggested by La Marca *in* Frost, 1985). Instead, they asserted that they suspected a possible relationship with *Sphaenorhynchus* or with *H. picta* (from the *H. godmani* species group) based on ‘‘oral disc and mouth position’’ of the tadpoles. We could not obtain samples of this species for our analysis.

Hyla warreni: This species, known only from two adult females, was described by Duellman and Hoogmoed (1992), who did not associate it with any other species or species group. Unfortunately, we could not obtain samples of this species for our analysis.

Other Genera

Aplastodiscus: The taxonomy and history of this genus was recently reviewed thoroughly by Garcia et al. (2001a). According to these authors the monophyly of the genus is supported by four putative synapomorphies: (1) the absence of webbing between toes I and II and basal webbing between the other toes; (2) bicolored iris; (3) females with unpigmented eggs; and (4) great development of internal metacarpal and metatarsal tubercles. Based on overall morphological and advertisement call similarities B. Lutz (1950) suggested a close relationship of this genus with *Hyla albosignata*. Garcia et al. (2001a) suggest that *Aplastodiscus* could be related with the *H. albofrenata* and *H. albosignata* complexes of the *H. albomarginata* group, as defined by Cruz and Peixoto (1984), based on the presence of enlarged internal metacarpal and metatarsal tubercles, and unpigmented eggs. Haddad et al. (2005) described the reproductive mode of *A. perviridis* and noticed that it was the same as that described by Haddad and Sawaya (2000) and Hartmann et al. (2004) in species included in *H. albofrenata* and *H. albosignata* complexes. Based on this, Haddad et al. (2005) suggested a possible relationship between these two species complexes and *Aplastodiscus*. *Aplastodiscus* is composed of two species, *Aplastodiscus cochranae* and *A. perviridis;* we include both in our analysis.

Nyctimantis: This monotypic Neotropical genus was considered a member of the Hemiphractinae by Duellman (1970) and Trueb (1974). Duellman and Trueb (1976) reviewed the taxon and placed it in Hylinae. Duellman and Trueb (1976) considered *Nyctimantis* to be related with *Anotheca spinosa* because both share the medial ramus of the pterygoid that is juxtaposed squarely against the anterolateral corner of the ventral ledge of the otic capsule. Also, frogs of both genera are known (*Anotheca*; Taylor, 1954; Jungfer, 1996) or suspected (*Nyctimantis*; Duellman and Trueb, 1976) to deposit their eggs in water-filled tree cavities. However, Duellman (2001) latter placed *Anotheca* in the Middle American/Holarctic clade, implicitly suggesting no relationship with *Nyctimantis*. Considering the uncertainty of the position of *Nyctimantis* within hylines, at this stage it is difficult to interpret which character states are autapomorphic. We include the single species *Nyctimantis rugiceps* in this analysis.

Phyllodytes: The history of this genus was reviewed by Bokermann (1966b). Possible synapomorphies of the taxon are the presence of odontoids on the mandible and on the cultriform process of the parasphenoid (Peters, ‘‘1872’’ [1873]), something unique within the Hylinae. Peixoto and Cruz (1988) noticed that among the six species recognized at that time, four species (*P. acuminatus*, *P. brevirostris*, *P. luteolus*, and *P. tuberculosus*) share the presence of series of enlarged tubercles on the venter and an enlarged tubercle on each side at the origin of the thigh (Bokermann, 1966b: fig. 6). The other two species, *P. auratus* and *P. kautskyi*, have uniform granulation on the venter and lack enlarged tubercles on the thighs, as also seems to be the case in *P. melanomystax*, a species described later (see Caramaschi et al., 1992). Peixoto et al. (2003) described two additional species, *P. edelmoi* and *P. gyrinaethes*; both have a tubercle on each side at the origin of the thigh. *Phyllodytes edelmoi* has a series of indistinct tubercles on the venter; in *P. gyrinaethes* they do not form series. Caramaschi and Peixoto (2004) added *P. punctatus*, which has two medial, poorly distinct rows of tubercles. Caramaschi et al. (2004a) resurrected *P. wuchereri*. Peixoto et al. (2003) suggested three different species groups based on color pattern, and Caramaschi et al. (2004) further expanded the definitions. The *P. luteolus* group is characterized by a plain pattern with a variably defined dorsolateral dark brown to black line on canthus rostralis and/or behind the corner of eye. This group includes *P. acuminatus*, *P. brevirostris*, *P. edelmoi*, *P. kautskyi*, *P. luteolus*, and *P. melanomystax*. The *P. tuberculosus* group has a pale brown dorsum with scattered dark brown dots and includes *P. punctatus* and *P. tuberculosus*. The *P. auratus* group has a dorsal pattern of two dorsolateral, longitudinal white or yellowish stripes, with each stripe being bordered by a dark brown or black line from posterior corner of eye to groin. This group includes *P. auratus* and *P. wuchereri*. Finally, *P. gyrinaethes* is placed in its own group for having red color on hidden surfaces of thighs and a highly modified tadpole. It is unclear if any of these groups is monophyletic. Tissues were available for *P. luteolus* and an unidentified species, *Phyllodytes* sp., from Bahia, Brazil.

Lysapsus and *Pseudis*: The monophyly of the former subfamily Pseudinae has not been historically controversial; it is supported by the presence of a long, ossified intercalary element between the ultimate and penultimate phalanges. Haas (2003) added several synapomorphies from larval morphology, based on the study of larvae of two species of *Pseudis*. The limits and definitions of *Pseudis* and *Lysapsus* were reviewed by Savage and Carvalho (1953) and by Klappenbach (1985). From their observations it is unclear which character states support the monophyly of either genus. Savage and Carvalho (1953: 199) implicitly proposed the paraphyly of *Pseudis*, when they suggested that *Lysapsus* ''seems to have arisen from *Pseudis*.'' Garda et al. (2004) recently distinguished both genera on the basis of sperm morphology. In *Lysapsus laevis* (the only species of *Lysapsus* available to them) the subacrosomal cone is nearly absent, but it is clearly present in the four species of *Pseudis* they studied. Regardless, the monophyly of either genus has not been satisfactorily documented.

Morphological diversity within *Pseudis* includes large species, several of which were included in the past in the synonymy of *P. paradoxa* and were recently resurrected (Caramaschi and Cruz, 1998), and smaller species with a double vocal sac, *P. cardosoi* and *P. minuta* (Klappenbach, 1985; Kwet, 2000). *Lysapsus* includes three species, *L. caraya*, *L. laevis* and *L. limellum*; we include in our analysis the last two. *Pseudis* is composed of six species: *P. bolbodactyla*, *P. cardosoi*, *P. fusca*, *P. minuta*, *P. paradoxa*, and *P. tocantins*, of which we include in our analysis *P. minuta* and *P. paradoxa*.

Scarthyla: Duellman and de Sá (1988) and Duellman and Wiens (1992) suggested that this monotypic genus was sister to *Scinax*, but more recently, Darst and Cannatella (2003) presented evidence supporting a sister group relationship between *Scarthyla* and ''pseudids''. The single species, *Scarthyla goinorum*, is included in our analysis.

Scinax: With roughly 86 recognized species, *Scinax* is the second largest genus within Hylinae. This genus includes the species formerly placed in the *Hyla catharinae* and *H. rubra* groups; a taxonomic history was presented by Faivovich (2002). The relationships among the species of *Scinax* were recently addressed by Faivovich (2002), who performed a phylogenetic analysis using 38 species representing the five species groups then recognized. Although he employed eight outgroups, the analysis is not a strong test of the monophyly of *Scinax* nor of the relationships of *Scinax* with other hylines. Duellman and Wiens (1992) suggested that *Scinax* is the sister group of *Scarthyla* and that this clade is sister to *Sphaenorhynchus*. Faivovich (2002) did not test this assertion because his selection of outgroups was heavily influenced by da Silva's results (1998), which did not suggest a close relationship between *Scinax* and these two genera. Taxon choice in the present study will test more appropriately the hypothesis of (*Scinax* + *Scarthyla*) + *Sphaenorhynchus*.

Faivovich's (2002) results suggested that *Scinax* contains two major clades: (1) a *S. ruber* clade composed of species that had been previously grouped into the *S. rostratus*, *S. ruber*, and *S. staufferi* groups; and (2) a *S. catharinae* clade composed of the species that were included in the *S. catharinae* and *S. perpusillus* groups. Faivovich (2002) continued recognition of these two species groups within the *S. catharinae* clade, as well as the *S. rostratus* group within the *S. ruber* clade, as the individual monophyly of the *S. catharinae* and *S. rostratus* groups were corroborated by his analysis. The *S. perpusillus* group is recognized because its monophyly could not be tested, and it still awaits a rigorous test. All species previously included in the nonmonophyletic groups of *S. ruber* and *S. staufferi* are included in the larger *S. ruber* clade, without being assigned to any group. For a list of the species currently included in *Scinax*, see page 95.

In anticipation of a forthcoming study of the phylogeny of *Scinax* by Faivovich and associates, we include only *S. berthae* and *S. catharinae* as exemplars of the *S. catharinae* clade, and *S. acuminatus*, *S. boulengeri*, *S. elaeochrous*, *S. staufferi*, *S. fuscovarius*, *S. ruber*, *S. squalirostris*, and *S. nasicus* as exemplars of the *S. ruber* clade.

Sphaenorhynchus: More has been written about nomenclatural confusion surrounding *Sphaenorhynchus* than about its systematics (see Frost, 2004). This genus has been reviewed by Caramaschi (1989). Duellman and Wiens (1992) proposed the following synapomorphies for *Sphaenorhynchus*: posterior ramus of pterygoid absent; zygomatic ramus of squamosal absent or reduced to a small knob; pars facialis of maxilla and alary process of premaxilla reduced; postorbital process of maxilla reduced, not in contact with quadratojugal; neopalatine reduced to a sliver or absent; pars externa plectri entering tympanic ring posteriorly (rather than dorsally); pars externa plectri round; hyale curved medially; coracoids and clavicle elongated; transverse process of presacral vertebra IV elongate, oriented posteriorly; and prepollex ossified, bladelike. The genus is composed of 11 species: *S. bromelicola*, *S. carneus*, *S. dorisae*, *S. lacteus*, *S. orophilus*, *S. palustris*, *S. pauloalvini*, *S. planicola*, *S. prasinus*, *S. platycephalus*, and *S. surdus*. In our analysis we include *S. dorisae* and *S. lacteus*.

Xenohyla: This genus was named by Izecksohn (1996) for the bizarre frog *Hyla truncata*, which had previously been suggested to be related to *Sphaenorhynchus* by Izecksohn (1959, 1996) and Lutz (1973). According to Izecksohn (1996), *Xenohyla* shares with *Sphaenorhynchus* the reduced number of maxillary teeth, a relatively short urostyle, and the development of the transverse processes of presacral vertebra IV; furthermore, *Xenohyla* shares with *Sphaenorhynchus* the quadratojugal not in contact with the maxilla. Izecksohn (1996) suggested also a close relationship with *Scinax* based on the presence in *Xenohyla* of a coracoid ridge and an internal, subgular vocal sac. While the coracoid ridge is present in *Scinax*, it is also present in several other hylines (e.g., see Faivovich, 2002). The internal, subgular vocal sac is not a synapomorphy of all *Scinax*, but only of the *S. catharinae* clade. Caramaschi (1998) added *X. eugenioi*, a second species for the genus. We include *X. truncata* in our study.

CHARACTER SAMPLING

GENE SELECTION

Because this study involves the simultaneous analysis of taxa of disparate levels of divergence, we assembled a large data set, including four mitochondrial and five nuclear genes, spanning a broad range of variation, from the fast-evolving cytochrome *b* (Graybeal, 1993) to the much conserved nuclear genes such as 28S (Hillis and Dixon, 1991).

Ribosomal mitochondrial genes and cytochrome *b* have been employed recently in several phylogenetic studies of various anuran groups at various levels of divergence (Read et al., 2001; Vences and Glaw, 2001; Cunningham, 2002; Salducci et al., 2002). Nuclear genes have been poorly explored for their use in anuran phylogenetics. The 28S ribosomal nuclear gene has been used in amphibians by Hillis et al. (1993). The protein-coding genes rhodopsin, tyrosinase, RAG-1, and RAG-2 were used to study problems at different levels by Bossuyt and Milinkovitch (2000), Biju and Bossuyt (2003), and Hoegg et al. (2004). In this study we include 12S, tRNA valine, 16S, and fragments of cytochrome b, rhodopsin, tyrosinase, 28S, RAG-1, and seventh in absentia. The last gene is used here for the first time in amphibians.

DNA ISOLATION AND SEQUENCING

Whole cellular DNA was extracted from frozen and ethanol-preserved tissues (usually liver or muscle) using either phenol-chloroform extraction methods or the DNeasy (QIAGEN) isolation kit. See table 2 for a list and sources of the primers employed.

Amplification was carried out in a 25-μl-

TABLE 2

Primers Used in this Study

Primer	Sequence	Reference
MVZ59	5′-ATAGCACTGAAAAYGCTDAGATG-3′	Graybeal (1997)
12L1	5′-AAAAAGCTTCAAACTGGGATTAGATACCCCACTAT-3′	Feller and Hedges (1998)
12SM	5′-GGCAAGTCGTAACATGGTAAG-3′	Darst and Cannatella (2004)
MVZ50	5′-TYTCGGTGTAAGYGARAKGCTT-3′	Graybeal (1997)
12sL13	5′-TTAGAAGAGGCAAGTCGTAACATGGTA-3′	Feller and Hedges (1998)
16sTitus I	5′-GGTGGCTGCTTTTAGGCC-3′	Titus and Larson (1996)
16sL2A	5′-CCAAACGAGCCTAGTGATAGCTGGTT-3′	Hedges (1994)
16sH10	5′-TGATTACGCTACCTTTGCACGGT-3′	Hedges (1994)
16sAR	5′-CGCCTGTTTATCAAAAACAT-3′	Palumbi et al. (1991)
16sBR	5′-CCGGTCTGAACTCAGATCACGT-3′	Palumbi et al. (1991)
16sWilk2	5′-GACCTGGATTACTCCGGTCTGA-3′	Wilkinson et al. (1996)
MVZ15	5′-GAACTAATGGCCCACACWWTACGNAA-3′	Moritz et al. (1992)
H15149(H)	5′-AAACTGCAGCCCCTCAGAAATGATATTTGTCCTCA-3′	Kocher at al. (1989)
Rhod1A	5′-ACCATGAACGGAACAGAAGGYCC-3′	Bossuyt and Milinkovitch (2000)
Rhod1C	5′-CCAAGGGTAGCGAAGAARCCTTC-3′	Bossuyt and Milinkovitch (2000)
Rhod1D[a]	5′-GTAGCGAAGAARCCTTCAAMGTA-3′	Bossuyt and Milinkovitch (2000)
R1-GFF	5′-GAGAAGTCTACAAAAAVGGCAAAG-3′	Taran Grant and Julian Faivovich
R1-GFR	5′-GAAGCGCCTGAACAGTTTATTAC-3′	Taran Grant and Julian Faivovich
Tyr 1C	5′-GGCAGAGGAWCRTGCCAAGATGT-3′	Bossuyt and Milinkovitch (2000)
Tyr 1G	5′-TGCTGGGCRTCTCTCCARTCCCA-3′	Bossuyt and Milinkovitch (2000)
sia1[b]	5′-TCGAGTGCCCCGTGTGYTTYGAYTA-3′	Bonacum et al. (2001)
sia2	5′-GAAGTGGAAGCCGAAGCAGSWYTGCATCAT-3′	Bonacum et al. (2001)
28SV	5′-AAGGTAGCCAAATGCCTCGTCATC-3′	Hillis and Dixon (1991)
28SJJ	5′-AGTAGGGTAAAACTAACCT-3′	Hillis and Dixon (1991)

[a] This primer, instead of Rhod1C, was used to amplify this gene in the 30-chromosome *Hyla*.

[b] The primer pair sia1-2 was used together with the universal primers T3 and T7, as done by Bonacum et al. (2001).

volume reaction using either puRe Taq Ready-To-Go PCR beads (Amersham Biosciences, Piscataway, NJ) or Invitrogene PCR SuperMix. For all the amplifications, the PCR program included an initial denaturing step of 30 seconds at 94°C, followed by 35 or 38 cycles of amplification (94°C for 30 seconds, 48–60°C for 60 seconds, 72°C for 60 seconds), with a final extension step at 72°C for 6 min.

Polymerase chain reaction (PCR)-amplified products were cleaned either with a QIAquick PCR purification kit (QIAGEN, Valencia, CA) or with ARRAY-IT (TeleChem International, Sunnyvale, CA) and labeled with fluorescent-dye labels terminators (ABI Prism Big Dye Terminators v. 3.0 cycle sequencing kits; Applied Biosystems, Foster City, CA). Depending on whether the cleaned product was purified with QIAquick or Array-It, the sequencing reaction was carried out in either 10 μl or 8 μl volume reaction following standard protocols. The labeled PCR products were isopropanol-precipitated following the manufacturer's protocol. The products were sequenced either with an ABI 3700 or with an ABI Prism 377 sequencer. Most samples were sequenced in both directions.

Chromatograms obtained from the automated sequencer were read and contigs made using the sequence editing software Sequencher 3.0. (Gene Codes, Ann Arbor, MI). Complete sequences were edited with BioEdit (Hall, 1999).

MORPHOLOGY

Because the present study is mostly based on molecular data, the failure to include a thorough morphological data set doubtless is its weakest point. As trained morphologists, most of the authors of this paper think that a phylogenetic hypothesis that explains all the available data is the best hypothesis that we can aspire to, and that no class of data is better than any other. Apart from da Silva's unpublished dissertation, which is commented upon below, published comparative studies involving a diversity of hylid exemplars are rare. Major exceptions are the thorough osteological studies by Trueb (1970a) and those on hand muscles of Pelodryadinae (Burton, 1996), distal extensor muscles of anurans (Burton, 1998a), and foot muscles of Hylidae (Burton, 2004). Explicit character descriptions in the context of phylogenetic comparisons include those by Duellman and Trueb (1983), Campbell and Smith (1992), Duellman and Campbell (1992), Duellman and Wiens (1992), Fabrezi and Lavilla (1992), Kaplan (1994, 1999), Cocroft (1994), Burton (1996, 1998a, 2004), Haas (1996, 2003), da Silva (1997), Duellman et al. (1997), Kaplan and Ruiz-Carranza (1997), Mendelson et al. (2000), Sheil et al. (2001), Faivovich (2002), and Alcalde and Rosset (''2003'' [2004]). Most of these studies were targeted in general to very specific apparent clades or to very large clades using very few terminals, which leaves particular sets of characters known for very few terminals. Unfortunately, for the inclusion of the characters employed in these studies to be informative, detailed anatomic work would be required on a very large number of terminals (besides the potentially serious need to redefine several characters), a task that we find impossible to pursue at this time. Much to our regret, we find that there are almost no published studies from which we could derive character scorings to enrich our data set without extensive work. The only data set that we thought could be included, due to its relatively dense taxon sampling, is the one resulting from the collection of observations presented by Burton (2004). Although its sampling of nonhylid taxa that match our sampled taxa is particularly sparse, we consider Burton's study to be an important addition to this analysis. Characters are listed and discussed in appendix 3.

da Silva's (1998) Dissertation

da Silva (1998) presented his Ph.D. dissertation on phylogeny of hylids with emphasis on Hylinae. Although da Silva's dissertation has not been published, some of its results and conclusions were described and commented in detail by Duellman (2001). Because the present paper deals specifically with the phylogeny of Hylinae, we cannot avoid a few comments dealing with da Silva's work. Considering the mostly coincident scope of both da Silva's dissertation and this paper, it is evident that a thorough discussion and comparison of his results with ours would almost amount to the publication of his chapter on Hylinae relationships. This is a situation with which we feel most uncomfortable, because we think that this is a responsibility that rests on Helio R. da Silva.

From a purely practical perspective, at this point the integration of da Silva's data set with ours is impracticable for two reasons: (1) The data matrix as printed in the dissertation distributed by the University of Michigan is incomplete, as it lacks the scorings for 10 characters (chars. 110–120) for all taxa. This is also the situation with the thesis that is deposited at the Department of Herpetology library of the University of Kansas, Natural History Museum (Faivovich, personal obs.). (2) A few scorings for groups that we are familiar with are not coincident with our observations on the same species, something suggestive either of polymorphism in those characters or mistaken scorings.[21] If this were the case, it would not be surprising, as scoring mistakes are to be expected in such an impressive data set. The problem with them is that once detected, they have to be corrected and the analysis has to be redone. It is evident that a revision of the data set is necessary before any integration can take place.

PHYLOGENETIC ANALYSIS

Our optimality criterion to choose among trees is parsimony. The logical basis of parsimony as an optimality criterion has been presented by Farris (1983). However, parsi-

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[21] For example, character 60 (anterior process of the hyale) is scored 0 (absent) in *Aplastodiscus*, where it is present in the material available to us (Faivovich, 2002; Garcia, personal obs.). Character 61 (anterolateral process of the hyoid plate) is scored 0 (absent) in *Hyla albofrenata*, *H. albomarginata*, *H. albopunctata*, *H. albosignata*, *H. faber*, and *H. multifasciata*, whereas it is present in the specimens available to us (Garcia and Faivovich, personal obs.)

mony has repeatedly been attacked from different perspectives, all of which tend to portray parsimony as inferior to such model-based approaches as maximum likelihood. Criticisms of parsimony have centered on two main topics: statistical inconsistency and the notion that parsimony is an overparameterized likelihood model. As stated by Goloboff (2003), the emphasis on statistical consistency decreased following several studies showing that: (1) maximum likelihood can be inconsistent even with minor violations of the model when they were generated with a mix of models (Chang, 1996); (2) given some evolutionary models, maximum likelihood estimators could be inconsistent (Steel et al., 1994; Farris, 1999); (3) parsimony can be consistent (Steel et al., 1993); (4) assuming likelihood as a more accurate method, inferences based on trees suboptimal under the maximum likelihood could be less reliable than inferences made on trees optimal under otherwise inferior but faster criteria (Sanderson and Kim, 2000); and (5) at least under some conditions, parsimony may be more likely than maximum likelihood to find the correct tree, given finite amounts of data (Yang, 1997; Siddall; 1998; Pol and Siddall, 2001). Tuffley and Steel (1997) demonstrated that parsimony is a maximum likelihood estimator when each site has its own branch length. Farris (1999, 2000) and Siddall and Kluge (1999) suggested that the results of Tuffley and Steel (1997) were an indication that the model implied by parsimony (‘‘no special model of evolution’’ or ‘‘no common mechanism model’’) was indeed more realistic. However, likelihood advocates (Steel and Penny, 2000; Lewis, 2001; Steel, 2002) countered that models that assume constant probabilities of change across all sites are to be preferred on the grounds of simplicity (i.e., as having fewer parameters to estimate). Goloboff (2003) demonstrated that parsimony could actually be derived from models that require even fewer parameters than the commonly used likelihood models.

The use of Bayesian Markov chain Monte Carlo (BMCMC) techniques has become quite popular among evolutionary biologists. However, for reasons outlined by Simmons et al. (2004), the posterior probability values of the clades cannot be interpreted as values of truth or support. Furthermore, Kolaczkowski and Thornton (2004) demonstrated, by using simulations in the presence of heterogeneous data, that parsimony performs better than both maximum likelihood and BMCMC over a wide range of conditions.

We contend that all serious criticisms of parsimony have been rebutted. We consider that while the first point mentioned (inconsistency of likelihood when the data are generated with different models) could certainly occur in any analysis, it is particularly problematic in the present one, because we are combining morphology with both mitochondrial and nuclear coding and non-coding genes. Furthermore, for a data set of this size, maximum likelihood is quite impractical to apply for computational reasons.

For the phylogenetic analyses of the DNA sequence data, we used the method of Direct Optimization (Wheeler, 1996, 1998, 2002), as implemented in the program POY (Wheeler et al., 2002), a heuristic approximation to the optimal tree alignment methods of Sankoff (1975) and Sankoff and Cedergren (1983). Sequence alignment and tree searching have traditionally been treated as two independent steps in phylogenetic analyses: sequences are first aligned, and a fixed or static multiple alignment is then treated as a standard character matrix that is the basis for tree searching in the test of character congruence. However, there may be other equally defensible multiple sequence alignments that would require fewer hypothesized transformations to explain the observed sequence variation; an explanation that requires fewer transformations is more parsimonious and is therefore objectively preferred over explanations that require a greater number of transformations (see De Laet [2005] for a much more sophisticated approach to the problems of constructing multiple alignments prior to tree searching). Direct Optimization seeks the cladogram-alignment combination (i.e., the optimal tree alignment) that minimizes the total number of hypothesized transformation events required to explain the observations. Within this framework, insertion/deletion events (indels, gaps) are historical evidence that is taken into account when hypothesizing common ancestry.

The simplest minimization of transformations is obtained when tree searches are conducted under equal weights for indels and all substitutions (1:1:1, this is the ratio of the cost of opening gap:extension gap:substitutions) (Frost et al., 2001). This weighting scheme implies that indels are as costly as the number of nucleotides they span. This is not a situation with which we are comfortable, inasmuch as a single deletion event could entail more than a single nucleotide and hence necessarily require a lower cost than if all the nucleotides it includes were lost independently of each other. However, theoretical justifications for the selection of differential costs for gap opening and gap extension are not evident.

De Laet and Smets (1998) suggested that parsimony analysis searches for the trees on which the highest number of compatible independent pairwise similarities can be accommodated; that is, they described parsimony as a two-taxon analysis. When dealing with static data sets, this approach and the minimization of transformations give the same rank of tress. However, De Laet (2005) showed that when considering parsimony as a two-taxon analysis in the presence of inapplicable character states (e.g., unequal-length sequences), the minimization of transformations (as obtained under 1:1:1) does not maximize the number of accommodated compatible independent pairwise a priori similarities. De Laet (2005) suggested that sequence homology has two components, homology of subsequences (the fragments of sequences that are comparable across a branch) and base-to-base homology within homologous subsequences. When maximization of homology is transformed into a problem of minimization of changes, the optimization of the two components that maximizes the accommodated independent pairwise similarities is obtained by summing up the cost regimes that are involved for each component. The number of subsequences is quantified by counting the number of insertion/deletion events (independent of their length, and therefore represented each as a whole by a unit opening gap). Base-to-base homology within homologous subsequences is maximized when substitutions are weighted twice as much as unit gaps (Smith et al., 1981). These result in a substitution cost of 2, a gap opening cost of 2 + 1 (the same cost of a substitution plus the cost of the first unit gap), and a gap extension cost of 1. All this development rests on the perspective of parsimony as a two-taxon analysis (De Laet and Smets, 1998). The most immediately appealing aspect of De Laet's perspective is that it offers a rationale for the use of gap-extension costs different from substitution costs, thus avoiding giving an insertion/deletion event of *n* nucleotides the same weight of *n* substitutions.

We conducted our searches using equal weights for minimizing transformations. In order to examine the effect of the gap treatment in our results, and following De Laet's development (2005), we also submitted our final tree to a round of tree-bisection and reconnection branch swapping (TBR) by using a weighting scheme of 2 for substitutions and morphological transformations, 3 for a gap opening, and 1 for a gap extension.

This study is guided by the idea that a simultaneous analysis of all available evidence maximizes explanatory power (Kluge, 1989; Nixon and Carpenter, 1996). Consequently, we analyzed all molecular and available morphological evidence simultaneously. The analysis was performed using subclusters of 60–100 processors of the American Museum of Natural History parallel computer cluster.

Heuristic algorithms applied to both tree searching and length calculation (i.e., alignment cost) were employed throughout the analysis. As with any heuristic solution, the optimal solution from these analyses under Direct Optimization represents the upper bound, and more exhaustive searching could result in an improved solution. Considering the large size of our data set, we tried two different approaches. The first strategy tries to collect many locally optimal trees from many replications to input them into a final round of tree fusing (Goloboff, 1999). For the second strategy, quick concensus estimates (Goloboff and Farris, 2001) are used as constraints for additional tree searching, following the suggestion of Pablo Goloboff (personal commun.).

For maximizing the number of trees for tree fusing, we employed two different routines:

1. Three hundred fifty random addition sequences were done in groups of 5 or 10, followed by a round of tree fusing, sending the best tree to 10–25 parsimony ratchet cycles (Nixon, 1999a) using TBR, reweighting between 15 and 35% of the fragments, keeping one tree per cycle, and by setting the character weight multiplier between two and five in different replicates, with a final round of TBR branch swapping. Tree fusing was always done fusing sectors of at least three taxa with two successive rounds of fusing.
2. One hundred fifty random addition sequences were built in groups of 5, 7, or 10 by submitting the best of each group to 10–25 ratchet cycles using TBR.

The 40 best trees resulting from these analyses where submitted to tree fusing in groups of five, and the resulting eight trees were subsequently fused. This final tree was submitted to 30 replicates of Ratchet using the same settings as above, with the resulting trees being submitted to a final round of TBR branch swapping.

Alternatively, we did 50 random addition sequences followed by a round of TBR and made an 85% majority rule consensus, as suggested by Goloboff and Farris (2001) to quickly estimate the groups actually present in the consensus of large data sets without having to do intensive searches. The approach of Goloboff and Farris (2001) assumes that groups that are present in all or most independent searches are more likely to be actually supported by the data. To speed up the searches for the estimation of the quick consensus, we treated the partial sequences of the RAG-1, rhodopsin, SIA, and tyrosinase genes as prealigned. Once the quick consensus was estimated, it was inputted in POY as a constraint file, with which we built 100 Wagner trees, each followed by 10 ratchet replicates. All trees resulting from these constrained searches were fused in groups of different size, and the final trees were submitted to a round of TBR. The original constraint file was not used during the fusing and final TBR steps.

While all searches were done using standard direct optimization, all were submitted to final rounds of TBR under the command ‘‘iterative pass’’ (Wheeler, 2003a). This routine does a three-dimensional optimization, taking into account the states of the three adjacent nodes of the internal node of interest. Because any change in the reconstructed sequence could potentially affect adjacent nodes, the procedure is done iteratively until stabilization is achieved.

The large size of the data set imposes a heavy burden in computer times to estimate support measures. Bremer supports (Bremer, 1988) were calculated using POY, without using ‘‘iterative pass’’. Parsimony Jackknife values (Farris et al., 1996) were calculated using the implied alignment (Wheeler, 2003b) of the best topology. In turn, this implies that the parsimony jackknife values could be overestimated. Parsimony Jackknife was calculated in TNT (Goloboff et al., 2000); 1000 pseudoreplicates were performed. For each pseudoreplicate the best topology was searched for by using sectorial searches and tree fusing, starting with two Wagner trees generated through random addition sequences.

Final tree lengths under the 1:1:1 weighting scheme were checked with TNT. Lists of synapomorphies were generated with TNT; only unambiguous transformations common to all most parsimonious trees were considered.

For the analysis, the complete 12S-tRNA valine-16S sequence was cut into 14 fragments and the partial 28S sequence was cut into 4 fragments coincident with conserved regions (Giribet, 2001). Although this constrains homology assessment, the universe of alternative ancestral sequences that has to be explored is a more tractable problem than using long single fragments. The sequence files as they were input into POY are available from http://research.amnh.org/users/julian. Tree editing was done using WinClada (Nixon, 1999b).

RESULTS

In total, we sequenced 256 terminals. The contiguous 12S, tRNA valine, and 16S genes were sequenced for all but seven terminals. For these terminals we were unable to amplify or sequence one or two of the overlapping PCR fragments. The partial cytochrome *b* fragment was sequenced for all but 12 terminals. The success with the nuclear loci varied from 232 terminals sequenced for the first exon of rhodopsin to as few as 166 sequenced for 28S. See appendix 2 for a complete list of the loci sequenced for each taxon, voucher specimens, locality data, and GenBank accessions. All sequences were produced for this project and for that of Faivovich et al. (2004) with the exception of 21 sequences taken from GenBank that were produced by Bijou and Bossuyt (2003) and by Darst and Cannatella (2004). The fact that the morphological characters are not scored for 70% of the terminals led to several ambiguous optimizations. A list of nonambiguous morphological synapomorphies is provided in appendix 3, many of which are mentioned throughout the discussion and in the section ''Taxonomic Conclusions: A New Taxonomy of Hylinae and Phyllomedusinae''.

The phylogenetic analysis resulted in four most parsimonious trees of 65,717 steps. One of these trees resulted from one of the rounds of tree fusing of the trees resulting from the constrained search, and the other three trees were obtained after a round of TBR swapping of the first one. Parsimony Jackknife and Bremer support values are generally high. Most of the 272 nodes of the strict consensus (figs. 1–5) are well supported, with 226 nodes having a Bremer support of ≥10 and 162 nodes with a Bremer support of ≥20; additionally, 255 nodes have a jackknife value of ≥75% and 245 nodes have a jackknife value of ≥90%.

All conflict among the trees is restricted to two points: (1) the relationships among *Hyla circumdata*, *H. hylax*, and the undescribed species *Hyla* sp. 4 (fig. 3); and (2) the relationships of *H. femoralis* with the *H. versicolor* and *H. eximia* groups (fig. 5).

When the best trees were submitted to a round of TBR using a weighting scheme of 3:1:2 as suggested by De Laet (in press) and mentioned earlier, the resulting tree differs from the original ones only in that (1) the clade composed of *Cryptobatrachus* and *Stefania* moves to be the sister group of *Flectonotus* and *Gastrotheca* (fig. 2), and (2) the clade composed of *Lysapsus*, *Pseudis*, and *Scarthyla* moves from the sister taxon of *Scinax* to the sister taxon of the 30-chromosome *Hyla* groups, *Sphaenorhynchus*, and *Xenohyla* (fig. 4).

DISCUSSION

MAJOR PATTERNS OF RELATIONSHIPS OF HYLIDAE AND OUTGROUPS

As in previous analyses (Ruvinsky and Maxson, 1996; Haas, 2003; Darst and Cannatella, 2004), our results do not recover Hylidae as a monophyletic taxon (figs. 1, 2). Hemiphractinae appears as only distantly related to the Hylinae, Pelodryadinae, and Phyllomedusinae, each of which is monophyletic. For this reason, we exclude Hemiphractinae from Hylidae, being thereby restricted to Hylinae, Pelodryadinae, and Phyllomedusinae. In the same way, Centrolenidae, for a long time suspected to be related with hylids, appears as a distantly related clade, as suggested by previous studies (Haas, 2003; Darst and Cannatella, 2004).

Hylidae, as understood here, excludes the Hemiphractinae. Otherwise, the major clades within the Hylidae are coincident with the remaining subfamilies currently recognized. The Pelodryadinae is the sister taxon of Phyllomedusinae, corroborating the results of Darst and Cannatella (2004); in turn, Pelodryadinae + Phyllomedusinae is the sister taxon of Hylinae (figs. 1, 2).

Ranoids appear as monophyletic, with the two microhylid exemplars being the sister taxon of the Astylosternidae + remaining ranoids (fig. 2). Ranidae forms a paraphyletic melange, with the exemplars of Hemisotidae, Mantellidae, and Rhacophoridae being nested among the few ranid exemplars. Ranoids are the sister taxon of all remaining terminals (fig. 2).

Within hyloids, as expected, Leptodactylidae is rampantly paraphyletic, with all other included families nested within it (figs. 1, 2). Ceratophryinae, Eleutherodactylinae, Leptodactylinae, and Telmatobiinae are not monophyletic (fig. 2).

At the base of hyloids, the two exemplars of *Eleutherodactylus* are the sister taxon of a clade composed of *Hemiphractus helioi*, *Brachycephalus ephippium*, and *Phrynopus* sp. This situation renders Eleutherodactylinae and Hemiphractinae nonmonophyletic (fig. 2). The nonmonophyly of Hemiphractinae is further given by the fact that in the 1:1:1 analysis, *Stefania* + *Cryptobatrachus* and *Gastrotheca* + *Flectonotus* are not monophyletic but occur as a grade leading to the other hyloids (fig. 2); however, the group is monophyletic in the 3:1:2 analysis. Moving upward in the tree finds two large clades: one composed of Hylidae in the sense used here (i.e., excluding Hemiphractinae), and the other composed of the remaining hyloid families and subfamilies of Leptodactylidae. Leptodactylinae as defined by Laurent (1986) is not monophyletic in that *Limnomedusa* is only distantly related to the remaining ‘‘Leptodactylinae’’, being the sister taxon of *Odontophrynus*. Note that this arrangement is congruent with Leptodactylinae as defined by Lynch (1971). Centrolenidae obtains as monophyletic and as the sister taxon of Allophrynidae. The only cycloramphine exemplar, *Crossodactylus schmidti*, is the sister taxon of the dendrobatid exemplars.

Telmatobiinae is not monophyletic for having one of the Ceratophryinae exemplars, *Ceratophrys cranwelli*, nested within it. Furthermore, the other two Telmatobiinae exemplars, *Alsodes gargola* and *Euspsophus calcaratus*, form a clade with the Leptodactylinae exemplar *Limnomedusa macroglossa* and the other Ceratophryinae exemplar *Odontophrynus americanus*. This clade is also the sister taxon of all Bufonidae exemplars (fig. 2).

In general, most results concerning the relationships among outgroup taxa should be considered cautiously, because the taxon sampling of this analysis was not designed to address those specific questions. Some results are nonetheless expected or at least suggestive. In the former group we include, for example, the monophyly of Bufonidae, Dendrobatidae, Centrolenidae, and Ranoidea. The relationship between *Crossodactylus* and dendrobatids is consistent with the results of Haas (2003).

The fact that hemiphractines are not related to the Hylidae, and are likely nonmonophyletic, requires a change in how study of this group is approached. For instance, relationships of Hemiphractinae as recovered here are quite different from the results of the cladistic analysis based on morphology and life-history data presented by Mendelson et al. (2000). These authors found *Hemiphractus* to be nested within *Gastrotheca*, a result that Duellman (2001) considered implausible. Although we did not incorporate their data set into our analysis, the fact that they employed only hylid outgroups could have affected their results. With the important difference that we do not recover a monophyletic Hemipractinae, our results corroborate the sister taxon relationship between the northern Andean *Cryptobatrachus* and the Guayanan *Stefania*, as well as the sister group relationship between *Flectonotus* and *Gastrotheca*, as suggested by Duellman and Hoogmoed (1984) and Wassersug and Duellman (1984). Regarding the monophyly and actual position of Hemiphractinae within Neobatrachia, our results are inconclusive (similar to those of Darst and Cannatella, 2004) most likely because of a lack of the appropriate taxon sampling to address the problem. Their positions in the tree suggest that a much denser taxon sampling of ‘‘Leptodactylidae’’ and perhaps Eleutherodactylinae will be necessary to better understand their relationships.

PELODRYADINAE AND PHYLLOMEDUSINAE

Our results of a monophyletic Pelodryadinae + Phyllomedusinae corroborate early suggestions by Trewavas (1933), Duellman (1970), Bagnara and Ferris (1975), and more recent results by Darst and Cannatella (2004) and Hoegg et al. (2004). The monophyly of Pelodryadinae and Phyllomedusinae was not recovered in the analyses by Duellman (2001), Burton (2004), and Haas (2003). Discrepancies between the analyses of Burton (2004) and Haas (2003) and our’s may be the result of different taxon sampling and assumptions. Duellman (2001) assumed that Hylidae, in the classical sense (including Hemiphractinae), was monophyletic, and

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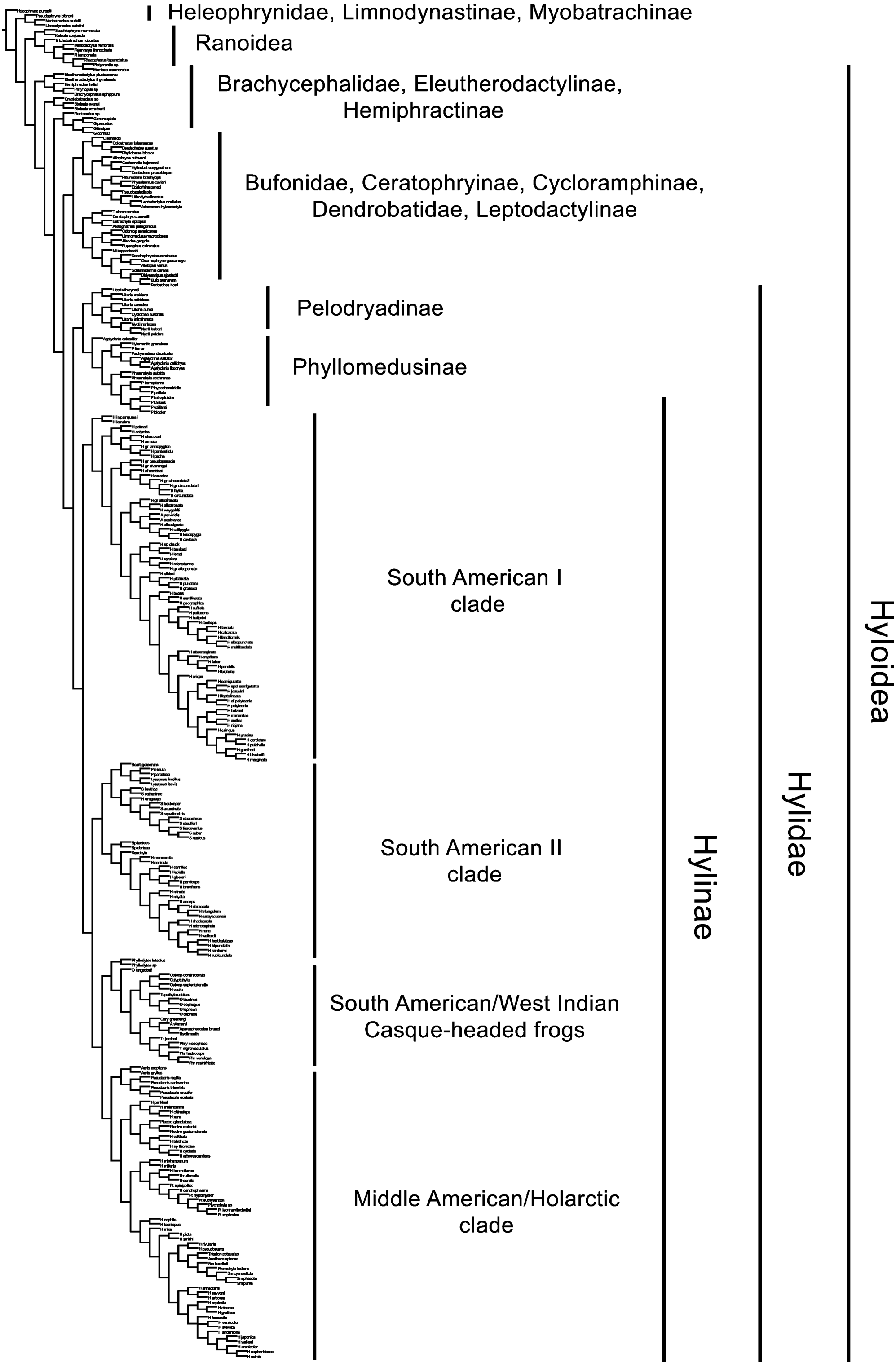
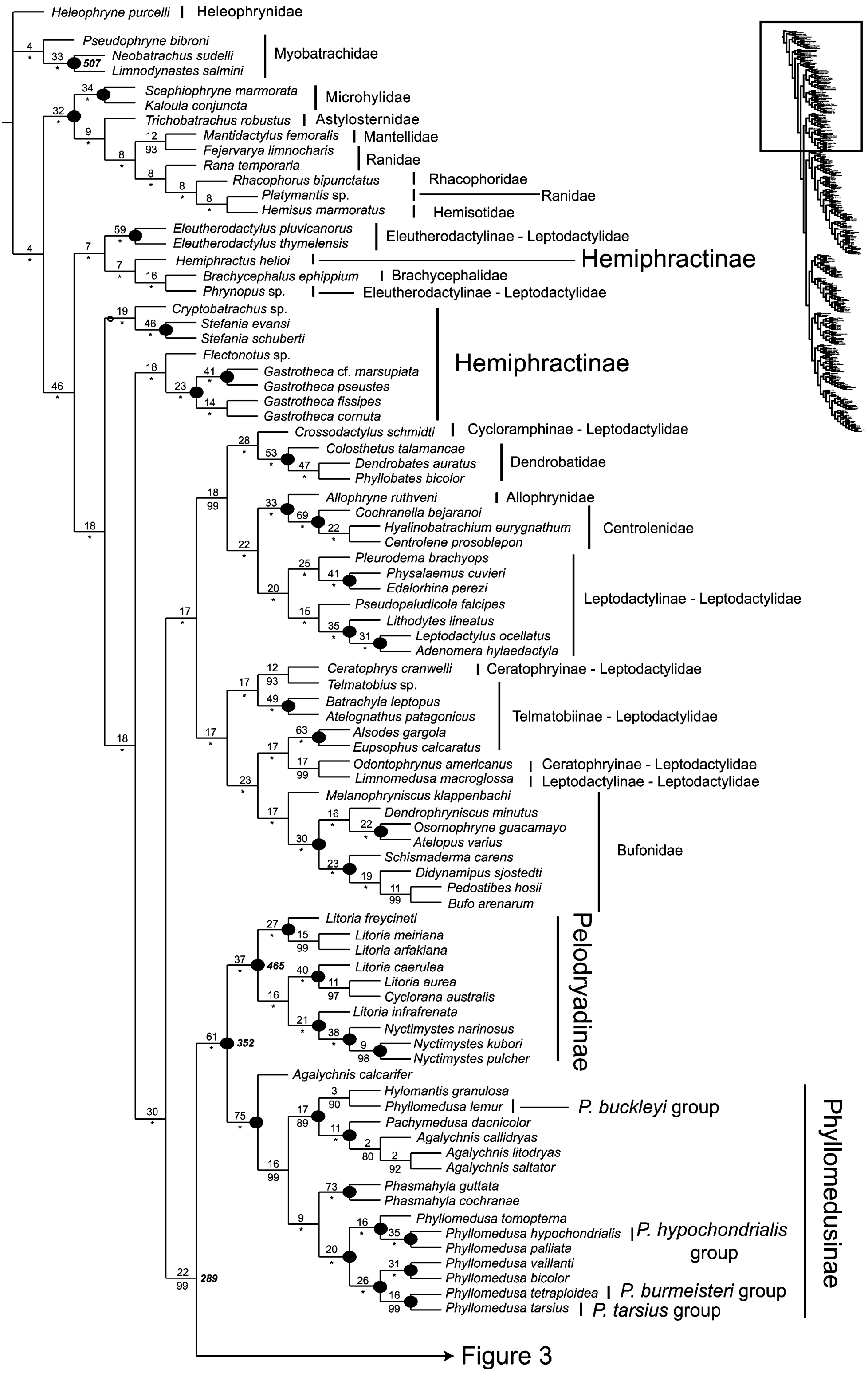
Fig. 1. A reduced image of the strict consensus of the four most parsimonious trees showing the major patterns of relationships of the outgroups, hylid subfamilies, and the four major clades of Hylinae recovered in the analysis.


Heleophryne purcelli
Pseudophryne bibroni
Neobatrachus sudelli
Limnodynastes salmini
Scaphiophryne marmorata
Kaloula conjuncta
Trichobatrachus robustus
Mantidactylus femoralis
Fejervarya limnocharis
R temporaria
Rhacophorus bipunctatus
Platymantis sp
Hemisus marmoratus
Eleutherodactylus pluvicanorus
Eleutherodactylus thymelensis
Hemiphractus helioi
Phrynopus sp
Brachycephalus ephippium
Cryptobatrachus sp
Stefania evansi
Stefania schuberti
Flectonotus sp
G marsupiata
G pseustes
G fissipes
G cornuta
C schmidti
Colostethus talamancae
Dendrobates auratus
Phyllobates bicolor
Allophryne ruthveni
Cochranella bejaranoi
Hyalinobat eurygnathum
Centrolene prosoblepon
Pleurodema brachyops
Physalaemus cuvieri
Edalorhina perezi
Pseudopaludicola
Lithodytes lineatus
Leptodactylus ocellatus
Adenomera hylaedactyla
T cfmarmoratus
Ceratophrys cranwelli
Batrachyla leptopus
Atelognathus patagonicus
Odontop americanus
Limnomedusa macroglossa
Alsodes gargola
Eupsophus calcaratus
M klappenbachi
Dendrophryniscus minutus
Osornophryne guacamayo
Atelopus varius
Schismaderma carens
Didynamipus sjostedti
Bufo arenarum
Pedostibes hosii
Litoria freycineti
Litoria meiriana
Litoria arfakiana
Litoria caerulea
Litoria aurea
Cyclorana australis
Litoria infrafrenata
Nycti narinosa
Nycti kubori
Nycti pulchra
Agalychnis calcarifer
Hylomantis granulosa
P lemur
Pachymedusa dacnicolor
Agalychnis saltator
Agalychnis callidryas
Agalychnis litodryas
Phasmahyla guttata
Phasmahyla cochranae
P tomopterna
P hypochondrialis
P palliata
P tetraploidea
P tarsius
P vaillanti
P bicolor
H inparquesi
H kanaima
H palmeri
H colymba
H charazani
H armata
H gr larinopygion
H pantosticta
H pacha
H gr pseudopseudis
H gr alvarengai
H cf martinsi
H astartea
H gr circumdata2
H gr circumdata1
H hylax
H circumdata
H gr albofrenata
H albofrenata
H weygoldti
A perviridis
A cochranae
H albosignata
H callipygia
H leucopygia
H cavicola
H sp chuck
H benitezi
H lemai
H roraima
H microderma
H gr albopunctu
H sibleszi
H picturata
H punctata
H granosa
H boans
H semilineata
H geographica
H rufitela
H pellucens
H heilprini
H raniceps
H fasciata
H calcarata
H lanciformis
H albopunctata
H multifasciata
H albomarginata
H crepitans
H faber
H pardalis
H biobeba
H ericae
H semiguttata
H spcf semiguttata
H joaquini
H leptolineata
H cf polytaenia
H polytaenia
H balzani
H marianitae
H andina
H riojana
H caingua
H prasina
H cordobae
H pulchella
H guentheri
H bischoffi
H marginata
Scart goinorum
P minuta
P paradoxa
Lysapsus limellus
Lysapsus laevis
S berthae
S catharinae
H uruguaya
S boulengeri
S acuminata
S squalirostris
S elaeochroa
S staufferi
S fuscovarius
S ruber
S nasicus
Sp lacteus
Sp dorisae
Xenohyla
H marmorata
H senicula
H carnifex
H labialis
H giesleri
H parviceps
H brevifrons
H minuta
H miyatai
H anceps
H ebraccata
H triangulum
H sarayacuensis
H rhodopepla
H microcephala
H nana
H walfordi
H berthalutzae
H bipunctata
H sanborni
H rubicundula
Phyllodytes luteolus
Phyllodytes sp
O langsdorfi
Osteop dominicensis
Calyptahyla
Osteop septentrionalis
H vasta
Tepuihyla edelcae
O taurinus
O oophagus
O leprieuri
O cabrerai
Cory greeningi
A siemersi
Aparasphenodon brunoi
Nyctimantis
Tr jordani
Phry mesophaea
T nigromaculatus
Phr hadroceps
Phr venulosa
Phr resinifictrix
Acris crepitans
Acris gryllus
Pseudacris regilla
Pseudacris cadaverina
Pseudacris triseriata
Pseudacris crucifer
Pseudacris ocularis
H perkinsi
H melanomma
H chimalapa
H xera
Plectro glandulosa
Plectro matudai
Plectro guatemalensis
H calthula
H bistincta
H sp thorectes
H cyclada
H arborescandens
H miotympanum
H miliaria
H bromeliacea
D ruliocculis
D sorafia
Pt spinipollex
H dendrophasma
Pt hypomykter
Pt euthysanota
Ptychohyla sp
Pt leonhardschultzei
Pt zophodes
H nephila
H taeniopus
H mixe
H picta
H smithi
H rivularis
H pseudopuma
Triprion petasatus
Anotheca spinosa
Sm baudinii
Pternohyla fodiens
Sm cyanosticta
Sm phaeota
Sm puma
H annectans
H savygni
H arborea
H squirella
H cinerea
H gratiosa
H femoralis
H versicolor
H avivoca
H andersonii
H japonica
H walkeri
H arenicolor
H euphorbiacea
H eximia
Heleophrynidae, Limnodynastinae, Myobatrachinae
Ranoidea
Brachycephalidae, Eleutherodactylinae, Hemiphractinae
Bufonidae, Ceratophryinae, Cycloramphinae, Dendrobatidae, Leptodactylinae
Pelodryadinae
Phyllomedusinae
South American I clade
South American II clade
South American/West Indian Casque-headed frogs
Middle American/Holarctic clade
Hylinae
Hylidae
Hyloidea


Heleophryne purcelli
Heleophrynidae
Pseudophryne bibroni
Neobatrachus sudelli
Limnodynastes salmini
507
Myobatrachidae
Scaphiophryne marmorata
Kaloula conjuncta
Microhylidae
Trichobatrachus robustus
Astylosternidae
Mantidactylus femoralis
Mantellidae
Fejervarya limnocharis
Rana temporaria
Ranidae
Rhacophorus bipunctatus
Rhacophoridae
Platymantis sp.
Ranidae
Hemisus marmoratus
Hemisotidae
Eleutherodactylus pluvicanorus
Eleutherodactylus thymelensis
Eleutherodactylinae - Leptodactylidae
Hemiphractus helioi
Hemiphractinae
Brachycephalus ephippium
Brachycephalidae
Phrynopus sp.
Eleutherodactylinae - Leptodactylidae
Cryptobatrachus sp.
Stefania evansi
Stefania schuberti
Flectonotus sp.
Gastrotheca cf. marsupiata
Gastrotheca pseustes
Gastrotheca fissipes
Gastrotheca cornuta
Hemiphractinae
Crossodactylus schmidti
Cycloramphinae - Leptodactylidae
Colosthetus talamancae
Dendrobates auratus
Phyllobates bicolor
Dendrobatidae
Allophryne ruthveni
Allophrynidae
Cochranella bejaranoi
Hyalinobatrachium eurygnathum
Centrolene prosoblepon
Centrolenidae
Pleurodema brachyops
Physalaemus cuvieri
Edalorhina perezi
Pseudopaludicola falcipes
Lithodytes lineatus
Leptodactylus ocellatus
Adenomera hylaedactyla
Leptodactylinae - Leptodactylidae
Ceratophrys cranwelli
Ceratophryinae - Leptodactylidae
Telmatobius sp.
Batrachyla leptopus
Atelognathus patagonicus
Alsodes gargola
Eupsophus calcaratus
Telmatobiinae - Leptodactylidae
Odontophrynus americanus
Ceratophryinae - Leptodactylidae
Limnomedusa macroglossa
Leptodactylinae - Leptodactylidae
Melanophryniscus klappenbachi
Dendrophryniscus minutus
Osornophryne guacamayo
Atelopus varius
Schismaderma carens
Didynamipus sjostedti
Pedostibes hosii
Bufo arenarum
Bufonidae
Litoria freycineti
Litoria meiriana
Litoria arfakiana
465
Litoria caerulea
Litoria aurea
Cyclorana australis
Litoria infrafrenata
Nyctimystes narinosus
Nyctimystes kubori
Nyctimystes pulcher
Pelodryadinae
352
Agalychnis calcarifer
Hylomantis granulosa
Phyllomedusa lemur
P. buckleyi group
Pachymedusa dacnicolor
Agalychnis callidryas
Agalychnis litodryas
Agalychnis saltator
Phasmahyla guttata
Phasmahyla cochranae
Phyllomedusa tomopterna
Phyllomedusa hypochondrialis
Phyllomedusa palliata
P. hypochondrialis group
Phyllomedusa vaillanti
Phyllomedusa bicolor
Phyllomedusa tetraploidea
P. burmeisteri group
Phyllomedusa tarsius
P. tarsius group
Phyllomedusinae
289
Figure 3

Burton (2004) assumed that Hylidae, Centrolenidae, and Allophrynidae formed a monophyletic group. Our analysis did not include the morphological characters employed by Haas (2003) in his analysis, nor does our pelodryadine taxon sampling match his. For this reason, our results are not directly comparable to his, and we do not consider the monophyly of the Pelodryadinae a settled issue.

In our analysis, the presence of a tendon of the m. flexor ossis metatarsi II arising only from distal tarsal 2–3 is a synapomorphy of Pelodryadinae plus Phyllomedusinae. Furthermore, the presence of the pigment pterorhodin (Bagnara and Ferris, 1975) may be a synapomorphy of this clade, although the distribution of this character state requires further elucidation. Both Pelodryadinae and Phyllomedusinae share the presence of supplementary elements of the m. intermandibularis. These elements are apical in Pelodryadinae and posterolateral in Phyllomedusinae (Tyler, 1971). Both character states have previously been considered nonhomologs (Tyler and Davies, 1978a) that separately support the monophyly of each of these groups (Duellman, 2001). In the context of our analysis, however, the sole presence of supplementary elements is more parsimoniously interpreted as a putative synapomorphy of this clade, while it is ambiguous which of the positions of the elements (apical or posterolateral) is the plesiomorphic state. Note that this ambiguity is a potential challenge to the only known morphological synapomorphy of Pelodryadinae. Future anatomical work will corroborate whether these two morphologies could be considered as states of the same transformation series, as is tentatively being done here.

PELODRYADINAE

As stated previously, our analysis does not include enough of a comprehensive taxon sampling of Pelodryadinae to address its internal relationships in a meaningful way. Nonetheless, our results corroborate the long-held idea (see previous discussions) that *Cyclorana* and *Nyctimystes* are nested within *Litoria*. For the reasons detailed earlier, our analysis is not an overly strong test of the positions of the former two genera within *Litoria*. Nevertheless, the single exemplar of *Cyclorana* is the sister taxon of *L. aurea*, an exemplar of the *L. aurea* group with which *Cyclorana* is supposed to be related based on various sources of evidence (King et al., 1979; Tyler, 1979; Tyler et al., 1981). *Nyctimystes* is the sister taxon of *L. infrafrenata*, one of the groups of *Litoria* that Tyler and Davies (1979) considered as possibly related to *Nyctimystes* based on morphological similarities of its skull with that of *N. zweifeli*. The other groups they considered are mostly the montane species of *Litoria*; from these we included a single exemplar, *L. arfakiana*, that is quite distant from *Nyctimystes*, being the sister taxon of *L. meiriana* (with which, incidentally, it also shares the presence of a flange in the medial surface of metacarpal III; Tyler and Davies, 1978b). In our analysis, the fibrous origin of the m. extensor brevis superficialis digiti III on the distal end of the fibulare is a synapomorphy of Pelodryadinae; we are skeptical, however, that this optimization will hold with better sampled outgroups for muscular characters, because Burton (2004) found the same character state in several leptodactylids, none of which is included in our outgroup sample.

PHYLLOMEDUSINAE

Several authors (Funkhouser, 1957; Duellman, 1970; Donnelly et al., 1987; Hoogmoed

←

Fig. 2. A partial view of the strict consensus showing the relationships of the outgroups, Pelodryadinae, and Phyllomedusinae. Numbers above nodes are Bremer support values. Numbers below nodes are Parsimony Jackknife absolute frequencies; those with an asterisk (*) have a 100% frequency. Numbers in boldfaced italic are node numbers for the list of morphological synapomorphies (see appendix 3). Black circles denote nodes that are present in the quick consensus estimation. The arrow shows alternative placement of the (*Cryptobatrachus* + *Stefania*) clade when using the 3:1:2 weighting scheme (see text).

and Cadle, 1991) noticed the distinctiveness of *Agalychnis calcarifer* and its presumed sister taxon, *A. craspedopus*, from the other species of *Agalychnis*. Corroborating the results of Duellman (2001), we found no evidence for the monophyly of *Agalychnis*. Our results indicate that *A. calcarifer* is the sister group of the remaining Phyllomedusinae, and it has no close relationship with the other exemplars of *Agalychnis*.

Phyllomedusa lemur, the only exemplar of the *P. buckleyi* group available for this analysis, is recovered, although with low Bremer support (3), as the sister group of *Hylomantis*, and it is only distantly related with the other exemplars of *Phyllomedusa*. This situation corroborates previous suggestions (Funkhouser, 1957; Cannatella, 1980; Jungfer and Weygoldt, 1994) that the *P. buckleyi* group should not be included in *Phyllomedusa*. Cruz (''1988'' [1989]) suggested, on the basis of iris coloration, skin texture, poor development of webbing, and slender body, that *Hylomantis* is related to two species of the *P. bukleyi* group, *P. buckleyi* and *P. psilopygion*. On the basis of the same character states, Cruz (1990) associated the *P. buckleyi* group with both *Hylomantis* and *Phasmahyla*. Our results support these ideas only in part, because while our only exemplars of *Hylomantis* and the *P. buckleyi* group are each monophyletic, *Phasmahyla* is more closely related to *Phyllomedusa* (excluding the *P. buckleyi* group).

We had no clear idea regarding the position of *Hylomantis* and *Phasmahyla*. Morphologically, the evidence is conflicting in that each one shares at least one different possible synapomorphy with the restricted *Phyllomedusa* (*Phyllomedusa* excluding the *P. buckleyi* group). *Phasmahyla* has the same type of nest where the eggs are wrapped in a leaf; nests are unknown in *Hylomantis*, but species of this genus share with *Phyllomedusa* (excluding the *P. buckleyi* group) the presence of the slip of the m. depressor mandibulae that originates from the dorsal fascia at the level of the m. dorsalis scapulae (Cruz, 1990; Duellman et al., 1988b), a character state that is absent in all other Phyllomedusinae. Our analysis recovers *Phasmahyla* as the sister group of the restricted *Phyllomedusa*, suggesting that the eggs wrapped in a leaf are a synapomorphy of this clade.

MAJOR PATTERNS OF RELATIONSHIPS WITHIN HYLINAE

For purposes of discussion, we consider Hylinae to be composed of four major clades (fig. 1), called here: (1) the South American clade I; (2) South American clade II (SA-II); (3) Middle American/Holarctic clade; and (4) South American/West Indian Casque-headed Frogs. These major sections and their subclades will be discussed in this order.

SOUTH AMERICAN CLADE I

This clade is composed of all Gladiator Frogs, the Andean stream-breeding *Hyla*, the genus *Aplastodiscus*, and a Tepuian clade of *Hyla*. It contains five major clades (fig. 3). The first of these is called the Tepuian clade, and is composed solely of two exemplars of the *H. aromatica* and *H. geographica* groups. The second clade is composed of all Andean stream-breeding *Hyla*. The third is composed of all the exemplars of the *H. circumdata*, *H. martinsi*, and *H. pseudopseudis* groups, from southeastern Brazil, and we are calling it informally the Atlantic/Cerrado clade. The fourth is composed of the southeastern Brazilian *H. albosignata* and *H. albofrenata* complexes of the larger, nonmonophyletic *H. albomarginata* group plus the two species of *Aplastodiscus*, and we are calling it informally the Green clade. The fifth clade is composed of all the remaining species groups (*H. geographica*, *H. pulchella*, *H. boans*, *H. granosa*, *H. punctata*, *H. albomarginata* complex of the *H. albomarginata* group) and unassigned species associated in the past with the Gladiator Frogs, and we are calling it informally the TGF clade (for True Gladiator Frogs.)

Six currently recognized species groups within the South American clade I are not monophyletic. The *Hyla albomarginata* group is not monophyletic because its three ''complexes'' defined by Cruz and Peixoto (''1985'' [1987]) are spread throughout the Green clade and the TGF clade. The *H. albomarginata* complex is not monophyletic, with its species being related with different groups in the TGF clade (see below). The *H.*

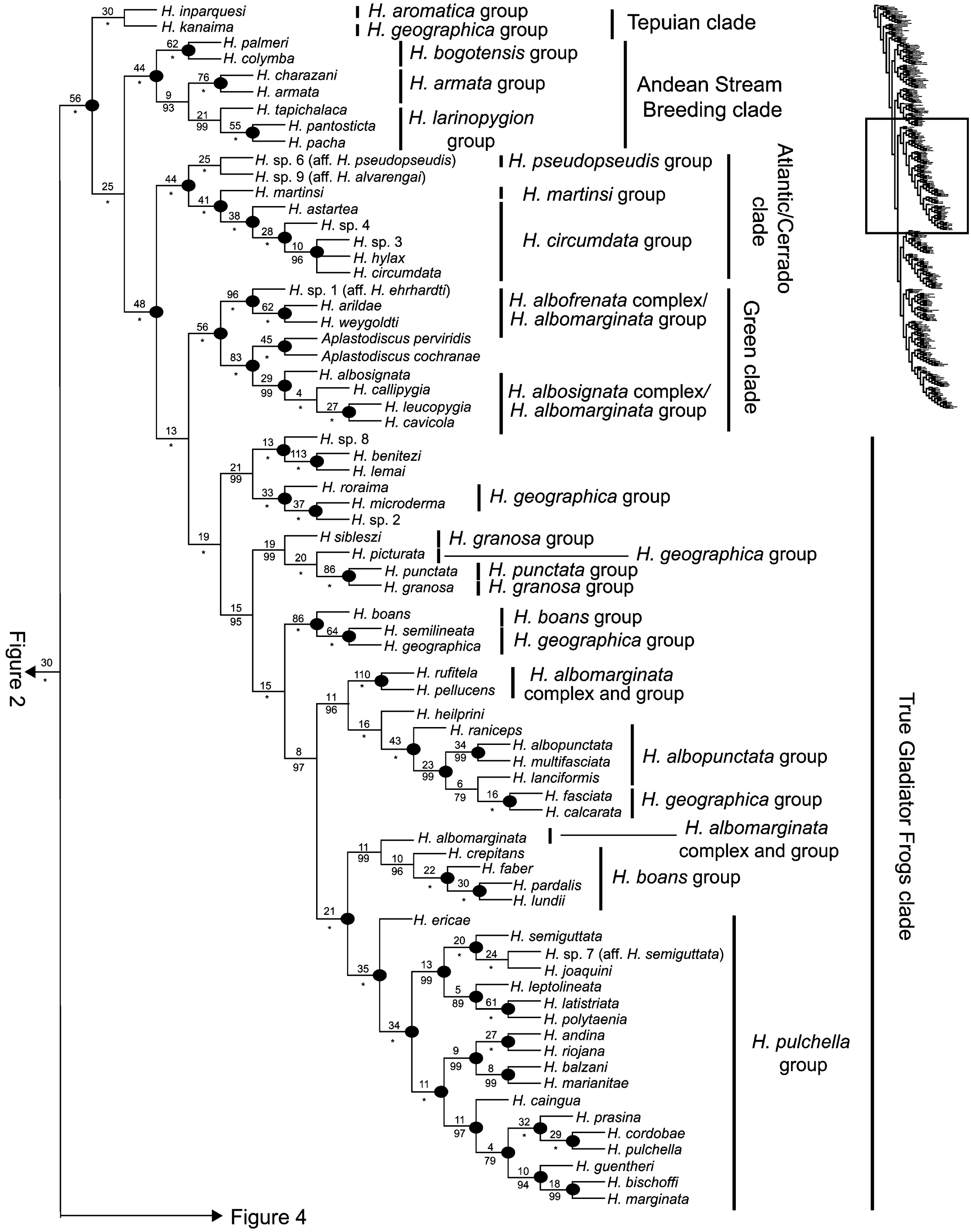


Fig. 3. A partial view of the strict consensus showing the relationships of the South American I clade and its correspondence with the currently recognized species groups. Numbers above nodes are Bremer support values. Numbers below nodes are Parsimony Jackknife absolute frequencies; those with an asterisk (*) have a 100% frequency. Black circles denote nodes that are present in the quick consensus estimation.

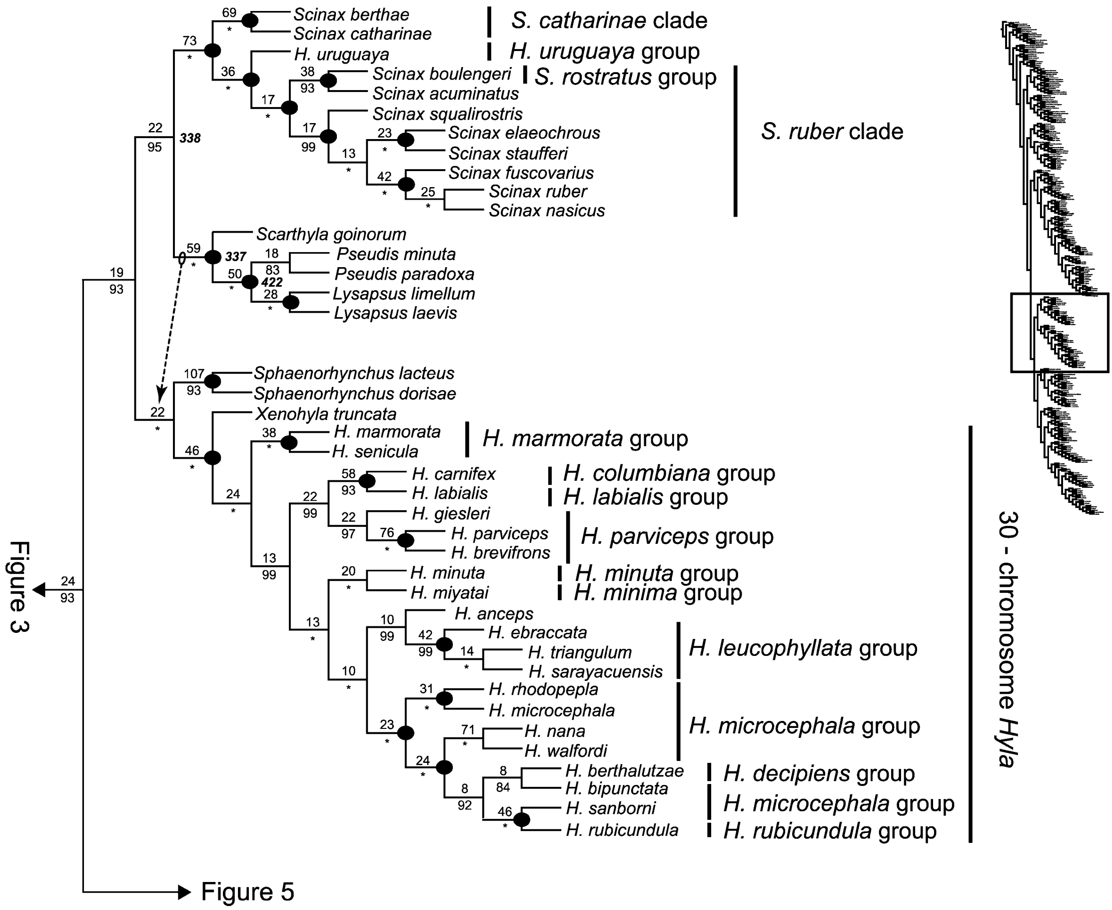


Fig. 4. A partial view of the strict consensus showing the relationships of the South American II clade and its correspondence with the currently recognized species groups. Numbers above nodes are Bremer support values. Numbers below nodes are Parsimony Jackknife absolute frequencies; those with an asterisk (*) have a 100% frequency. Numbers in boldfaced italic are node numbers for the list of morphological synapomorphies (see appendix 3). Black circles denote nodes that are present in the quick consensus estimation. The arrow shows alternative placement of the (*Scarthyla* + (*Lysapsus* + *Pseudis*)) clade when using the 3:1:2 weighting scheme (see text).

albosignata complex is monophyletic, as is the *H. albofrenata* complex. These two complexes, however, do not form a monophyletic group, because *Aplastodiscus* is the sister group to the *H. albosignata* complex, and this clade is sister to the *H. albofrenata* complex. Within the TGF Clade, the only group that is not represented by a single exemplar (the *Hyla punctata* group) that results as monophyletic is the *H. pulchella* group. The *H. albomarginata* complex, *H. albopunctata*, *H. boans*, *H. geographica*, and *H. granosa* groups are nonmonophyletic.

Hyla pellucens and *H. rufitela* are the sister group of the clade composed of *H. heilprini* and the paraphyletic *H. albopunctata* group (see below); *H. albomarginata* is the sister taxon of a fragment of the *H. boans* group (see below). The *H. albopunctata* group is paraphyletic inasmuch as *H. fasciata* plus *H. calcarata* is nested within it. The *H. boans* group is polyphyletic because the mostly southeastern Brazil/northeastern Argentina exemplars (*H. faber*, *H. lundii*, *H. pardalis*, *H. crepitans*, and *H. albomarginata*) together with *H. albomarginata* are the sister taxon of the *H. pulchella* group and are only distantly related to *H. boans*. *Hyla* *boans* is the sister taxon of *H. geographica* plus *H. semilineata*. The *H. geographica* group is rampantly polyphyletic, with its exemplars partitioned into five different clades within the South American clade I: (1) *H. kanaima* is the sister taxon of *H. inparquesi*, the single exemplar of the *H. aromatica* group; (2) *H. roraima* and *H. microderma* form a monophyletic group with four Guayanese and one Amazonian species; (3) *Hyla picturata* is related to the exemplars of the *H. punctata* and *H. granosa* groups; (4) *Hyla semilineata* + *H. geographica* are related to *H. boans*; and (5) *H. fasciata* + *H. calcarata* are nested within the *H. albopunctata* group as detailed above. The *H. granosa* group is paraphyletic by having *H. picturata* and *H. punctata* nested within it.

Andean Stream-Breeding *Hyla* and the Tepuian Clade

The monophyly of the Andean stream-breeding *Hyla* is congruent with suggestions presented by Duellman et al. (1997) and Mijares-Urrutia (1997), who noticed similarities in larval morphology of the *H. bogotensis* and *H. larinopygion* groups. Duellman et al. (1997) presented a phylogenetic analysis restricted to wholly or partially Andean species groups of *Hyla*. In their most parsimonious tree, the *H. armata*, *H. bogotensis*, and *H. larinopygion* groups formed a monophyletic group supported by three transformations in tadpole morphology: the enlarged, ventrally oriented oral disc; the complete marginal papillae; and a labial tooth row formula 4/6 or higher.

Duellman et al. (1997) suggested a close relationship between the *H. armata* and *H. larinopygion* groups based on the presence in males of a greatly enlarged prepollex lacking a projecting spine. While our results are congruent with this, note that males of the *H. bogotensis* group also have a prepollex with the same external morphology as those of the *H. armata* and *H. larinopygion* groups. Kizirian et al. (2003) suggested that the *H. armata* group was nested in the *H. larinopygion* group. Our results do not support this suggestion. However, this could be a consequence of the few exemplars of the *H. larinopygion* group available for our study.

Kizirian et al. (2003) had doubts about the placement of *Hyla tapichalaca*. Faivovich et al. (2004) showed that this species is related to the *H. armata–H. larinopygion* groups (although they only included *H. armata* in their analysis). Our results go a step further, indicating a closer relationship with the *H. larinopygion* group.

Hyla inparquesi and *H. kanaima* forming the sister taxon of all the remaining South American clade I is an unexpected result. On the basis of morphology, we expected our only exemplar of the *H. aromatica* group, *H. inparquesi*[22], to be related to the Andean stream-breeding clade of *Hyla*, because both share the character states that Duellman et al. (1997) suggested as synapomorphies in support of the monophyly of the Andean stream-breeding *Hyla*: (1) known larvae with ventral, enlarged oral discs; (2) complete marginal papillae; and (3) with a minimum labial tooth row formula of 4/6. Furthermore, adults of the *H. aromatica* group share a greatly enlarged prepollex without a projecting spine in males that, as we mentioned above, is present in most species of Andean stream-breeding *Hyla* (the only known exception being *H. tapichalaca*; Kizirian et al., 2003).

This sister-group relationship between the Tepuian clade and all the remaining groups of the South American clade I has further implications. Based on the available material, Duellman et al. (1997) considered the prepollex greatly enlarged without a projecting spine to be an intermediate state in an ordered transformation series from prepollex not greatly enlarged to prepollex greatly enlarged with a projecting spine. Our topology implies that the greatly enlarged prepollex without a projecting spine is a synapomorphy of the whole South American clade I (with subsequent transformations, including the development of a projecting spine). However, *H. kanaima* does not have an enlarged prepollex as prominent as that found in the *H. armata*, *H. aromatica*, *H. bogotensis*, and *H. larinopygion* groups. In order to clarify this situation, it would be necessary to (1) define the prepollex character states osteologically, and (2) include a denser sampling

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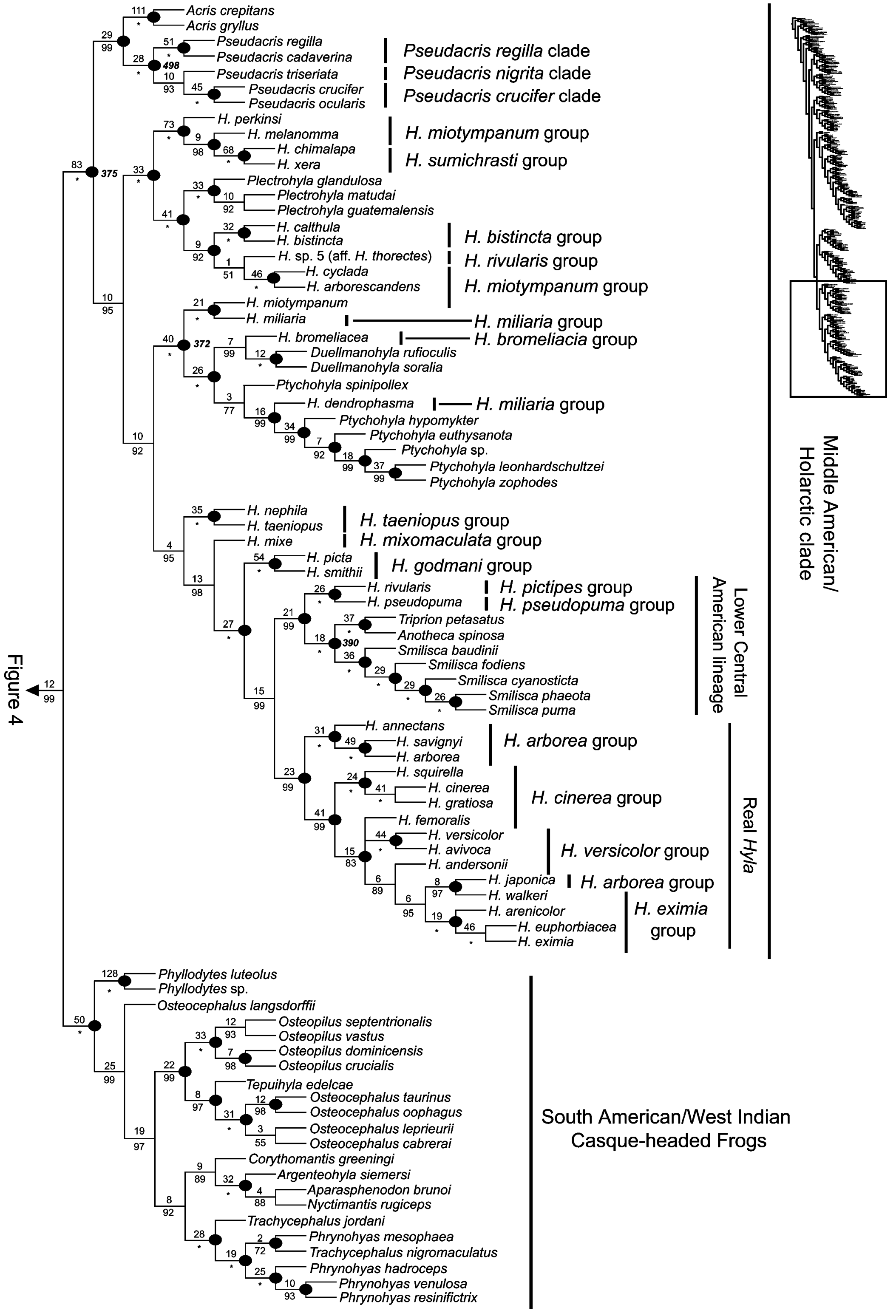
[22] The tadpole of *Hyla kanaima* is unknown.


Acris crepitans
Acris gryllus
Pseudacris regilla
Pseudacris cadaverina
Pseudacris triseriata
Pseudacris crucifer
Pseudacris ocularis
Pseudacris regilla clade
Pseudacris nigrita clade
Pseudacris crucifer clade
H. perkinsi
H. melanomma
H. chimalapa
H. xera
H. miotympanum group
H. sumichrasti group
Plectrohyla glandulosa
Plectrohyla matudai
Plectrohyla guatemalensis
H. calthula
H. bistincta
H. sp. 5 (aff. H. thorectes)
H. cyclada
H. arborescandens
H. bistincta group
H. rivularis group
H. miotympanum group
H. miotympanum
H. miliaria
H. miliaria group
H. bromeliacea
H. bromeliacia group
Duellmanohyla rufioculis
Duellmanohyla soralia
Ptychohyla spinipollex
H. dendrophasma
H. miliaria group
Ptychohyla hypomykter
Ptychohyla euthysanota
Ptychohyla sp.
Ptychohyla leonhardschultzei
Ptychohyla zophodes
H. nephila
H. taeniopus
H. taeniopus group
H. mixe
H. mixomaculata group
H. picta
H. smithii
H. godmani group
H. rivularis
H. pictipes group
H. pseudopuma
H. pseudopuma group
Triprion petasatus
Anotheca spinosa
Smilisca baudinii
Smilisca fodiens
Smilisca cyanosticta
Smilisca phaeota
Smilisca puma
Lower Central American lineage
H. annectans
H. savignyi
H. arborea
H. arborea group
H. squirella
H. cinerea
H. gratiosa
H. cinerea group
H. femoralis
H. versicolor
H. avivoca
H. versicolor group
H. andersonii
H. japonica
H. walkeri
H. arborea group
H. arenicolor
H. euphorbiacea
H. eximia
H. eximia group
Real Hyla
Middle American/Holarctic clade
Figure 4
Phyllodytes luteolus
Phyllodytes sp.
Osteocephalus langsdorffii
Osteopilus septentrionalis
Osteopilus vastus
Osteopilus dominicensis
Osteopilus crucialis
Tepuihyla edelcae
Osteocephalus taurinus
Osteocephalus oophagus
Osteocephalus leprieurii
Osteocephalus cabrerai
Corythomantis greeningi
Argenteohyla siemersi
Aparasphenodon brunoi
Nyctimantis rugiceps
Trachycephalus jordani
Phrynohyas mesophaea
Trachycephalus nigromaculatus
Phrynohyas hadroceps
Phrynohyas venulosa
Phrynohyas resinifictrix
South American/West Indian Casque-headed Frogs

of the *H. aromatica* group, to better understand its relationship with *H. kanaima*. (Perhaps the character state of *H. kanaima* could be interpreted as a reversal.)

Our topology implies an interesting scenario regarding the evolution of larval morphology in the South American clade I; that is, that larval morphology of the Atlantic/Cerrado, Green, and TGF clades evolved from an ancestor with the highly modified morphology typical of stream larvae (including large numbers of labial tooth rows, a large oral disc with complete marginal papillae, and relatively low fins) that during evolution, underwent a transformation of these character states (specifically, reduction in labial tooth row formulae, a reduced oral disc, and formation of an anterior gap in the marginal papillae). These transformations were coincident with distributional shifts from high-elevation mountain streams (as in the Tepuian and Andean stream-breeding clades) toward lower elevation forest mountain streams (the cases of the Atlantic/Cerrado clade, the Green clade, and, and some taxa of the TGF clade), and Amazonian lowlands and the Cerrado-Chaco (several taxa of the TGF clade).

Gladiator Frogs

Duellman et al. (1997) suggested the existence of a clade composed of the *Hyla albomarginata*, *H. albopunctata*, *H. boans*, *H. circumdata*, *H. geographica*, and *H. pulchella* groups. The synapomorphy supporting this clade is, according to these authors, the presence of ‘‘an enlarged prepollical spine lacking a quadrangular base’’. Faivovich et al. (2004), based on the analysis of mitochondrial DNA sequences and on the observation (Garcia and Faivovich, personal obs.) that *H. punctata* and the *H. polytaenia* group show the same morphology of the prepollical spine, argued that these additional groups also belong to that clade (these authors further included the *H. polytaenia* group within the *H. pulchella* group), which was called earlier in this paper ‘‘Gladiator Frogs’’. Our results indicate that a clade with the composition suggested by Duellman et al. (1997) and Faivovich et al. (2004) is paraphyletic because *Aplastodiscus* is nested within it; furthermore, *H. kanaima* of the *H. geographica* group is only distantly related to this clade.

Atlantic/Cerrado Clade

Our results corroborate the long-suspected association of the *Hyla circumdata* group with the groups of *H. pseudopseudis* and *H. martinsi* (Bokermann, 1964a; Cardoso, 1983; Caramaschi and Feio, 1990; Pombal and Caramaschi, 1995), even though the monophyly of these two groups could not be tested by our analysis. We also consider as corroborated the suspected relationship of the *Hyla circumdata* and *H. pseudopseudis* groups with *H. alvarengai* (Bokermann, 1964a; Duellman et al., 1997), because *Hyla* sp. 9 (aff. *H. alvarengai*) is nested in this clade.

Unfortunately, due to the unavailability of samples, we could not test the relationships of the *Hyla claresignata* group with this clade. Considering the phylogenetic context of the Atlantic/Cerrado clade within the South American clade I, we must revisit the apparent synapomorphies of the *H. claresignata* group mentioned earlier (oral disc completely surrounded by marginal papillae, and 7/12–8/13 labial tooth rows). The presence and distribution of these character states in the Tepuian and Andean stream-breeding *Hyla* clades is suggestive, not of a closer relationship of the *H. claresignata* group with any of them (these character states are plesiomorphies in this context), but of the nature of its relationship with the Atlantic/Cerrado clade. Perhaps the *H. claresignata* group is not a

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Fig. 5. A partial view of the strict consensus showing the relationships of the Middle American–Holarctic and South American/West Indian Casqued-headed frog clades and it correspondence with the currently recognized species groups. Numbers above nodes are Bremer support values. Numbers below nodes are Parsimony Jackknife absolute frequencies; those with an asterisk (*) have a 100% frequency. Numbers in boldfaced italic are node numbers for the list of morphological synapomorphies (see appendix 3). Black circles denote nodes that are present in the quick consensus estimation.

member of the Atlantic/Cerrado clade, but is a basal group related either to the Tepuian or Andean stream-breeding clade, or perhaps it is even the sister taxon of the clade composed of the Atlantic/Cerrado, Green, and TGF clades. At this point we are not aware of evidence favoring any of these alternatives.

Green Clade

Lutz (1950) was the first to suggest that *Aplastodiscus* was related to species latter included in the *Hyla albosignata* complex, as defined by Cruz and Peixoto (''1985'' [1987]). This was supported by Garcia et al. (2001a) based on the presence of enlarged internal metacarpal and metatarsal tubercles and unpigmented eggs. More recently, Haddad et al. (2005) described the reproductive mode of *Aplastodiscus perviridis*, which includes egg deposition in a subterranean nest excavated by the male, where exotrophic larvae spend the early stages of development until flooding releases them to a nearby water body. This mode is the same as that observed in one species of the *H. albosignata* complex, *H. leucopygia* (Haddad and Sawaya, 2000), and for the undescribed species of the *H. albofrenata* complex included in our analysis, *Hyla* sp.1 (aff. *H. ehrhardti*) (Hartmann et al., 2004); this mode is further suspected to occur in all species of both the *H. albosignata* and *H. albofrenata* complexes (Haddad and Sawaya, 2000, Hartmann et al., 2004). Species included in the *H. albomarginata* complex instead lay their eggs on the water film surface (Duellman, 1970). Based on the shared reproductive mode, Haddad et al. (2005) suggested that *Aplastodiscus* could be related to the *H. albofrenata* and *H. albosignata* complexes. Our results support the monophyly of both the *H. albofrenata* and *H. albosignata* complexes and their close relationship with *Aplastodiscus*, that is the sister taxon of the *H. albosignata* complex.

While we are not aware of nonmolecular synapomorphies for several nodes supported by molecular evidence, the few osteological data available for the South American clade I indicate that the Green clade and the TGF clade share the presence of transverse processes of the sacral diapophyses notably expanded distally, while species of the Atlantic/Cerrado clade (Bokermann, 1964a; Garcia 2003) and *H. tapichalaca* (Kizirian et al., 2003), the only Andean stream-breeding *Hyla* with any described postcranial osteology, have the transverse processes poorly expanded or not expanded at all. However, the distribution of this character state is in conflict with the presence of a prepollical spine in the Atlantic/Cerrado clade and the TGF clade, which is absent in the Green clade, where there is a fairly enlarged prepollex but no spine. A detailed study of prepollex morphology in these taxa would help to better define the relevant transformation series and it transformation sequences in the tree.

True Gladiator Frog Clade

The results imply the nonmonophyly of several species groups within this clade, as described earlier. This situation is not unexpected considering the paucity of evidence of monophyly previously available for most of them.

The monophyly of the group composed of the two unassigned species from the Guayana Highlands, *Hyla benitezi*, *H. lemai*, *Hyla* sp. 2, two members of the *H. geographica* group (*H. microderma* and *H. roraima*), and *Hyla* sp. 8 is further supported by the presence of a mental gland in males (Faivovich et al., in prep.)

In the DNA-based phylogenetic analysis of the *Hyla pulchella* group performed by Faivovich et al. (2004), *H. punctata* is the sister species of *H. granosa*, with this overall clade forming the sister taxon of a clade composed of the *H. albopunctata*, *H. geographica*, *H. albomarginata*, *H. boans*, and *H. pulchella* groups. In our analysis, *H. punctata*, our only exemplar of the group, is the sister taxon of *H. granosa*, and this taxon is at the apex of a pectinated series that includes *H. sibleszi* and, curiously, *H. picturata*. Prior to the analysis, we had no idea as to with which species group *H. picturata* would be related, but certainly we did not expect this colorful frog to be nested within a group of green species.

Our results lend only partial support for a relationship between *Hyla heilprini* and the *H. albomarginata* group, as tentatively suggested by Duellman (1974) and Trueb and Tyler (1974) based on overall pigmentation and the white peritoneum, because *H. heilprini* is the sister taxon of the *H. albopunctata* group (including a fragment of the *H. geographica* group), with *H. heilprini* plus this unit being the sister taxon of a fragment of the *H. albomarginata* group. The nonmonophyly of the *H. albopunctata* group corroborates comments advanced by de Sá (1995, 1996) as to the lack of evidence for its monophyly.

Hyla crepitans, *H. faber*, *H. lundii*, and *H. pardalis* form, together with *H. albomarginata*, a monophyletic group only distantly related to *H. boans*, the species that gives the name to the former group. Within this clade, the nest builders[23] *H. faber*, *H. lundii*, and *H. pardalis*, are monophyletic.

The polyphyly of the *Hyla boans* group has implications for the evolution of reproductive modes, in that it implies independent origins of nest-building behavior by males. Although theoretically possible, certainly no author had ever suggested that such a characteristic behavior as the nest building could be a homoplastic feature.[24] However, the molecular evidence points that way, and further evidence indicates that this or a similar reproductive mode also occurs in at least some species of the *H. circumdata* group (Pombal and Haddad, 1993, Pombal and Gordo, 2004), implying then at least three independent occurrences within the South American clade I. In a wider context, nest building was reported as well in Pelodryadinae in males of *Litoria jungguy* (Richards, 1993; using the name *L. lesueuri*, see Donnellan and Mahony [2004]), thus implying a fourth instance of homoplasy within Hylidae.

Our topology for the *Hyla pulchella* group is identical to that of Faivovich et al. (2004), including the exemplars of the former *H. polytaenia* group nested within it. Following Faivovich et al. (2004), we continue to recognize a *H. polytaenia* clade within the *H. pulchella* group. These authors stated that the lack of any pattern on the hidden surfaces of thighs was one of two possible morphological synapomorphies of this clade (with the other being the mostly striped dorsal pattern). This observation is mistaken, because the same character state occurs in *H. ericae* (Caramaschi and Cruz, 2000), *H. joaquini*, *H. marginata*, *H. melanopleura*, *H. palaestes*, and *H. semiguttata* (Duellman et al., 1997; Garcia et al., 2001b), suggesting that it actually may be a synapomorphy of a more inclusive clade whose contents are still undefined.

SOUTH AMERICAN II CLADE

The South American II clade (fig. 4) is composed of the 30-chromosome *Hyla*, the *Hyla uruguaya* group, *Lysapsus*, *Pseudis*, *Scarthyla*, *Scinax*, *Sphaenorhynchus*, and *Xenohyla*. It contains two main clades: one composed of *Lysapsus*, *Pseudis*, *Scarthyla*, and *Scinax* (including the *H. uruguaya* group), and the other composed of *Sphaenorhynchus*, *Xenohyla*, and all the exemplars of 30-chromosome *Hyla* species groups.

Within this clade, *Scinax* and the *Hyla microcephala* group are not monophyletic. *Scinax* has *H. uruguaya*, an exemplar of the *H. uruguaya* group, nested within it. The *H. microcephala* group is paraphyletic with respect to the available exemplars of the *H. decipiens* and *H. rubicundula* groups.

Relationships of *Scinax*

Several hypotheses have been advanced on the relationships of *Scinax*. *Aparasphenodon* was considered by Trueb (1970a) to be closely related to *Corythomantis* and, in turn, she considered these two genera to be nested within the (then) *Hyla rubra* group (currently the genus *Scinax*), based on overall similarities in cranial morphology. *Scarthyla* was considered to be related to *Scinax* by Duellman and de Sá (1988). Duellman and Wiens (1992) extended this to suggest that *Scarthyla* is the sister taxon of *Scinax*, which together form the sister taxon of *Sphaenorhynchus*. According to Duellman and Wiens (1992), character states supporting the monophyly of these three genera are narrow sacral diapophyses, anteriorly inclined ala-

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[23] Caldwell (1992) referred to the facultative nature of nest building in males of *Hyla crepitans* on specimens from Venezuela, far away from the range of *H. crepitans* in Brazil. Other authors (Lynch and Suarez-Mayorga, 2001), expressed doubts regarding the taxonomic status of northwestern South American *H. crepitans*, and unpublished molecular data from Faivovich and Haddad indicate that more than one species is involved.

[24] Our surprise with these results led us to sequence an additional sample of each *Hyla boans* and *H. faber* to check for the possibility of cross-contaminations; both were identical with the sequences we already had.

ry processes of the premaxillae, and tadpoles with large, laterally placed eyes. Duellman and Wiens (1992) suggested that possible morphological synapomorphies of *Scinax* and *Scarthyla* are reduced webbing on the hand and the presence of an anterior process of the hyale. *Tepuihyla* was suggested to be closely related with *Scinax*, this being supported by the absence or extreme reduction of webbing between toes I and II, adhesive discs wider than long, and the presence of double-tailed sperm (Ayarzagüena et al., ‘‘1992’’ [1993b]). This association was questioned by Duellman and Yoshpa (1996) on the grounds that the absence or extreme reduction of webbing between toes I and II was homoplastic among hylids (although Duellman and Wiens [1992] suggested this same character state to be a synapomorphy of *Scinax*). These authors suggested that the only evidence uniting *Tepuihyla* with *Scinax* could be the double-tailed sperm reported by Ayarzagüena et al. (‘‘1992’’ [1993b]) for *Tepuihyla* and by Fouquette and Delahoussaye (1977) for *Scinax*.[25]

Mijares-Urrutia et al. (1999) again suggested a close relationship of *Tepuihyla* with *Scinax*, but also with *Scarthyla* and *Sphaenorhynchus*–*Scinax* relatives, as suggested by Duellman and Wiens (1992). Mijares-Urrutia et al. (1999) also noted that *Tepuihyla* has rounded sacral diapophyses as found in these three genera (Duellman and Wiens, 1992).

Our results do not support a relationship of *Scinax* with *Aparasphenodon*, *Corythomantis*, or *Tepuihyla* because these three genera are nested within the South American/West Indies Casque-headed Frog clade. Furthermore, *Scinax* is not the sister group of *Scarthyla* but of a clade composed of *Scarthyla* plus *Lysapsus* and *Pseudis* (in the 1:1:1 analysis) or of all the remaining genera included in the South American II clade (in the 3:1:2 analysis).

Scinax is also paraphyletic with respect to the *Hyla uruguaya* group, for which Bokermann and Sazima (1973a) and Langone (1990) could not suggest affinities with any other hylids. Most recently, Kolenc et al. (‘‘2003’’ [2004]) observed in the larvae of *H. uruguaya* and *H. pinima* the morphological synapomorphies of the larvae of the *Scinax ruber* clade that were reported by Faivovich (2002), and they suggested a possible relationship between the *H. uruguaya* group and the *Scinax ruber* clade. Adults of the *H. uruguaya* group are quite characteristic morphologically, and perhaps as a consequence this group was never associated with any species of *Scinax* prior to Kolenc et al. (‘‘2003’’ [2004]).

Our results reveal that none of the outgroups employed by Faivovich (2002) in the phylogenetic analysis of *Scinax* is particularly close to *Scinax*; instead, all other components of the South American II clade are much more suitable to establish character-state polarities in this genus. Consequently, exemplars of these closer neighbors of *Scinax* need to be added, and the synapomorphies of *Scinax* resulting from that analysis need to be reevaluated.

Lysapsus, *Pseudis*, and *Scarthyla*

The sister-group relationship between *Scarthyla goinorum* and ‘‘pseudids’’ (*Lysapsus* + *Pseudis*), and this group being nested within Hylinae, corroborates recent findings by Darst and Cannatella (2004) and Haas (2003). Burton (2004) reported a likely synapomorphy for the *Scarthyla* plus the ‘‘pseu-

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[25] The interpretation of the double-tailed sperm as a putative synapomorphy is problematic for two practical reasons: (1) Taboga and Dolder (1998), Kuramoto (1998), and Costa et al. (2004) suggested that previous reports of double-tailed spermatozoa in several Anura based on optical microscopy are in error, because scanning electron microscopy and transmission electron microscopy of ultrathin serial sections show that actually there is a single axoneme/paraxonemal rod and the axial fiber. This suggests that there could be a problem of homology between the structures present in *Scinax* and those in *Tepuihyla*. (2) Even if we would assume that the problem is only about the correct interpretation of two different states in the optical microscopy (i.e., whether the ‘‘double tail’’ is actually a double flagellum or an axoneme/paraxonemal rod and the axial fiber), we find that the studied hylid taxa using optical microscopy are not numerous. Although Fouquette and Delahoussaye (1977) mentioned that they studied several hylines, an exhaustive list of those taxa was not given, and published records only include *Acris* (Delahoussaye, 1966), 10 species of *Hyla* (Delahoussaye, 1966; Pyburn, 1993; Kuramoto, 1998; Taboga and Dolder, 1998; Costa et al., 2004), 1 species of *Pseudacris* (Delahoussaye, 1966), *Pseudis* and *Lysapsus* (Garda et. al., 2004), *Scarthyla goinorum* (Duellman and de Sá, 1988), several species of *Scinax* (Fouquette and Delahoussaye, 1977; Taboga and Dolder, 1998; Costa et al., 2004), and *Sphaenorhynchus lacteus* (Fouquette and Delahoussaye, 1977).

did'' clade that is corroborated in the present analysis; that is, the m. transversus metatarsus II oblique, with a narrow, proximal connection to metatarsus II, and a broad, distal connection to metatarsus III. Another character state described by Burton (2004), the undivided tendon of the m. flexor digitorum brevis superficialis, optimizes in this analysis as a synapomorphy of this clade plus *Scinax*.

Besides the molecular data, the monophyly of *Lysapsus* plus *Pseudis* is further supported by the tendo superficialis pro digiti III arising from the m. flexor digitorum brevis superficialis, with no contribution from the aponeurosis plantaris; the origin of m. flexor ossis metatarsi IV and the joint tendon of origin of mm. flexores ossum metatarsorum II and III crossing each other; the m. flexor ossis metatarsi IV very short, inserting on the proximal two-thirds of metatarsal IV or less; absence of a tendon from the m. flexor digitorum brevis superficialis to the medial slip of the medial m. lumbricalis brevis digiti V; and m. transversus metatarsus III oblique, with a narrow, proximal connection onto metatarsal III, and a broad, distal connection to metatarsal IV. Another likely morphological synapomorphy is the elongated intercalary elements.

Vera Candioti (2004) noticed that *Lysapsus limellum* and most of the 30-chromosome *Hyla* (*H. nana* and *H. microcephala*) studied by her and Haas (2003) share two of the synapomorphies that Haas (2003) reported for *Pseudis paradoxa* and *P. minuta*: insertion of the m. levator mandibulae lateralis in the nasal sac, and a distinct gap in the m. subarcualis rectus II–IV. Haas (2003) observed different character states for *H. ebraccata* (the m. levator mandibulae lateralis inserts in tissue close to posterodorsal process of suprarostral cartilage or adrostral tissue; continuous m. subarcualis rectus II–IV), suggesting the need for additional studies on its taxonomic distribution within the 30-chromosome *Hyla* and in the other genera of the South American II clade.

Sphaenorhynchus, *Xenohyla* and the 30-Chromosome *Hyla*

Izecksohn (1959, 1996) suggested possible relationships of *Xenohyla* with *Sphaenorhynchus* and *Scinax* (Izecksohn, 1996). These ideas are partially corroborated by our 1:1:1 results, with the exception that they also suggest that *Xenohyla* is the sister group of the 30-chromosome *Hyla*. The karyotype is still unknown in *Xenohyla*, and this poses an obstacle to our understanding of the limits of the 30-chromosome *Hyla*. Interestingly, while both *Sphaenorhynchus* and *Xenohyla* do have a quadratojugal, in both cases it does not articulate with the maxilla (Duellman and Wiens, 1992; Izecksohn, 1996), which could be seen as an intermediate step before the extreme reductions of the quadratojugal seen in the 30-chromosome *Hyla* (Duellman and Trueb, 1983). Tadpoles of *Xenohyla* and several species of 30-chromosome *Hyla* share the presence of the tail tip extended into a flagellum, as well as the presence of high caudal fins (e.g., see Bokermann, 1963; Kenny, 1969; Gomes and Peixoto, 1991a, 1991b; Izecksohn, 1996; Peixoto and Gomes, 1999).

Phylogenetic hypotheses of the 30-chromosome *Hyla* species groups using morphological characters were presented by Duellman and Trueb (1983), Duellman et al. (1997), Kaplan (1991, 1994), and Kaplan and Ruíz (1997); none of these tested the monophyly of the contained species groups. A summary of their proposals and the supporting evidence are depicted in figure 6.

Chek et al. (2001) presented a phylogenetic analysis using partial 16S and cytochrome *b* sequences of the *Hyla leucophyllata* group, including exemplars of other 30-chromosome *Hyla* species groups. Because they did not include non-30-chromosome hylids, they did not test the monophyly of this clade.

The distribution of certain characters in several species associated with the currently recognized species groups suggests problems in our phylogenetic understanding of these frogs. The monophyly of a group composed of the *Hyla leucophyllata*, *H. marmorata*, *H. microcephala*, and *H. parviceps* groups is currently supported by the absence of labial tooth rows in their larvae (Duellman and Trueb, 1983). However, within the *H. parviceps* group, *H. microps* (Santos et al., 1998) and *H. giesleri* (Bokermann, 1963; Santos et al., 1998) have at least one labial tooth row. Similarly, Gomes and Peixoto (1991a) and

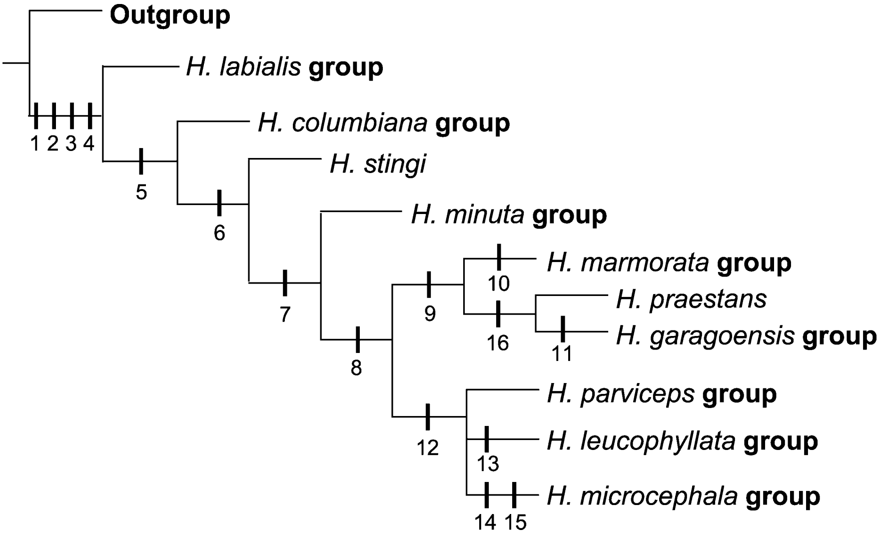

Fig. 6. Current state of phylogenetic knowledge of the 30-chromosome *Hyla*. Redrawn from Duellman (2001: 857) with the addition of Kaplan's (2000) suggestion regarding the relationships of *Hyla praestans* with the *H. garagoensis* group. Numbered synapomorphies, as textually described by these authors, are: 1, 30 chromosomes; 2, reduced quadratojugal; 3, 1/2 labial tooth rows; 4, nuptial excrescences absent; 5, tadpole tail xiphicercal; 6, tadpole mouth terminal; 7, 0/1 labial tooth rows; 8, 0/0 labial tooth rows; 9, one ventral row of small labial papillae in tadpoles; 10, extensive axillary membrane; 11, longitudinal stripes on hindlimbs of tadpoles; 12, one ventral row of large labial papillae in tadpoles; 13, tadpole body violin-shaped in dorsal view; 14, body of tadpole depressed; 15, labial papillae absent in tadpoles; 16, internal surface of the arytenoids with a small medial depression.

Peixoto and Gomes (1999) noticed in the *H. marmorata* group the presence of one labial tooth row in the larvae of *H. nahdereri*, *H. senicula*, and *H. soaresi*. Based on these facts and similarities in tail depth, tail color, general body shape, and predatory habits, they suggested that the *H. marmorata* group could instead be more closely related to *H. minuta* than to the groups suggested by Duellman and Trueb (1983). Gomes and Peixoto (1991b) pointed out the presence of a labial tooth row in the larva of *H. elegans*. Wild (1992) further noted the absence of marginal papillae (an apparent synapomorphy of the *H. microcephala* group) in the larva of *H. allenorum* (a species of the *H. parviceps* group).

The reproductive modes of the different species are also informative. According to Duellman and Crump (1974), *Hyla parviceps* deposits its eggs directly in the water, as does *H. microps* (Bokermann, 1963), whereas *H. bokermanni* and *H. brevifrons* oviposit on leaves overhanging ponds; upon hatching, the tadpoles drop into the water where they complete development. *Hyla ruschii* oviposits on leaves overhanging streams (Weygoldt and Peixoto, 1987). The oviposition on leaves occurs in most species of the *H. leucophyllata* group, whereas both reproductive modes occur in the *H. microcephala* group.

Our results recover the 30-chromosome *Hyla* species as monophyletic; however, our topology differs from previous hypotheses. In our topology, the root is placed between the *H. marmorata* group and the other exemplars, instead of between the *H. labialis* group and the other exemplars, as was assumed in previous analyses (Duellman and Trueb, 1983; Kaplan, 1991, 1994, 1999; Chek et al., 2001).

Topological differences from previous hypotheses are not due merely to a re-rooting of the previously accepted tree; the relationships obtained by our analysis are quite different from previous proposals. Our analysis does not recover as monophyletic the exemplars of the three species groups once thought to be monophyletic on the basis of lacking labial tooth rows, that is, the *Hyla leucophyllata*, *H. microcephala*, and *H. parviceps* groups. Instead, the *H. microcephala* group (including the taxa imbedded within it) is the sister taxon of a clade composed of *H. anceps* and the exemplars of the *H. leucophyllata* group. The exemplars of the *H. parviceps* group are the sister taxon of a clade composed of the exemplars of the *H. columbiana* and *H. labialis* groups. This shows that the scenario of labial tooth row evolution is more complex than previously thought, because it implies several transformations in both directions between presence and absence of labial teeth within the clade.

Observations by Wassersug (1980), Spirandeli Cruz (1991), and Kaplan and Ruiz-Carranza (1997) on the internal oral features of larvae of representatives of the *Hyla leucophyllata* (*H. ebraccata* and *H. sarayacuensis*), *H. microcephala* (*H. microcephala*, *H. nana*, *H. phlebodes*, and *H. sanborni*), and *H. garagoensis* (*H. padreluna* and *H. virolinensis*) groups revealed a reduction of internal oral structures (including reduction of most internal papillation, reduction of branchial baskets, reduction or absence of secretory ridges and secretory pits) that is most extreme in the representatives of the *H. microcephala* group. *Hyla minuta* does not show the reductions seen in these species groups (Spirandeli Cruz, 1991). This species also shares with representatives of the *H. leucophyllata* group described by Wassersug (1980) a reduction in the density of the filter mesh of the branchial baskets in comparison with other hylid tadpoles. It is clear that the study of internal oral features will provide several additional characters relevant for the study of the 30-chromosome species of *Hyla*.

The exemplars of the *Hyla parviceps* group obtain as monophyletic. However, we included only 3 of the 15 species currently included in this problematic group. We are not confident that the monophyly of the *H. parviceps* group will be maintained as more taxa are added. Regarding the exemplars of the *H. leucophyllata* group, their relationships are equivalent to those obtained by Chek et al. (2001).

The sister-group relationship of *Hyla anceps* and the *H. leucophyllata* group corroborates early suggestions by Lutz (1948, 1973) that these could be related on the basis of sharing a large axilar membrane and flash coloration.

While we could not test the monophyly of the *Hyla minima* and *H. minuta* groups, our exemplars of these groups are sister taxa, and they are only distantly related with the exemplars of the *H. parviceps* group. This position does not support Duellman's (2001) tentative suggestion that the species of the *H. minima* group should be included in the *H. parviceps* group.

The paraphyly of the *Hyla microcephala* group with respect to the *H. rubicundula* group is an expected result, as historically its species were associated with *H. nana* and *H. sanborni* (Lutz, 1973). Nevertheless, the association of the *H. microcephala* and *H. rubicundula* groups were reinforced by Pugliese et al. (2001), who described the larva of *H. rubicundula* and noted similarities (like the lack of marginal papillae) with the larvae of members of the *H. microcephala* group. In particular, these authors noticed similarities with *H. nana* and *H. sanborni*, with the latter being the sister taxon of *H. rubicundula* in our analysis.

Carvalho e Silva et al. (2003) segregated the *Hyla decipiens* group from the *H. microcephala* group on the basis that the larvae of these species lack the possible morphological synapomorphies currently diagnostic of the *H. microcephala* group (body of tadpole depressed, labial papillae absent in tadpoles) and the putative clade composed of the *H. leucophyllata*, *H. microcephala*, and *H. parviceps* groups (absence of labial tooth rows). However, as mentioned above, our results imply a complex scenario for labial tooth row transformations and place the *H. decipiens* group within the *H. microcephala* group. The available taxon sampling did not allow testing the monophyly of the *H. decipiens* group. The fact that its known species share the oviposition on leaves above the water, and the reversals in larval morphology that led Carvalho e Silva et al. (2003) to consider them unrelated to the *H. microcephala* group, probably indicates that, even if nested inside this group, the species assigned to the *H. decipiens* group could be a monophyletic unit.

The relationships of the *Hyla garagoensis* group, from which no exemplar was available for this study, were discussed by Kaplan and Ruiz-Carranza (1997). Based on the absence of labial tooth rows, they placed the *H. garagoensis* group in a polytomy together with the *H. marmorata* group and the clade composed of the *H. microcephala*, *H. parviceps*, and *H. leucophyllata* groups. Duellman et al. (1997) presented a cladogram for most of the 30-chromosome *Hyla* groups, where the *H. garagoensis* and *H. marmorata* groups appear together as a clade supported by the presence of one ventral row of small marginal papillae in larvae. This character state needs further assessment, as indicated by Gomes and Peixoto (1991a) and Peixoto and Gomes (1999), because tadpoles of the *H. marmorata* group have either one (*H. nahdereri*) or two rows of marginal papillae (*H. senicula*; *H. soaresi*); the tadpoles of *H. padreluna*, a species of the *H. garagoensis* group, also has a double row (Kaplan and Ruiz-Carranza, 1997). Considering this and earlier comments, we do not see evidence that associates the *H. garagoensis* group with the *H. marmorata* group more than with any other group within the 30-chromosome *Hyla* clade.

MIDDLE AMERICAN/HOLARCTIC CLADE

This clade is composed of most of the Middle American/Holarctic genera and species groups of treefrogs (fig. 5). For the purposes of discussion, we divide it into four large clades. The first of these includes *Acris* and *Pseudacris*. The second includes *Plectrohyla*, the *Hyla bistincta* group, the *H. sumichrasti* group, and various elements of the *H. miotympanum* group. The third clade includes *Duellmanohyla*, *Ptychohyla*, *H. miliaria*, *H. bromeliacia* (the sole exemplar of the *H. bromeliacia* group), and one element of the *H. miotympanum* group. The fourth clade includes *Smilisca*, *Triprion*, *Anotheca*, and the exemplars of the *H. arborea*, *H. cinerea*, *H. eximia*, *H. godmani*, *H. mixomaculata*, *H. pictipes*, *H. pseudopuma*, *H. taeniopus*, and *H. versicolor* groups.

Within the Middle American/Holarctic clade, the genera *Ptychohyla* and *Smilisca*, as well as the *Hyla arborea*, *H. cinerea*, *H. eximia*, *H. miotympanum*, *H. tuberculosa*, and *H. versicolor* groups, are not monophyletic. The *H. miotympanum* group is polyphyletic; its exemplars split among three different clades: *H. miotympanum* is the sister taxon of one of the exemplars of the *H. tuberculosa* group, *H. miliaria*; *H. arborescandens* and *H. cyclada* are related to an undescribed species close to *H. thorectes*, and together are related to exemplars of the *H. bistincta* group; *H. melanomma* and *H. perkinsi* are at the base of the *H. sumichrasti* group. *Smilisca* is not monophyletic, having *Pternohyla fodiens* nested within it. *Ptychohyla* is paraphyletic with respect to *H. dendrophasma* (*H. tuberculosa* group). The *H. arborea* group is polyphyletic, with *H. japonica* nested within the *H. eximia* group. The *H. cinerea* group is not monophyletic, with *H. femoralis* being more closely related to members of the *H. eximia* and *H. versicolor* groups than to *H. cinerea*, *H. gratiosa*, and *H. squirella*. The *H. versicolor* group is not monophyletic because *H. andersonii* is more closely related to the *H. eximia* group.

The monophyly of all genera and species groups of *Hyla* contained in this clade was maintained by Duellman (1970, 2001) based mostly on biogeographic grounds, because morphological evidence of monophyly was lacking. Duellman (2001) further presented a diagram depicting ‘‘suggested possible evolutionary relationships’’ among Middle and North American Hylinae, using as terminals the species groups of *Hyla* and the different genera (redrawn here as fig. 7). Duellman (2001) envisioned a North American basal lineage being the sister taxon of what he called the Middle American basal lineage. This Middle American basal lineage is further divided into a lower Central American lineage (itself divided into an isthmian highland lineage and a lowland lineage) and the Mexican-Nuclear Central American lineage (in turn divided into a Mexican-Nuclear Central American highland lineage and a lowlands lineage).

While the basal position of *Acris* and *Pseudacris* in this clade is consistent with Duellman’s (2001) intuitive suggestion of a North American basal lineage, it differs in that the Holarctic species groups of *Hyla* are only distantly related to them.

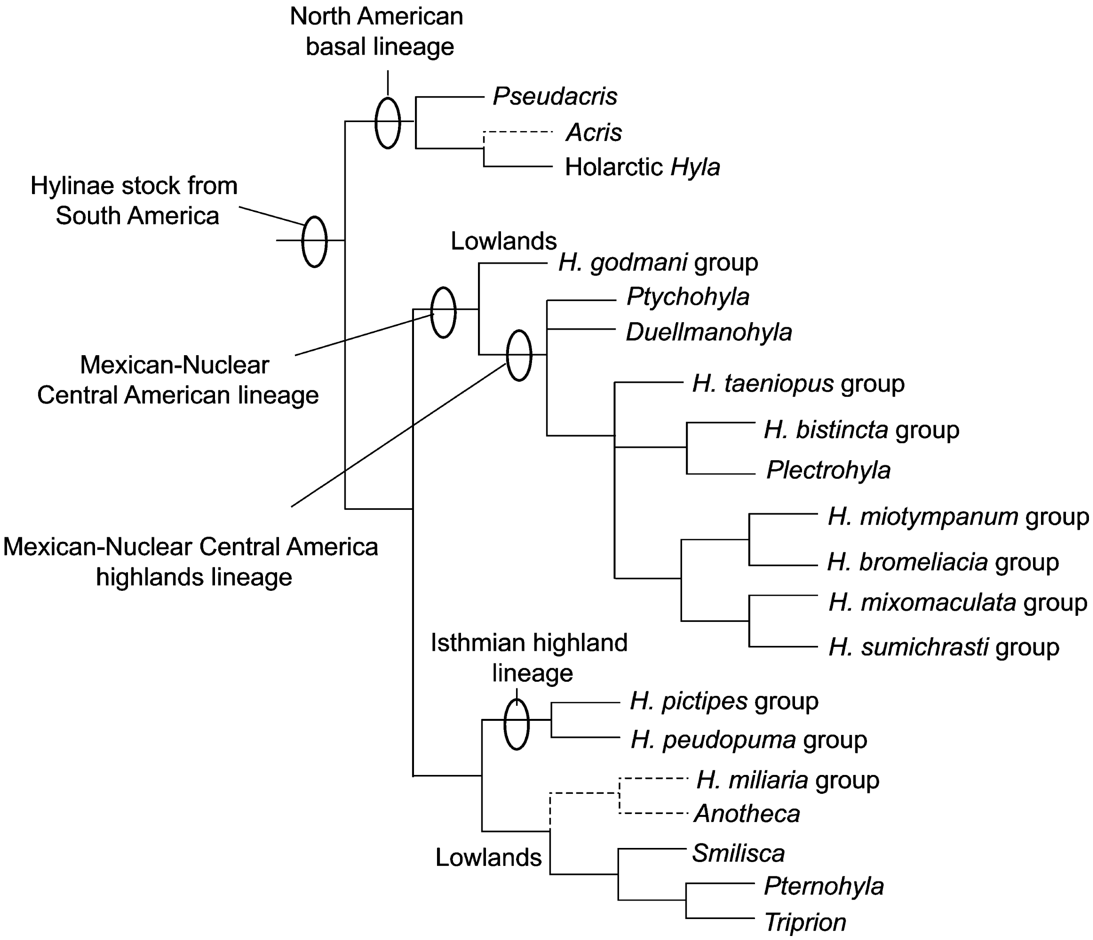

Fig. 7. Relationships of Middle American and North American Hylinae as envisioned by Duellman (2001). Broken lines are tentative placements.

We found no evidence supporting Duellman's (2001) exclusively Mexican-Nuclear Central American lineage, nor of his Mexican-Nuclear Central American highland lineage. The latter has nested within it the Mexican-Nuclear Central American lowland clade (the *H. godmani* group), a clade reminiscent of Duellman's (2001) isthmian highland-lowlands lineage, and also all species groups of Holarctic *Hyla*. Biogeographic implications of the discordant nature of our results with Duellman's suggested relationships between Middle- and North American Hylinae will be dealt with from a biogeographic perspective later in this paper.

The nonmonophyly of North American Hylinae does not agree with previous analyses (Hedges, 1986; Cocroft, 1994; da Silva, 1997; Moriarty and Cannatella, 2004) because those analyses assumed implicitly that *Acris*, the Holarctic *Hyla*, and *Pseudacris* are monophyletic. In spite of this, the internal relationships of *Pseudacris* recovered in this analysis are consistent to those obtained by Moriarty and Cannatella (2004).

Previous analyses either did not find evidence that *Acris* was particularly close to any group of North American hylids (Cocroft, 1994), or else suggested relationships with different species groups of North American *Hyla* (Hedges, 1986; da Silva, 1997). Two morphological synapomorphies of this *Acris*

+ *Pseudacris* clade could be the spherical or ovoid testes (as opposed to elongate testes) and the presence of dark pigmentation in the peritoneum surrounding the testes (Ralin, 1970, as cited by Hedges, 1986).

The nonmonophyly of the *Hyla miotympanum* group is not surprising because, as discussed in the section on taxon sampling, it did not appear that any of its putative synapomorphies could withstand a test with a broader taxon sampling. Duellman (2001) merged the formerly recognized *H. pinorum* group (Duellman, 1970) with the *H. miotympanum* group. With the notable exception of *H. miotympanum*, our results are close to recovering both groups as originally envisioned by Duellman (1970), because *H. cyclada* and *H. arborescandens* (*H. miotympanum* group) are recovered as monophyletic, and the former *H. pinorum* group is recovered as a paraphyletic assemblage that includes the *H. sumichrasti* group nested within it. In his analysis (Duellman, 2001: 912), the two species included by Duellman (1970) in the *H. pinorum* group (*H. melanomma* and *H. pinorum*), plus the two species that were later associated with this group (*H. perkinsi* and *H. juanitae*), form a monophyletic group supported by a single synapomorphy, the presence of an extensive (equal to or more than one-half length of upper arm) axillary membrane.

The dubious monophyly of the 17 species assigned to the *Hyla bistincta* group was not seriously tested in our analysis, because only 2 species were available. These two exemplars form the sister group of two taxa previously associated with the *H. miotympanum* group, and together they form the sister taxon of *Plectrohyla*. According to Duellman and Campbell (1992), character states supporting a monophyletic *H. bistincta* group plus *Plectrohyla* are: medial ramus of pterygoid long, in contact with otic capsule; dorsal skin thick (but see Mendelson and Toal [1995] and Duellman [2001] for discussions of this character); complete marginal papillae of the oral disc; and presence of at least one row of submarginal papillae (called by these authors accessory labial papillae) on the posterior labium (but see Wilson et al. [1994a] for discussion of this character state). From these, the complete marginal papillae of the oral disc occur in all known larvae of the clade containing *Plectrohyla*, and the *H. bistincta*, *H. sumichrasti*, and fragments of the *H. miotympanum* group, as well as in larvae of several other nearby clades (*Ptychohyla*, *Duellmanohyla*, the *H. mixomaculata*, and *H. taeniopus* groups; see Duellman 1970, 2001). Furthermore, the row of submarginal papillae in the larval oral disc presents a fair amount of variation in the extent and distribution of the papillae, within which could probably be subsumed the morphology seen in all known larvae of the clade mentioned above (see illustrations of all these oral discs in Duellman, 1970, 2001). Besides discussions provided by Mendelson and Toal (1995) and Duellman (2001) regarding the definition of the character state ‘‘thick skin’’, it does not occur in the following species currently assigned to the *H. bistincta* group: *H. calvicollina*, *H. charadricola*, *H. chryses*, *H. labedactyla*, and *H. sabrina* (Duellman, 2001). Considering that 15 of 17 species currently included in the *H. bistincta* group and 15 of 18 included in *Plectrohyla* could not be included in the analysis, we do not consider our results a strong test of their intrarelationships, particularly when several species of the *H. bistincta* group that present suspicious character state combinations, like the ones mentioned above, were not available. Our results relating *H. arborescandens* with species of the *H. bistincta* group corroborate earlier suggestions by Caldwell (1974) that relate this species to species currently placed in the *H. bistincta* group (*H. mykter*, *H. robertsorum*, and *H. siopela*.). Mendelson and Toal (1996) also suggested affinities of *H. arborescandens* and *H. hazalae* with the *H. bistincta* group on the basis of unpublished osteological data.

Duellman (2001) noted the lack of evidence for the monophyly of the *Hyla tuberculosa* group. Although poor, our taxon sampling does not recover it as monophyletic, because *H. dendrophasma* is nested within *Ptychohyla*, and *H. miliaria* is the sister taxon of *H. miotympanum*. Duellman (2001) also referred to the possibility advanced by da Silva (1997) of a relationship of the *H. tuberculosa* group with the Gladiator Frogs; at this point the evidence presented herein does not support this idea, but in case a denser sampling of the group still corroborates its polyphyly, we would not be surprised if some of its elements (particularly *H. tuberculosa*[26]) are shown to be related with the TGF clade.

Hyla miotympanum has repeatedly been considered a generalized Middle American hyline (Duellman, 1963, 1970; Campbell and Smith, 1992; Duellman, 2001), largely because the larva of *H. miotympanum* exhibits a labial tooth row formula of 2/3 and a relatively small oral disc with an anterior gap in the marginal papillae. We are not aware of any morphological synapomorphy supporting its relationship with *H. miliaria*, although our molecular data firmly place it there. According with our results, there is a morphological synapomorphy supporting the monophyly of the clade composed of these two species plus *Duellmanohyla*, the *H. bromeliacia* group, and *Ptychohyla* (including *H. dendrophasma*): the tendo superficialis hallucis that tapers from an expanded corner of the aponeurosis plantaris, with fibers of the m. transversus plantae distalis originating on distal tarsal 2–3 that insert on the lateral side of the tendon.

Considering its overall external appearance, we are surprised by the position of the poorly known *Hyla dendrophasma*. This species was originally considered to be a member of the *H. tuberculosa* group (Campbell et al., 2000) based on its large snout–vent length and extensive hand webbing, although with the caveat that it lacks dermal fringes, the only character state shared by all other species placed in the *H. tuberculosa* group. DNA was isolated and sequenced twice from tissues of the female holotype, the only known specimen (Campbell et al., 2000). Inasmuch as most previous notions of relationships among species of *Ptychohyla* derive from adult male morphology and tadpoles, the discovery of at least one male specimen of *H. dendrophasma* could hopefully allow us to better understand its relationships within *Ptychohyla*.

Campbell and Smith (1992) and Duellman (2001) suggested five morphological synapomorphies for *Ptychohyla*. One of these is apparently unique to *Ptychohyla* (pars palatina of the premaxilla with well-developed lingual flange), while the other four show a more extensive taxonomic distribution. (1) The cluster of ventrolateral mucous glands in breeding males is present in *Duellmanohyla chamulae*, *D. ignicolor*, and *D. schmidtorum* (Campbell and Smith, 1992; see also Thomas et al., 1993). (2) The presence in the ventrolateral edge of forearm of tubercles coalesced into a ridge (as opposed to the absence of tubercles) was reported for *D. lythrodes*, *D. salvavida*, *D. schmidtorum*, and *D. soralia* (Duellman, 1970; 2001); *H. bromeliacia* has an indistinct row of tubercles that do not coalesce into a ridge (absent in *H. dendroscarta*) (Duellman, 1970). (3) The double row of marginal papillae is present as well in larvae of the *H. bromeliacia* group (Duellman, 1970). Finally, (4) larvae of the *H. bromeliacia* group have a labial tooth row formula of 2/4 or 2/5, and all known larvae of *Duellmanohyla* have a labial tooth row formula of 3/3; the minimum known for a species of *Ptychohyla* is 3/5 (*P. legleri* and *P. salvadorensis*) (Duellman, 1970, 2001; Campbell and Smith, 1992).

The monophyly of the group composed of *Ptychohyla euthysanota*, *P. hypomykter*, *P. leonhardschultzei*, and *P. zophodes* is congruent with the results of Duellman (2001), who supported the monophyly of these taxa based on the presence of a thick, rounded tarsal fold. These species further share the presence of hypertrophied ventrolateral glands in breeding males with two species we could not include in our analysis: *P. macrotympanum* and *P. panchoi*. Furthermore, all these species also share with *P. spinipollex* the presence of the nuptial excrescences composed of enlarged individual spines. The states of these characters are unknown in *Ptychohyla* sp. and *Hyla dendrophasma* because the only available specimens are females. The nonmonophyly of *P. hypomykter* plus *P. spinipollex* is most surprising, considering that both were considered to be a

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[26] The other South American species of the *Hyla tuberculosa* group, *H. phantasmagoria*, is known only from the holotype. It was considered a junior synonym of *H. miliaria* by Duellman (1970), who later resurrected it (Duellman, 2001). Besides a few comments by this author, no morphological comparisons with other species of the group are available.

single species (Wilson and McCranie, 1989; see also McCranie and Wilson, 1993).

Although we included several species of *Ptychohyla* in our analysis, we do not think that we have apprehended a good representation of the morphological diversity of the group, and the absence of species like *P. erythromma*, *P. legleri*, and *P. sanctaecrucis* certainly weakens the test of monophyly of *Ptychohyla*. This is more so considering the fact that several of the putative morphological synapomorphies of *Ptychohyla* are actually shared with some species of its sister taxon, as discussed earlier, and that the monophyly of our exemplars of *Ptychohyla* is weakly supported. The low Bremer support (3) for *Ptychohyla* also suggests that the evidence for its monophyly deserves further attention.

The *Hyla bromeliacia* group was tentatively associated with the polyphyletic *H. miotympanum* group by Duellman (2001: 779). Other than this, we are not aware of it being associated with any other group. Besides the molecular evidence, we are aware of at least one likely morphological synapomorphy supporting the monophyly of *Duellmanohyla* plus the *Hyla bromeliacia* group: the presence of pointed serrations of the larval jaw sheaths (Campbell and Smith, 1992; Duellman, 1970; 2001). These are apparently longer in some species of *Duellmanohyla* than in the *H. bromeliacia* group, but both seem to be notably more pointed than in *Ptychohyla* (see descriptions and illustrations in Duellman, 1970).

We share with Duellman (2001) and Mendelson and Campbell (1999) doubts regarding the monophyly of the *Hyla taeniopus* group. Nevertheless, our two exemplars are recovered as monophyletic in the analysis. Duellman (2001) examined the possibility of a relationship between this group and the *H. bistincta* group, based on the fact that both have large stream-adapted tadpoles with small, ventral oral discs with complete marginal papillae and bear a labial tooth row formula of 2/3 (but noting that the tooth-row formula is slightly higher for *H. nephila* and *H. trux*). Our results suggest instead that the *H. taeniopus* group is the sister taxon of a clade composed of *H. mixe* (the only available exemplar of the *H. mixomaculata* group) plus the clade composed of the Holarctic *Hyla* groups, the *H. godmani*, *H. pictipes*, and *H. pseudopuma* groups, and *Anotheca*, *Smilisca* (including *Pternohyla*), and *Triprion*. Furthermore, in the context of our results, the ventral oral disc with complete marginal papillae seems to be a synapomorphy of the whole Middle American clade, with subsequent transformations in the clade just mentioned and in other points of the tree.

We were unable to test the monophyly of the *Hyla mixomaculata* group, because *H. mixe* was the only taxon available. Regardless, and until a rigorous test is possible, the monophyly of this group could be reasonably assumed based on the presence of the enlarged oral disc with 7/10 or 11 labial tooth rows. At this point it should be stressed that the sequenced sample comes from a tadpole that was assigned to the *H. mixomaculata* group based that on that characteristic, and that it was tentatively assigned to *H. mixe* for being the only species of the group known from the region where the larva was collected; thus, considering the uncertainty in its determination, its position in the tree should be viewed cautiously.

Duellman (2001) included the species of the former *Hyla picta* group in the *H. godmani* group. Unfortunately, the two exemplars available to us for this analysis are only the two members of the former *H. picta* group and none of the restricted *H. godmani* group; therefore, this is not a satisfactory test of the monophyly of the *H. godmani* group (sensu lato).

The Lower Central American Lineage

The monophyly of the included exemplars of the *Hyla pictipes* and *H. pseudopuma* groups, and its relationship with a clade composed of *Anotheca*, *Smilisca*, *Triprion*, and *Pternohyla*, is quite consistent (in the sense that it contains almost the same groups) with Duellman's intuitive proposal of a lower Central American clade that contains an Isthmian Highland lineage and a Lowland lineage (fig. 7), with the only exception being that he tentatively considered the *H. miliaria* group related to *Anotheca*.

The monophyly of a group composed of *Hyla pseudopuma* and *H. rivularis*, the only two exemplars available from the *H. pseudopuma* and *H. pictipes* groups, could be suggestive of a lineage of highland isthmian Hylinae as suggested by Duellman (2001). Although the monophyly of each of these two groups has not been tested here, the position of the undescribed Mexican species *Hyla* sp. 5 (aff. *H. thorectes*) deserves some comments.

Duellman (1970) recognized the *Hyla hazelae* group in which he included the nominal species and *H. thorectes*. Reasons for recognizing this group were ''the combination of large hands with vestigial webbing, half webbed feet . . . and presence of a tympanum are external features which separate these species from other small stream-breeding Mexican *Hyla*. Furthermore both species have small, relatively narrow tongues and large tubercles below the anal opening. The nature of the nasals and sphenethmoid are unique among northern Middle American hylids'' (Duellman, 1970: 384). It is unclear if any of these character states could have been considered as evidence of monophyly of the group. It is also unclear on what basis Duellman (2001) dismantled the group and placed *H. hazelae* in the *H. miotympanum* group, while *H. thorectes* was transferred to the *H. pictipes* group. Wilson et al. (1994b) suggested that *H. thorectes* could be related to *H. insolita* and *H. calypsa* (under the name *H. lancasteri*; see Lips, 1996) because they share oviposition on leaves overhanging streams and have dark ventral pigmentation; these character states were not included in Duellman's (2001) analysis of the group. Although we do not have data to take a position regarding these actions, the fact that *Hyla* sp. 5 (aff. *H. thorectes*) is unrelated to *H. rivularis* is here taken as evidence that *H. thorectes* should not be included in the *H. pictipes* group. Furthermore, all character states advanced by Duellman (2001) as shared by *H. thorectes* and the species of the *H. pictipes* group are also shared by *H. thorectes* and the taxa to which *Hyla* sp. 5 (aff. *H. thorectes*) appears to be closely related in our analysis. Because we were unable to include *H. calypsa*, *H. insolita*, or *H. lancasteri*, we do not have elements to test the hypothesis of Wilson et al. (1994b) regarding the close relationship of *H. calypsa*, *H. insolita*, and *H. thorectes*.

In order to better understand the relationships of the *Hyla pictipes* group, it would be important to add to this analysis exemplars of the former *H. zeteki* and *H. lancasteri* groups, because together with the original *H. pictipes* and *H. rivularis* groups (as defined by Duellman, 1970) they represent the three main morphological extremes of the group. The fact that so few exemplars of these two groups were available is one of the weaker points of our analysis.

The paraphyly of *Smilisca* is partly consistent with Duellman's (2001) phylogenetic analysis of this genus in that *Pternohyla* is nested within it. However, we did not recover *Triprion* nested within *Smilisca*, as did Duellman (2001).

A possible relationship between *Triprion* and *Anotheca* was first advanced by Lutz (1968) because she considered them to be the extreme of one specialization consisting ''in excessive ossification of the head, accompanied at some stages by extra dentition'' (Lutz, 1968: 10). Within this same line, she included all casque-headed frogs, including together South American and Middle American forms. Duellman and Trueb (1976) suggested a possible link of *Anotheca* with *Nyctimantis* (discussed below). Duellman (2001: 332) proposed a tentative relation of *Anotheca* with the *Hyla miliaria* group based on the oophagous tadpoles that develop in bromeliads or tree-holes (known for the only species of the *H. tuberculosa* group with a known tadpole, *H. salvaje*; see Wilson et al., 1985). While our results support a sister-group relationship of *Anotheca* and *Triprion* as suggested by Lutz (1968), it occurs within the Holarctic/Middle American clade and not within a group composed of all casque-headed frogs as she suggested. In the context of this analysis, both *Triprion* and *Anotheca* share the posterior expansion of the frontoparietals that cover almost all the otoccipital dorsally (see figures in Duellman, 1970).

Our analysis indicates that the insertion of m. extensor digitorum comunis longus on metatarsal II is a synapomorphy of a group composed of *Anotheca*, *Triprion*, and the paraphyletic *Smilisca*. Furthermore, *Smilisca* (including *Pternohyla*) and *Triprion* share the type I septomaxillary (see Trueb, 1970a) and bifurcated cavum principale of the olfactory capsule (Trueb, 1970a); the distribution of these character states should be studied in *Anotheca* and nearby groups to determine the level of inclusiveness of these possible synapomorphies.

Real *Hyla*

Our results concerning the relationships between the North American and Eurasiatic species groups of *Hyla* differ from previous analyses, in part likely because of the previous assumption of monophyly of North American/Holarctic Hylinae. In the first place, the molecular evidence supports a clade containing all North American and Eurasiatic species groups of *Hyla*, a result that differs from previous analyses where relationships either were unresolved (Cocroft, 1994) or were paraphyletic with respect to *Acris* and/or *Pseudacris* (Hedges, 1986; da Silva, 1997). The polyphyly of the *Hyla arborea* group and the paraphyly of the *H. eximia* group corroborate previous ideas by Anderson (1991) and Borkin (1999) regarding their nonmonophyly and the closer relationship of *H. japonica* with the *H. eximia* and *H. versicolor* groups. A likely synapomorphy of the *H. eximia* and *H. versicolor* groups, including *H. japonica* and *H. andersonii*, is the nucleolar organizer region (NOR) present in chromosome 6 instead of chromosome 10 (Anderson, 1991).

South American/West Indian Casque-Headed Frogs

This clade (fig. 5) is composed of *Phyllodytes*, *Phrynohyas*, *Nyctimantis*, and all South American/West Indian casque-headed frogs: *Argenteohyla*, *Aparasphenodon*, *Corythomantis*, *Osteopilus*, *Osteocephalus*, *Trachycephalus*, and *Tepuihyla*. It is divided basally in a group composed of the two exemplars of *Phyllodytes*, and another group composed of all casque-headed frog genera, including *Phrynohyas* and *Nyctimantis*.

Within this clade, other than those genera that are not monotypic (*Argenteohyla*, *Nyctimantis*, *Corythomantis*) or represented in this analysis by a single species (*Aparasphenodon*, *Tepuihyla*), *Phyllodytes* and *Osteopilus* are monophyletic, and *Osteocephalus*, *Phrynohyas*, and *Trachycephalus* are not monophyletic. *Osteocephalus* is not monophyletic because *O. langsdorffii* (the only species of the genus distributed in the Atlantic forest) is not related to the remaining exemplars of *Osteocephalus*, which form a monophyletic group that is the sister taxon of *Tepuihyla*. *Phrynohyas* is not monophyletic, having *Trachycephalus nigromaculatus* nested within it, and *Trachycephalus* is not monophyletic, with *T. jordani* forming the sister taxon of ‘‘*Phrynohyas*’’ + *T. nigromaculatus*.

With respect to *Phyllodytes*, we were unable to find any published hypothesis regarding its relationships, and considering the scant information available on its morphology, we had no previous clue as to other groups of Hylidae with which it might be related. The only morphological character state of which we are aware that *Phyllodytes* shares with several members of the South American/West Indian Casque-headed Frogs clade is the presence of at least four posterior labial tooth rows in the tadpole oral disc (see below, ‘‘Taxonomic Conclusions: A New Taxonomy of Hylinae and Phyllomedusinae’’, for further details).

The polyphyly of *Osteocephalus* was not unexpected considering the lack of any evidence of its monophyly. This polyphyly results because of the position of *O. langsdorffii*. This is the only species of the genus present in the Atlantic forest and a species that had been particularly poorly discussed in the context of the systematics of *Osteocephalus* (Duellman, 1974). While we do not test the monophyly of the bromeliad-breeding/single vocal sac species (here represented by a *O. oophagus*), our results show that our exemplars with lateral vocal sacs are paraphyletic with respect to *O. oophagus*.

The monophyly of *Tepuihyla* was not tested in this analysis. Its sister-group relationship with *Osteocephalus* (excluding *O. langsdorffii*) is supported by our data, instead of with *Scinax* as first suggested (Ayarzagüena et al., ‘‘1992’’ [1993b]; see earlier discussion on the relationships of *Scinax*). This situation requires changes in the original interpretation of two character states that provided evidence of the relationships of *Te-*

puihyla with other hylids. The presence of spicules in the dorsum of males is more parsimoniously interpreted as a putative synapomorphy of *Tepuihyla* plus *Osteocephalu*s, instead of a homoplasy, as advanced by Ayarzagüena et al. (''1992'' [1993b]). Similarly, the reduction of webbing between toes I and II is more parsimoniously interpreted as a putative synapomorphy of *Tepuihyla* (homoplastic with *Scinax*) instead of a synapomorphy of *Scinax* + *Tepuihyla*.

The monophyly of the four exemplars of *Osteopilus* corroborates in a much broader taxonomic context the results of Maxson (1992), Hedges (1996), and Hass et al. (2001), based on albumin immunological distances and still unpublished sequence data regarding its monophyly, and the recent taxonomic changes summarized by Powell and Henderson (2003b). Unfortunately, we could not include in our analysis *O. marianae*, *O. pulchrilineatus*, and *O. wilderi*, and we are not aware of any possible morphological synapomorphy supporting their monophyly. In the absence of other evidence, it could be suggested that the oviposition and development in bromeliads, which occurs in these three species and *O. brunneus*, is a possible synapomorphy uniting these with *O. crucialis*, which apparently also has this reproductive mode (Hedges, 1987).

The presence of paired lateral vocal sacs and biogeographic considerations led Trueb (1970b) and Trueb and Duellman (1971) to suggest the collective monophyly of *Argenteohyla*, *Osteocephalus*, *Phrynohyas*, and *Trachycephalus* (at that time the species of *Osteocephalus* having a single subgular vocal sac were still unknown). Furthermore, these authors considered *Trachycephalus* and *Phrynohyas* to be a monophyletic group on the basis of sharing vocal sacs that are more lateral and protrude posteriorly to the angles of the jaws when inflated. Trueb and Tyler (1974) suggested that the West Indian *Osteopilus* and the former *Calyptahyla crucialis* (now *Osteopilus crucialis*) were also related to this clade, although they exhibit a single, subgular vocal sac. Our results corroborate the monophyly of *Phrynohyas* plus *Trachycephalus* (see below), but they also suggest a more complex situation where the casque-headed frogs with double vocal sacs are paraphyletic, with all of the genera of casque-headed frogs that have a single subgular sac being nested within them.

Duellman and Trueb (1976) suggested that *Nyctimantis* was related to *Anotheca*, because both share the medial ramus of the pterygoid being juxtaposed squarely against the anterolateral corner of the ventral ledge of the otic capsule. Also, frogs of both genera are known (*Anotheca*; Taylor, 1954; Jungfer, 1996) or suspected (*Nyctimantis*; Duellman and Trueb, 1976) to deposit their eggs in water-filled tree cavities. Our results suggest a radically different picture, with *Nyctimantis* nested within the South American/West Indian Casque-headed Frogs, while *Anotheca* is nested within the Middle American/Holarctic clade, being the sister taxon of *Triprion*.

The topology has some discrepancies with previous suggestions as to the relationships of *Argenteohyla*, *Aparasphenodon*, and *Corythomantis* (for the latter two genera, see also comments for *Scinax* above). *Argenteohyla siemersi* was segregated by Trueb (1970b) from *Trachycephalus*, where it had been placed by Klappenbach (1961), because it lacks the diagnostic character states of *Trachycephalus* established by Trueb (1970a). Further, she suggested that *Argenteohyla* is a close ally of *Osteocephalus* based on the presence of paired lateral vocal sacs. Although Trueb (1970a) suggested that *Aparasphenodon* and *Corythomantis* are sister taxa, our evidence suggests that both *Argenteohyla* and *Nyctimantis* are closer to *Aparasphenodon* than to *Corythomantis*.

Most species in the South American/West Indies Casque-headed Frog clade frequently live in or seek refuge in bromeliads or treeholes. This has been reported for *Aparasphenodon* (Paolillo and Cerda, 1981; Teixeira et al., 2002), *Argenteohyla* (Barrio and Lutz, 1966; Cespedez, 2000), *Corythomantis* (Jared et al., 1999), *Nyctimantis* (Duellman and Trueb, 1976), *Osteocephalus langsdorffii* (Haddad, personal obs.), *Phrynohyas* (Goeldi, 1907; Prado et al., 2003), *Tepuihyla* (Ayarzagüena et al., ''1992'' [1993b]), and *Trachycephalus* (Lutz, 1954; Bokermann, 1966c). Furthermore, all species of *Phyllodytes* (Peixoto et al., 2003), some species of *Osteocephalus* (Jungfer and Schiesari, 1995;

Jungfer and Weygoldt, 1999; Jungfer and Lehr, 2001), some species of *Osteopilus* (Hedges, 1987; Lannoo et al., 1987), and at least two species of *Phrynohyas* (Goeldi, 1907; Lescure and Marty, 2000) even lay their eggs in phytotelmata or treeholes where their exotrophic larvae develop. While bromeliads and treeholes are used as refuges or for reproduction in other groups of hylids (e.g., *Anotheca spinosa*, the *Hyla bromeliacia* group, the two bromeliad breeding frogs of the *H. pictipes* group, *H. astartea*, the *H. tuberculosa* group, *Scinax alter*, the *Scinax perpusillus* group of the *S. catharinae* clade), the South American/West Indian Casque-headed Frog clade seems to be the largest clade of hylids that consistently makes use of bromeliads or treeholes.

The phylogenetic structure of the South American/West Indies Casque-headed Frog clade implies a minimum of one instance of reversal from presence of heavily exostosed and co-ossified skulls to normal looking, albeit heavily built skulls (the case of *Phrynohyas*), and at least a possible second and third instance involving reversals from exostosed skulls (the cases of *Tepuihyla* and *Osteopilus vastus*).

From a morphological perspective, the paraphyly of *Phrynohyas* with respect to *Trachycephalus nigromaculatus* and the concomitant nonmonophyly of *Trachycephalus* are most interesting and surprising. Herpetologists have been noticing for years that *T. nigromaculatus* and *Phrynohyas mesophaea* produce hybrids throughout their overlapping ranges of distribution (Haddad, personal obs.; Pombal, personal commun.; Ramos and Gasparini, 2004). The possibility of hybridization leads us to think that perhaps the introgression of *P. mesophaea* mitochondria could actually be the reason for the recovered paraphyly of *Trachycephalus*. However, phylogenetic analyses using either tyrosinase or rhodopsin alone (the only two nuclear genes that were successfully sequenced in *T. nigromaculatus*) still recover a paraphyletic *Trachycephalus* (results not shown).

TAXONOMIC CONCLUSIONS: A NEW TAXONOMY OF HYLINAE AND PHYLLOMEDUSINAE

Below we present a new taxonomic arrangement of Hylinae and Phyllomedusinae, based on the results discussed above. While our data clearly point to the fact that we could hardly have a more paraphyletic and uninformative hylid taxonomy as the current one, we foresee some resistance to this new monophyletic taxonomy, due mostly to the lack of morphological evidence in the analysis with consequent few morphological synapomorphies in the diagnoses (for many of the groups, only the molecular evidence presented here provides the evidence of monophyly) or to insufficient numbers of exemplars. The lack of a complete, well-researched nonmolecular data set is admittedly a weakness of this project. However, our study represents the largest amount of evidence for the largest number of terminals ever put together and analyzed in a consistent way to address the phylogenetic relationships of hylids. Until a nonmolecular data set is assembled, we are left only with the evidence provided by our analysis. The alternatives are evident: either we ignore the present results and stick to the traditional, grossly uninformative taxonomy, or we dare to present a new monophyletic taxonomy based on the evidence provided here. The latter option is far closer to the goals of phylogenetic systematics than is the former one. The new taxonomy is the result of our attempt to reconcile the need to recognize only monophyletic groups and to minimize changes to the existing taxonomy while keeping it informative (e.g.: we could have included all currently recognized genera of Hylinae in the synonymy of *Hyla*; this would have resulted in a perfectly monophyletic though utterly uninformative taxonomy).

We have not tested the monophyly of several genera and species groups either because we could not sample them at all (e. g. the cases of *Phrynomedusa* and the *Hyla claresignata* and *H. garagoensis* group) or because of insufficiency in sampling (e.g., the *H. pictipes*, *H. pseudopuma*, and *H. mixomaculata* groups). There are, as well, seven species that we could not associate with any group (see ‘‘Incertae Sedis and Nomina Dubia’’ below and appendix 4). Nevertheless, we are being bold in the recognition of groups. We recognize all groups that were previously recognized but for which we have not sampled sufficiently to test their monophyly (i.e., only one species was available). These are noted in text. We also assume that the transformation series supporting the monophyly of the exemplars of any given clade are correctly extrapolated as being evidence of the monophyly of the whole group. In the worse case scenario, we will be shown to be wrong; in the best case our hypotheses will withstand further testing. By default, we hope our arrangement will stimulate further research.

The former subfamily Hemiphractinae is now tentatively considered to be part of the paraphyletic Leptodactylidae, pending further research on this vast nonmonophyletic conglomerate of hyloids.

The total number of DNA transformations supporting the monophyly of each relevant clade is informed in the respective diagnoses, with the exception of species groups whose monophyly has not been tested in our analysis. See figure 8 for a summary of the new taxonomy and figures 9–12 for the strict consensus of our analysis updated with the new taxonomy. See appendix 5 for details regarding the number of transitions, transversions, and inferred insertion/deletion events as well as the specific positions involved for each gene.

HYLINAE RAFINESQUE, 1815

SYNONYMS: See sections for tribes.

DIAGNOSIS: This subfamily is diagnosed by 32 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these transformations. Possible morphological synapomorphies are the tendo superficialis digiti V (manus) with an additional tendon that arises ventrally from m. palmaris longus (da Silva, 1998, as cited by Duellman, 2001).

COMMENTS: The 2n = 24 chromosomes may be another putative synapomorphy of this clade, but it will be necessary to better understand its distribution in the more basal members of the different tribes.

COPHOMANTINI HOFFMANN, 1878

Cophomantina Hoffmann, 1878. Type genus: *Cophomantis* Peters, 1870.

DIAGNOSIS: This tribe is diagnosed by 65 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these transformations. Possible morphological synapomorphies include a ventral oral disc, and complete marginal papillae in larvae, (these character states subsequently transform in more inclusive groups within this clade).

COMMENTS: This tribe includes the genera *Aplastodiscus*, *Bokermannohyla* new genus, *Hyloscirtus*, *Hypsiboas*, and *Myersiohyla* new genus.

The increase in the number of labial tooth rows is likely another synapomorphy of Cophomantini, because all known larvae of *Hyloscirtus* and *Myersiohyla* new genus colectively have a minimum of 6/7 labial tooth rows. However, at this time the minimum number of labial tooth rows that is synapomorphic for Cophomantini is ambiguous, because the tadpole is still unknown in *H. kanaima*.

An enlarged prepollex is present in all species of *Hyloscirtus* and in most species of *Myersiohyla*, new genus. (Unlike species of the *H. aromatica* group, in *H. kanaima*, the prepollex is not enlarged.) This characteristic could be a synapomorphy of Cophomantini as an intermediate state leading to the enlarged prepollex with a projecting spine, as proposed by Duellman et al. (1997). In order to understand whether this character state is a synapomorphy of Cophomantini, further research is required, including (1) more osteological work to define the character states involved, and (2) additional studies on the phylogenetic relationships within *Myersiohyla*, new genus, to understand whether the character state present in the former *H. kanaima* could be interpreted as a reversal.

Burton (2004) suggested that the tendo superficialis hallucis tapering from an expanded corner of the aponeurosis plantaris, with fibers of the m. transversus plantae distalis originating on distal tarsal 2–3 inserting on the lateral side of the tendon, provides evidence of monophyly of a group composed of the *H. albomarginata*, *H. albopunctata*, *H. boans*, *H. geographica*, and *H. pulchella* groups. The lack of information on the taxonomic distribution of this character state within several terminals of Cophomantini renders its optimization ambiguous in all our most parsimonious trees. While it is clear that it is a synapomorphy of some component of Cophomantini, at this point we do not know its level of inclusiveness. (Burton points out its presence in *H. phyllognatha*, the only member of the *H. bogotensis* group that he studied.) The same point holds for the presence of an accessory tendon of the m. lumbricalis longus digiti III, which Burton (2004) considered characteristic of those same species groups.

There are other character states that were observed in exemplars of this tribe whose taxonomic distribution needs to be assessed in its most basal taxa in order to know with more precision the limits of the clade or clades they diagnose. One of these is the point of insertion of the tendon of the m. extensor brevis medius digiti IV that Faivovich (2002) found to insert in the medial proximal margin of phalanx 2 in the exemplars of this tribe that he studied (*Aplastodiscus perviridis*, *Hyla albopunctata*, *H. faber*, and *H. raniceps*). In other hyloids this tendon is known to insert in the anterior medial margin of metacarpal IV (Burton, 1996, 1998b; Faivovich, 2002). Subsequently, this character state was observed in other species available for studies (*H. albomarginata*, *H. andina*, *H. circumdata*, *H. clepsydra*, *H. geographica*, *H. granosa*, *H. multifasciata*, and *H. polytaenia*; Faivovich, personal obs.).

There are at least two other character states whose taxonomic distribution within this tribe deserve further scrutiny. The first of these is the presence in the dorsal surface of the larval oral cavity of an anteromedial loop of the prenarial wall into the prenarial arena. Wassersug (1980) described and reported it in *Hyla rufitela*, Spirandeli Cruz (1991) in *Aplastodiscus perviridis*, *H. faber*, *H. lundii*, and *H. prasina*, and D'Heursel and de Sá (1999) in *H. geographica* and *H. semilineata*. The second character state is the presence of one (most frequently) or more (a few species of the *H. bogotensis* group; Mijares-Urrutia, 1992b) fleshy projections of variable shape (triangular, round, or elliptic; sometimes called papillae) in the inner margin of the nostrils of the larvae, which various authors (Kenny, 1969; Peixoto, 1981; Peixoto and Cruz, 1983; Lavilla, 1984; Mijares-Urrutia, 1992b; Wild, 1992; Ayarzagüena and Señaris, ‘‘1993’’ [1994]; de Sá, 1995, 1996; Duellman et al., 1997; Faivovich, 2002; Gomes and Peixoto, 2002; Faivovich, personal obs.) noticed in several species: *Aplastodiscus perviridis*, *Hyla albofrenata*, *H. albomarginata*, *H. albopunctata*, *H. albosignata*, *H. alemani*, *H. andina*, *H. aromatica*, *H. charazani*, *H. balzani*, *H. carvalhoi*, *H. circumdata*, *H. faber*, *H. fasciata*, *H. granosa*, *H. inparquesi*, *H. jahni*, *H. leucopygia*, *H. multifasciata*, *H. palaestes*, *H. platydactyla*, *H. punctata*, *H. raniceps*, *H. sibleszi*, and an undescribed species of the *H. aromatica* group. Although not explicitly mentioned in the descriptions, this character state seems evident in illustrations of other larvae: *H. goiana*, *H. joaquini*, *H. marginata*, *H. polytaenia*, and *H. pulchella* (Eterovick et al., 2002; Gallardo, 1964; Garcia et al., 2001b, 2003).

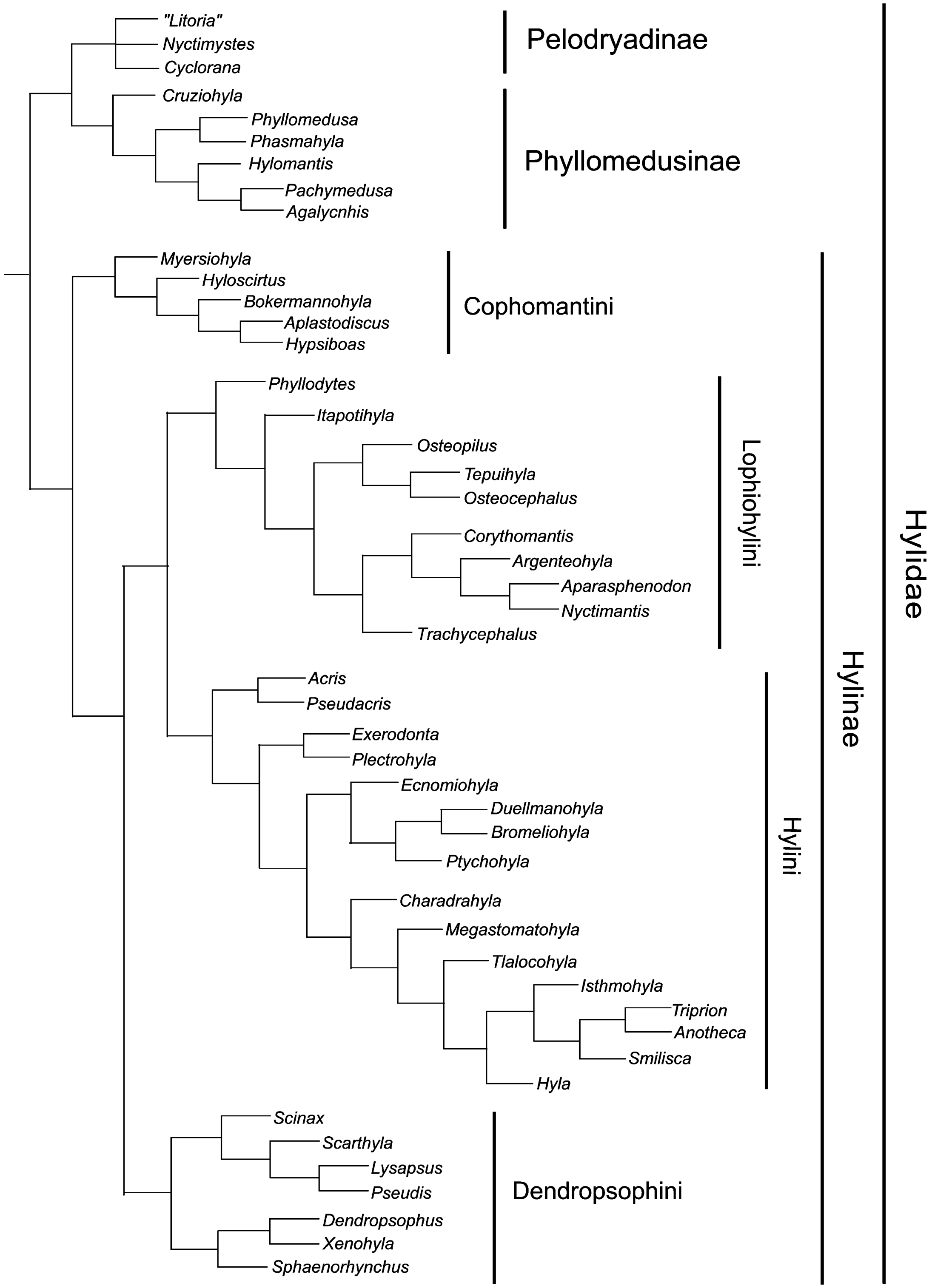
Aplastodiscus A. Lutz *in* B. Lutz, 1950

TYPE SPECIES: *Aplastodiscus perviridis* A. Lutz *in* B. Lutz, 1950, by original designation.

DIAGNOSIS: This genus is diagnosed by 72 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Other apparent synapomorphies of this clade are the particular reproductive modes, where the male constructs a subterranean nest in the muddy side of streams and ponds, and where larvae spend early stages of development; subsequent to flooding, the exotrophic larvae live in ponds or streams (Haddad and Sawaya, 2000; Hartmann et al., 2004, Haddad et al., 2005). The presence of proportionally very developed

→

Fig. 8. A schematic summary of the new taxonomy of Hylidae proposed here, as indicated by the phylogenetic relationships of the genera of Hylinae, Pelodryadinae, and Phyllomedusinae. The genus *Phrynomedusa* was unavailable for this study and is not included.


"Litoria"
Nyctimystes
Cyclorana
Pelodryadinae
Cruziohyla
Phyllomedusa
Phasmahyla
Hylomantis
Pachymedusa
Agalycnhis
Phyllomedusinae
Myersiohyla
Hyloscirtus
Bokermannohyla
Aplastodiscus
Hypsiboas
Cophomantini
Phyllodytes
Itapotihyla
Osteopilus
Tepuihyla
Osteocephalus
Corythomantis
Argenteohyla
Aparasphenodon
Nyctimantis
Trachycephalus
Lophiohylini
Acris
Pseudacris
Exerodonta
Plectrohyla
Ecnomiohyla
Duellmanohyla
Bromeliohyla
Ptychohyla
Charadrahyla
Megastomatohyla
Tlalocohyla
Isthmohyla
Triprion
Anotheca
Smilisca
Hyla
Hylini
Scinax
Scarthyla
Lysapsus
Pseudis
Dendropsophus
Xenohyla
Sphaenorhynchus
Dendropsophini
Hylinae
Hylidae

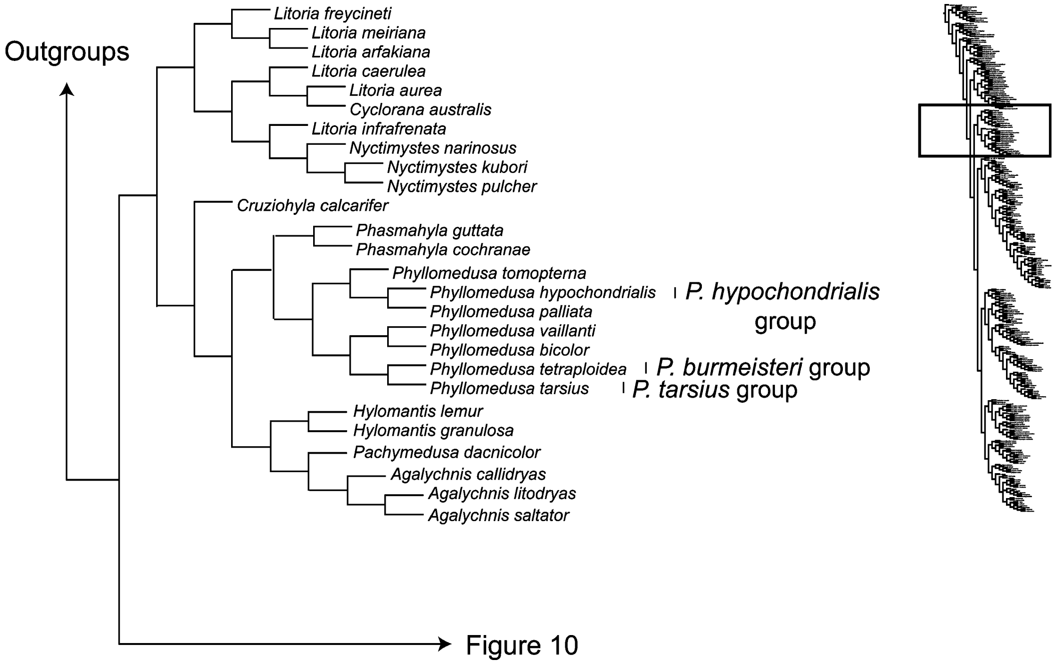


Fig. 9. A partial view of the strict consensus, updated with the new taxonomy for Phyllomedusinae proposed here.

metacarpal and metatarsal tubercles is a possible morphological synapomorphy of the genus (Garcia et al., 2001).

COMMENTS: Our results imply a clade composed of *Aplastodiscus* and two complexes of the former *Hyla albomarginata* group, as defined by Cruz and Peixoto (‘‘1985’’ [1987]): the *H. albofrenata* and *H. albosignata* complexes, which are here included in *Aplastodiscus*.

Garcia et al. (2001) suggested four synapomorphies for *Aplastodiscus* as then understood (that is, containing only *A. cochranae* and *A. perviridis*): (1) lack of webbing between toes I and II, and very reduced webbing in the remaining toes, (2) bicolored iris, (3) females with unpigmented eggs, and (4) highly developed inner metacarpal and metatarsal tubercles. The lack of webbing between toes I and II, the reduction of webbing among the remaining toes, and the bicolored iris occur only in the two species originally contained in *Aplastodiscus*. These species, *A. cochranae* and *A. perviridis*, are here included in the *A. perviridis* group, and therefore these two character states are possibly synapomorphic only of this group, not of *Aplastodiscus* as redefined here. The very developed inner metacarpal and metatarsal tubercles are also present in all species of the *Hyla albofrenata* and *H. albosignata* complexes (Cruz and Peixoto ‘‘1984’’ [1985], ‘‘1985’’ [1987]; Cruz et al., 2003), and we consider this feature as a putative synapomorphy of *Aplastodiscus* as redefined here. The presence of unpigmented eggs is known to occur in all species of the former *H. albofrenata* and *H. albosignata* complexes with known eggs (Haddad and Sawaya, 2000; Garcia et al., 2001; Hartmann et al., 2004; Haddad et al., 2005). However, the taxonomic distribution of egg pigmentation within Cophomantini is not well known. It is possible that unpigmented eggs are actually a synapomorphy of a more inclusive clade, as they are known to occur in at least some species of *Hyloscirtus* (*H. jahni*, *H. larinopygion*, *H. palmeri*, and *H. platydactyla*; La Marca, 1985, and Faivovich, personal obs.), *Hypsiboas* (*H. lemai*, Duellman [1997], and the undescribed species here called *Hyla* sp. 2), and *Myersiohyla* new genus (*Hyla inparquesi*; Faivo-

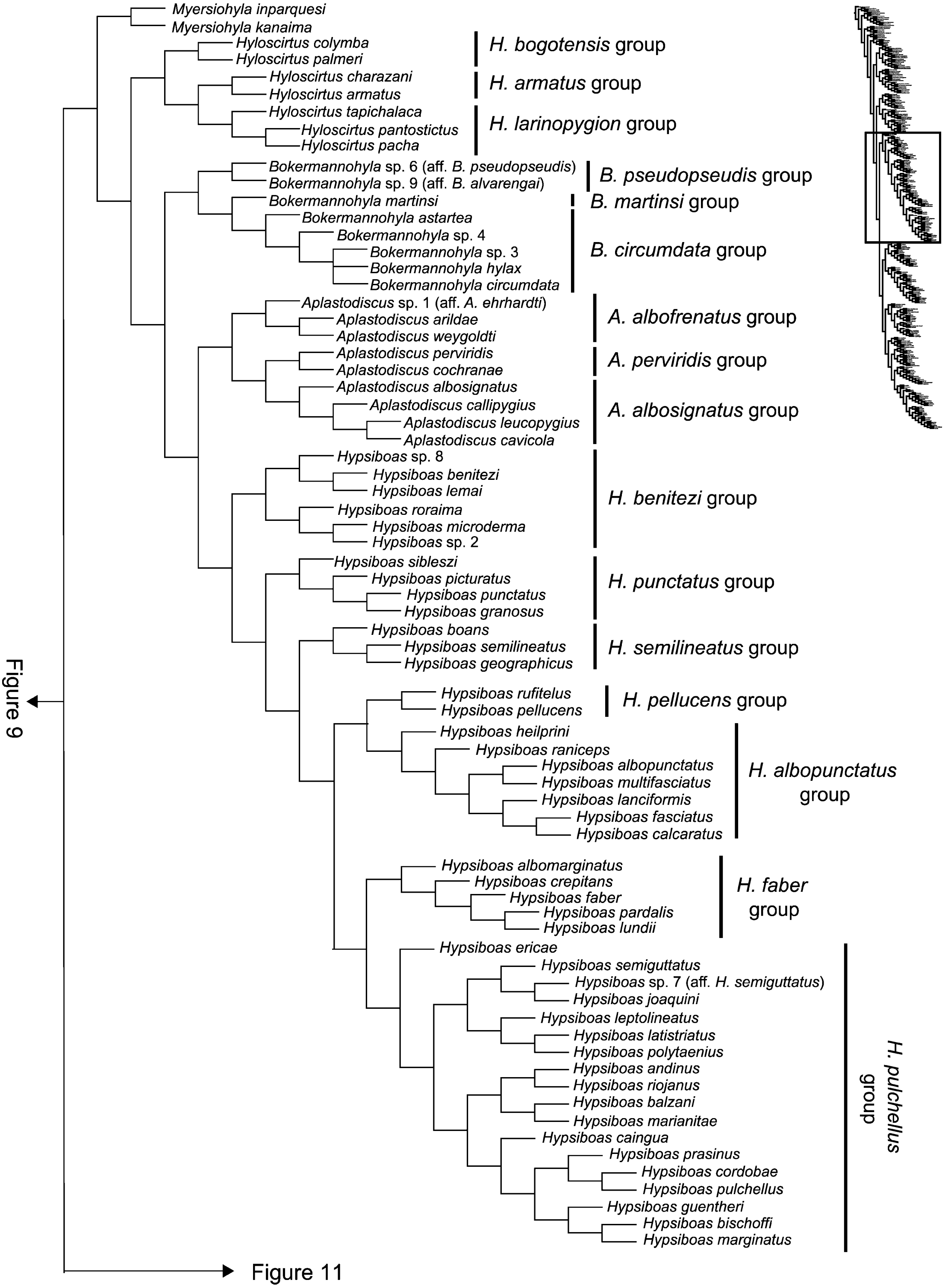


Fig. 10. A partial view of the strict consensus, updated with the new taxonomy for the tribe Cophomantini.

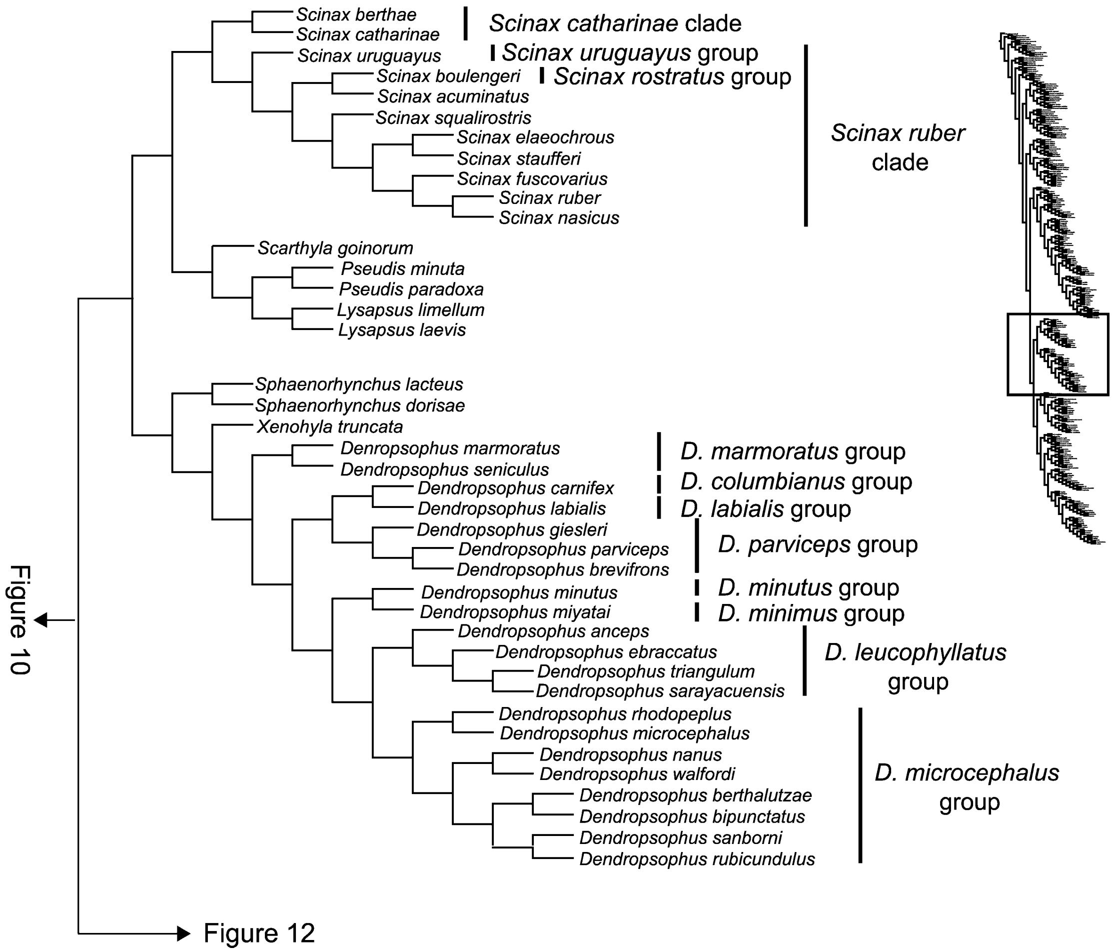


Fig. 11. A partial view of the strict consensus, updated with the new taxonomy for the tribe Dendropsophini.

vich, Myers, and McDiarmid, in prep.; eggs of *M. kanaima* are pigmented, Duellman and Hoogmoed, 1992); the only known eggs of species of *Bokermannohyla*, new genus have a pigmented animal pole (Sazima and Bokermann, 1977; Eterovick and Brandão, 2001).

Most species of *Aplastodiscus*, as redefined here, possess a white parietal peritoneum (Garcia and Faivovich, personal obs.), as it occurs in some other Cophomantini (*Hyla bogotensis*, *H. granosa*, and *H. punctata* groups, *H. marginata*; Ruiz-Carranza and Lynch [1991: 4]; Garcia [2003]; Faivovich, personal obs.). While this could be a possible synapomorphy of *Aplastodiscus*, the taxonomic distribution of this character state is still poorly known in various components of the Cophomantini, so we prefer to await further research on the issue, before hypothesizing polarities.

Bokermann (1967c) pointed out the overall similarity among advertisement calls of the *Hyla albofrenata* and *H. albosignata* complexes and *Aplastodiscus perviridis*. Future research will define whether any character state related to the advertisement calls could be considered as a synapomorphy of *Aplastodiscus* as redefined here, or of any of its internal clades.

CONTENTS: Fourteen species included in three species groups.

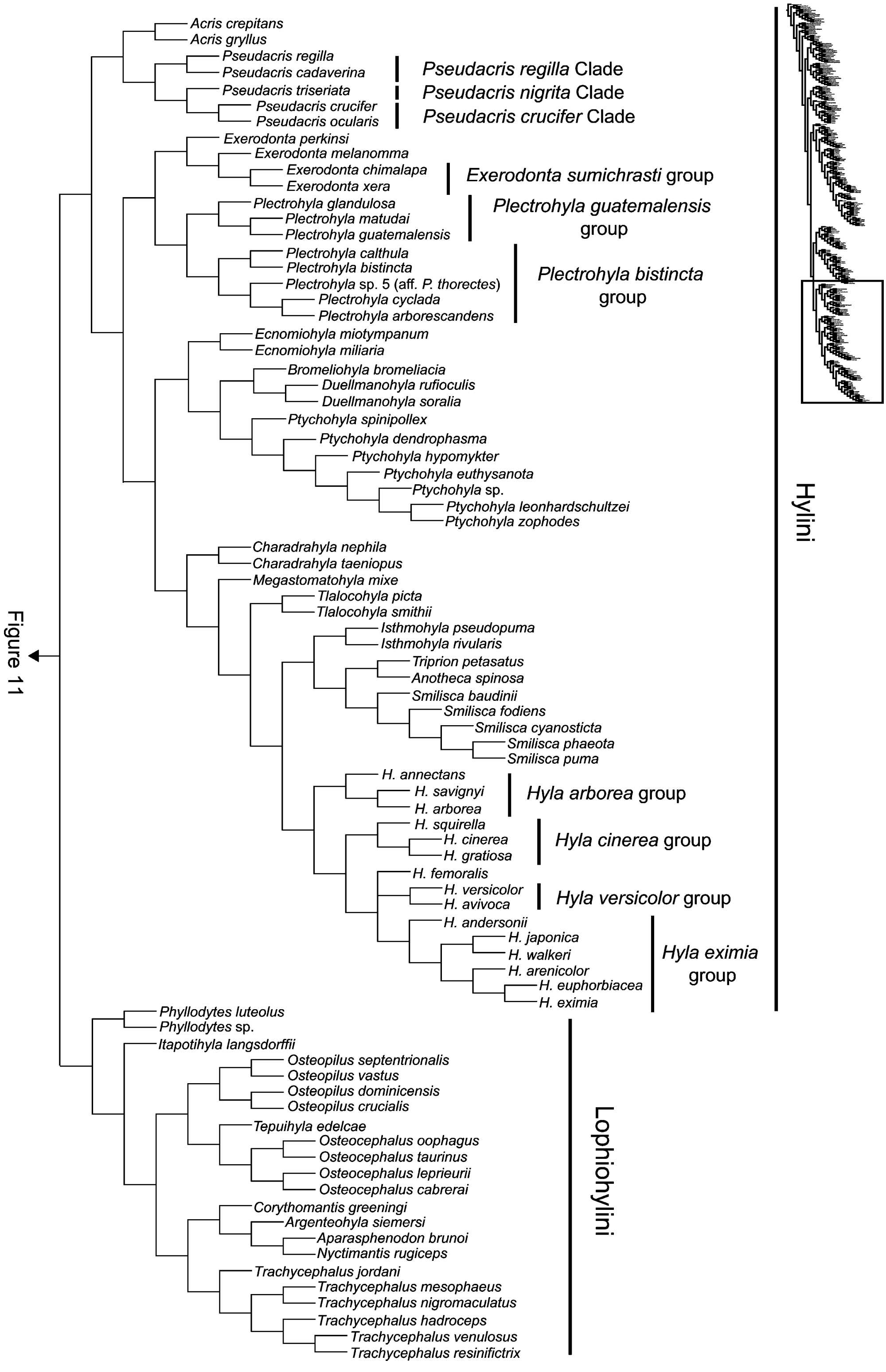


Fig. 12. A partial view of the strict consensus, updated with the new taxonomy for the tribes Hylini and Lophiohylini.

Aplastodiscus albofrenatus Group

DIAGNOSIS: This species group is diagnosed by 114 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these transformations. We are not aware of any morphological synapomorphies for this group.

CONTENTS: Six species. *Aplastodiscus albofrenatus* (A. Lutz, 1924), new comb.; *Aplastodiscus arildae* (Cruz and Peixoto, ‘‘1985’’ [1987]), new comb.; *Aplastodiscus ehrhardti* (Müller, 1924), new comb.; *Aplastodiscus musicus* (B. Lutz, 1948), new comb.; *Aplastodiscus weygoldti* (Cruz and Peixoto, ‘‘1985’’ [1987]), new comb.

Aplastodiscus albosignatus Group

DIAGNOSIS: This species group is diagnosed by 42 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. A possible morphological synapomorphy of this group is the presence of elaborate tubercles and ornamentation around the cloacal region (Cruz and Peixoto, ‘‘1985’’ [1987]).

CONTENTS: Seven species. *Aplastodiscus albosignatus* (A. Lutz and B. Lutz, 1938), new comb.; *Aplastodiscus callipygius* (Cruz and Peixoto, ‘‘1984’’ [1985]), new comb.; *Aplastodiscus cavicola* (Cruz and Peixoto, ‘‘1984’’ [1985]), new comb.; *Aplastodiscus flumineus* (Cruz and Peixoto, ‘‘1984’’ [1985]), new comb.; *Aplastodiscus ibirapitanga* (Cruz, Pimenta, and Silvano, 2003), new comb.; *Aplastodiscus leucopygius* (Cruz and Peixoto, ‘‘1984’’ [1985]), new comb.; *Aplastodiscus sibilatus* (Cruz, Pimenta, and Silvano, 2003), new comb.

Aplastodiscus perviridis Group

DIAGNOSIS: This species group is diagnosed by 58 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Apparent morphological synapomorphies of this group include the bicolored iris and the absence of webbing between toes I and II (known instances of homoplasy within hylids occur in some *Scinax* and in various groups of Lophiohylini) and reduction of webbing between the other toes (Garcia et al., 2001).

CONTENTS: Two species. *Aplastodiscus cochranae* (Mertens, 1952); *Aplastodiscus perviridis* A. Lutz *in* B. Lutz, 1950.

Bokermannohyla, new genus

TYPE SPECIES: *Hyla circumdata* Cope, ‘‘1870’’ [1871].

DIAGNOSIS: This genus is diagnosed by 65 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy.

ETYMOLOGY: This genus is dedicated to Werner Carlos Augusto Bokermann (1929–1995), as homage to his contribution to the knowledge of Brazilian anurans. He also described several species now included in the new genus. The name derives from Bokermann + connecting *-o* + *Hyla*. We are adopting the ending *-hyla* for several of the new genera described here, most of which contain species groups formerly placed in *Hyla*. The gender is feminine.

COMMENTS: *Bokermannohyla* includes all species previously allocated in the *Hyla circumdata*, *H. martinsi*, and *H. pseudopseudis* groups. We include tentatively the *H. claresignata* group pending the inclusion of its species in the analysis, because it was associated to the *H. circumdata* group by Bokermann (1972) and Jim and Caramaschi (1979). *Hyla alvarengai* is also included because our analysis shows that *Hyla* sp. 9 (aff. *H. alvarengai*) is nested within this new genus. These species groups should be maintained within *Bokermannohyla* until their monophyly is rigorously tested.

CONTENTS: Twenty-three species, placed in four species groups.

Bokermannohyla circumdata Group

DIAGNOSIS: This species group is diagnosed by 52 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. A putative morphological synapomorphy of this group is the presence of (usually thin) dark vertical stripes on the posterior surface of the thigh (Heyer, 1985).

CONTENTS: Fifteen species. *Bokermannohyla ahenea* (Napoli and Caramaschi, 2004), new comb.; *Bokermannohyla astartea* (Bokermann, 1967), new comb.; *Bokermannohyla caramaschii* (Napoli, 2005) new comb.; *Bokermannohyla carvalhoi* (Peixoto, 1981), new comb.; *Bokermannohyla circumdata* (Cope, ''1870'' [1871]), new comb.; *Bokermannohyla feioi* (Napoli and Caramaschi, 2004), new comb.; *Bokermannohyla gouveai* (Peixoto and Cruz, 1992), new comb.; *Bokermannohyla hylax* (Heyer, 1985), new comb.; *Bokermannohyla ibitipoca* (Caramaschi and Feio, 1990), new comb.; *Bokermannohyla izeckshoni* (Jim and Caramaschi, 1979), new comb.; *Bokermannohyla lucianae* (Napoli and Pimenta, 2003), new comb.; *Bokermannohyla luctuosa* (Pombal and Haddad, 1993), new comb.; *Bokermannohyla nanuzae* (Bokermann and Sazima, 1973), new comb.; *Bokermannohyla ravida* (Caramaschi, Napoli and Bernardes, 2001), new comb.; *Bokermannohyla sazimai* (Cardoso and Andrade, ''1982'' [1983]), new comb.

Bokermannohyla claresignata Group

DIAGNOSIS: We are not aware of any synapomorphy supporting the monophyly of this group; see below.

COMMENTS: We did not include any exemplar of this group, and as such we did not test its monophyly. See the earlier discussion regarding its position in the South American I clade. Considering the topology of Cophomantini, synapomorphies suggested for the *Bokermannohyla claresignata* group can only be maintained if assumed to be reversals (i.e., a enlarged larval oral disc, complete marginal papillae, and large number of labial tooth rows are also present in *Myersiohyla* new genus and the *Hyloscirtus armatus* group; complete marginal papillae and large number of labial tooth rows are also present in the *H. bogotensis* and *H. larinopygion* groups; the marginal papillae are also complete or with an extremely reduced gap in other species of *Bokermannohyla*). This would be unproblematic if it were a result of the analysis, but we prefer not to assume it a priori. While these character states cannot be considered at this stage to support the monophyly of the *B. claresignata* group, considering that its two species are barely distinguishable from each other, we think its nonmonophyly is unlikely and we continue to recognize the group as a hypothesis to be tested.

CONTENTS: Two species. *Bokermannohyla claresignata* (A. Lutz and B. Lutz, 1939), new comb.; *Bokermannohyla clepsydra* (A. Lutz, 1925), new comb.

Bokermannohyla martinsi Group

DIAGNOSIS: Apparent morphological synapomorphies of this group are the development of the humeral crest into a hook-like projection, and a bifid prepollex (Bokermann, 1965b).

COMMENTS: We included a single exemplar of this group, and as such we did not test its monophyly. We continue recognizing it on the basis of the morphological evidence noted above.

CONTENTS: Two species. *Bokermannohyla langei* (Bokermann, 1965), new comb.; *Bokermannohyla martinsi* (Bokermann, 1964), new comb.

Bokermannohyla pseudopseudis Group

DIAGNOSIS: This group is diagnosed by 48 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy for this group.

COMMENTS: Considering our results, which show the undescribed species of the *Hyla pseudopseudis* group (*Hyla* sp. 6) to be the sister taxon of an undescribed species similar with *H. alvarengai* (*Hyla* sp. 9), we are tentatively including the *H. alvarengai* in this species group. Eterovick and Brandão (2001) characterized this group on the basis of the presence of short, lateral irregular tooth rows and for having more tooth rows (between six and eight rows) in the oral discs of the larvae than do those of the *Bokermannohyla circumdata* group. However, the tadpole of *H. ibitiguara*, included in this group by Caramaschi et al. (2001), has a labial tooth formula of 2/4 (Cardoso, 1983) and seems to lack the short, lateral irregular tooth rows, as do tadpoles of *H. alvarengai* (Sazima and Bokermann, 1977).

CONTENTS: Four species. *Bokermannohyla alvarengai* (Bokermann, 1956), new comb.; *Bokermannohyla ibitiguara* (Cardoso, 1983), new comb.; *Bokermannohyla pseudopseudis* (Miranda-Ribeiro, 1937), new comb.; *Bokermannohyla saxicola* (Bokermann, 1964), new comb.

Hyloscirtus Peters, 1882

TYPE SPECIES: *Hyloscirtus bogotensis* Peters, 1882.

Hylonomus Peters, 1882. Type species: *Hylonomus bogotensis* Peters, 1882, by monotypy. Primary homonym of *Hylonomus* Dawson, 1860.

DIAGNOSIS: This genus is diagnosed by 56 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. The only putative morphological synapomorphy that we are aware of for this genus is the wide dermal fringes on fingers and toes.

COMMENTS: This genus contains all species included in the *Hyla armata*, *H. bogotensis*, and *H. larinopygion* species groups. The groups are maintained unchanged within *Hyloscirtus* until the monophyly of each of them is properly tested with denser taxon sampling.

While the wide dermal fringes in fingers and toes are present in the three species groups, in the *H. armatus* group they are more obvious in the first manual digit. In the *H. bogotensis* and *H. larinopygion* groups the fringes look even wider, apparently due to a combination of proportionally smaller discs and wider fringe, which gives the finger or toe the appearance of being almost as wide as the disc.

CONTENTS: Twenty-eight species placed in three species groups.

Hyloscirtus armatus Group

DIAGNOSIS: This species group is diagnosed by 103 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Duellman et al. (1997) suggested four synapomorphies of the *H. armatus* group: the presence of keratin-covered bony spines on the proximal ventral surface of the humerus, on the expanded distal element of the prepollex, and on the first metacarpal; forearms hypertrophied; tadpole tail long with low fins and bluntly rounded tip; and the presence of a ‘‘shelf’’ on the larval upper jaw sheath.

COMMENTS: Our observations of breeding males of the two species of this group indicate the presence of darkly pigmented, keratinized spicules in the dorsum, head (particularly lips), forelimbs, undersides of forelimbs, and pectoral and abdominal region. As the breeding biology of this and the other two species groups of the genus becomes better known, it will be possible to understand if the presence of these spicules are a putative synapomorphy of the *H. armatus* group.

CONTENTS: Two species. *Hyloscirtus armatus* (Boulenger, 1902), new comb.; *Hyloscirtus charazani* (Vellard, 1970), new comb.

Hyloscirtus bogotensis Group

DIAGNOSIS: This species group is diagnosed by 95 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these transformations. The only morphological synapomorphy that has been proposed for this group is the presence of a mental gland in adult males (Duellman, 1972b). See appendix 4 for a justification of the inclusion of ‘‘*Hyalinobatrachium*’’ *estevesi* (Rivero, 1968) in this species group.

COMMENTS: Species of the *Hyloscirtus bogotensis* group have a white parietal peritoneum (Ruiz-Carranza and Lynch, 1991: 4), as do some other Cophomantini (see comments for *Aplastodiscus*). Further research on the taxonomic distribution of this character state in the other species groups of *Hyloscirtus*, and in the other genera of Cophomantini, would clarify which group or groups are diagnosed by this synapomorphy.

CONTENTS: Sixteen species. *Hyloscirtus albopunctulatus* (Boulenger, 1882), new comb.; *Hyloscirtus alytolylax* (Duellman, 1972), new comb.; *Hyloscirtus bogotensis* Peters, 1882; *Hyloscirtus callipeza* (Duellman, 1989), new comb.; *Hyloscirtus colymba*

(Dunn, 1931), new comb.; *Hyloscirtus denticulentus* (Duellman, 1972), new comb.; *Hyloscirtus estevesi* (Rivero, 1968), new comb.; *Hyloscirtus jahni* (Rivero, 1961), new comb.; *Hyloscirtus lascinius* (Rivero, 1969), new comb.; *Hyloscirtus lynchi* (Ruiz-Carranza and Ardila-Robayo, 1991), new comb.; *Hyloscirtus palmeri* (Boulenger, 1908), new comb.; *Hyloscirtus phyllognathus* (Melin, 1941), new comb.; *Hyloscirtus piceigularis* (Ruiz-Carranza and Lynch, 1982), new comb.; *Hyloscirtus platydactylus* (Boulenger, 1905), new comb.; *Hyloscirtus simmonsi* (Duellman, 1989), new comb.; *Hyloscirtus torrenticola* (Duellman and Altig, 1978), new comb.

Hyloscirtus larinopygion Group

DIAGNOSIS: This species group is diagnosed by 32 transformations in mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy for this group.

CONTENTS: Ten species. *Hyloscirtus caucanus* (Ardila-Robayo, Ruiz-Carranza, and Roa-Trujillo, 1993), new comb.; *Hyloscirtus larinopygion* (Duellman, 1973), new comb.; *Hyloscirtus lindae* (Duellman and Altig, 1978), new comb.; *Hyloscirtus pacha* (Duellman and Hillis, 1990), new comb.; *Hyloscirtus pantostictus* (Duellman and Berger, 1982), new comb.; *Hyloscirtus psarolaimus* (Duellman and Hillis, 1990), new comb.; *Hyloscirtus ptychodactylus* (Duellman and Hillis, 1990) new comb.; *Hyloscirtus sarampiona* (Ruiz-Carranza and Lynch, 1982) new comb.; *Hyloscirtus staufferorum* (Duellman and Coloma, 1993), new comb.; *Hyloscirtus tapichalaca* (Kizirian, Coloma, and Paredes-Recalde, 2003), new comb.

Hypsiboas Wagler, 1830

TYPE SPECIES: *Hyla palmata* Daudin, 1802 (= *Rana boans* Linnaeus, 1758), by subsequent designation by implication of Duellman, 1977 (not monotypy as stated by Duellman, 1977: 24).

Boana Gray, 1825. Type species: *Rana boans* Linnaeus, 1758, by monotypy. Coined as a synonym of *Hyla* and never subsequently validated as available under article 11.6.1 (ICZN, 1999).

Auletris Wagler, 1830. Type species: *Rana boans* Linnaeus, 1758, by subsequent designation of Stejneger (1907).

Lobipes Fitzinger, 1843. Type species: *Hyla palmata* Daudin, 1801 (= *Rana boans* Linnaeus, 1758), by original designation.

Phyllobius Fitzinger, 1843. Type species: *Hyla albomarginata* Spix, 1824, by original designation. Primary homonym of *Phyllobius* Schoenherr, 1824.

Centrotelma Burmeister, 1856. Type species: *Hyla infulata* Wied-Neuwied, 1824 (= *H. albomarginata* Spix, 1824), by subsequent implication by Duellman (1977) (not monotypy as stated by Duellman, 1977: 24).

Hylomedusa Burmeister, 1856. Type species: *Hyla crepitans* Wied-Neuwied, 1825, by subsequent designation by implication of Duellman (1977) (not monotypy as stated by Duellman, 1977: 24).

Cinclidium Cope, 1867. Type species: *Cinclidium granulatum* Cope, 1867 (= *Rana boans* Linnaeus, 1758), by monotypy. Primary homonym of *Cinclidium* Blyth, 1842.

Cophomantis Peters, 1870. Type species: *Cophomantis punctillata* Peters, 1870 (= *Hyla semilineata* Spix, 1824) by monotypy.

Cincliscopus Cope, ''1870'' [1871]. *Replacement* name for *Cinclidium* Cope, 1867.

DIAGNOSIS: This genus is diagnosed by 33 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy for this genus.

COMMENTS: This genus is resurrected for all species formerly included in the *Hyla albopunctata*, *H. boans*, *H. geographica*, *H. granosa*, *H. pulchella*, and *H. punctata* species groups, the *H. albomarginata* complex, and several species previously unassigned to any group. Most of the former species groups are retained using the new combinations and its contents are redefined in accordance with our results to avoid paraphyly.

It is tempting to suggest that the presence of a prepollical spine is a possible synapomorphy of this group. However, as discussed earlier, further anatomical studies are necessary to determine whether this character state is homologous with that present in *Bokermannohyla*.

Duellman (2001) and Savage (2002b) suggested that the name *Boana* Gray, 1825 could be applied to a clade of Gladiator

Frogs. Gray (1825) suggested the name *Boana* as a synonym of *Hyla*, and Stejneger (1907) subsequently designated *Hyla boans* as its type species. Unfortunately, as far as we can determine from literature research, the name *Boana* has never been used in combination with an active species name, therefore failing to fulfill the criterion established by article 11.6.1 (ICZN, 1999) for the availability of names originally proposed as synonyms. Duellman (2001) further stated that if *Hyla punctata* were included within this group, ‘‘the generic *Hylaplesia* Boie would be included in the synonymy of *Boana*.’’ However, this is not the case since, as discussed by Dubois (1982), the type species of *Hylaplesia* is *Rana tinctoria* Cuvier, 1797 (= *Dendrobates tinctorius*), by subsequent designation of Duméril and Bibron (1841).

Wagler (1830) did not combine *Hypsiboas* with any of the species included in this genus. Subsequent authors (e.g., Tschudi, 1838; Fitzinger, 1843, Cope, 1862) considered it masculine, as we are doing here.

CONTENTS: Seventy species placed in seven species groups, plus two species unassigned to group.

Hypsiboas albopunctatus Group

DIAGNOSIS: This species group is diagnosed by 43 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy.

COMMENTS: To avoid paraphyly, we include *Hyla fasciata* and *H. calcarata* in the group, and to avoid the creation of a species group for a single species, we also include the sister taxon of the former *H. albopunctata* group, *H. heilprini*. Larvae so far known of the group (*H. albopunctata*, *H. calcarata*, *H. fasciata*, *H. multifasciata*, *H. raniceps*), with the exception of *H. heilprini* and *H. lanciformis* are reported to have the mediodistal portion of the internal wall of the spiracle separated from the body wall (de Sá, 1995; 1996; Faivovich, 2002, personal obs.; Peixoto and Cruz, 1983; Wild, 1992). Peixoto and Cruz (1983) reported the same character state for larvae of *H. albomarginata*. Additional studies on the taxonomic distribution of this peculiar character state are needed to know the limits of the clade or clades it diagnoses. Wild (1992) noticed that larvae of *H. calcarata*, *H. fasciata*, and *H. lanciformis* share the presence of pigmented caudal vertical bands that interconnect laterally along the musculature, with this pattern occurring as well in *H. raniceps* (Faivovich, personal obs.).

Hyla dentei was originally associated with both *H. raniceps* and the former *H. geographica* group. We are tentatively including it in the *Hypsiboas albopunctatus* group in view of its overall similarities with *Hyla calcarata* and *H. fasciata*.

CONTENTS: Nine species. *Hypsiboas albopunctatus* (Spix, 1824), new comb.; *Hypsiboas calcaratus* (Troschel, 1848), new comb.; *Hypsiboas dentei* (Bokermann, 1967), new comb.; *Hypsiboas fasciatus* (Günther, 1858), new comb.; *Hypsiboas heilprini* (Noble, 1923), new comb.; *Hypsiboas lanciformis* Cope, 1871; *Hypsiboas leucocheilus* (Caramaschi and Niemeyer, 2003), new comb.; *Hypsiboas multifasciatus* (Günther, 1859), new comb.; *Hypsiboas raniceps* Cope, 1862.

Hypsiboas benitezi Group

DIAGNOSIS: This species group is diagnosed by 30 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. A putative synapomorphy of this group is the presence of a flat mental gland in males (Faivovich et al., in prep.) (known instance of homoplasy in *Hyla granosa*).

COMMENTS: This new species group includes the clade composed of three species from the Guayana Highlands and three species from the northwestern Amazon Basin. Because one of the Guayanan and one of the Amazonian species are still undescribed, they are not further considered. Two species, *Hyla microderma* and *H. roraima,* are a fragment of the former *H. geographica* group. We are also including tentatively *H. hutchinsi* and *H. rhythmicus*, based on their overall similarity with *H. benitezi*. See appendix 4 for a justification of the inclusion of *Hyla pulidoi* (Rivero, 1968) in this species group.

CONTENTS: Seven species. *Hypsiboas benitezi* (Rivero, 1961), new comb.; *Hypsiboas hutchinsi* (Pyburn and Hall, 1984), new comb.; *Hypsiboas lemai* (Rivero, 1971), new comb.; *Hypsiboas microderma* (Pyburn, 1977), new comb.; *Hypsiboas pulidoi* (Rivero, 1968), new comb.; *Hypsiboas rhythmicus* (Señaris and Ayarzagüena. 2002), new comb.; *Hypsiboas roraima* (Duellman and Hoogmoed, 1992), new comb.

Hypsiboas faber Group

DIAGNOSIS: This species group is diagnosed by 28 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy for this group.

COMMENTS: We are including in this group a clade of some species resulting from the fragmentation of the *Hyla boans* group. Our results indicate that *H. crepitans*, *H. faber*, *H. lundii*, and *H. pardalis* form, together with *H. albomarginata* (a component of the *Hyla albomarginata* group), a monophyletic group only distantly related to *H. boans*, the species that gives the name to the former group. For this reason, we recognize this clade as the *Hypsiboas faber* species group. We tentatively include *Hyla exastis* in this group because Caramaschi and Rodrigues (2003) related it to *H. lundii* and *H. pardalis* on the basis of the lichenous color pattern and the rugose dorsal skin texture.

A likely behavioral synapomorphy of most species of this group, with the exception of *Hyla albomarginata*, is the construction of nests by males (with two instances of homoplasy within Hylinae, some species of the now called *Hypsiboas semilineatus* group (see p. 88), and the *Bokermannohyla circumdata* group.) The inclusion of *Hyla pugnax* and *H. rosenbergi* is tentative, based on the fact that males construct nests, but they lack the reticulated palpebral membrane, a likely synapomorphy present in most species of the now called *Hypsiboas semilineatus* group (see below). Future research will test this bold hypothesis.

CONTENTS: Eight species. *Hypsiboas albomarginatus* (Spix, 1824), new comb.; *Hypsiboas crepitans* (Wied-Neuwied, 1824), new comb.; *Hypsiboas exastis* (Caramaschi and Rodrigues, 2003), new comb.; *Hypsiboas faber* (Wied-Neuwied, 1821), new comb.; *Hypsiboas lundii* (Burmeister, 1856), new comb.; *Hypsiboas pardalis* (Spix, 1824), new comb.; *Hypsiboas pugnax* (O. Schmidt, 1857), new comb.; *Hypsiboas rosenbergi* (Boulenger, 1898), new comb.

Hypsiboas pellucens Group

DIAGNOSIS: This species group is diagnosed by 115 transformations in mitochondrial ribosomal genes. See appendix 5 for a complete list of these transformations. We are not aware of any morphological synapomorphy for the group.

COMMENTS: We recognize this new species group to include the clade composed of the fragment of the former *Hyla albomarginata* complex that includes *H. pellucens* and *H. rufitela*. The inclusion of *H. rubracyla* is tentative, based on its previous association with *H. pellucens*.

CONTENTS: Three species. *Hypsiboas pellucens* (Werner, 1901), new comb.; *Hypsiboas rubracylus* (Cochran and Goin, 1970), new comb.; *Hypsiboas rufitelus* (Fouquette, 1958), new comb.

Hypsiboas pulchellus Group

DIAGNOSIS: This species group is diagnosed by 55 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Observations by Faivovich and Garcia (unpubl.) suggest that the absence of the slip of the m. depressor mandibulae that originates on the dorsal fascia at the level of the m. dorsalis scapularis (present in all other exemplars so far studied of *Hypsiboas*, and also of *Aplastodiscus*, *Hyloscirtus*, and *Bokermannohyla*) is a possible synapomorphy of the group.

COMMENTS: We continue to recognize within this species group a *Hypsiboas polytaenius* clade that includes *Hyla beckeri*, *H. buriti*, *H. cipoensis*, *H. goiana*, *H. latistriata*, *H. leptolineata*, *H. phaeopleura*, *H. polytaenia*, and *H. stenocephala*. Besides molecular data, a likely morphological synapomorphy that supports this clade is the dorsally striped pattern (homoplastic in *Hyla bischoffi* where a striped pattern occurs on some individuals).

CONTENTS: Thirty species. *Hypsiboas alboniger* (Nieden, 1923), new comb.; *Hypsiboas andinus* (Müller, 1926), new comb.; *Hypsiboas balzani* (Boulenger, 1898), new comb.; *Hypsiboas beckeri* (Caramaschi and Cruz, 2004), new comb.; *Hypsiboas bischoffi* (Boulenger, 1887), new comb.; *Hypsiboas buriti* (Caramaschi and Cruz, 1999), new comb.; *Hypsiboas caingua* (Carrizo, ''1990'' [1991]), new comb.; *Hypsiboas callipleura* (Boulenger, 1902), new comb.; *Hypsiboas cipoensis* (B. Lutz, 1968), new comb.; *Hypsiboas cordobae* (Barrio, 1965), new comb.; *Hypsiboas cymbalum* (Bokermann, 1963), new comb.; *Hypsiboas ericae* (Caramaschi and Cruz, 2000), new comb.; *Hypsiboas freicanecae* (Carnaval and Peixoto, 2004), new comb.; *Hypsiboas goianus* (B. Lutz, 1968), new comb.; *Hypsiboas guentheri* (Boulenger, 1886), new comb.; *Hypsiboas joaquini* (B. Lutz, 1968), new comb.; *Hypsiboas latistriatus* (Caramaschi and Cruz, 2004), new comb.; *Hypsiboas leptolineatus* (P. Braun and C. Braun, 1977), new comb.; *Hypsiboas marginatus* (Boulenger, 1887), new comb.; *Hypsiboas marianitae* (Carrizo, 1992), new comb.; *Hypsiboas melanopleura* (Boulenger, 1912), new comb.; *Hypsiboas palaestes* (Duellman, De la Riva, and Wild, 1997), new comb.; *Hypsiboas phaeopleura* (Caramaschi and Cruz, 2000), new comb.; *Hypsiboas polytaenius* (Cope, 1870), new comb.; *Hypsiboas prasinus* (Burmeister, 1856), new comb.; *Hypsiboas pulchellus* (Duméril and Bibron, 1841), new comb.; *Hypsiboas riojanus* (Koslowsky, 1895), new comb.; *Hypsiboas secedens* (B. Lutz, 1963), new comb.; *Hypsiboas semiguttatus* (A. Lutz, 1925), new comb.; *Hypsiboas stenocephalus* (Caramaschi and Cruz, 1999), new comb.

Hypsiboas punctatus Group

DIAGNOSIS: This species group is diagnosed by 30 transformations in mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy for the group.

COMMENTS: We do not see any reason to keep the former *Hyla granosa* and *H. punctata* groups separated, as our analysis shows that the two nominal species form a monophyletic group and they are phenotypically similar, so we include all the species in the *Hypsiboas punctatus* group. The inclusion of *Hyla alemani*, *H. atlantica*, *H. hobbsi*, and *H. ornatissima* is tentative, based on their previous association with the former *H. granosa* and *H. punctata* groups. The inclusion of *Hyla picturata* is based on our analysis.

CONTENTS: Eight species. *Hypsiboas alemani* (Rivero, 1964), new comb.; *Hypsiboas atlanticus* (Caramaschi and Velosa, 1996), new comb.; *Hypsiboas granosus* (Boulenger, 1882), new comb.; *Hypsiboas hobbsi* (Cochran and Goin, 1970), new comb.; *Hypsiboas ornatissimus* (Noble, 1923), new comb.; *Hypsiboas picturatus* (Boulenger, 1882), new comb.; *Hypsiboas punctatus* (Schneider, 1799), new comb.; *Hypsiboas sibleszi* (Rivero, 1971), new comb.

Hypsiboas semilineatus Group

DIAGNOSIS: This species group is diagnosed by 128 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. A possible morphological synapomorphy of this species group is the presence of a reticulated palpebral membrane (with instances of homoplasy in other species of *Hypsiboas*: *H. hutchinsi* and *H. microderma*).

COMMENTS: We include in this group the fragments of the former *Hyla boans* and *H. geographica* groups that form a monophyletic group. We prefer to call it the *Hypsiboas semilineatus* group because the use of either the *H. boans* or *H. geographicus* groups would only cause confusion regarding its contents. The inclusion of *Hyla wavrini* is based on the combination of the same reproductive mode of *H. boans* (eggs deposited in a basin built by the male) and a reticulated palpebral membrane (Hoogmoed, 1990). *Hyla pombali* is tentatively included based on comments by Caramaschi et al (2004a) stressing its similarities with *H. semilineata*, but with the caveat that it lacks the reticulated palpebral membrane. Schooling behavior has been reported for tadpoles of *H. geo-*

graphica (Caldwell, 1989) and *H. semilineata* (D'Heursel and Haddad, 2002), and this may be a synapomorphy for at least these two species.

CONTENTS: Six species. *Hypsiboas boans* (Linnaeus, 1758), new comb.; *Hypsiboas geographicus* (Spix, 1824), new comb.; *Hypsiboas pombali* (Caramaschi, Silva, and Feio, 2004); *Hypsiboas semilineatus* (Spix, 1824), new comb.; *Hypsiboas wavrini* (Parker, 1936), new comb.

Species of *Hypsiboas* Unassigned to Group

There are two species of *Hypsiboas* that we do not assign to any group because we do not have evidence favoring a relationship with any of the species groups that we are recognizing for the genus. These species are *Hypsiboas fuentei* (Goin and Goin, 1968), new comb., and *Hypsiboas varelae* (Carrizo, 1992), new comb.

Myersiohyla, new genus

TYPE SPECIES: *Hyla inparquesi* Ayarzagüena and Señaris (''1993'' [1994]).

DIAGNOSIS: This genus is diagnosed by 48 transformations in mitochondrial protein and ribosomal genes. See appendix 5 for complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy for this group.

ETYMOLOGY: Dedicated to Charles W. Myers in recognition of his contributions to herpetology, particularly to the herpetofauna of the Guayana Highlands. The name derives from *Myersius* (latinized Myers) + connecting *-o* + *Hyla*. The gender is feminine (Myers and Stothers, MS).

COMMENTS: This new genus includes the species of *Hyla aromatica* group and *H. kanaima*, a former member of the *H. geographica* group. Ayarzagüena and Señaris (''1993'' [1994]) included the presence of a strong odor in the definition of the *Hyla aromatica* group; this could be a possible synapomorphy of *Myersiohyla*. The presence of a strong odor has yet to be recorded in *H. kanaima*. It should be noted that the sample we included of *H. inparquesi* was not collected in the type locality, but in Cerro de la Neblina, ca. 300 km southward.

CONTENTS: Four species. *Myersiohyla aromatica* (Ayarzagüena and Señaris, ''1993'' [1994]), new comb.; *Myersiohyla inparquesi* (Ayarzagüena and Señaris, ''1993'' [1994]), new comb.; *Myersiohyla loveridgei* (Rivero, 1961), new comb.; *Myersiohyla kanaima* (Goin and Wodley, 1961), new comb.

DENDROPSOPHINI FITZINGER, 1843

Dendropsophi Fitzinger, 1843. Type genus: *Dendropsophus* Fitzinger, 1843.

DIAGNOSIS: This tribe is diagnosed by 23 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Apparent morphological synapomorphies of this tribe are the absence of lingual papillae in the larvae (known instances of reversal in *Lysapsus* and *Pseudis*) and the absence of nuptial excrescences (with instances of homoplasy in some species of *Sphaenorhynchus* and several Cophomantini).

COMMENTS: This tribe contains the genera *Dendropsophus*, *Lysapsus*, *Pseudis*, *Scarthyla*, *Scinax*, *Sphaenorhynchus*, and *Xenohyla*. The absence of lingual papillae in the larvae is the condition reported in all species of *Dendropsophus*, *Scarthyla*, and *Scinax*, whose larvae have been studied (Wassersug, 1980; Duellman and de Sá, 1988; Echeverria, 1997; Faivovich, 2002; Vera Candioti et al., 2004); a reversal occurs in *Lysapsus* and *Pseudis* (de Sá and Lavilla, 1997; Vera Candioti, 2004). This character state is still unknown in *Sphaenorhynchus* and *Xenohyla*. Another possible morphological synapomorphy is the absence of keratinized nuptial excrescences. Duellman et al. (1997) and Duellman (2001) suggested that the absence of nuptial excrescences was a synapomorphy of the 30-chromosome *Hyla*. Nuptial excrescences are also absent in *Lysapsus*, *Pseudis*, *Scarthyla*, *Scinax*, some species of *Sphaenorhynchus*, and *Xenohyla* (Caramaschi, 1989; Duellman and Wiens, 1992; Faivovich, personal obs.; Rodriguez and Duellman, 1994). Note that, while pigmented keratinized structures are absent in all these groups, nuptial pads are present at least in some species of *Dendropsophus*, *Scarthyla*, and *Scinax* (Faivovich, personal obs.).

Dendropsophus Fitzinger, 1843

TYPE SPECIES: *Hyla frontalis* Daudin, 1800 (= *Rana leucophyllata* Beireis, 1783), by original designation.

Lophopus Tschudi, 1838. Type species: *Hyla marmorata* Daudin (= *Bufo marmoratus* Laurenti, 1768), by monotypy. Primary homonym of *Lophopus* Duméril, 1837.

Hylella Reinhardt and Lütken, ''1861'' [1862]. Type species: *Hylella tenera* Reinhardt and Lütken, 1862 (= *Hyla bipunctata* Spix, 1824), by subsequent designation of Smith and Taylor (1948).

Güntheria Miranda-Ribeiro, 1926. Type species: *Hyla dasynota* Günther, 1869 (= *Hyla senicula* Cope, 1868), by monotypy.

DIAGNOSIS: This genus is diagnosed by 33 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Karyological evidence is the presence of 30 chromosomes. Morphological synapomorphies of this clade are possibly the extreme reduction in the quadratojugal (also occurs in some Cophomantini and Hylini) and a 1/2 labial tooth row formula (known instance of homoplasy in *Hyla anceps*; subsequent reductions in the formula in some clades) (Duellman and Trueb, 1983; Wogel et al., 2000).

COMMENTS: This genus contains all species formerly placed in *Hyla* that are known or suspected to have 30 chromosomes. However, the fact that the karyotype of its sister taxon, *Xenohyla*, is still unknown, precludes the 30-chromosome condition to be considered a synapomorphy of *Dendropsophus*, because it could be a synapomorphy of *Dendropsophus* + *Xenohyla*. A similar situation occurs with two muscle characters. Burton (2004) suggested that the m. contrahentis hallucis reduced or absent and the presence of m. flexor teres hallucis are synapomorphies of this group. Unfortunately, both transformations optimize ambiguously because corresponding character states are still unknown in *Xenohyla*.

While we consider the extreme reduction of the quadratojugal to be a possible morphological synapomorphy of *Dendropsophus*, we warn that the condition requires further study, because the quadratojugal is reduced as well in *Sphaenorhynchus* and *Xenohyla* (Caramaschi, 1989; Duellman and Wiens, 1992; Izecksohn, 1996), although apparently not to the level seen in *Dendropsophus*.

Bogart (1973), Gruber (2002), Skuk and Langone (1991), and Kaiser et al. (1996) described variation in chromosome morphology for several species of *Dendropsophus*.

CONTENTS: Eighty-eight species, most of them placed in nine species groups, and seven unassigned to group.

Dendropsophus columbianus Group

DIAGNOSIS: The only morphological synapomorphy suggested for this group is the presence of two close, triangular lateral spaces between the cricoid and arytenoids at the posterior part of the larynx (Kaplan, 1999).

COMMENTS: We included a single exemplar of this group, and as such we did not test its monophyly, but following Kaplan (1999) we recognize it on the basis of the evidence mentioned above.

CONTENTS: Three species. *Dendropsophus bogerti* (Cochran and Goin, 1970), new comb.; *Dendropsophus carnifex* (Duellman, 1969), new comb.; *Dendropsophus columbianus* (Boettger, 1892), new comb.

Dendropsophus garagoensis Group

DIAGNOSIS: A possible morphological synapomorphy of this group is the internal surface of the arytenoids with a small medial depression (Kaplan, 1999).

COMMENTS: We did not include any exemplar of this group in the analysis. We recognize it following Kaplan (1999), who considered *Hyla praestans* to be the sister taxon of the *H. garagoensis* group on the basis of them sharing the aforementioned putative synapomorphy. We find it more informative at this stage to include it in the group than to consider it as a species unassigned to any group.

CONTENTS: Four species. *Dendropsophus garagoensis* (Kaplan, 1991), new comb.; *Dendropsophus padreluna* (Kaplan and Ruiz-Carranza, 1997), new comb.; *Dendropsophus praestans* (Duellman and Trueb, 1983), new comb.; *Dendropsophus viroli-*

nensis (Kaplan and Ruiz-Carranza, 1997), new comb.

Dendropsophus labialis Group

DIAGNOSIS: We are not aware of any synapomorphy for this group.

COMMENTS: We included a single exemplar of this group in the analysis, and as such we did not test its monophyly. Following Duellman and Trueb (1983) and Duellman (1989), we continue to recognize the group pending a rigorous test of its monophyly.

CONTENTS: Three species. *Dendropsophus labialis* (Peters, 1863), new comb.; *Dendropsophus meridensis* (Rivero, 1961) new comb.; *Dendropsophus pelidna* (Duellman, 1989), new comb.

Dendropsophus leucophyllatus Group

DIAGNOSIS: This species group is diagnosed by 35 transformations in mitochondrial ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies.

COMMENTS: On the basis of our molecular results, we are including *Hyla anceps* in this group. With the exception of this species, all other members of the group share the presence of pectoral glands in males and females (Duellman, 1970).

CONTENTS: Eight species. *Dendropsophus anceps* (A. Lutz, 1929), new comb.; *Dendropsophus bifurcus* (Andersson, 1945), new comb.; *Dendropsophus ebraccatus* (Cope, 1874), new comb.; *Dendropsophus elegans* (Wied-Neuwied, 1824), new comb.; *Dendropsophus leucophyllatus* (Beireis, 1783), new comb.; *Dendropsophus rossalleni* (Goin, 1959), new comb.; *Dendropsophus sarayacuensis* (Shreve, 1935), new comb.; *Dendropsophus triangulum* (Günther, ‘‘1868’’ [1869]), new comb.

Dendropsophus marmoratus Group

DIAGNOSIS: This species group is diagnosed by 73 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Possible morphological synapomorphies of this group are the warty skin around the margin of the lower lip, the crenulated margin of limbs, and the dorsal marbled pattern (Bokermann, 1964b) (instances of homoplasy in other Hylinae). Furthermore, as it is discernible from the illustrations presented by Gomes and Peixoto (1991b) and Peixoto and Gomes (1999), and confirmed by Peixoto (personal commun. cited in Altig and McDiarmid, 1999a), known larvae of this species group share the presence of a thick sheath of tissue in the basal portion of the tail muscle and adjacent fins, another likely morphological synapomorphy.

COMMENTS: Bokermann (1964b) diagnosed this group as having large vocal sacs. While this could be a synapomorphy, we are hesitant to consider it as such until more anatomical and comparative studies are done in *Dendropsophus*. In connection with the large vocal sacs of the species of this group, Tyler (1971) mentioned that in *Hyla marmorata* the pectoral lymphatic septum is modified in a way that permits the inflated sac to intrude into sub-humeral spaces.

CONTENTS: Eight species. *Dendropsophus acreanus* (Bokermann, 1964), new comb.; *Dendropsophus dutrai* (Gomes and Peixoto, 1996), new comb.; *Dendropsophus marmoratus* (Laurenti, 1768), new comb.; *Dendropsophus melanargyreus* (Cope, 1887), new comb.; *Dendropsophus nahdereri* (B. Lutz and Bokermann, 1963), new comb.; *Dendropsophus novaisi* (Bokermann, 1968) new comb.; *Dendropsophus seniculus* (Cope, 1868), new comb.; *Dendropsophus soaresi* (Caramaschi and Jim, 1983), new comb.

Dendropsophus microcephalus Group

DIAGNOSIS: This species group is diagnosed by 42 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Morphological synapomorphies include the lack of labial tooth rows and marginal papillae (Duellman and Trueb, 1983) (a reversal occurs in the *Dendropsophus decipiens* clade).

COMMENTS: This group now includes all species from the *Hyla decipiens*, *H. microcephala*, and *H. rubicundula* groups. We did not test the monophyly of the *H. decipiens* or *H. rubicundula* groups. We continue recognition of the *Dendropsophus microcephalus* group and within it, pending a rigorous test, a *D. decipiens* clade (including *H. berthalutzae*, *H. decipiens*, *H. haddadi*, and *H. oliveirai*), and a *D. rubicundulus* clade (including *H. anataliasiasi*, *H. araguaya*, *H. cachimbo*, *H. cerradensis*, *H. elianeae*, *H. jimi*, *H. rhea*, *H. rubicundula*, and *H. tritaeniata*). Putative synapomorphies of the *D. decipiens* clade are the oviposition on leaves overhanging water (homoplastic with the *D. leucophyllatus* group and some species of the now *D. parviceps* group) and the presence of a posterior row of marginal papillae (a reversal). A putative synapomorphy of the *D. rubicundulus* clade is the green dorsum in life that changes to pinkish or violet when preserved (Napoli and Caramaschi, 1998).

It seems likely that additional synapomorphies for at least some species of *Dendropsophus microcephalus* group will be hypothesized as larval anatomy is carefully studied. For example, the four species of the group studied by Spirandeli Cruz (1991) and Wassersug (1980) (*H. microcephala*, *H. nana*, *H. phlebodes*, *H. sanborni*) show knob-like vestiges of the filter rows in larvae. It also remains to be seen whether the peculiarities of the mannicoto glandulare described by Lajmanovich et al. (2000) for *H. nana* are common to other larvae of the group.

CONTENTS: Thirty-three species. *Dendropsophus anataliasiasi* (Bokermann, 1972), new comb.; *Dendropsophus araguaya* (Napoli and Caramaschi, 1998), new comb.; *Dendropsophus berthalutzae* (Bokermann, 1962), new comb.; *Dendropsophus bipunctatus* (Spix, 1824), new comb.; *Dendropsophus branneri* (Cochran, 1948), new comb.; *Dendropsophus decipiens* (A. Lutz, 1925), new comb.; *Dendropsophus cachimbo* (Napoli and Caramaschi, 1999), new comb.; *Dendropsophus cerradensis* (Napoli and Caramaschi, 1998) new comb.; *Dendropsophus cruzi* (Pombal and Bastos, 1998), new comb.; *Dendropsophus elianeae* (Napoli and Caramaschi, 2000), new comb.; *Dendropsophus gryllatus* (Duellman, 1973), new comb.; *Dendropsophus haddadi* (Bastos and Pombal, 1996), new comb.; *Dendropsophus jimi* (Napoli and Caramaschi, 1999), new comb.; *Dendropsophus joannae* (Köhler and Lötters, 2001), new comb.; *Dendropsophus leali* (Bokermann, 1964), new comb.; *Dendropsophus mathiassoni* (Cochran and Goin, 1970), new comb.; *Dendropsophus meridianus* (B. Lutz, 1954), new comb.; *Dendropsophus microcephalus* (Cope, 1886), new comb.; *Dendropsophus minusculus* (Rivero, 1971), new comb.; *Dendropsophus nanus* (Boulenger, 1889), new comb.; *Dendropsophus oliveirai* (Bokermann, 1963), new comb.; *Dendropsophus phlebodes* (Stejneger, 1906), new comb.; *Dendropsophus pseudomeridianus* (Cruz et al., 2000), new comb.; *Dendropsophus rhea* (Napoli and Caramaschi, 1999), new comb.; *Dendropsophus rhodopeplus* (Günther, 1858), new comb.; *Dendropsophus robertmertensi* (Taylor, 1937), new comb.; *Dendropsophus rubicundulus* (Reinhardt and Lütken, ''1861'' [1862]), new comb.; *Dendropsophus sanborni* (Schmidt, 1944), new comb.; *Dendropsophus sartori* (Smith, 1951), new comb.; *Dendropsophus studerae* (Carvalho e Silva, Carvalho e Silva, and Izecksohn, 2003), new comb.; *Dendropsophus tritaeniatus* (Bokermann, 1965), new comb.; *Dendropsophus walfordi* (Bokermann, 1962), new comb.; *Dendropsophus werneri* (Cochran, 1952), new comb.

Dendropsophus minimus Group

DIAGNOSIS: No synapomorphy is known for this group.

COMMENTS: We included a single species of this group in the analisis, and as such we did not test its monophyly and we are not aware of any evidence supporting it. Following Duellman (1982), we continue to recognize it pending a rigorous test of its monophyly.

CONTENTS: Four species. *Dendropsophus aperomeus* (Duellman, 1982), new comb.; *Dendropsophus minimus* (Ahl, 1933), new comb.; *Dendropsophus miyatai* (Vigle and Goberdhan-Vigle, 1990), new comb.; *Dendropsophus riveroi* (Cochran and Goin, 1970), new comb.

Dendropsophus minutus Group

DIAGNOSIS: No synapomorphy is known for this group

COMMENTS: We included a single species of this group in the analysis, and as such we did not test its monophyly. Following Martins and Cardoso (1987), we continue to recognize the species group pending a rigorous test of its monophyly. Considering similarities between *Hyla minuta* and *H. limai* (Haddad, personal obs.), we tentatively include the latter in the group.

CONTENTS: Four species. *Dendropsophus delarivai* (Köhler and Lötters, 2001), new comb.; *Dendropsophus limai* (Bokermann, 1962), new comb.; *Dendropsophus minutus* (Peters, 1872), new comb.; *Dendropsophus xapuriensis* (Martins and Cardoso, 1987), new comb.

Dendropsophus parviceps Group

DIAGNOSIS: This species group is diagnosed by 27 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy supporting the monophyly of this group.

COMMENTS: We expressed our scepticism regarding the monophyly of this group, as currently defined, but found no evidence to reject monophyly. We recognize the group pending a rigorous test of its monophyly.

CONTENTS: Fifteen species. *Dendropsophus allenorum* (Duellman and Trueb, 1989), new comb.; *Dendropsophus bokermanni* (Goin, 1960), new comb.; *Dendropsophus brevifrons* (Duellman and Crump, 1974), new comb.; *Dendropsophus gaucheri* (Lescure and Marty, 2001), new comb.; *Dendropsophus giesleri* (Mertens, 1950), new comb.; *Dendropsophus grandisonae* (Goin, 1966), new comb.; *Dendropsophus koechlini* (Duellman and Trueb, 1989), new comb.; *Dendropsophus luteoocellatus* (Roux, 1927), new comb.; *Dendropsophus microps* (Peters, 1872), new comb.; *Dendropsophus parviceps* (Boulenger, 1882), new comb.; *Dendropsophus pauiniensis* (Heyer, 1977), new comb.; *Dendropsophus ruschii* (Weygoldt and Peixoto, 1987), new comb.; *Dendropsophus schubarti* (Bokermann, 1963), new comb.; *Dendropsophus subocularis* (Dunn, 1934), new comb.; *Dendropsophus timbeba* (Martins and Cardoso, 1987), new comb.

Species of *Dendropsophus* Unassigned to Group

There are several species of *Dendropsophus* that have not been associated with any group. These are: *Dendropsophus amicorum* (Mijares-Urrutia, 1998), new comb.; *Dendropsophus battersbyi* (Rivero, 1961), new comb.; *Dendropsophus haraldschultzi* (Bokermann, 1962), new comb.; *Dendropsophus stingi* (Kaplan, 1994), new comb.; *Dendropsophus tintinnabulum* (Melin, 1941), new comb.; *Dendropsophus yaracuyanus* (Mijares-Urrutia and Rivero, 2000), new comb.

Lysapsus Cope, 1862

TYPE SPECIES: *Lysapsus limellum* Cope, 1862, by monotypy.

Podonectes Steindachner, 1864. Type species: *Podonectes palmatus* Fitzinger, 1864 (= *Lysapsus limellum* Cope, 1862), by monotypy.

DIAGNOSIS: This genus is diagnosed by 47 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these transformations. A possible morphological synapomorphy of this genus is the near absence of subacrosomal cone in the sperm (Garda et al., 2004).

CONTENTS: Three species. *Lysapsus caraya* Gallardo, 1964; *Lysapsus laevis* Parker, 1935; *Lysapsus limellum* Cope, 1862.

Pseudis Wagler, 1830

TYPE SPECIES: *Rana paradoxa* Linnaeus, 1758, by monotypy.

Batrachychthys Pizarro, 1876. Type species: not designated; based on larvae of *Pseudis paradoxa* (Linnaeus, 1758), according to Caramaschi and Cruz (1998).

DIAGNOSIS: This genus is diagnosed by 28 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these transformations. We are not aware of any morphological synapomorphy for this genus.

COMMENTS: Garda et al. (2004) distinguished *Lysapsus* and *Pseudis* on the basis of the ultrastructure of the sperm acrosome complex, but they stated that the morphology present in *Lysapsus* (near absence of subacrosomal cone) is the apomorphic condition, with only the plesiomorphic condition being found in *Pseudis* and therefore not providing evidence of its monophyly.

CONTENTS: Six species. *Pseudis bolbodactyla* A. Lutz, 1925; *Pseudis cardosoi* Kwet, 2000; *Pseudis fusca* Garman, 1883; *Pseudis minuta* Günther, 1858; *Pseudis paradoxa* (Linnaeus, 1758); *Pseudis tocantins* Caramaschi and Cruz, 1998.

Scarthyla Duellman and de Sá, 1988

TYPE SPECIES: *Scarthyla ostinodactyla* (= *Hyla goinorum* Bokermann, 1962), by original designation.

DIAGNOSIS: Molecular autapomorphies include 227 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular autapomorphies. Apparent morphological autapomorphies include the ability of its tadpoles to propel themselves out of the water, elongated tadpoles (Duellman and Wiens, 1992) and the presence of a labial arm on the oral disc (McDiarmid and Altig, 1990).

COMMENTS: The oral structure known as the labial arm has also been reported for the *Scinax rostratus* group (McDiarmid and Altig, 1990; Faivovich, 2002) and for four other species of *Scinax* (Heyer et al., 1990; Alves and Carvalho e Silva, 2002; Alves et al., 2004). Suarez Mayorga and Lynch (2001b) recently reported a similar structure in the larvae of *Sphaenorhynchus dorisae*, adding that as yet unpublished studies suggest that the structures present in *Scinax*, *Scarthyla*, and *Sphaenorhynchus* are not homologs.

CONTENTS: Monotypic. *Scarthyla goinorum* (Bokermann, 1962)

Scinax Wagler, 1830

TYPE SPECIES: *Hyla aurata* Wied-Neuwied 1821, by subsequent designation of Stejneger (1907).

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

Garbeana Miranda-Ribeiro, 1926. Type species: *Garbeana garbei* Miranda-Ribeiro, 1926, by monotypy.

DIAGNOSIS: This genus is diagnosed by 83 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Morphological synapomorphies include webbing between toes I and II that does not extend beyond the subarticular tubercle of toe I, ability to bend finger I and toe I, origin of the m. pectoralis abdominalis through well-defined tendons, and m. pectoralis abdominalis overlapping m. obliquus externus (da Silva, 1998; Faivovich, 2002).

COMMENTS: Besides the first five character states mentioned above, Faivovich (2002) considered as synapomorphies of *Scinax* the round or poorly expanded sacral diapophyses, the occluded frontoparietal fontanelle, single origin of the m. extensor brevis superficialis digiti III from the ulnare, and the presence of the m. lumbricalis longus digiti V that originates from the lateral corner of the aponeurosis palmaris. As mentioned earlier, the position of *Scinax* within Hylinae suggests that outgroups employed by Faivovich (2002) are phylogenetically distant from *Scinax*. Because of this, we contend that the taxonomic distribution of the aforementioned character states needs to be reassessed, at least among the other Dendropsophini, before considering them synapomorphies of *Scinax*. For example, it seems evident that the round or poorly expanded sacral diapophyses are not a synapomorphy of *Scinax*, but of a more inclusive group (also present, at least, in *Scarthyla* and *Sphaenorhynchus*; Duellman and Wiens, 1992), whose limits are still unclear. In the same way, the absence of the lingual papillae, as mentioned earlier, might be a synapomorphy of Dendropsophini. The truncated discs of the digits were considered a synapomorphy of *Scinax* by Duellman and Wiens (1992) and Faivovich (2002). The phylogenetic position of the single exemplar of the *H. uruguaya* group in the analysis, as sister group of the *S. ruber* clade, complicates this interpretation. Discs in the two species of the group, *H. uruguaya* and *H. pinima*, are proportionally reduced in size with respect to most species of *Scinax*, cannot be considered truncated, and therefore determine an ambiguous optimization of this character state.

Burton (2004) considered that m. flexor ossis metatarsus IV with insertions on both metatarsi IV and V was a synapomorphy of

Scinax. Because this character state is still unknown in our two exemplars of the *S. catharinae* clade, and in the exemplar of *Hyla uruguaya* group, it optimizes ambiguously in our analysis; it is unclear if it is a synapomorphy of *Scinax* or of a more exclusive clade.

The *Hyla uruguaya* group is being included in *Scinax* to avoid rendering *Scinax* paraphyletic. Larvae of the two species of the *H. uruguaya* group share with members of the *S. ruber* clade some synapomorphies (the proctodeal tube not reaching the free margin of the lower fin, and the presence of keratinized spurs behind the lower jaw sheath and over the infralabial papillae [Kolenc et al., ‘‘2003’’ [2004]]). However, preliminary observations on *H. uruguaya* indicate that adults show at least one conflicting character state, the m. depressor mandibulae without an origin from the dorsal fascia at the level of the m. dorsalis scapulae (Faivovich, personal obs.)—a character state that optimized as a synapomorphy of the *S. catharinae* clade in the analysis of Faivovich (2002). This controversy may be resolved when all the conflicting evidence is analyzed, including a much denser sampling of *Scinax*. In the meantime, since the molecular evidence indicates affinities with the *S. ruber* clade, we tentatively include the two species of the *H. uruguaya* group in this clade, where they are recognized as a separate group.

CONTENTS: Eighty-eight species placed in two major clades.

Scinax catharinae Clade

DIAGNOSIS: This clade is diagnosed by 90 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Morphological synapomorphies suggested for this clade by Faivovich (2002) are absence of the anterior process of the suprascapula, internal vocal sac, distal division of the middle branch of the m. extensor digitorum comunis longus, and insertion of the medial side of this branch on the tendon of the m. extensor brevis medius digiti IV.

COMMENTS: Regardless of problems imposed by the present results to interpretation of the possible synapomorphies of *Scinax* resulting from Faivovich’s (2002) analysis, the sparse available knowledge on the taxonomic distribution of the transformations supporting the monophyly of the very distinctive *S. catharinae* clade suggests that most of them still hold in the present analysis. An exception is the m. depressor mandibulae without an origin from the dorsal fascia at the level of the m. dorsalis scapulae, which also occurs in *Hyla uruguaya*, rendering its optimization ambiguous in our analysis.

Scinax catharinae Group

DIAGNOSIS: Because we only included two species of the *Scinax catharinae* group as exemplars of the *S. catharinae* clade, the molecular transformations that diagnose this group are redundant with those diagnosing the *S. catharinae* clade. Presumed morphological synapomorphies of this group include the posterior part of the cricoid ring extensively elongated and curved, the partial mineralization of intercalary elements between ultimate and penultimate phalanges, and the laterodistal origin of the m. extensor brevis distalis digiti III (Faivovich, 2002).

CONTENTS: Twenty-seven species. *Scinax agilis* (Cruz and Peixoto, 1983); *Scinax albicans* (Bokermann, 1967); *Scinax angrensis* (B. Lutz, 1973); *Scinax argyreornatus* (Miranda-Ribeiro, 1926); *Scinax ariadne* (Bokermann, 1967); *Scinax aromothyella* Faivovich, 2005; *Scinax berthae* (Barrio, 1962); *Scinax brieni* (De Witte, 1927); *Scinax canastrensis* (Cardoso and Haddad, 1982); *Scinax carnevalli* (Caramaschi and Kisteumacher, 1989); *Scinax catharinae* (Boulenger, 1888); *Scinax centralis* (Pombal and Bastos, 1996); *Scinax flavoguttatus* (A. Lutz and B. Lutz, 1939); *Scinax heyeri* (Peixoto and Weygoldt, 1986); *Scinax hiemalis* (Haddad and Pombal, 1987); *Scinax humilis* (B. Lutz, 1954); *Scinax jureia* (Pombal and Gordo, 1991); *Scinax kautskyi* (Carvalho e Silva and Peixoto, 1991); *Scinax littoralis* (Pombal and Gordo, 1991); *Scinax longilineus* (B. Lutz, 1968); *Scinax luizotavioi* (Caramaschi and Kisteumacher, 1989); *Scinax machadoi* (Bokermann and Sazima, 1973); *Scinax obtriangulatus* (B. Lutz, 1973); *Scinax ranki* (Andrade and Cardoso, 1987); *Scinax rizi-*

bilis (Bokermann, 1964); *Scinax strigilatus* (Spix, 1824); and *Scinax trapicheiroi* (B. Lutz, 1954).

Scinax perpusillus Group

DIAGNOSIS: Presumed synapomorphies of this group are the oviposition in bromeliads and the extreme reduction of webbing between toes II and III (Peixoto, 1987; Faivovich, 2002).

COMMENTS: The monophyly of this group was not tested by Faivovich (2002) because only one species of the group was available for his analysis, where it obtained as the sister taxon of all exemplars of the *S. catharinae* clade. For these two reasons, we continue recognizing this group until its monophyly is rigorously tested.

CONTENTS: Seven species. *Scinax alcatraz* (B. Lutz, 1973); *Scinax arduous* Peixoto, 2002; *Scinax atratus* (Peixoto, 1989); *Scinax littoreus* (Peixoto, 1988); *Scinax melloi* (Peixoto, 1989); *Scinax perpusillus* (A. Lutz and B. Lutz, 1939); *Scinax v-signatus* (B. Lutz, 1968).

Scinax ruber Clade

DIAGNOSIS: This clade is supported by 53 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. A morphological synapomorphy suggested for this clade by Faivovich (2002) is the proctodeal tube positioned above the margin of the lower fin.

COMMENTS: Faivovich (2002) was skeptical about the monophyly of the *S. ruber* clade; however, the present analysis recovers it as monophyletic, with a considerable number of transformations supporting its monophyly.

As in the case of several of the synapomorphies suggested by Faivovich's (2002) analysis for *Scinax*, we are unsure as to whether the suggested morphological synapomorphies are optimized identically in our analysis. In particular, we do not know the taxonomic distribution within Dendropsophini for two other synapomorphies proposed for this clade (Faivovich, 2002): the arytenoids with a dorsal prominence developed over the pharyngeal margin, and absence of the lateral m. extensor brevis distalis digiti V (pes). Preliminary observation on the larvae of some species of *Sphaenorhynchus* (*Sphaenorhynchus bromelicola*, *S. orophilus*, *S. pauloalvini*, and *S. prasinus*; Faivovich, personal obs.) indicate that their proctodeal tubes are attached to the free margin of the lower fin, similar to the *S. catharinae* clade, instead of having the characteristic position seen in larvae of the *S. ruber* clade.

Scinax megapodius and *S. trachythorax* are considered here to be junior synonyms of *S. fuscovarius* for reasons discussed in appendix 4. There are two species, *Hyla dolloi* and *H. karenanneae*, that upon examination of their type series we consider to be species of *Scinax* (see appendix 4 for further comments on them).

CONTENTS: Fifty-six species. Eleven assigned to two groups, 43 unassigned to any group.

Scinax rostratus Group

DIAGNOSIS: Putative morphological synapomorphies of this group include the juxtaposed inner margins of the vomers; overlap of the otic plate of the crista parotica due to a broad otic plate; nonfenestration of the cartilaginous plate of the squamosal with the oblique cartilage; pointed tubercle on heel; absence of the m. extensor brevis distalis digiti II; presence of m. extensor brevis distalis digiti I (pes); discontinuity of lateral margins with the posterior portion of the oral disc; third posterior labial tooth row placed on a labial arm; reduction of the third posterior labial tooth to one-quarter the length of the second row; absence of keratinized spurs behind the lower jaw sheath; and head-down calling position (Faivovich, 2002).

CONTENTS: Nine species. *Scinax boulengeri* (Cope, 1887); *Scinax garbei* (Miranda-Ribeiro, 1926); *Scinax jolyi* (Lescure and Marty, 2001); *Scinax kennedyi* (Pyburn, 1973); *Scinax nebulosus* (Spix, 1824); *Scinax pedromedinae* (Henle, 1991); *Scinax proboscideus* (Brongersma, 1933); *Scinax rostratus* (Peters, 1870); *Scinax sugillatus* (Duellman, 1973).

Scinax uruguayus Group

DIAGNOSIS: Putative morphological synapomorphies of this group include the bicolored iris and the presence of two keratinized and pigmented plates on the sides of the lower jaw sheath (Kolenc et al., ''2003'' [2004]).

COMMENTS: The marginal papillae of the posterior margin of the oral disc being larger than those of the lateral margins (Kolenc et al., ''2003'' [2004]) and the reduction in toe webbing could be other synapomorphies of the group.

CONTENTS: Two species. *Scinax pinima* (Bokermann and Sazima, 1973) new comb.; *Scinax uruguayus* (Schmidt, 1944) new comb.

Species of the *Scinax ruber* Clade Unassigned to a Species Group

We follow Faivovich (2002) in not recognizing the former *Scinax ruber* and *S. staufferi* groups, as both were not monophyletic on his analysis. We are considering all species formerly included in these groups as members of the *S. ruber* clade, although we consider them as unassigned to any group. These species are *Scinax acuminatus* (Cope, 1862); *Scinax altae* (Dunn, 1933); *Scinax alter* (B. Lutz, 1973); *Scinax auratus* (Wied-Neuwied, 1821); *Scinax baumgardneri* (Rivero, 1961); *Scinax blairi* (Fouquette and Pyburn, 1972); *Scinax boesemani* (Goin, 1966); *Scinax caldarum* (B. Lutz, 1968); *Scinax cardosoi* (Carvalho e Silva and Peixoto, 1991); *Scinax castroviejoi* De la Riva, 1993; *Scinax chiquitanus* (De la Riva, 1990); *Scinax crospedospilus* (A. Lutz, 1925); *Scinax cruentommus* (Duellman, 1972); *Scinax curicica* Pugliese, Pombal, and Sazima, 2004; *Scinax cuspidatus* (A. Lutz, 1925); *Scinax danae* (Duellman, 1986); *Scinax dolloi* (Werner, 1898) new comb.; *Scinax duartei* (B. Lutz, 1951); *Scinax elaeochrous* (Cope, 1875); *Scinax eurydice* (Bokermann, 1964); *Scinax exiguus* (Duellman, 1986); *Scinax flavidus* La Marca, 2004; *Scinax funereus* (Cope, 1874); *Scinax fuscomarginatus* (A. Lutz, 1925); *Scinax fuscovarius* (A. Lutz, 1925); *Scinax granulatus* (Peters, 1871); *Scinax hayii* (Barbour, 1909); *Scinax ictericus* Duellman and Wiens, 1993; *Scinax karenanneae* (Pyburn, 1992) comb. nov.; *Scinax lindsayi* Pyburn, 1992; *Scinax manriquei* Barrio-Amorós, Orellana, and Chacon, 2004; *Scinax maracaya* (Cardoso and Sazima, 1980); *Scinax nasicus* (Cope, 1862); *Scinax oreites* Duellman and Wiens, 1993; *Scinax pachycrus* (Miranda-Ribeiro, 1937); *Scinax parkeri* (Gaige, 1926); *Scinax perereca* Pombal, Haddad, and Kasahara, 1995; *Scinax quinquefasciatus* (Fowler, 1913); *Scinax ruber* (Laurenti, 1768); *Scinax similis* (Cochran, 1952); *Scinax squalirostris* (A. Lutz, 1925); *Scinax staufferi* (Cope, 1865); *Scinax trilineatus* (Hoogmoed and Gorzula, 1977); *Scinax wandae* (Pyburn and Fouquette, 1971); *Scinax x-signatus* (Spix, 1824).

Sphaenorhynchus Tschudi, 1838

TYPE SPECIES: *Hyla lactea* Daudin, 1801, by original designation.

Dryomelictes Fitzinger, 1843. Type species: *Hyla lactea* Daudin, 1802, by original designation.

Dryomelictes Cope, 1865. Type species: *Hyla aurantiaca* Daudin, 1802, by original designation. Junior homonym of *Dryomelictes* Fitzinger, 1843.

Hylopsis Werner, 1894. Type species: *Hylopsis platycephalus* Werner, 1894, by monotypy.

Sphoenohyla Lutz and Lutz, 1938. Substitute name (explicit subgenus of *Hyla*) for *Sphaenorhynchus* thought erroneously to be preoccupied by *Sphenorhynchus* Lichtenstein, 1823.

DIAGNOSIS: This genus is diagnosed by 157 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Duellman and Wiens (1992) proposed the following synapomorphies for *Sphaenorhynchus*: posterior ramus of pterygoid absent; zygomatic ramus of squamosal absent or reduced to a small knob; pars facialis of maxilla and alary process of premaxilla reduced; postorbital process of maxilla reduced, not in contact with quadratojugal; neopalatine reduced to a sliver or absent; pars externa plectri entering tympanic ring posteriorly (rather than dorsally); pars externa plectri round; hyale curved medially; coracoids and clavicle elongated; and prepollex ossified, bladelike. Other likely synapomorphies include the differentiation of the m. intermandibularis into a small apical supplementary element, and the extreme development of the m. interhyoideus (Tyler, 1971).

COMMENTS: Duellman and Wiens (1992)

considered that the transverse process of presacral vertebra IV elongate, oriented posteriorly is a synapomorphy of *Sphaenorhynchus*. The presence of this character state in *Xenohyla* (Izecksohn, 1996) suggests that in the context of our topology, its optimization is ambiguous. There are also some larval features that could be considered synapomorphies of at least some species of *Sphaenorhynchus*, such as the morphology and position of the nostrils and the presence of some notably large marginal papillae (see Kenny, 1969; Bokermann, 1973; Cruz, 1973; Cruz and Peixoto, 1980; Suarez-Mayorga and Lynch, 2001b). The presence of a white peritoneum in five species (*S. carneus*, *S. lacteus*, *S. planicola*, *S. prasinus*, and *S. surdus*; Haddad and Faivovich, personal obs.) may be another synapomorphy of this genus (with several instances of homoplasy within Hylinae). Observations on six species (*S. carneus*, *S. dorisae*, *S. lacteus*, *S. planicola*, *S. prasinus*, and *S. surdus*) suggest that they are ant specialists (Duellman, 1978; Rodriguez and Duellman, 1994; Parmalee, 1999; Haddad, personal obs.), another likely synapomorphy whose taxonomic distribution within the group deserves additional study.

CONTENTS: Eleven species. *Sphaenorhynchus bromelicola* Bokermann, 1966; *Sphaenorhynchus carneus* (Cope, 1868); *Sphaenorhynchus dorisae* (Goin, 1967); *Sphaenorhynchus lacteus* (Daudin, 1801); *Sphaenorhynchus orophilus* (A. Lutz and B. Lutz, 1938); *Sphaenorhynchus palustris* Bokermann, 1966; *Sphaenorhynchus pauloalvini* Bokermann, 1973; *Sphaenorhynchus planicola* (A. Lutz and B. Lutz, 1938); *Sphaenorhynchus platycephalus* (Werner, 1894); *Sphaenorhynchus prasinus* Bokermann, 1973; *Sphaenorhynchus surdus* (Cochran, 1953).

Xenohyla Izecksohn, 1996

TYPE SPECIES: *Hyla truncata* Izecksohn, 1959, by original designation.

DIAGNOSIS: For the purposes of this paper, we consider that the 128 transformations in mitochondrial protein and ribosomal genes autapomorphic of *Xenohyla truncata* are synapomorphies of this genus. See appendix 5 for a complete list of these molecular synapomorphies. Although species of *Xenohyla* are very distinctive, we are aware of only three putative morphological synapomorphies: the retention in adults of the scars of the windows of forelimbs emergence (but see Comments below); the presence of a small, transverse process in the urostyle; and frugivorous habits (reported for *X. truncata* by da Silva et al. [1989] and Izecksohn [1996]; unknown in *X. eugenioi*).

COMMENTS: We included a single species of this genus in the analysis, and as such we did not test its monophyly, but consider it very likely on the basis of the evidence noted above and its unique external aspect. Izecksohn (1996) and Caramaschi (1998) noticed that adults of *Xenohyla* retain scars of the large windows of forelimb emergence that are evident in recently metamorphosed individuals. Each of these scars actually corresponds to a thick pectoral patch of glands that is macroscopically evident upon superficial dissection (Faivovich, personal obs.).

CONTENTS: Two species. *Xenohyla eugenioi* Caramaschi, 2001; *Xenohyla truncata* (Izecksohn, 1959).

HYLINI RAFINESQUE, 1815

Hylarinia Rafinesque, 1815. Type genus: *Hylaria* Rafinesque, 1814 (an unjustified emendation of *Hyla* Laurenti, 1768).
Hylina Gray, 1825. Type genus: *Hyla* Laurenti, 1768.
Dryophytae Fitzinger, 1843. Type genus: *Dryophytes* Fitzinger, 1843.
Acridina Mivart, 1869. Type genus: *Acris* Duméril and Bibron, 1841.
Triprioninae Miranda-Ribeiro, 1926. Type genus: *Triprion* Cope, 1866.

DIAGNOSIS: This tribe is diagnosed by 107 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. The only known morphological synapomorphy is the undivided tendon of the m. flexor digitorum brevis superficialis (there are several instances of homoplasy within Hylidae including at least *Scinax*, *Scarthyla* + *Pseudis*, and a reversal within Hylini).

COMMENTS: The tribe Hylini is proposed for the clade of Middle American/Holarctic hylids. It includes *Acris*, *Anotheca*, *Duellmanohyla*, *Exerodonta*, *Hyla*, *Pseudacris*, *Ptychohyla*, *Smilisca* (including *Pternohyla*), *Triprion*, and six new genera, *Bromeliohyla* new gen., *Charadrahyla* new gen., *Ecnomiohyla* new gen., *Isthmohyla* new gen., *Megastomatohyla* new gen., and *Tlalocohyla* new gen. Morescalchi (1973) recognized the tribe Hylini in which he included most genera currently placed in Hylinae. Subsequent authors have not used Hylini in the sense that Morescalchi (1973) used it.

Acris Duméril and Bibron, 1841

TYPE SPECIES: *Rana gryllus* LeConte, 1825, by subsequent designation of Fitzinger (1843).

DIAGNOSIS: This genus is diagnosed by 138 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Other apparent synapomorphies include the differentiation of the m. intermandibularis into an apical supplementary element (Tyler, 1971), and diploid chromosome number of 22 (Bushnell et al., 1939; Cole, 1966; Duellman, 1970).

CONTENTS: Two species. *Acris crepitans* Baird, 1854; *Acris gryllus* (LeConte, 1825).

Anotheca Smith, 1939

TYPE SPECIES: *Gastrotheca coronata* Stejneger, 1911 (= *Hyla spinosa* Steindachner, 1864), by original designation.

DIAGNOSIS: This monotypic genus is diagnosed by 219 transformations of nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these transformations. Morphological autapomorphies include the tendo superficialis hallucis that tapers from an expanded corner of the aponeurosis plantaris; with fibers of the m. transversus plantae distalis originating on distal tarsal 2–3 inserting on the lateral side of the tendon (several of homoplasy, see appendix 1); the unique skull ornamentation composed of sharp, dorsally pointed spines in the margins of frontoparietal, maxilla, nasal (including canthal ridge), and squamosal, and character states that result in its reproductive mode, including maternal provisioning of trophic eggs to tadpoles (see Jungfer, 1996).

CONTENTS: Monotypic. *Anotheca spinosa* (Steindachner, 1864).

Bromeliohyla, new genus

TYPE SPECIES: *Hyla bromeliacia* Schmidt, 1933.

DIAGNOSIS: For the purposes of this paper we consider that the 141 transformations in nuclear and mitochondrial protein and ribosomal genes autapomorphic of *Bromeliohyla bromeliacia* are synapomorphies of this genus. See appendix 5 for a complete list of these molecular synapomorphies. Possible nonmolecular synapomorphies of this genus are the reproductive mode, where eggs are laid in water accumulated in bromeliads (several instances of homoplasy, e.g., two species of *Isthmohyla*, *Phyllodytes*, some species *Osteopilus*, and the *Scinax perpusillus* group), and tadpoles with dorsoventrally flattened bodies and elongated tails.

ETYMOLOGY: From *Bromelia* + *Hyla*, in reference to the bromeliad breeding habits of its species. The gender is feminine.

COMMENTS: We included a single species of this genus, and as such we did not test its monophyly. We consider it likely based on the evidence noted above.

CONTENTS: Two species. *Bromeliohyla bromeliacia* (Schmidt, 1933), new comb.; *Bromeliohyla dendroscarta* (Taylor, 1940), new comb.

Charadrahyla, new genus

TYPE SPECIES: *Hyla taeniopus* Günther, 1901.

DIAGNOSIS: This genus is diagnosed by 56 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy supporting this genus.

ETYMOLOGY: Derived from the Greek word *charadra-* (ravine) + *Hyla*. In reference to the habits of these frogs. The gender is feminine.

COMMENTS: This new genus includes the species formerly placed in the *Hyla taeniopus* group.

CONTENTS: Five species. *Charadrahyla altipotens* (Duellman, 1968), new comb.;

Charadrahyla chaneque (Duellman, 1961), new comb.; *Charadrahyla nephila* (Mendelson and Campbell, 1999), new comb.; *Charadrahyla taeniopus* (Günther, 1901), new comb.; *Charadrahyla trux* (Adler and Denis, 1972), new comb.

Duellmanohyla Campbell and Smith, 1992

TYPE SPECIES: *Hyla uranochroa* Cope, 1876, by original designation.

DIAGNOSIS: This genus is diagnosed by 48 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Likely morphological synapomorphies of this group are the red iris, the labial stripe expanded below orbit, the lack of nuptial excrescences, the ventrally oriented funnel-shaped oral disc in larvae, labial tooth rows reduced in length, and absence of lateral processes on upper jaw sheath (Duellman, 2001).

CONTENTS: Eight species. *Duellmanohyla chamulae* (Duellman, 1961); *Duellmanohyla ignicolor* (Duellman, 1961); *Duellmanohyla lythrodes* (Savage, 1968); *Duellmanohyla rufioculis* (Taylor, 1952); *Duellmanohyla salvavida* (McCranie and Wilson, 1986); *Duellmanohyla schmidtorum* (Stuart, 1954); *Duellmanohyla soralia* (Wilson and McCranie, 1985); *Duellmanohyla uranochroa* (Cope, 1876).

Ecnomiohyla, new genus

TYPE SPECIES: *Hypsiboas miliarius* Cope, 1886.

DIAGNOSIS: This genus is diagnosed by 37 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy supporting this genus.

ETYMOLOGY: From the Greek, *ecnomios*, meaning marvelous, unusual; an obvious reference to the incredible frogs of the *Hyla tuberculosa* group. The gender is feminine.

COMMENTS: This new genus contains the *Hyla tuberculosa* group, excluding *H. dendrophasma*, and including one species of the *H. miotympanum* group as well. Erecting a new genus for this clade is the only way of being consistent with the new monophyletic taxonomy that is proposed for hylids. Although naming the former *H. tuberculosa* group as a genus constitutes a testable claim of monophyly, we expect that it will ultimately be found to be two or three different clades, with one of these being the one named here.

CONTENTS: Ten species. *Ecnomiohyla echinata* (Duellman, 1962), new comb.; *Ecnomiohyla fimbrimembra* (Taylor, 1948), new comb.; *Ecnomiohyla miliaria* (Cope, 1886), new comb.; *Ecnomiohyla minera* (Wilson, McCranie, and Williams, 1985), new comb.; *Ecnomiohyla miotympanum* (Cope, 1863), new comb.; *Ecnomiohyla phantasmagoria* (Dunn, 1943); *Ecnomiohyla salvaje* (Wilson, McCranie, and Williams, 1985), new comb.; *Ecnomiohyla thysanota* (Duellman, 1966), new comb.; *Ecnomiohyla tuberculosa* (Boulenger, 1882), new comb.; *Ecnomiohyla valancifer* (Firschein and Smith, 1956), new comb.

Exerodonta Brocchi, 1879

TYPE SPECIES: *Exerodonta sumichrasti* Brocchi, 1879, by monotypy.

DIAGNOSIS: This genus is diagnosed by 80 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy supporting this genus.

COMMENTS: *Exerodonta* is resurrected for the species previously placed in the *Hyla sumichrasti* group and a fragment of the former *H. miotympanum* group as defined by Duellman (2001) that corresponds to the traditionally recognized *H. pinorum* group (Duellman 1970). Although we did not include the type species, *E. sumichrasti*, in the analysis, but only *H. chimalapa* and *H. xera*, we consider that these two species and *H. sumichrasti* and *H. smaragdina* are so similar that we are not hesitant to consider them closely related. Although we are not aware of any synapomorphy supporting the monophyly of the former *H. pinorum* group (Duellman, 1970), and our results suggest it is paraphyletic with respect to the *H. sumichrasti* group, we are tentatively including the other species associated with it, *H. abdivita*, *H. bivocata*, *H. catracha*, and *H. juanitae* by Snyder (1972), Porras and Wilson (1987), and Campbell and Duellman (2000), in this resurrected genus.

CONTENTS: Eleven species, four placed in one species group, seven unassigned to group.

Exerodonta sumichrasti Group

DIAGNOSIS: This species group is diagnosed by 76 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Putative morphological synapomorphies of this group are the massive nasals (Duellman, 1970) and, in the species with a known tadpole, the enlarged larval oral disc (homoplastic with the former *Hyla mixomaculata* group), and the 3/6 to 7 labial tooth row formula (Canseco-Márquez et al., 2003; Duellman, 1970).

COMMENTS: The illustrations of the oral discs of *Hyla smaragdina*, *H. sumichrasti* (Duellman, 1970), and *H. xera* (Canseco-Márquez et al., 2003) show that they share the multiple interruption of the last posterior labial tooth row into shorter rows, possibly another synapomorphy.

CONTENTS: Four species. *Exerodonta chimalapa* (Mendelson and Campbell, 1994), new comb.; *Exerodonta smaragdina* (Taylor, 1940), new comb.; *Exerodonta sumichrasti* Brocchi, 1879; *Exerodonta xera* (Mendelson and Campbell, 1994), new comb.

Species of *Exerodonta* Unassigned to Group

Considering that in our analysis *Hyla melanomma* and *H. perkinsi* are a grade leading to the *E. sumichrasti* group, we are not assigning to any group these and the other species associated with the former *Hyla pinorum* group (Duellman, 1970; Snyder, 1972; Porras and Wilson, 1987; Campbell and Duellman, 2000). These species are: *Exerodonta abdivita* (Campbell and Duellman, 2000), new comb.; *Exerodonta bivocata* (Duellman and Hoyt, 1961), new comb.; *Exerodonta catracha* (Porras and Wilson, 1987), new comb.; *Exerodonta juanitae* (Snyder, 1972), new comb.; *Exerodonta melanomma* (Taylor, 1940), new comb.; *Exerodonta perkinsi* (Campbell and Brodie, 1992), new comb.; *Exerodonta pinorum* (Taylor, 1937), new comb.

Hyla Laurenti, 1768

TYPE SPECIES: *Hyla viridis* Laurenti, 1768 (= *Rana arborea* Linnaeus, 1758), by subsequent designation of Stejneger (1907).

Calamita Schneider, 1799. Type species: *Rana arborea* Linnaeus, 1758, by subsequent designation of Stejneger (1907).
Hylaria Rafinesque, 1814. Unjustified emendation for *Hyla*.
Hyas Wagler, 1830. Type species: *Rana arborea* Linnaeus, 1758, by monotypy. Junior homonym of *Hyas* Leach, 1815.
Dendrohyas Wagler, 1830. Substitute name for *Hyas* Wagler, 1830.
Dryophytes Fitzinger, 1843. Type species: *Hyla versicolor* LeConte, 1825, by original designation.
Epedaphus Cope, 1885. Type species: *Hyla gratiosa* LeConte, 1856, by monotypy.

DIAGNOSIS: This genus is diagnosed by 25 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy for the genus.

COMMENTS: *Hyla* is restricted to all species previously placed in the *H. arborea*, *H. cinerea*, *H. eximia*, and *H. versicolor* groups, which are redefined herein.

CONTENTS: Thirty-two species, with 31 placed in four species groups and one species unassigned to group.

Hyla arborea Group

DIAGNOSIS: This species group is diagnosed by 37 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy supporting this group.

COMMENTS: The contents of the *Hyla arborea* group are restricted to avoid its paraphyly. The inclusion of the species that were not included in the present analysis and do not show the NOR in chromosome 6 is tentative, because no evidence, other than the molecular data presented here, is known to support its monophyly.

CONTENTS: Fourteen species. *Hyla annectans* (Jerdon, 1870); *Hyla arborea* (Linnaeus, 1758); *Hyla chinensis* Günther, 1858; *Hyla hallowellii* Thomson, 1912; *Hyla immaculata* Boettger, 1888; *Hyla intermedia* Boulenger, 1882; *Hyla meridionalis* Boettger, 1874; *Hyla sanchiangensis* Pope, 1929; *Hyla sarda* (De Betta, 1853); *Hyla savignyi* Audouin, 1827; *Hyla simplex* Boettger, 1901; *Hyla tsinlingensis* Liu and Hu, 1966; *Hyla ussuriensis* Nikolsky, 1918; *Hyla zhaopingensis* Tang and Zhang, 1984.

Hyla cinerea Group

DIAGNOSIS: This species group is diagnosed by 35 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy supporting this group.

COMMENTS: *Hyla femoralis* is excluded from the *H. cinerea* group to avoid the paraphyly of the group.

CONTENTS: Three species. *Hyla cinerea* (Schneider, 1799); *Hyla gratiosa* LeConte, ‘‘1856’’ [1857]; *Hyla squirella* Bosc, 1800.

Hyla eximia Group

DIAGNOSIS: This species group is diagnosed by 17 transformations in mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy supporting this group.

COMMENTS: The inclusion of *Hyla suweonensis* is tentative, based on the fact that Anderson (1991) reported a NOR in chromosome 6, a character state shared by *H. femoralis* and the *H. eximia* and *H. versicolor* groups.

CONTENTS: Eleven species. *Hyla andersonii* Baird, 1854; *Hyla arboricola* Taylor, 1941; *Hyla arenicolor* Cope, 1886; *Hyla bocourti* (Mocquard, 1889); *Hyla euphorbiacea* Günther, 1859; *Hyla eximia* Baird, 1854; *Hyla japonica* Günther, ‘‘1858’’ [1859]; *Hyla plicata* Brocchi, 1877; *Hyla suweonensis* Kuramoto, 1980; *Hyla walkeri* Stuart, 1954; *Hyla wrightorum* Taylor, 1939.

Hyla versicolor Group

DIAGNOSIS: This species group is diagnosed by 51 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy supporting this group.

COMMENTS: *Hyla andersonii* is transferred to the *H. eximia* group to avoid the paraphyly of the *H. versicolor* group.

CONTENTS: Three species. *Hyla avivoca* Viosca, 1928; *Hyla chrysoscelis* Cope, 1880; *Hyla versicolor* LeConte, 1825.

Species of *Hyla* Unassigned to Group

Considering that relationships of *Hyla femoralis* Bosc, 1800 with the *H. versicolor* and *H. eximia* groups are unresolved, we prefer to keep this species unassigned as a more stable alternative to merging the *H. versicolor* and the *H. eximia* groups into a single group.

Isthmohyla, new genus

TYPE SPECIES: *Hyla pseudopuma* Günther, 1901.

DIAGNOSIS: This genus is diagnosed by 42 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy for the genus.

ETYMOLOGY: From *Isthmo*, Greek, in reference to the mostly isthmian distribution of these frogs (the only exception is *Hyla insolita*) + *Hyla*. The gender is feminine.

COMMENTS: This new genus includes all species of the *Hyla pseudopuma* and *H. pictipes* groups, as defined by Duellman (2001), with the exception of *H. thorectes*, which is transferred to *Plectrohyla*. Our taxon sampling of the relevant species groups was too sparse to result in a test of their respective monophyly. We tentatively recognize these species groups as reviewed by Duellman (2001), with the exception that *H. thorectes* is excluded from the former *H. pictipes* group and not included in *Isthmohyla*.

CONTENTS: Fourteen species placed in two species groups.

Isthmohyla pictipes Group

DIAGNOSIS: We are not aware of any synapomorphy supporting the monophyly of this group.

COMMENTS: We included a single exemplar of this group, and as such we did not test its monophyly. It is being tentatively recognized following Duellman (2001) until a rigorous test is performed. This species group is formed by the former *Hyla lancasteri, H. pictipes*, *H. rivularis*, and *H. zeteki* groups (Duellman, 1970, 2001). The monophyly of the former *H. zeteki* group does not seem to be controversial, as its two species share massive temporal musculature, bromeliad dwelling larvae, a terminal oral disc, and a labial tooth row formula of 1/1. The monophyly of the group composed of the former *H. rivularis* and *H. pictipes* groups (as defined by Duellman, 1970) is supported by the presence of an enlarged oral disc (Duellman, 2001) with a broad band of conic submarginal papillae on the posterior part of the disc, about three rows on the anterior part, and an M-shaped upper jaw sheath[27] (Faivovich, personal obs.; see also illustrations in Duellman, 2001). The monophyly of the former *H. lancasteri* group seems to be supported by the presence of granular dorsal skin (Duellman, 2001; known homoplastic instance in *H. debilis*), a short snout, and the presence of dark ventral pigmentation (Wilson et al., 1994b, known homoplastic instance in *H. thorectes*.)

CONTENTS: Ten species. *Isthmohyla calypsa* (Lips, 1996), new comb.; *Isthmohyla debilis* (Taylor, 1952), new comb.; *Isthmohyla insolita* (McCranie, Wilson, and Williams, 1993), new comb.; *Isthmohyla lancasteri* (Barbour, 1928), new comb.; *Isthmohyla picadoi* (Dunn, 1937), new comb.; *Isthmohyla pictipes* (Cope, 1876), new comb.; *Isthmohyla rivularis* (Taylor, 1952), new comb.; *Isthmohyla tica* (Starret, 1966), new comb.; *Isthmohyla xanthosticta* (Duellman, 1968), new comb.; *Isthmohyla zeteki* (Gaige, 1929), new comb.

Isthmohyla pseudopuma Group

DIAGNOSIS: We are not aware of any synapomorphy supporting the monophyly of this group.

COMMENTS: We included a single exemplar of this group, and as such we did not test its monophyly. It is being tentatively recognized following Duellman (2001) until a rigorous test is performed.

CONTENTS: Four species. *Isthmohyla angustilineata* (Taylor, 1952), new comb.; *Isthmohyla graceae* (Myers and Duellman, 1982), new comb.; *Isthmohyla infucata* (Duellman, 1968), new comb.; *Isthmohyla pseudopuma* (Günther, 1901), new comb.

Megastomatohyla, new genus

TYPE SPECIES: *Hyla mixe* Duellman, 1965.

DIAGNOSIS: For the purposes of this paper, we consider that the 209 transformations in nuclear and mitochondrial protein and ribosomal genes autapomorphic of *Hyla mixe* are synapomorphies of this genus. See appendix 5 for a complete list of these molecular synapomorphies. A possible morphological synapomorphy of this genus is the greatly enlarged oral disc of the known larvae bearing 7–10 anterior rows and 10–11 posterior rows.

ETYMOLOGY: From the Greek, *mega*, large, plus the stem of the genitive *stomatos*, mouth, in reference to the enlarged oral disc of the larvae + *Hyla*. The gender is feminine.

COMMENTS: We included a single species of this genus, and as such we did not test its monophyly, but consider it very likely on the basis of the evidence noted above. As mentioned earlier, the sequenced sample comes from a tadpole that was assigned to the *Hyla mixomaculata* group based on the enlarged oral disc and the labial tooth row formula and tentatively assigned to *H. mixe* for being the only species of the group known from the region where it was collected. Considering the uncertainty in its determination, its position in the tree should be viewed cautiously. This is not a situation we feel most comfortable with, but for a matter of being consistent with the general approach of this

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[27] The description and illustrations of the tadpole of *Hyla debilis* by Duellman (1970) do not show these character states.

contribution, we consider that it is better to describe a new genus for the *H. mixomaculata* group than to leave it as incerta sedis. Although we did not test the monophyly of the group, as stated earlier, we consider it based on the morphological synapomorphy for larvae mentioned above. Another possible synapomorphy of this group could be the lack of vocal slits (Duellman, 1970), but this is contingent on the internal relationships of the nearby *Charadrahyla*; *C. chaneque* is the only species of that genus known to lack vocal slits (Duellman, 2001). If future studies show it to be the sister group of the remaining species of *Charadrahyla*, it could render the optimization of the lack of vocal slits as ambiguous for both *Charadrahyla* and *Megastomatohyla*. Males of species included in *Megastomatohyla* lack nuptial excrescences on the thumb (Duellman, 1970). The polarity of this character state is unclear because it also occurs in *Charadrahyla altipotens* and in *Hyla godmani* and *H. loquax* (Duellman, 1970).

CONTENTS: Four species. *Megastomatohyla mixe* (Duellman, 1965), new comb.; *Megastomatohyla mixomaculata* (Taylor, 1950), new comb.; *Megastomatohyla nubicola* (Duellman, 1964), new comb.; *Megastomatohyla pellita* (Duellman, 1968), new comb.

Plectrohyla Brocchi, 1877

TYPE SPECIES: *Plectrohyla guatemalensis* Brocchi, 1877, by original designation.

Cauphias Brocchi, 1877. Replacement name for *Plectrohyla* Brocchi, 1877.

DIAGNOSIS: This genus is supported by 43 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy supporting this genus as redefined here.

COMMENTS: We are including in *Plectrohyla* all species formerly placed in the *Hyla bistincta* group and some of the members of the former *H. miotympanum* (*H. cyclada* and *H. arborescandens*) and *H. pictipes* (*H. thorectes*) groups. *H. thorectes* is being tentatively included because a still undescribed species, very similar to *H. thorectes* (*Hyla* sp. 5) is nested within this clade. *Hyla hazelae* is tentatively included because of its similarities with *H. thorectes*. 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. The facts that no apparent morphological synapomorphies are known for the *H. bistincta* group and that some authors raised doubts regarding the limits between it and *Plectrohyla* support the conservative stance of including all these species in *Plectrohyla*. We preserve a *Plectrohyla guatemalensis* group for all the species of *Plectrohyla* as defined in the past and tentatively recognize a group that contains all members of the *H. bistincta* group plus the species of other groups shown to be related with it in this analysis.

The reasons why we are not considering some of the characters states shared by *Plectrohyla* and the *Hyla bistincta* group that were advanced by Duellman (2001) as synapomorphies of the redefined *Plectrohyla* were discussed earlier in this paper (p. 68). The only character state that seems to be inclusive of *Plectrohyla* and the *H. bistincta* group is the long medial ramus of the pterygoid in contact with the otic capsule. However, both *H. arborescandens* and *H. cyclada* were reported by Duellman (2001) to have a short medial ramus that does not contact the prootic. In a more densely sampled context, this character state could probably be interpreted as a reversal; however, in the present context it optimized ambiguously, so we do not consider it a morphological synapomorphy of the redefined *Plectrohyla*.

CONTENTS: Thirty-nine species placed in two species groups.

Plectrohyla bistincta Group

DIAGNOSIS: Exemplars of this species group in our analysis are diagnosed by 16 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these transformations.

We are not aware of any morphological synapomorphy supporting this group.

CONTENTS: Twenty-one species. *Plectrohyla ameibothalame* (Canseco-Márquez, Mendelson, and Gutiérrez-Mayén et al., 2002), new comb.; *Plectrohyla arborescandens* (Taylor, ''1938''[1939]), new comb.; *Plectrohyla bistincta* (Cope, 1877), new comb.; *Plectrohyla calthula* (Ustach, Mendelson, McDiarmid, and Campbell, 2000), new comb.; *Plectrohyla calvicollina* (Toal, 1994), new comb.; *Plectrohyla celata* (Toal and Mendelson, 1995), new comb.; *Plectrohyla cembra* (Caldwell, 1974), new comb.; *Plectrohyla charadricola* (Duellman, 1964), new comb.; *Plectrohyla chryses* (Adler, 1965), new comb.; *Plectrohyla crassa* (Brocchi, 1877), new comb.; *Plectrohyla cyanomma* (Caldwell, 1974), new comb.; *Plectrohyla cyclada* (Campbell and Duellman, 2000) new comb.; *Plectrohyla hazelae* (Taylor, 1940), new comb.; *Plectrohyla labedactyla* (Mendelson and Toal, 1996), new comb.; *Plectrohyla mykter* (Adler and Dennis, 1972), new comb.; *Plectrohyla pachyderma*, (Taylor, 1942), new comb.; *Plectrohyla pentheter* (Adler, 1965), new comb.; *Plectrohyla psarosema* (Campbell and Duellman, 2000), new comb.; *Plectrohyla robertsorum* (Taylor, 1940), new comb.; *Plectrohyla sabrina* (Caldwell, 1974), new comb.; *Plectrohyla siopela*, (Duellman, 1968), new comb.; *Plectrohyla thorectes* (Adler, 1965), new comb.

Plectrohyla guatemalensis Group

DIAGNOSIS: This group is diagnosed by 34 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these transformations. Possible morphological synapomorphies of this species group are bifurcate alary process of the premaxilla; sphenethmoid with anterior part ossified; frontoparietals abbuting posteriorly, exposing only small part of the frontoparietal fontanelle; humerus having well-developed flanges; hypertrophied forearm; prepollex enlarged and ossified in both sexes; prepollex truncate; and absence of lateral labial folds in larvae (Duellman and Campbell, 1992; Duellman, 2001).

CONTENTS: Eighteen species. *Plectrohyla acanthodes* Duellman and Campbell, 1992; *Plectrohyla avia* Stuart, 1952; *Plectrohyla chrysopleura* Wilson, McCranie, and Cruz-Díaz, 1994; *Plectrohyla dasypus* McCranie and Wilson, 1981; *Plectrohyla exquisitia* McCranie and Wilson, 1998; *Plectrohyla glandulosa* (Boulenger, 1883); *Plectrohyla guatemalensis* Brocchi, 1877; *Plectrohyla hartwegi* Duellman, 1968; *Plectrohyla ixil* Stuart, 1942; *Plectrohyla lacertosa* Bumhanzen and Smith, 1954; *Plectrohyla matudai* Hartweg, 1941; *Plectrohyla pokomchi* Duellman and Campbell, 1984; *Plectrohyla psiloderma* McCranie and Wilson, 1992; *Plectrohyla pycnochila* Rabb, 1959; *Plectrohyla quecchi* Stuart, 1942; *Plectrohyla sagorum* Hartweg, 1941; *Plectrohyla tecunumani* Duellman and Campbell, 1984; *Plectrohyla teuchestes* Duellman and Campbell, 1992.

Pseudacris Fitzinger, 1843

TYPE SPECIES: *Rana nigrita* LeConte, 1825, by monotypy.

Chorophilus Baird, 1854. Type species: *Rana nigrita* LeConte, 1825, by original designation.
Helocaetes Baird, 1854. Type species: *Hyla triseriata* Wied-Neuwied, 1839, by subsequent designation of Schmidt (1953).
Hyliola Mocquard, 1899. Type species: *Hyla regilla* Baird and Girard, 1852, by subsequent designation of Stejneger (1907).
Limnaoedus Mittleman and List, 1953. Type species: *Hyla ocularis* Bosc and Daudin, 1801, by original designation.
Parapseudacris Hardy and Borrough, 1986. Type species: *Hyla crucifer* Wied-Neuwied, 1838, by original designation.

DIAGNOSIS: This genus is diagnosed by 37 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. The m. transversus metatarsus II broad, occupying the entire length of metatarsus II optimizes in this analysis as a morphological synapomorphy of this genus.

CONTENTS: Fourteen species placed in four clades.

Pseudacris crucifer Clade

DIAGNOSIS: This clade is diagnosed by molecular data presented by Moriarty and Cannatella (2004).

CONTENTS: Two species. *Pseudacris cru-*

cifer (Wied-Neuwied, 1838); *Pseudacris ocularis* (Bosc and Daudin, 1801).

Pseudacris ornata Clade

DIAGNOSIS: This clade is diagnosed by molecular data presented by Moriarty and Cannatella (2004).

CONTENTS: Three species. *Pseudacris illinoensis* Smith, 1951; *Pseudacris ornata* (Holbrook, 1836); *Pseudacris streckeri* A.A. Wright and A.H. Wright, 1933.

Pseudacris nigrita Clade

DIAGNOSIS: This clade is diagnosed by molecular data presented by Moriarty and Cannatella (2004).

COMMENTS: According to Moriarty and Cannatella (2004), this clade contains a more exclusive clade that contains all species but *P. brimleyi* and *P. brachyphona*.

CONTENTS: Seven species. *Pseudacris brachyphona* (Cope, 1889); *Pseudacris brimleyi* Brandt and Walker, 1933; *Pseudacris clarkii* (Baird, 1854); *Pseudacris feriarum* (Baird, 1854); *Pseudacris maculata* (Agassiz, 1850); *Pseudacris nigrita* (LeConte, 1825); *Pseudacris triseriata* (Wied-Neuwied, 1838).

Pseudacris regilla Clade

DIAGNOSIS: This clade is diagnosed by molecular data presented by Moriarty and Cannatella (2004).

CONTENTS: Two species. *Pseudacris cadaverina* (Cope, 1866); *Pseudacris regilla* (Baird and Girard, 1852).

Ptychohyla Taylor, 1944

TYPE SPECIES: *Ptychohyla adipoventris* Taylor, 1944 (= *Hyla leonhardschultzei* Ahl, 1934), by original designation.

DIAGNOSIS: This genus is diagnosed by 11 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. An apparent morphological synapomorphy of this group is the well-developed lingual flange of the pars palatina of premaxillar (Campbell and Smith, 1992).

COMMENTS: To avoid paraphyly, we are including *Hyla dendrophasma* in *Ptychohyla*. As mentioned earlier in the discussion, other synapomorphies of *Ptychohyla* proposed by Campbell and Smith (1992) and Duellman (2001) are also present in some species of its sister taxon (*Bromeliohyla* + *Duellmanohyla*), so we do not recognize them as synapomorphies until a phylogenetic analysis including that evidence is performed. Known males of the exemplars of *Ptychohyla* included in the analysis share the presence of enlarged individual nuptial spines and hypertrophied ventrolateral glands (Duellman, 2001), as do males of *P. macrotympanum* and *P. panchoi*. Discovery of males of *H. dendrophasma* will confirm whether this character state is an apparent synapomorphy of these species or of a less inclusive clade.

CONTENTS: Thirteen species. *Ptychohyla acrochorda* Campbell and Duellman, 2000; *Ptychohyla dendrophasma* (Campbell, Smith, and Acevedo, 2000), new comb.; *Ptychohyla erythromma* (Taylor, 1937); *Ptychohyla euthysanota* Kellogg, 1928; *Ptychohyla hypomykter* McCranie and Wilson, 1993; *Ptychohyla legleri* (Taylor, 1958); *Ptychohyla leonhardschultzei* (Ahl, 1934); *Ptychohyla macrotympanum* (Tanner, 1957); *Ptychohyla panchoi* Duellman and Campbell, 1982; *Ptychohyla salvadorensis* (Mertens, 1952); *Ptychohyla sanctaecrucis* Campbell and Smith, 1992; *Ptychohyla spinipollex* (Schmidt, 1936); *Ptychohyla zophodes* Campbell and Duellman, 2000.

Smilisca Cope, 1865

TYPE SPECIES: *Smilisca daulinia* Cope, 1865 (= *Hyla baudinii* Duméril and Bibron, 1841), by monotypy.

Pternohyla Boulenger, 1882. Type species *Pternohyla fodiens* Boulenger, 1882, by monotypy. NEW SYNONYMY.

DIAGNOSIS: This genus is diagnosed by 38 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy.

COMMENTS: *Pternohyla* is included in the synonymy of *Smilisca* to avoid paraphyly.

CONTENTS: Eight species. *Smilisca baudinii* (Duméril and Bibron, 1841); *Smilisca cyanosticta* (Smith, 1953); *Smilisca dentata* (Smith, 1957), new comb.; *Smilisca fodiens*

(Boulenger, 1882), new comb.; *Smilisca phaeota* (Cope, 1862); *Smilisca puma* (Cope, 1885); *Smilisca sila* (Duellman and Trueb, 1966); *Smilisca sordida* (Peters, 1863).

***Tlalocohyla*,** new genus

TYPE SPECIES: *Hyla smithii* Boulenger, 1902.

DIAGNOSIS: This genus is diagnosed by 92 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy.

ETYMOLOGY: From Tlaloc, the Olmec God of the rain, + connecting *-o* + *Hyla*. The gender is feminine.

COMMENTS: The inclusion of *Hyla godmani* and *H. loquax* is tentative and based on its association with *H. picta* and *H. smithii* in the former *H. godmani* group by Duellman (2001). The larvae of *H. loquax* and *H. smithii* share a reduction in the length of the third posterior tooth row (Caldwell, 1986; Lee, 1996). This feature is not present in the larvae of *H. godmani* as described by Duellman (1970).

CONTENTS: Four species. *Tlalocohyla godmani* (Günther, 1901), new comb.; *Tlalocohyla loquax* (Gaige and Stuart, 1934), new comb.; *Tlalocohyla picta* (Günther, 1901), new comb.; *Tlalocohyla smithii* (Boulenger, 1902), new comb.

Triprion Cope, 1866

TYPE SPECIES: *Pharyngodon petasatus* Cope, 1865, by monotypy.

Pharyngodon Cope, 1865. Junior homonym of *Pharyngodon* Diesing, 1861. Type species: *Pharyngodon petasatus* Cope, 1865, by monotypy.

Diaglena Cope, 1887. Type species: *Triprion spatulatus* Günther, 1882, by monotypy.

DIAGNOSIS: For the purposes of this paper we consider that the 125 transformations in nuclear and mitochondrial protein and ribosomal genes autapomorphic of *Triprion petasatus* are synapomorphies of this genus. See appendix 5 for a complete list of these molecular synapomorphies. In Duellman's (2001) phylogenetic analysis of *Pternohyla*, *Smilisca*, and *Triprion*, the monophyly of *Triprion* is supported by three synapomorphies[28]: maxilla greatly expanded laterally; prenasal bone present (known homoplastic instance in *Aparasphenodon*); and presence of parasphenoid odontoids.

COMMENTS: We included a single species of this genus, and as such we did not test its monophyly, but we do not consider it controversial on the basis of the morphological evidence mentioned above.

CONTENTS: Two species. *Triprion petasatus* (Cope, 1865); *Triprion spatulatus* Günther, 1882.

LOPHIOHYLINI MIRANDA-RIBEIRO, 1926

Lophiohylinae Miranda-Ribeiro, 1926. Type genus: *Lophyohyla* Miranda-Ribeiro, 1926.

Trachycephalinae B. Lutz, 1969. Type genus: *Trachycephalus* Tschudi, 1838.

DIAGNOSIS: This tribe is diagnosed by 63 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. A putative morphological synapomorphy of this tribe is the presence of at least four posterior labial tooth rows in the larval oral disc (e.g., Bokermann, 1966b; Duellman, 1974; de Sá, 1983; Lannoo et al., 1987; McDiarmid and Altig, 1990; Schiesari et al., 1996; da Silva *in* Altig and McDiarmid, 1999b; Wogel et al., 2000) (reversals in *Osteopilus marianae*, *O. crucialis*, *O. wilderi* [Dunn, 1926] and in *Osteocephalus oophagus* [Jungfer and Schiesari, 1995]).

COMMENTS: This tribe contains all South American and West Indian casque-headed frogs and related groups. It includes *Aparasphenodon*, *Argenteohyla*, *Corythomantis*, *Osteopilus*, *Phyllodytes*, *Tepuihyla*, a new monotypic genus, and the genera *Osteocephalus* and *Trachycephalus* as redefined here.

Recently, Kasahara et al. (2003) noticed that *Aparasphenodon brunoi*, *Corythomantis*

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[28] Note that on his preferred tree (fig. 410) one of these character transformations is numbered 18, which seems to be a typographical error for 12, the only other character that supports this clade but that is not shown in the tree.

greeningi, and *Osteocephalus langsdorffii* share similar chromosome morphology, where there is a clear discontinuity in the chromosome lengths of the first five pairs and the remaining seven pairs. Furthermore, they share the presence of a secondary constriction in pair 10. Available information on karyotypes of other casque-headed frogs of this clade suggests that the discontinuity in chromosome lengths occurs as well in *Argenteohyla* (apparent from plates published by Morand and Hernando, 1996), *Phrynohyas venulosa* (apparent from plates published by Bogart, 1973), and some species of *Osteopilus* (*O. brunneus*, *O. dominicensis*, *O. marianae*, *O. septentrionalis*), but not in *Osteocephalus taurinus*, the only species of the genus *Osteocephalus*, as redefined here, whose karyotype was studied (Anderson, 1996). The position of the secondary constriction also varies, having been observed in chromosome 4 in *Argenteohyla* (Morand and Hernando, 1996), chromosome 9 in *Osteopilus brunneus*, *O. dominicensis*, *O. septentrionalis*, and *O. wilderi* (Anderson, 1996), chromosome 10 in *Phrynohyas venulosa* (apparent from plates published by Bogart, 1973), and in chromosome 12 in *Osteocephalus taurinus*. The taxonomic distribution of these character states needs further study to define the inclusiveness of the clades they support.

Delfino et al. (2002) noticed that serous skin glands of *Osteopilus septentrionalis* and *Phrynohyas venulosa* produce secretory granules with a dense cortex and a pale medulla; they observed the same in a photograph of a section of skin of *Corythomantis greeningi* published by Toledo and Jared (1995). Very few hylid taxa were studied for serous gland histology, and these include a few species of *Phyllomedusa*, Holarctic *Hyla*, *Scinax*, and *Pseudis paradoxa* (see Delfino et al., 2001, 2002). The taxonomic distribution of these peculiar secretory granules requires additional study to assess its level of generality and the clade or clades that it diagnoses.

Aparasphenodon Miranda-Ribeiro, 1920

TYPE SPECIES: *Aparasphenodon brunoi* Miranda-Ribeiro, 1920, by monotypy.

DIAGNOSIS: For the purposes of this paper we consider that the 83 transformations in nuclear and mitochondrial protein and ribosomal genes autapomorphic of *Aparasphenodon brunoi* are synapomorphies of this genus. See appendix 5 for a complete list of these molecular synapomorphies. A possible morphological synapomorphy of this genus is the presence of a prenasal bone (Trueb, 1970a.)

COMMENTS: We included a single species of this genus, and as such we did not test its monophyly, but we consider it possible based on the morphological evidence mentioned above.

CONTENTS: Three species. *Aparasphenodon bokermanni* Pombal, 1993; *Aparasphenodon brunoi* Miranda-Ribeiro, 1920; *Aparasphenodon venezolanus* (Mertens, 1950).

Argenteohyla Trueb, 1970

TYPE SPECIES: *Hyla siemersi* Mertens, 1937, by original designation.

DIAGNOSIS: Molecular autapomorphies include 102 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Apparent morphological autapomorphies of this taxon include the articulation of the zygomatic ramus of the squamosal with the pars fascialis of the maxillary, and the noticeable reduction in the size of discs of fingers and toes (Trueb, 1970b.)

CONTENTS: Monotypic. *Argenteohyla siemersi* (Mertens, 1937).

Corythomantis Boulenger, 1896

TYPE SPECIES: *Corythomantis greeningi* Boulenger, 1896, by monotypy.

DIAGNOSIS: Molecular autapomorphies include 132 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these transformations. Morphological autapomorphies of this monotypic genus include the absence of palatines, and nasals that conceal the alary processes of premaxillaries (Trueb, 1970a).

CONTENTS: Monotypic. *Corythomantis greeningi* Boulenger, 1896.

Itapotihyla, new genus

TYPE SPECIES: *Hyla langsdorffii* Duméril and Bibron, 1841.

DIAGNOSIS: Molecular autapomorphies include 122 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these transformations. A possible morphological autapomorphy is the presence of a prominent subcloacal flap.

ETYMOLOGY: From Itapoti + *-Hyla*. The generic name is an allusion to the resemblance of the unique known species of this genus with lichens and mosses. Itapoti is a Tupi-Guarani term, a composition of ''itá'' (= rock) with ''poti'' (= flower or to flourish), which means lichen or moss.

CONTENTS: Monotypic. *Itapotihyla langsdorffii* (Duméril and Bibron, 1841), new comb.

Nyctimantis Boulenger, 1882

TYPE SPECIES: *Nyctimantis rugiceps* Boulenger, 1882, by monotypy.

DIAGNOSIS: Molecular autapomorphies include 139 transformations in mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Possible morphological autapomorphies are the development of an irregular orbital flange in the frontoparietal, and the sphenethmoid almost completely concealed dorsally by the frontoparietals and nasals (Duellman and Trueb, 1976).

CONTENTS: Monotypic. *Nyctimantis rugiceps* Boulenger, 1882.

Osteocephalus Steindachner, 1862

TYPE SPECIES: *Osteocephalus taurinus* Steindachner, 1862, by subsequent designation of Kellogg (1932).

DIAGNOSIS: This genus is diagnosed by 34 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy supporting this genus.

CONTENTS: Seventeen species. *Osteocephalus buckleyi* (Boulenger, 1882); *Osteocephalus cabrerai* (Cochran and Goin, 1970); *Osteocephalus deridens* Jungfer, Ron, Seipp, and Almendáriz, 2000; *Osteocephalus elkejungingerae* (Henle, 1981); *Osteocephalus exophthalmus* Smith and Noonan, 2001; *Osteocephalus fuscifacies* Jungfer, Ron, Seipp, and Almendáriz, 2000; *Osteocephalus heyeri* Lynch, 2002; *Osteocephalus leoniae* Jungfer and Lehr, 2001; *Osteocephalus leprieurii* (Duméril and Bibron, 1841); *Osteocephalus mutabor* Jungfer and Hödl, 2002; *Osteocephalus oophagus* Jungfer and Schiesari, 1995; *Osteocephalus pearsoni* (Gaige, 1929); *Osteocephalus planiceps* Cope, 1874; *Osteocephalus subtilis* Martins and Cardoso, 1987; *Osteocephalus taurinus* Steindachner, 1862; *Osteocephalus verruciger* (Werner, 1901); *Osteocephalus yasuni* Ron and Pramuk, 1999.

Osteopilus Fitzinger, 1843

TYPE SPECIES: *Trachycephalus marmoratus* Duméril and Bibron, 1841 (= *Hyla septentrionalis* Duméril and Bibron, 1841).

Calyptahyla Trueb and Tyler, 1974. Type species: *Trachycephalus lichenatus* Gosse, 1851 (= *Hyla crucialis* Harlan, 1826), by original designation.

DIAGNOSIS: This genus is diagnosed by 43 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. No morphological synapomorphies are known for this genus.

CONTENTS: Eight species. *Osteopilus brunneus* (Gosse, 1851); *Osteopilus crucialis* (Harlan, 1826); *Osteopilus dominicensis* (Tschudi, 1838); *Osteopilus marianae* (Dunn, 1926); *Osteopilus pulchrilineatus* (Cope ''1869'' [1870]); *Osteopilus septentrionalis* (Duméril and Bibron, 1841); *Osteopilus vastus* (Cope, 1871); *Osteopilus wilderi* (Dunn, 1925).

Phyllodytes Wagler, 1830

TYPE SPECIES: *Hyla luteola* Wied-Neuwied, 1824, by monotypy.

Amphodus Peters, ''1872'' [1873]. Type species: *Amphodus wuchereri* Peters, ''1872'' [1873], by original designation.

Lophyohyla Miranda-Ribeiro, 1923. Type species: *Lophyohyla piperata* Miranda-Ribeiro, 1923 (=

Hyla luteola Wied-Neuwied, 1824), by original designation.

DIAGNOSIS: This genus is diagnosed by 174 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Two morphological synapomorphies of this taxon are the presence of odontoids on the mandible and on the cultriform process of the parasphenoid (Noble, 1931).

CONTENTS: Eleven species placed in four species groups (Caramaschi et al., 2004a), one of which is monotypic.

Phyllodytes auratus Group

DIAGNOSIS: We are not aware of any possible synapomorphy for this group.

COMMENTS: We did not include any exemplar of this group, but we continue to recognize it following Caramaschi et al. (2004b) pending a rigorous test. Caramaschi et al. (2004b) diagnosed the different species groups based on color patterns; it is unclear if any of these patterns could be considered synapomorphic.

CONTENTS: Two species. *Phyllodytes auratus* (Boulenger, 1917); *Phyllodytes wuchereri* (Peters, ‘‘1872’’ [1873]).

Phyllodytes luteolus Group

DIAGNOSIS: We are not aware of any possible synapomorphy for this group.

COMMENTS: We included a single exemplar of this group and thus did not test its monophyly, but we continue to recognize it following Caramaschi et al. (2004b) pending a rigorous test. See comments for the *P. auratus* group.

CONTENTS: Six species. *Phyllodytes acuminatus* Bokermann, 1966; *Phyllodytes brevirostris* Peixoto and Cruz, 1988; *Phyllodytes edelmoi* Peixoto, Caramaschi, and Freire, 2003; *Phyllodytes kautskyi* Peixoto and Cruz, 1988; *Phyllodytes luteolus* (Wied-Neuwied, 1824); *Phyllodytes melanomystax* Caramaschi, Silva, and Britto-Pereira, 1992.

Phyllodytes tuberculosus Group

DIAGNOSIS: We are not aware of any possible synapomorphy for this group.

COMMENTS: We did not include any exemplar of this group, but we continue to recognize it following Caramaschi et al. (2004b) pending a rigorous test. See comments for the *P. auratus* group.

CONTENTS: Two species. *Phyllodytes punctatus* Caramaschi and Peixoto, 2004; *Phyllodytes tuberculosus* Bokermann, 1966.

Species of *Phyllodytes* Unassigned to Group

Peixoto et al. (2003) assigned *Phyllodytes gyrinaethes* Peixoto, Caramaschi, and Freire, 2003 to its own species group. As stated earlier in this paper, we consider that monotypic species groups are not informative.

Tepuihyla Ayarzagüena and Señaris, ‘‘1992’’ [1993]

TYPE SPECIES: *Hyla rodriguezi* Rivero, 1968, by original designation.

DIAGNOSIS: For the purposes of this paper we consider that the 90 transformations in nuclear and mitochondrial protein and ribosomal genes autapomorphic of *Tepuihyla edelcae* are synapomorphies of this genus. See appendix 5 for a complete list of these molecular synapomorphies. In the context of our results, the reduction of webbing between toes I and II is a putative morphological synapomorphy of this genus (Ayarzagüena et al., ‘‘1992’’ [1993b]; several instances of homoplasy within Lophiohylini, in *Phyllodytes*, and in the clade composed of *Corythomantis*, *Argenteohyla*, *Aparasphenodon*, and *Nyctimantis*).

COMMENTS: We included a single species of *Tepuihyla*, and as such we did not test its monophyly. We continue to recognize it following Ayarzagüena and Señaris (‘‘1992’’ [1993b]) until its monophyly is rigorously tested.

CONTENTS: Eight species. *Tepuihyla aecii* (Ayarzagüena, Señaris, and Gorzula, ‘‘1992’’ [1993]); *Tepuihyla celsae* Mijares-Urrutia, Manzanilla-Pupo, and La Marca, 1999; *Tepuihyla edelcae* (Ayarzagüena, Señaris, and Gorzula, ‘‘1992’’ [1993]); *Tepuihyla galani* (Ayarzagüena, Señaris, and Gorzula, ‘‘1992’’ [1993]); *Tepuihyla luteolabris* (Ayarzagüena, Señaris, and Gorzula, ‘‘1992’’ [1993]); *Tepuihyla rimarum* (Ayarzagüena, Señaris, and

Gorzula, ‘‘1992’’ [1993]); *Tepuihyla rodriguezi* (Rivero, 1968); *Tepuihyla talbergae* Duellman and Yoshpa, 1996.

Trachycephalus Tschudi, 1838

TYPE SPECIES: *Trachycephalus nigromaculatus* Tschudi, 1838, by monotypy.

Phrynohyas Fitzinger, 1843. Type species: *Hyla zonata* Spix, 1824 (= *Rana venulosa* Laurenti, 1768). NEW SYNONYMY.

Acrodytes Fitzinger, 1843. Type species: *Hyla venulosa* Daudin, 1802 (= *Rana venulosa* Laurenti, 1768), by original designation.

Scytopis Cope, 1862. Type species: *Scytopis hebes* Cope, 1862, by monotypy.

Tetraprion Stejneger and Test, 1891. Type species: *Tetraprion jordani* Stejneger and Test, 1891, by original designation.

DIAGNOSIS: This genus is diagnosed by 37 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. The only possible morphological synapomorphy that we are aware of for this genus is the presence of paired vocal sacs protruding posterior to the angles of the jaws when inflated (Trueb and Duellman, 1971; see also Tyler, 1971).

COMMENTS: We are including *Phrynohyas* in the synonymy of *Trachycephalus* to avoid the nonmonophyly of the two genera. There are other alternatives to resolve this situation, such as restricting *Trachycephalus* to the southeastern Brazilian taxa, including *P. mesophaea*, while retaining *Phrynohyas* for the remaining species currently placed in that genus, and resurrecting *Tetraprion* to accommodate *T. jordani*. We consider that the action taken here is the most conservative.

CONTENTS: Ten species. *Trachycephalus atlas* Bokermann, 1966; *Trachycephalus coriaceus* (Peters, 1867), new comb.; *Trachycephalus hadroceps* (Duellman and Hoogmoed, 1992), new comb.; *Trachycephalus imitatrix* (Miranda-Ribeiro, 1926), new comb.; *Trachycephalus lepidus* (Pombal, Haddad, and Cruz, 2003), new comb.; *Trachycephalus mesophaeus* (Hensel, 1867), new comb.; *Trachycephalus nigromaculatus* Tschudi, 1838; *Trachycephalus resinifictrix* (Goeldi, 1907), new comb.; *Trachycephalus venulosus* (Laurenti, 1768), new comb.

Incertae Sedis and Nomina Dubia

The taxonomic scheme introduced above comprises most of the valid species of Hylinae. However, there are a number of species of former *Hyla* whose position in this new taxonomy is uncertain. There are two likely reasons for this. (1) The species have known type material and/or are known from multiple specimens, but the available information is not sufficient to allow even the tentative assignment to any of the taxonomic groups, so they are here considered as incerta sedis. (2) The species are known mostly from their original descriptions or type materials are reported to be lost or lack clear locality data. These are considered nomina dubia. See appendix 4 for additional comments on some of these species. Within the first category fall *Hyla alboguttata* Boulenger, 1882, *Hyla chlorostea* Reynolds and Foster, 1992, *Hyla helenae* Ruthven, 1919, *Hyla imitator* (Barbour and Dunn, 1921), *Hyla inframaculata* Boulenger, 1882, *Hyla vigilans* Solano, 1971, and *Hyla warreni* Duellman and Hoogmoed, 1992. In the second category we include (those with extant type material are followed by an asterisk) *Calamita melanorabdotus* Schneider, 1799, *Calamita quadrilineatus* Schneider, 1799, *Hyla auraria** Peters, 1873, *Hyla fusca* Laurenti, 1768, *Hypsiboas hypselops* Cope, 1871, *Hyla molitor** Schmidt, 1857, *Hyla palliata* Cope, 1863, *Hyla roeschmanni* De Grys, 1938, *Hyla surinamensis* Daudin, 1802, and *Litoria americana** Duméril and Bibron, 1841.

PHYLLOMEDUSINAE GÜNTHER, 1858

Phyllomedusidae Günther, 1858. Type genus: *Phyllomedusa* Wagler, 1830.

Pithecopinae B. Lutz, 1969. Type genus: *Pithecopus* Cope, 1866.

DIAGNOSIS: The monophyly of this subfamily is supported by 95 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. A possible morphological synapomorphy is the pupil constricting to vertical ellipse (Duellman, 2001; known instance of homoplasy in *Nyctimystes*). There are several larval character states that may be synapomorphies, such as: the ventrolateral position of the spiracle; arcus subocularis of larval chondrocranium with distinct lateral processes; ultralow suspensorium; secondary fenestrae parietales; and absence of a passage between ceratohyal and ceratobranchial I (Haas, 2003).

COMMENTS: Duellman (2001) considered the presence of a process on the medial surface of metacarpal II a synapomorphy of Phyllomedusinae, with a known instance of homoplasy in Centrolenidae. However, because Phyllomedusinae appears to be the sister taxon of Pelodryadinae, the situation is more complex. As noticed by Tyler and Davies (1978b), this character state is also present in some species groups of *Litoria*, so the internal topology of Pelodryadinae will determine whether this character state is indeed a synapomorphy of Phyllomedusinae, with homoplastic instances in Pelodryadinae, or if it is a synapomorphy of Phyllomedusinae + Pelodryadinae, with subsequent reversals in the latter taxon. The supplementary posterolateral elements of the m. intermandibularis have been considered a synapomorphy of Phyllomedusinae (Duellman, 2001; Tyler, 1971). As mentioned earlier, because it is more parsimonious to interpret the sole presence of supplementary elements of the m. intermandibularis as a synapomorphy of Pelodryadinae + Phyllomedusinae, at this point it is ambiguous which of the positions (apical as present in Pelodryadinae or posterolateral as in Phyllomedusinae) is the plesiomorphic state of this clade.

The absence of the slip of the m. depressor mandibulae that originates from the dorsal fascia at the level of the m. dorsalis scapulae (which subsequently reverses in *Hylomantis* and *Phyllomedusa*, see below) could also be a synapomorphy of Phyllomedusinae; however, its taxonomic distribution among nonphyllomedusines needs to be assessed. This is most needed in Pelodryadinae, where as far as we are aware, all observations on this muscle are limited to Starrett's (1968) unpublished dissertation where she commented on its morphology in 2 of the 172 known valid species of the subfamily. Oviposition on leaves out of water could also be another synapomorphy of Phyllomedusinae, but this is dependent on the position of *Phrynomedusa* within Phyllomedusinae (species of this genus do not oviposit on leaves but on rock crevices or fallen trunks) and on the topology of Pelodryadinae (however, only two species of Pelodryadinae, *Litoria iris* and *L. longirostris*, are known to lay eggs out of water, and not necessarily on leaves; Tyler, 1963; McDonald and Storch, 1993).

Several transformations that resulted as synapomorphies of Phyllomedusinae in Burton's (2004) analysis optimize ambiguously in our trees because their distribution is unknown in *Cruziohyla* new genus. Consequently, it is unclear which transformations are synapomorphic of the subfamily and which ones support the monophyly of internal clades. These transformations are: two insertions of the m. flexor digitorum brevis superficialis; the tendon of the m. flexor digitorum brevis superficialis divided along its length into a medial tendon, from which arise tendo superficialis IV and m. lumbricalis longus digiti V, and a lateral tendon from which arise tendo superficialis V and m. lumbricalis longus digiti IV; tendo superficialis pro digiti II arising from a deep, triangular muscle, which originates on the distal tarsal 2–3; tendo superficialis pro digiti III arising entirely from the margin of the aponeurosis plantaris; two tendons of insertion of m. lumbricalis longus digiti V arising from two equal muscle slips; pennate insertion of the lateral slip of the medial m. lumbricalis brevis digiti V; m. transversus metatarsus II broad, occupying the entire length of metatarsal II; m. transversus metatarsus III broad, occupying more than 75% of the length of metatarsal III; m. extensor brevis superficialis digiti III with two insertions, a flat tendon onto basal phalanx III and a pennate insertion on metatarsus III; and finally the m. extensor brevis superficialis digiti IV with a single origin with belly undivided. The presence of m. flexor teres hallucis is shared with Pelodryadinae; however, Burton (2004) stressed that in that subfamily, presence or absence of this muscle is subject to great intraspecific variation, without providing information as to the states present in the particular specimens he studied, so the character was scored as missing data in our matrix.

There are several other character systems that will likely provide additional synapomorphies for this group of frogs. Manzano and Lavilla (1995b) and Manzano (1997) described several unique character states from musculature, whose taxonomic distribution across all Phyllomedusinae needs to be assessed. Tyler and Davies (1978a) mentioned that Phyllomedusinae are the only hylids where the mandibular branch of the trigeminal nerve subdivides into two twigs after traversing the mandible. Various authors (e.g., Kenny; 1969; Cruz, 1982; Lescure et al., 1995) noticed that larvae of several species of Phyllomedusinae are usually suspended in water in an oblique or even vertical position relative to the water surface. Bagnara (1974) observed a light-sensitive tail-darkening reaction in larvae of two phyllomedusines (*Pachymedusa dacnicolor* and *Phyllomedusa trinitatis*), and we observed a similar reaction in tadpoles of *Phyllomedusa tetraploidea* (Faivovich, pers. obs.). Further research will determine how inclusive is the clade or clades supported by these synapomorphies.

The presence of multiple bioactive peptides has been suggested as a distinctive character of Phyllomedusinae (Cei, 1985). Since the beginning of the biochemical prospecting, it has become evident that Phyllomedusinae have several different classes of bioactive peptides (Erspamer, 1994), some unique (e.g., sauvagine, deltorphins), some not (e.g., bombesins, caeruleins), as do the Pelodryadinae (Apponyi et al., 2004). Because there are multiple bioactive peptides, it seems reasonable to consider the different peptide families individually as potential synapomorphies of Phyllomedusinae, Pelodryadinae, or Phyllomedusinae + Pelodryadinae. More work needs to be done to better understand the taxonomic distribution of the different classes of peptides.

Agalychnis Cope, 1864

TYPE SPECIES: *Agalychnis callidryas* Cope, 1862, by original designation.

DIAGNOSIS: The monophyly of this group is supported by 23 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. *Agalychnis* has extensively developed webbing on hands and feet in relationship with *Pachymedusa*, *Hylomantis*, *Cruziohyla* new genus, *Phasmahyla*, and *Phyllomedusa*. Also, with the exception of *A. annae*, which has a yellow iris, the other species have either a red or a dark red iris.

COMMENTS: Considering the lack of knowledge regarding the internal structure of Pelodryadinae, where some species have extensive hand and foot webbing (e.g., Tyler, 1968), it is still unknown if these character states are plesiomorphic for Phyllomedusinae. Consequently, at this stage we do not know exactly in which point of the topology of Phyllomedusinae they are homoplastic (both hands and foot webbing are developed in *Cruziohyla* new genus and, somewhat less extensively, in *Phrynomedusa*).

CONTENTS: Six species. *Agalychnis annae* (Duellman, 1963); *Agalychnis callidryas* Cope, 1862; *Agalychnis litodryas* (Duellman and Trueb, 1967); *Agalychnis moreletii* (Duméril, 1853); *Agalychnis saltator* (Taylor, 1955); *Agalychnis spurrelli* (Boulenger, ‘‘1913’’ [1914].)

Cruziohyla, new genus

TYPE SPECIES: *Agalychnis calcarifer* Boulenger, 1902.

DIAGNOSIS: For the purposes of this paper we consider that the 171 transformations in nuclear and mitochondrial protein and ribosomal genes autapomorphic of *Cruziohyla calcarifer* are synapomorphies of this genus. See appendix 5 for a complete list of these molecular synapomorphies. Possible morphological synapomorphies include the extensive hand and foot webbing (but see comments for *Agalychnis*) and the development of tadpoles in water-filled depressions on fallen trees. See comments below.

ETYMOLOGY: The name comes from the Latinization of Cruz, *Cruzius* + connecting -*o* + *Hyla*. We dedicate this new genus to our colleague and friend Carlos Alberto Gonçalves da Cruz, in recognition of his various contributions to our knowledge of Phyllomedusinae.

COMMENTS: *Phrynomedusa*, the only genus of Phyllomedusinae missing from our analysis, shares with *Cruziohyla* a bicolored iris, developed foot webbing (although more extensively developed in *Cruziohyla*), and oral disc with complete marginal papillae in the larvae. However, they differ in that eggs of *Phrynomedusa* are laid in rock crevices (A. Lutz and B. Lutz, 1939; Weygoldt, 1991) or fallen trunk cavities above streams, from where tadpoles drop and develop. The larvae of *Cruziohyla*, unlike those of most other known Phyllomedusinae, develop in water-filed depressions of fallen trees (Donnelly et al., 1987; Hoogmoed and Cadle, 1991; Caldwell, 1994; Block et al., 2003). Hoogmoed and Cadle (1991) reported two situations where tadpoles associated with *Agalychnis craspedopus* were found in small pools in the forest, without a clear indication of where the eggs were laid. This could be interpreted either as a polymorphic reproductive trait or as an indication that more than one species is involved.

The oral disc with marginal papillae as a morphological synapomorphy of *Cruziohyla* + *Phrynomedusa* should be taken cautiously because of our general ignorance of the internal topology of Pelodryadinae. Some Pelodryadinae also have an oral disc with complete marginal papillae (see Anstis, 2002), and further analysis could show that this is actually a plesiomorphy for Phyllomedusinae. The same problem holds for the presence of foot webbing.

Instead of creating *Cruziohyla* to include *Agalychnis calcarifer* and *A. craspedopus*, we could place both species in *Phrynomedusa*. Both alternatives imply taxonomic risks (in particular, that *Cruziohyla* could be shown to be nested within *Phrynomedusa*). Taking into account our almost complete ignorance of the relationships of Pelodryadinae, and therefore character-state polarities at its base, and that *Phrynomedusa* could not be included in this analysis, we consider that at this stage it is more appropriate to create *Cruziohyla* than to enlarge *Phrynomedusa*, without being certain about character polarities at the base of Phyllomedusinae.

Agalychnis craspedopus could not be included in the analysis, but the close relationship between *A. craspedopus* and *A. calcarifer* seems uncontroversial, as both have been repeatedly associated by some authors (Duellman, 1970; Hoogmoed and Cadle, 1991; Duellman, 2001).

CONTENTS: Two species. *Cruziohyla calcarifer* (Boulenger, 1902), new comb., *Cruziohyla craspedopus* (Funkhouser, 1957), new comb.

Hylomantis Peters, ‘‘1872’’ [1873]

TYPE SPECIES: *Hylomantis aspera* Peters, ‘‘1872’’ [1873], by monotypy.

DIAGNOSIS: The monophyly of this group is supported by 38 transformations in mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. We are not aware of any morphological synapomorphy supporting this genus.

COMMENTS: Only *Phyllomedusa lemur* of the *P. buckleyi* group was included in the analysis, and it obtains as the sister group of our exemplar of *Hylomantis*, *H. granulosa*, but with a Bremer support value of 3. While it is evident that this group should be excluded from *Phyllomedusa*, the possible taxonomic actions (whether to create a new genus or to include it in *Hylomantis*) deserve further discussion. From the definition of the group given by Cannatella (1980), the only character state that could be considered a synapomorphy is the bright orange flanks in life. The other character states included by Cannatella (1980) are either likely symplesiomorphies (absence of the slip of the m. depressor mandibulae originating from the dorsal fascia at the level of the m. dorsalis scapulae; hands and feet less than one-fourth webbed; parotoid gland not differentiated; palpebrum unpigmented; frontoparietal fontanelle exposed, large, and oval; oral discs of larvae lacking marginal papillae anteriorly) or character states whose taxonomic distribution in Phyllomedusinae makes their polarity unclear (lack of spots or pattern on flanks; cream or white iris; size; dorsum uniformly green by day; presence or absence of calcars). Like the *P. buckleyi* group, the two species included in *Hylomantis* by Cruz (1990) also lack spots or pattern on flanks, which are light yellow (instead of bright orange). At this point, we have no evidence regarding the polarity of these two character states; consequently, we consider that the morphological evidence of monophyly of the *P. buckleyi* group is weak. Considering that we could not test the monophyly of the *P. buckleyi* group, and that available morphological evidence for its monophyly is not compelling, provisionally, and with the caveat that the molecular support for this grouping is rather weak, we prefer to include all species of this group in *Hylomantis*, where we recognize them as a separate species group, pending a rigorous test of its monophyly when a denser taxon sampling becomes available.

CONTENTS: Eight species placed in two species groups.

Hylomantis aspera Group

DIAGNOSIS: Possible morphological synapomorphies of this group are the lanceolate discs and presence of the slip of the m. depressor mandibulae originating from the dorsal fascia at the level of the m. dorsalis scapulae (known homoplastic instance in *Phyllomedusa* and several other anurans).

COMMENTS: We included a single species of this group, and as such we did not we did not test its monophyly, but we recognize it based on the aforementioned evidence.

CONTENTS: Two species. *Hylomantis aspera* Peters, ''1872'' [1873]; *Hylomantis granulosa* (Cruz, ''1988'' [1989]).

Hylomantis buckleyi Group

DIAGNOSIS: The only apparent morphological synapomorphy of this group is the possession of bright orange flanks in life (Cannatella, 1980).

COMMENTS: We included a single species of this group, and as such we did not we did not test its monophyly. We recognize it following Cannatella (1980), pending a rigorous test of its monophyly. Ruiz-Carranza et al. (1988) tentatively included *Phyllomedusa danieli* in the *P. buckleyi* group because of the reduced webbing, absence of parotoid glands, toe I shorter than toe II, presence of a calcar, and unpigmented palpebrum. As the authors noted, these characteristics are also shared with *Phasmahyla* and *Hylomantis* (they refer to these genera using the former species groups of *Phyllomedusa*), but some also with *Phrynomedusa*. One difference they noticed was the golden iris coloration instead of white; however, in the present scenario the polarity of this state is unclear (a white iris is present in *Phasmahyla* and *Hylomantis*, as redefined here). A difference is the large snout–vent length (SVL) of *P. danieli* compared with the species of *Hylomantis* (the only reported specimen of *P. danieli*, a female, is 81 mm SVL; females of the other species reach a maximum of 57 mm, according to Cannatella [1980]). *Phyllomedusa danieli* shares with the *Hylomantis buckleyi* group its only apparent morphological synapomorphy (but see comments above), the bright orange flanks in life. Because of this, we tentatively include *P. danieli* in *Hylomantis*.

CONTENTS: Six species. *Hylomantis buckleyi* (Boulenger, 1882), new comb.; *Hylomantis danieli* (Ruiz-Carranza, Hernández-Camacho, and Rueda-Almonacid, 1988), new comb.; *Hylomantis hulli* (Duellman and Medelson, 1995), new comb.; *Hylomantis lemur* (Boulenger, 1882), new comb.; *Hylomantis medinai* (Funkhouser, 1962), new comb.; *Hylomantis psilopygion* (Cannatella, 1980), new comb.

Pachymedusa Duellman, 1968

TYPE SPECIES: *Phyllomedusa dacnicolor* Cope, 1864.

DIAGNOSIS: Molecular autapomorphies include 105 transformations in nuclear and mitochondrial proteins and ribosomal genes. See appendix 5 for a complete list of these transformations. Possible morphological autapomorphies are the first toe opposable to others, reticulated palpebral membrane (homoplastic with some species of *Phyllomedusa*; Duellman et al., 1988b), and the iris reticulation (Duellman, 2001).

COMMENTS: Duellman (2001) also included the toes about one-fourth webbed as an autapomorphy of *Pachymedusa*. In the context of our results, this is probably not an autapomorphy, as the webbing is also equally or more reduced in *Hylomantis* (as redefined here), *Phasmahyla*, and *Phyllomedusa*.

CONTENTS: Monotypic. *Pachymedusa dacnicolor* (Cope, 1864).

Phasmahyla Cruz, 1990

TYPE SPECIES: *Phyllomedusa guttata* A. Lutz, 1924, by original designation.

DIAGNOSIS: The monophyly of this genus is supported by 94 transformations in mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these molecular synapomorphies. Possible morphological synapomorphies of this genus are the absence of a vocal sac, and the modification of the larval oral disc into an anterodorsal funnel-shaped structure (Cruz, 1990).

COMMENTS: Cruz (1990) mentioned the absense of parotoid glands in *Phasmahyla* but stressed the presence of a pair of latero-dorsal glands. While these glands could be cosidered as possible synapomorphies of *Phasmahyla*, additional work is needed in order to determine if they could be considered as homologous to the parotoid glands present in *Phyllomedusa*.

CONTENTS: Four species. *Phasmahyla cochranae* (Bokermann, 1966); *Phasmahyla exilis* (Cruz, 1980); *Phasmahyla guttata* (A. Lutz, 1924); *Phasmahyla jandaia* (Bokermann and Sazima, 1978).

Phrynomedusa Miranda-Ribeiro, 1923

TYPE SPECIES: *Phrynomedusa fimbriata* Miranda-Ribeiro, 1923, by subsequent designation of Miranda-Ribeiro (1926).

DIAGNOSIS: A likely synapomorphy of this taxon is the oviposition in rock crevices or fallen trunks overhanging streams (A. Lutz and B. Lutz, 1939; Weygoldt, 1991).

COMMENTS: We did not include any species of this genus in our analysis. Besides the place of oviposition, we are not aware of any other possible synapomorphy of *Phrynomedusa*. This is not a strong support for its monophyly, particularly if we consider that with the exception of Weygoldt's (1991) studies in captivity of *Phrynomedusa marginata*, reports on oviposition of *Phrynomedusa* are mostly anecdotal.

The most obvious difference between *Phrynomedusa* and *Cruziohyla* is the impressive SVL difference. Although the reduction in SVL could actually be a synapomorphy of *Phrynomedusa*, considering how rudimentary is our knowledge of the topology of Pelodryadinae, and considering its taxonomic distribution in Phyllomedusinae (*Phasmahyla*, *Hylomantis*, and *Cruziohyla* also have a proportionally smaller SVL, as do some species of *Phyllomedusa*), the polarity of SVL as a character, if definable at all, is far from clear. *Phrynomedusa* could either be the sister group of *Cruziohyla* or the remaining Phyllomedusinae.

CONTENTS: Five species. *Phrynomedusa appendiculata* (A. Lutz, 1925); *Phrynomedusa bokermanni* Cruz, 1991; *Phrynomedusa fimbriata* Miranda-Ribeiro, 1923; *Phrynomedusa marginata* (Izecksohn and Cruz, 1976); *Phrynomedusa vanzolinii* Cruz, 1991.

Phyllomedusa Wagler, 1830

TYPE SPECIES: *Rana bicolor* Boddaert, 1772 by monotypy.

Pithecopus Cope, 1866. Type species: *Phyllomedusa azurea* Cope, 1862.

Bradymedusa Miranda-Ribeiro, 1926. Type species: *Hyla hypochondrialis* Daudin, 1800, by subsequent designation of Vellard (1948).

DIAGNOSIS: The monophyly of this taxon is supported by 49 transformations in nuclear and mitochondrial protein and ribosomal genes. See appendix 5 for a complete list of these transformations. Apparent morphological synapomorphies of *Phyllomedusa* are the presence of parotoid glands, toe I longer than toe II, and presence of the slip of the m. depressor mandibulae originating from the dorsal fascia at the level of the m. dorsalis scapulae (known instance of homoplasy in the *Hylomantis granulosa* group, and several other anurans) (Duellman et al., 1988b).

COMMENTS: The transformation from presence to absence of the m. abductor brevis plantae hallucis optimizes ambiguously in our analysis because the state of this character is unknown in *Phasmahyla*.

Blaylock et al. (1976) described the peculiar wiping behavior in *P. boliviana* (as *P. pailona*), *P. hypochondrialis*, *P. sauvagii*, and *P. tetraploidea* (as *P. iheringii*). This behavior was subsequently reported in *P. distincta*, *P. tarsius* (Castanho and De Luca, 2001), and *P. iheringii* (Langone et al., 1985). Castanho and De Luca (2001) further noticed a peculiar daily molting behavior. Further research on the taxonomic distribution of these behaviors in *Phyllomedusa* will determine the limits of the group(s) they support. The presence of the so-called lipid glands has been so far been reported in the five species of *Phyllomedusa* that were studied (*P. bicolor*, *P. boliviana*, *P. hypochon-*

drialis, *P. sauvagii*, and *P. tetraploidea*; Blaylock et al., 1976; Delfino et al., 1998; Lacombe et al., 2000) and were noticed to be unique to the genus by Delfino et al. (1998), so they could likely be another synapomorphy. As noticed by Cruz (1982), and corroborated by most larval descriptions of Phyllomedusinae, the larvae of most species of *Phyllomedusa*,[29] as redefined here, have the third posterior row of labial teeth reduced in relation to the first and second posterior rows.

CONTENTS: Twenty-six species, some of them included in four species groups.

Phyllomedusa burmeisteri Group

DIAGNOSIS: We are not aware of any synapomorphy of this group.

COMMENTS: We included only a single species of this group in our analysis, and as such we did not test its monophyly, but we recognize it following Pombal and Haddad (1992), pending a rigorous test of its monophyly.

CONTENTS: Four species. *Phyllomedusa burmeisteri* Boulenger, 1882; *Phyllomedusa distincta* B. Lutz, 1950; *Phyllomedusa iheringii* Boulenger, 1885; *Phyllomedusa tetraploidea* Pombal and Haddad, 1992.

Phyllomedusa hypochondrialis Group

DIAGNOSIS: We are not aware of any synapomorphy of this group.

COMMENTS: We included a single species of this group, and as such we did not test its monophyly, but we recognize it following Brandão (2002), pending a rigorous test of its monophyly. Manzano and Lavilla (1995b) described the muscle epicoracoideus in *Phyllomedusa hypochondrialis*, and Manzano (1997) noticed its absence in other species that she studied (*P. atelopoides*, *P. boliviana*, and *P. sauvagii*). Our observations on the only other species of the group available to us, *P. rohdei* (AMNH A-20263), indicate that it also has the m. epicoracoideus, so we consider the presence of this muscle a possible synapomorphy of the group. All species of this group lack vomerine teeth, as do *Phasmahyla*, *Phyllomedusa palliata* and some species of *Phrynomedusa* (Brandão, 2002; Cruz, 1990). The taxonomic distribution of other myological peculiarities described by Manzano and Lavilla (1995b) in *P. hypochondrialis*, such as the presence of thin and/or shortened muscles, and unusual insertions of some of them, needs to be assessed in other Phyllomedusinae.

CONTENTS: Six species. *Phyllomedusa ayeaye* (B. Lutz, 1966); *Phyllomedusa centralis* Bokermann, 1965; *Phyllomedusa hypochondrialis* (Daudin, 1800); *Phyllomedusa megacephala* (Miranda-Ribeiro, 1926); *Phyllomedusa oreades* Brandão, 2002; *Phyllomedusa rohdei* Mertens, 1926.

Phyllomedusa perinesos Group

DIAGNOSIS: A possible synapomorphy of this group is the purple coloration on the hands, feet, flanks, and concealed surfaces, as well as the purple venter with white granules (Cannatella, 1982).

COMMENTS: We did not include any exemplar of this group in the analysis. Its monophyly is tentatively assumed following Cannatella (1982) and is based on the evidence mentioned above.

CONTENTS: Four species. *Phyllomedusa baltea* Duellman and Toft, 1979; *Phyllomedusa duellmani* Cannatella, 1982; *Phyllomedusa ecuatoriana* Cannatella, 1982; *Phyllomedusa perinesos* Duellman, 1973.

Phyllomedusa tarsius Group

DIAGNOSIS: We are not aware of any synapomorphy supporting the monophyly of this group.

COMMENTS: We included a single species of this group, and as such we did not test its monophyly, but we continue to recognize it following De la Riva (1999) until its monophyly is rigorously tested.

CONTENTS: Four species. *Phyllomedusa boliviana* Boulenger, 1902; *Phyllomedusa camba* De la Riva, 2000; *Phyllomedusa sauvagii* Boulenger, 1882; *Phyllomedusa tarsius* (Cope, 1868).

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[29] The only exception we are aware of is the larvae of *Phyllomedusa vaillanti*, where P-3 almost equals P-2 (Caramaschi and Jim, 1983).

Species of *Phyllomedusa* Unassigned to Group

There are several species that are currently not assigned to any group. These are: *Phyllomedusa atelopoides* Duellman, Cadle, and Cannatella, 1988; *Phyllomedusa bicolor* (Boddaert, 1772); *Phyllomedusa coelestis* (Cope, 1874); *Phyllomedusa palliata* Peters, ''1872'' [1873]; *Phyllomedusa tomopterna* (Cope, 1868); *Phyllomedusa trinitatis* Mertens, 1926; *Phyllomedusa vaillanti* Boulenger, 1882; and *Phyllomedusa venusta* Duellman and Trueb, 1967.

BIOGEOGRAPHICAL COMMENTARY

Our objective here is to comment on patterns of distribution among the major biogeographic/tectonic units and not to provide a detailed biogeographic analysis. The distribution/biogeographic units of our discussion are (1) Australia plus New Guinea, (2) continental South America, (3) Middle America (in the sense of being composed of tropical Mexico, the Chortis Block of Central America, and the Panamanian Isthmus), and (4) the temperate Holarctic. Clearly all of these regions have histories that provide clues as to movements and diversifications within these areas. Because of the enormity of the topic of biogeography for the entire Hylidae, our comments will be truncated, limited either by our taxonomic sampling, knowledge of earth history, or phylogenetic resolution. Nevertheless, there are obvious geographic patterns that warrant our attention.

The distribution of the Hylidae strongly suggests a southern-continent origin of the taxon, a conclusion in accord with suggestions based on different lines of evidence advanced over the last 80 years (Metcalf, 1923a, 1923b, 1928; Duellman, 1970, 2001; Savage, 2002a) and supported by the observation that all the major groups of hylids have their centers of diversity in southern continents, with only phylogenetically secondary centers of diversification existing in Middle America, North America, and even more attenuated areas of radiation in Eurasia.

Relationships Between Australia and South America

The relationship between Australian and South American taxa has been previously noted for the Hylidae (Darst and Cannatella, 2004; Hoegg et al., 2004) and in several other groups (see Sanmartín and Ronquist [2004] for a review). In our results (fig. 13), the Australopapuan Pelodryadinae forms the sister taxon of the predominantly South American Phyllomedusinae, a distribution which we think speaks to one of the earliest patterns in the entire Hylidae, that of an Australia–Antarctica–South American connection. We cannot address any other topics of pelodryadine biogeography due to our limited sampling.

Relationships Between South and Middle America

Having the sister taxon of the Phyllomedusinae in Australia strongly suggests a southern (South American) origin of the Phyllomedusinae, although distribution of the most basal taxon, *Cruziohyla calcarifer*, is in Chocó/lower Middle America, with the remaining taxa found from northwestern Mexico to southern Brazil. This distribution suggests that the phyllomedusine biogeographic pattern is not recent. Assuming a connection between Australia and South America was by way of Antarctica, one would be driven to the conclusion that South America is the home of the phyllomedusines. The fact that we could not include any exemplar of *Phrynomedusa*, an Atlantic Forest genus possibly related with *Cruziohyla*, could possibly cloud the general picture.

Apart from the Hylini, there are several instances of members of the other three tribes of Hylinae having a Middle American distribution (figs. 14–16), corroborating the suggestion of Duellman (2001) regarding the existence of several independent vicariance or dispersal events with hylids between South America and Middle America. Our results imply eight independent events of dispersal from South America into Middle America: (1) *Dendropsophus ebraccatus*, (2) *D. microcephalus*, (3) ancestor of Hylini, (4) *Hypsiboas boans*, (5) *H. rufitelus*, (6) *Scinax boulengeri*, (7) *S. elaeochrous* and *S. staufferi*, and (8) *Trachycephalus venulosus*. However, this number is a clear underestimation because we did not include other terminals that also have a Middle American distribution (e.g., *Dendropsophus phlebodes*, *D. robertmertensi*, *D. sartori*, *D. subocularis*, *Hypsiboas pugnax*, *H. rosenbergi*, *Scinax altae*, and *S. rostratus*) and which may represent additional entries into Middle America from South America. For some of these species (e.g., *Scinax altae* and *S. rostratus*) we consider it likely that they are related to other Middle American members of their respective phylogenetic nearest relatives (hence not adding to the number of independent biogeographic events). Other species (*Dendropsophus subocularis*) might imply additional events because they are probably nested within mostly South American clades. The uncertain position of the other species (e.g., *Dendropsophus phlebodes*, *D. robertmertensi*, *D. sartori*, *Hypsiboas pugnax*, *H. rosenbergi*) in our phylogenetic hypothesis does not allow us to suggest that their presence in Middle America either represents independent events or that they are contained within other groups of species whose ancestors moved into Middle America.

Considering the Hylinae with a Middle American origin, the results imply two biogeographic events to explain the presence of these lineages in South America: the cases of *Scinax elaeochrous* (fig. 15) and *Smilisca phaeota* (fig. 16). Once again, this is a minimal number of events. The monophyly of *Ecnomiohyla* could be in error, because most species were unavailable for study and at least *E. tuberculosa* (not studied) is possibly unrelated to the Middle American fringe-limbed treefrogs. Duellman (2001) suggested that *Smilisca sila* and *S. sordida* together are monophyletic (apparent synapomorphies: ventral oral disc in the larvae and small inner metatarsal tubercle) and together are the sister taxon of *S. puma*. If this hypothesis withstands further testing, it would represent a third independent biogeographic event involving a Middle American lineage present in northern South America.

SOUTH AMERICA

GUAYANA HIGHLANDS–ANDES–ATLANTIC FOREST

Within Cophomantini (fig. 14), the first four genera contain elements from three characteristic formations, quite distant geographically from each other: *Myersiohyla* is composed solely of Guayana Highlands species; *Hyloscirtus* is composed exclusively of Andean species; *Bokermannohyla* and *Aplastodiscus* are composed almost exclusively of species from the southeastern Brazilian Atlantic Forest and Rocky fields associated with this formation and to the Cerrado. We are not aware of any similar biogeographic pattern in any other animal group.

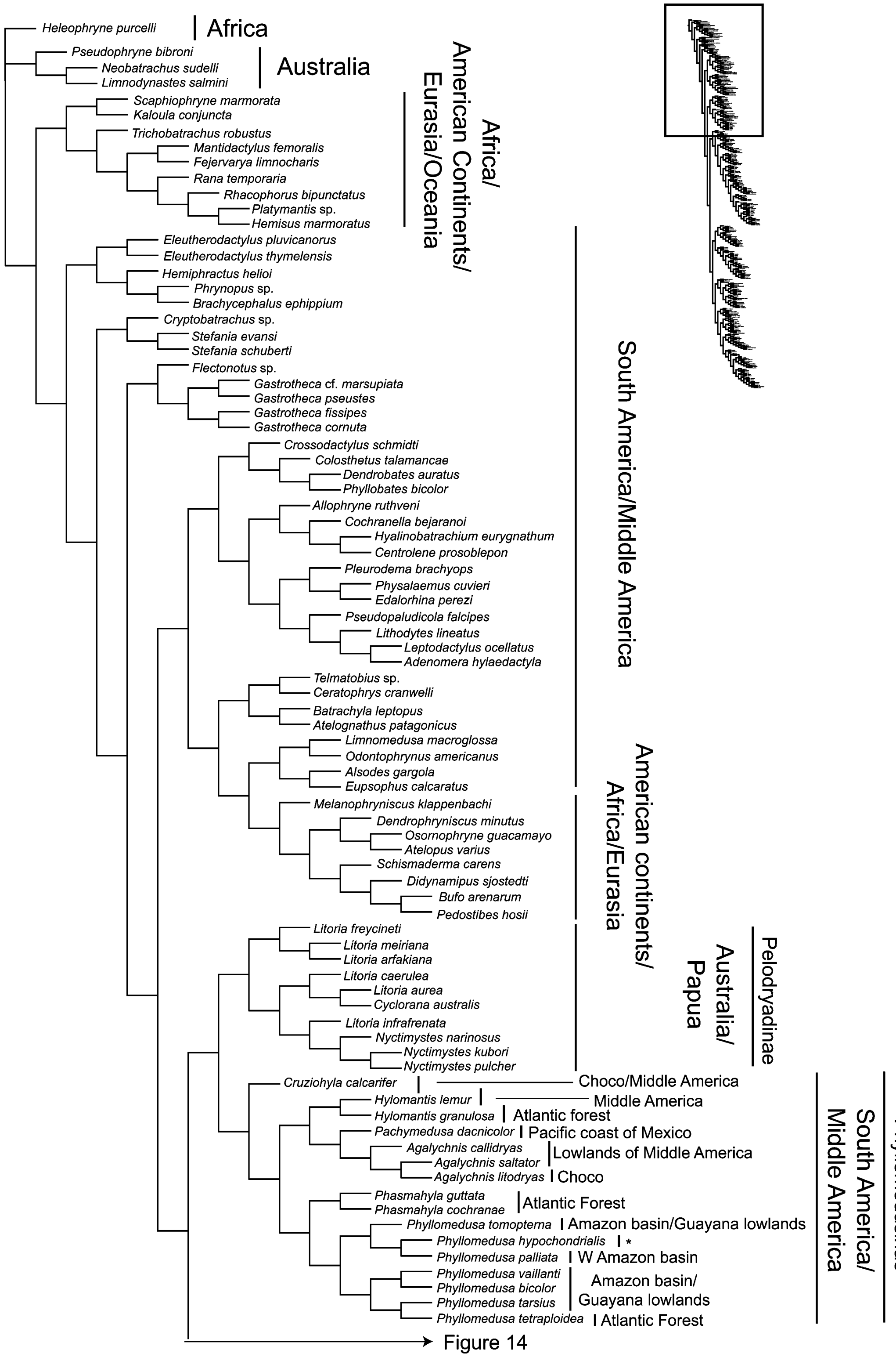
GUAYANA HIGHLANDS

Our analysis included 6 of the 19 hylid endemics (updated from Duellman's [1999] list by adding *Hypsiboas rhythmicus*) of the Guayana Highlands, plus two undescribed species. The topology suggests a minimum of four independent occurrences of endemic hylines in the Guayana Highlands (figs. 14, 16): (1) the *Hypsiboas benitezi* group (this group also contains three species from western Amazonia: *H. hutchinsi*, *H. microderma*, and *Hypsiboas* sp. 2), (2) *Hypsiboas sibleszi*, (3) *Myersiohyla*, and (4) *Tepuihyla*. In the *H. benitezi* group, it is ambiguous whether there is an origin in the Guayana Highlands with a subsequent dispersal/vicariance event into northwestern Amazonia, or two independent events that led to the presence of these species in the highlands.

Considering the 13 taxa from the Guayana Highlands that were unavailable for this study, all but two species are members of groups represented in the analysis. Seven are species of *Tepuihyla*, three are species of *Myersiohyla*, two are species of *Scinax* (*S. danae*, and *S. exiguus*), one is a species tentatively associated with the *Hypsiboas benitezi* group (*H. rhythmicus*), and one is incerta sedis (‘‘*Hyla warreni*’’). Phylogenetic relationships of the two species of *Scinax* with other species of the genus are still unknown, as is the position of ‘‘*Hyla warreni*’’. When considering relationships of the Guayana Highlands lineages with the other Hylinae, current evidence suggests they are related to elements from the Amazon Basin (*Osteocephalus*, *Hypsiboas microderma*, *Hypsiboas* sp. 2) and the Chocó (*Hypsiboas picturatus*).

IMPACT OF THE ANDES IN HYLINE EVOLUTION

The uplift of the Andes and subsequent climatic changes in the Quaternary have an


Heleophryne purcelli
Africa
Pseudophryne bibroni
Neobatrachus sudelli
Limnodynastes salmini
Australia
Scaphiophryne marmorata
Kaloula conjuncta
Trichobatrachus robustus
Mantidactylus femoralis
Fejervarya limnocharis
Rana temporaria
Rhacophorus bipunctatus
Platymantis sp.
Hemisus marmoratus
Africa/ American Continents/ Eurasia/Oceania
Eleutherodactylus pluvicanorus
Eleutherodactylus thymelensis
Hemiphractus helioi
Phrynopus sp.
Brachycephalus ephippium
Cryptobatrachus sp.
Stefania evansi
Stefania schuberti
Flectonotus sp.
Gastrotheca cf. marsupiata
Gastrotheca pseustes
Gastrotheca fissipes
Gastrotheca cornuta
Crossodactylus schmidti
Colosthetus talamancae
Dendrobates auratus
Phyllobates bicolor
Allophryne ruthveni
Cochranella bejaranoi
Hyalinobatrachium eurygnathum
Centrolene prosoblepon
Pleurodema brachyops
Physalaemus cuvieri
Edalorhina perezi
Pseudopaludicola falcipes
Lithodytes lineatus
Leptodactylus ocellatus
Adenomera hylaedactyla
Telmatobius sp.
Ceratophrys cranwelli
Batrachyla leptopus
Atelognathus patagonicus
Limnomedusa macroglossa
Odontophrynus americanus
Alsodes gargola
Eupsophus calcaratus
South America/Middle America
Melanophryniscus klappenbachi
Dendrophryniscus minutus
Osornophryne guacamayo
Atelopus varius
Schismaderma carens
Didynamipus sjostedti
Bufo arenarum
Pedostibes hosii
American continents/ Africa/Eurasia
Litoria freycineti
Litoria meiriana
Litoria arfakiana
Litoria caerulea
Litoria aurea
Cyclorana australis
Litoria infrafrenata
Nyctimystes narinosus
Nyctimystes kubori
Nyctimystes pulcher
Australia/ Papua
Pelodryadinae
Cruziohyla calcarifer
Choco/Middle America
Hylomantis lemur
Middle America
Hylomantis granulosa
Atlantic forest
Pachymedusa dacnicolor
Pacific coast of Mexico
Agalychnis callidryas
Agalychnis saltator
Lowlands of Middle America
Agalychnis litodryas
Choco
Phasmahyla guttata
Phasmahyla cochranae
Atlantic Forest
Phyllomedusa tomopterna
Amazon basin/Guayana lowlands
Phyllomedusa hypochondrialis
*
Phyllomedusa palliata
W Amazon basin
Phyllomedusa vaillanti
Phyllomedusa bicolor
Phyllomedusa tarsius
Amazon basin/ Guayana lowlands
Phyllomedusa tetraploidea
Atlantic Forest
South America/ Middle America
Phyllomedusinae
Figure 14

impressive correlation with large radiations of anuran groups, such as certain Bufonidae, Centrolenidae, Dendrobatidae, Hemiphractinae, and Eleutherodactylinae (e.g., Lynch, 1986; Coloma, 1995; Lynch and Duellman, 1997; Lynch et al., 1997; Lynch, 1998; Duellman, 1999). Previous knowledge of hylid distribution, as well as our results, suggests a much more limited impact of the Andes in hylid radiation and speciation, with three hyline radiations in the Andes (figs. 14, 16): *Hyloscirtus*, the Andean clade of the *Hypsiboas pulchellus* group, and the *Dendropsophus columbianus* + *D. labialis* groups clade. If we consider the taxa that were not included in this analysis, there are 41 with an Andean distribution: *Dendropsophus aperomeus*, *D. battersbyi*, ''*Hyla chlorostea*'', *D. delarivai*, *D. praestans*, *D. stingi*, *D. yaracuyanus*, ''*Hyla vigilans*'', *Osteocephalus elkejungingerae*, *O. leoniae*, *O. pearsoni*, *Scinax fuscovarius*, *S. castroviejoi*, *S. manriquei*, *S. oreites*, the four species of the *Dendropsophus garagoensis* group, plus 23 additional members of *Hyloscirtus*, the Andean clade of the *Hypsiboas pulchellus* group, and the *Dendropsophus columbianus* + *D. labialis* groups clade (Duellman, 1999; Mijares-Urrutia and Rivero, 2000; Jungfer and Lehr, 2001; Köhler and Lötters, 2001a; Barrio-Amorós et al., 2004). If the *D. garagoensis* group is not related to the *Dendropsophus columbianus* + *D. labialis* groups clade, then it would represent a fourth Andean radiation of hylids. Relationships of the Andean *D. aperomeus*, *D. battersbyi*, *D. delarivai*, *D. stingi*, and *D. yaracuyanus* within *Dendropsophus* are unknown, so they may represent as many as five additional events leading to the presence of hylids in the Andes. A similar situation occurs with ''*Hyla chlorostea*'', ''*Hyla vigilans*'', *Scinax manriquei*, *S. oreites*, and the species of *Osteocephalus*. *Scinax castroviejoi* and *S. fuscovarius* are sister species (Faivovich, unpubl. data), so they are considered another independent entrance into the Andes. Adding up all these species and clades gives a maximum total of 17 independent biogeographic events, of which 5 subsequently radiated and 13 are single taxa. If the Andean species of *Osteocephalus* were monophyletic, then the figure could decrease to 14 independent events, 6 of which subsequently radiated.

Considering the information outlined above, and returning to the beginning of this section, whereas now we have an upper and a lower limit for the number of independent radiations of hylids in the Andes, we have no idea as to the number of independent radiations of Bufonidae, Centrolenidae, Dendrobatidae, and Hemiphractinae in the Andes.

A question that might arise is why there is such poor diversification of hylids in the Andes (note that its complement, Why are there so many species in extra-Andean areas?, is equally valid). There are several scenarios that could answer this question. The presence in several areas of the Andes of anuran groups with obligate aquatic life-history stages dependent on either ponds or streams (Centrolenidae, Bufonidae) appears to be a strong argument against a hypothesis of lack of appropriate habitats. The fact that hylids are found in fairly high altitudes in the Andes (e.g., species in the Andean stream-breeding clade reach up to 2400 m; Duellman et al., 1997; species of the *D. labialis* group reach up to 3500 m; Lüddecke and Sanchez, 2002) and other places (e.g., several Hylini living between 2000 and 3000 m; see Duellman, 2001) could indicate that there may be few physiological constraints limiting the exploitation of higher areas.[30]

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[30] We understand that this argument is weak; perhaps the hylid groups that are not physiologically constrained are precisely those that could colonize and diversify in the highlands.

←

Fig. 13. A partial view of the strict consensus showing major biogeographic patterns among outgroups, Pelodryadinae and Phyllomedusinae, and the geographic distribution of the exemplars of Phyllomedusinae. Distributions are taken from Duellman (1999) and Frost (2002). Only collective groups referred in ''Biogeographic Commentary'' are shown. An asterisk (*) indicates the distribution of *Phyllomedusa hypochondrialis* that ranges from the Chaco/Cerrado through the Amazon Basin and Guayana lowlands up to the Llanos.

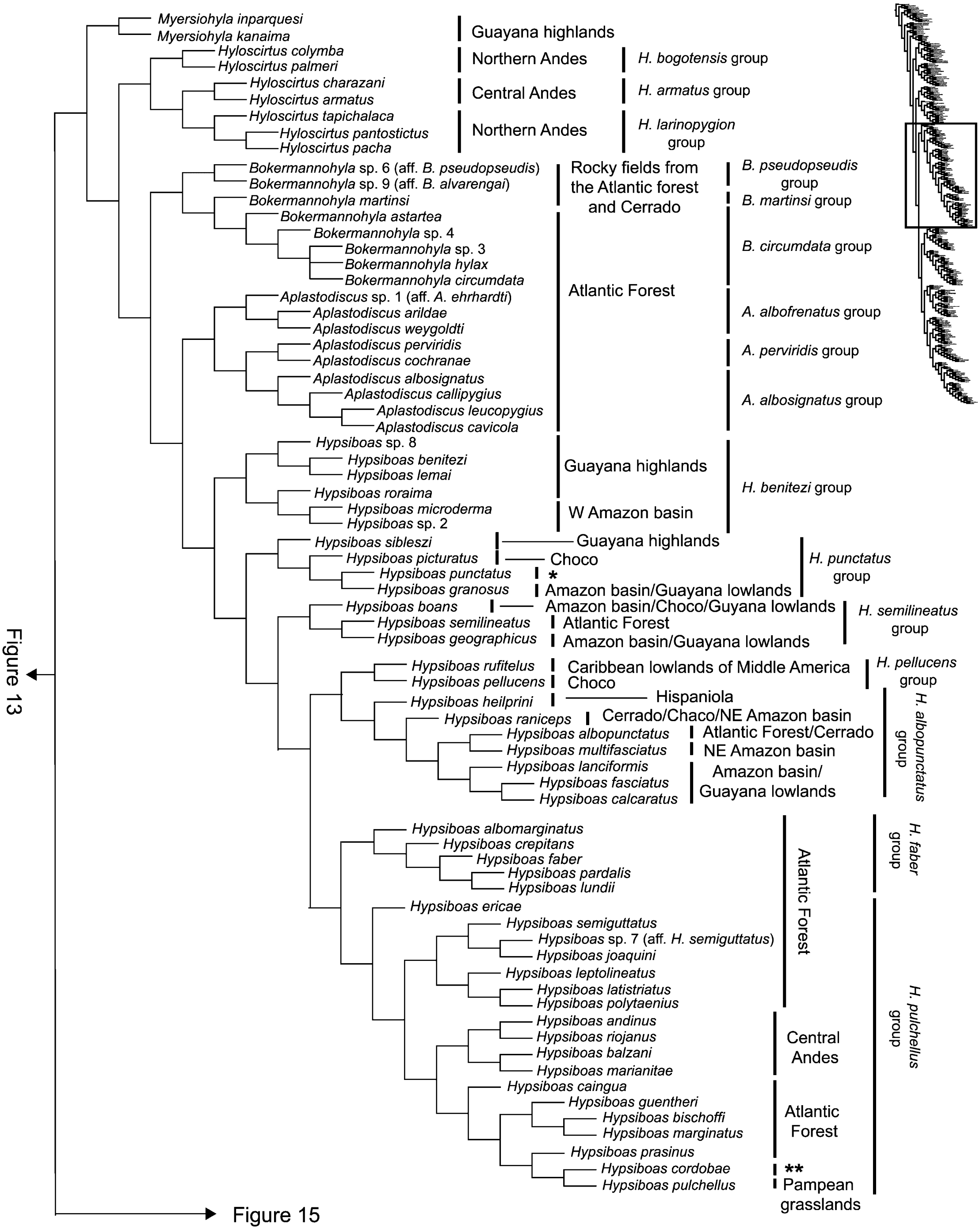

Fig. 14. A partial view of the strict consensus showing the geographic distribution of the components of Cophomantini. Distributions, in general, are taken from Duellman (1999). Only collective groups referred in ‘‘Biogeographic Commentary’’ are shown. An asterisk (*) indicates the distribution of *Hypsiboas punctatus* that ranges from the Chaco/Cerrado through the Amazon Basin and Guayana lowlands up to the Caribbean lowlands. Two asterisks (**) indicate the geographic distribution of *Hypsiboas cordobae* that is restricted to the Sierras of Central Argentina.

ATLANTIC FOREST

Of the several instances of hyline taxa present in the Atlantic Forest of Brazil, eight are single terminals and six are clades (figs. 14–16). The terminals are (1) *Aparasphenodon brunoi*, (2) *Dendropsophus anceps*, (3) *D. giesleri*, (4) *D. minutus*, (5) *D. seniculus*, (6) *Hypsiboas albopunctatus*, (7) *Scinax uruguayus*, and (8) *Xenohyla truncata*. The clades are (1) *Aplastodiscus*, (2) the *Hypsiboas faber* group plus the *H. pulchellus* group clade, (3) *Trachycephalus nigromaculatus* plus *T. mesophaeus*, (4) *Phyllodytes*, (5) the *Scinax catharinae* clade, and (6) *Bokermannohyla*. Including the approximately 134 hylid species that were unavailable for this study with a distribution in eastern Brazil would certainly increase the number of clades and terminals in an unpredictable way.

Faivovich (2002) observed that *Scinax* was divided in two clades, one endemic to the Atlantic Forest (the *S. catharinae* clade) and another that was widespread in the Neotropics (the *S. ruber* clade). Our results imply an ambiguous situation. The position of *S. uruguayus* as the sister taxon of the remaining species of the *S. ruber* clade suggests that *Scinax* could have as well originated in southeastern Brazil and colonized other areas of the Neotropics in subsequent events. A denser taxon sampling of *Scinax* would allow a test of this hypothesis.

In Lophiohylini, nearly all species of *Phyllodytes* are from the Atlantic Forest (the only exception being *P. auratus* from Trinidad), as is also true for *Itapotihyla langsdorffii* and several other species of the tribe. However, the situation here is equivocal because it would be equally parsimonious to postulate two independent events leading to the presence of *I. langsdorffii* and *Phyllodytes* in the Atlantic Forest.

Within *Bokermannohyla*, the *B. circumdata* species group, mostly from forested regions, is nested within a clade composed of species and species groups (*B. pseudopseudis* and *B. martinsi* groups) restricted to the highland formations of rocky fields (Bokermann and Sazima, 1973b; Eterovick and Brandão, 2001; Lugli and Haddad, in prep.). The facts that the other species included in the *B. martinsi* group, *B. langei*, is from forested areas (Bokermann, 1964a) and that two species of the *B. circumdata* group, *B. nanuzae* and *B. sazimai* are from rocky fields (Bokermann and Sazima, 1973b; Cardoso and Andrade ‘‘1982’’ [1983]) suggest that a denser taxon sampling of *Bokermannohyla* is necessary to better understand whether these frogs are an original element from the rocky fields that secondarily radiated in the forested areas or vice versa.

The clade composed of the *Hypsiboas faber* and *H. pulchellus* groups could be an example of an Atlantic Forest (or at least an eastern Brazilian[31]) origin with subsequent radiations into other regions. Faivovich et al. (2004) found that within the *H. pulchellus* group, an Andean clade was nested within an Atlantic Forest clade. Exactly the same pattern for the group is corroborated by our analysis (fig. 14).

ORIGIN OF WEST INDIAN HYLIDS

Our results support assertions made by Hass et al. (2001) and Hedges (1996), based on immunological distances and unpublished sequence data, regarding a diphyletic origin of West Indian hylids. *Osteopilus* is the sister group of a clade composed of *Osteocephalus* and the montane *Tepuihyla* (fig. 16). While the incomplete taxon sampling precludes a careful assessment of the distribution of the most basal taxa of these genera, our results are compatible with a northern South American origin for *Osteopilus*; *Tepuihyla* is restricted to highlands in Venezuela and Guyana (Ayarzagüena et al., ‘‘1992’’ [1993b], Duellman and Yoshpa, 1996; Mijares-Urrutia et al., 1999), and *Osteocephalus* is widespread in the Amazon Basin and surrounding regions, from Venezuela and French Guiana to Bolivia (e.g., De la Riva et al., 2000; Lescure and Marty, 2000; Jungfer and Lehr, 2001; Smith and Noonan, 2001).

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[31] *Hypsiboas crepitans* in Brazil occurs in some areas of the Atlantic forest and mostly in adjacent Cerrado Caatinga and Cerrado formations; however, we still think the observed pattern is meaningful, and the addition of the remaining species of the group will help to better define it. *Hypsiboas crepitans* also has wider distribution, including Panama, Colombia, Venezuela, and the Guayanas; however, the status of those populations needs to be reassessed (Lynch and Suarez-Mayorga, 2001), as do their relationships with the *H. faber* group.

Regarding the other West Indian hylid species, *Hypsiboas heilprini* and its sister-group relationship with the *H. albopunctatus* group (fig. 14) is notable in that the basal taxon of the group, *H. raniceps*, has a broad distribution through open areas of South America, spanning about 3500 km, from French Guiana (Lescure and Marty, 2000) to eastern central Argentina (Basso, 1995). The fact that both hylid lineages present in the West Indies clearly have a northern South American origin is coincident with the suggestions made by Hedges (1996).

MIDDLE AMERICA AND THE HOLARCTIC

The molecular evidence for Hylini does not support the idea of a basal split between an Isthmian–Lowlands clade and a Mexican–Nuclear Central American clade as was suggested by Duellman (2001). Instead, it suggests the existence of a clade composed primarily of, but not limited to, Mexican highlands-Nuclear Central American elements (fig. 15). Nested within this clade, there is a lineage composed of two lowland clades (*Tlalocohyla*, and the group composed of *Anotheca*, *Triprion*, and *Smilisca*), an Isthmian Highlands clade (*Isthmohyla*) and one North American–Eurasiatic clade (*Hyla*).

Within the Mexican Highlands–Nuclear Central American clade, and besides the major lineage that diversified outside this region (*Hyla*, *Isthmohyla*), there are two other instances of terminals distributed in lower Central America (fig. 15), *Duellmanohyla rufioculis* and *Ecnomiohyla miliaria*. There are also at least three more cases that were unavailable for this study: two species of *Duellmanohyla* (*D. lythrodes*, *D. uranochroa*), the lower Central American species of *Ecnomiohyla* (*E. fimbrimembra*, *E. thysanota*), and *Ptychohyla* (*P. legleri*). The two instances implied by our results are a lower limit; the addition of further exemplars of *Duellmanohyla*, *Ecnomiohyla*, and *Ptychohyla* will determine if there were other events as well.

Hylini is nested within a South American clade, supporting a South American origin for this group. It is interesting, however, to see a likely Mexican highlands–Nuclear Central American origin for the lowland lineages (*Anotheca*, *Tlalocohyla*, *Smilisca*, *Triprion*), and that the Isthmian Highlands *Isthmohyla* is nested within all these lineages. We see these situations as being at least partially compatible with the current paleogeographic scenario for Middle America (see Iturralde-Vinent and McPhee, 1999; Savage, 2002a).

The topology of the Mexican Highlands–Nuclear Central American clades also shows some fine-grained patterns, like the possible sister-taxon relationship between a clade from the Mexican highlands (*Plectrohyla bistincta* group) and one from the Nuclear Central American highlands (*Plectrohyla guatemalensis* group). The problem is that considering the scarce taxon sampling of these two species groups in our analysis, and the very likely possibility of further rearrangements upon addition of more exemplars of these groups (see comments in earlier discussion), it seems risky to hypothesize about the recovered pattern.

Most authors who have discussed the origin of Eurasiatic *Hyla* assumed its origin from western North American *Hyla* and its dispersion to Eurasia presumably through Beringia (Anderson, 1991; Borkin, 1999; Duellman, 2001; Kuramoto, 1980). The topology of *Hyla* (fig. 15) shows two Eurasiatic taxa. One of these, the *H. arborea* group, forms the sister taxon of the remaining *Hyla*. The other, *H. japonica*, is imbedded within the *H. eximia* group, which in turn is nested within a grade of eastern North American species. This situation implies two independent biogeographic events to explain the origin of Eurasiatic *Hyla*, as suggested by Anderson (1991) and Borkin (1999). While this pattern is partially compatible with the idea of a western North American origin of at least some Eurasiatic *Hyla* (those nested within the *H. eximia* group) claimed by previous authors, it remains at least equivocal for the clade that contains most exemplars of the *H. arborea* group. The only way of maintaining a western North American origin for this clade is to invoke a very important historical shift in the distribution of the currently eastern North American species groups or to accept an eastern North American–European (North Atlantic) vicariance or dispersal event. The position of the *H. eximia* group nested within eastern North American species groups requires a dispersal/vicariance

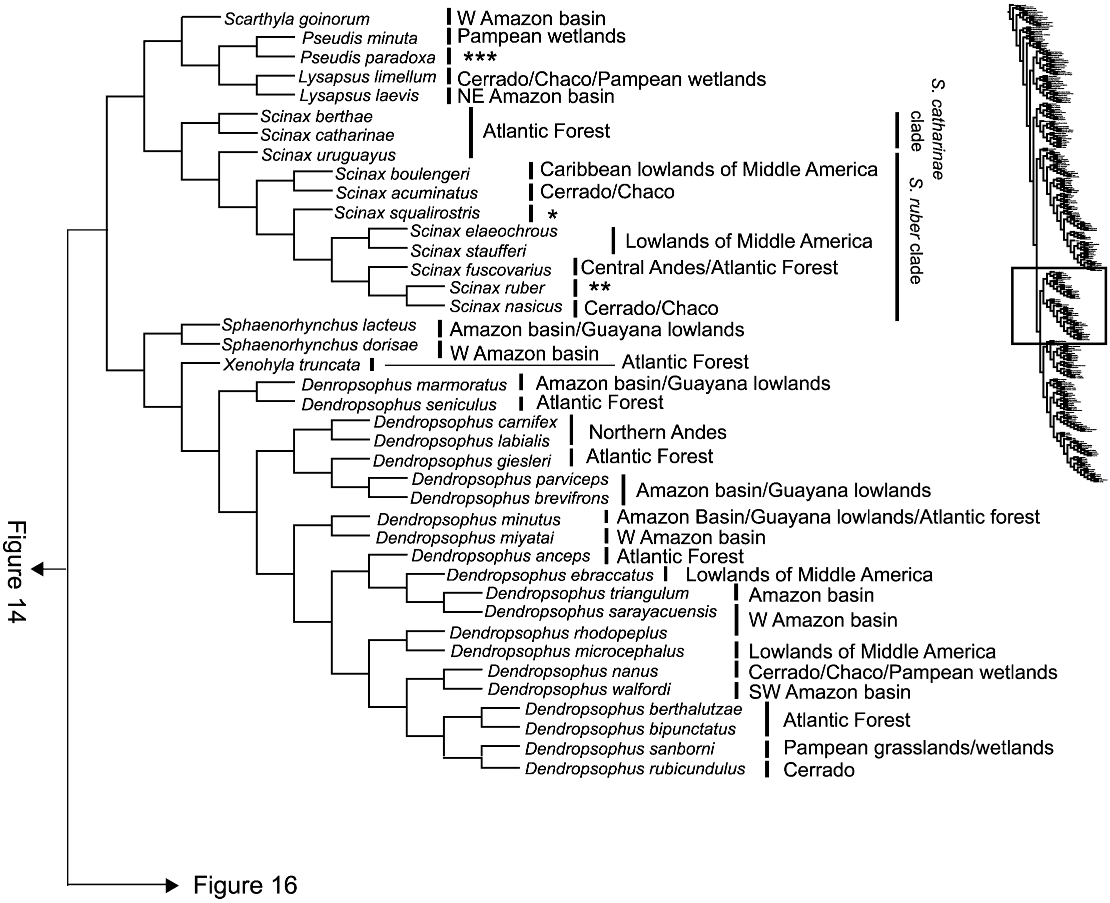


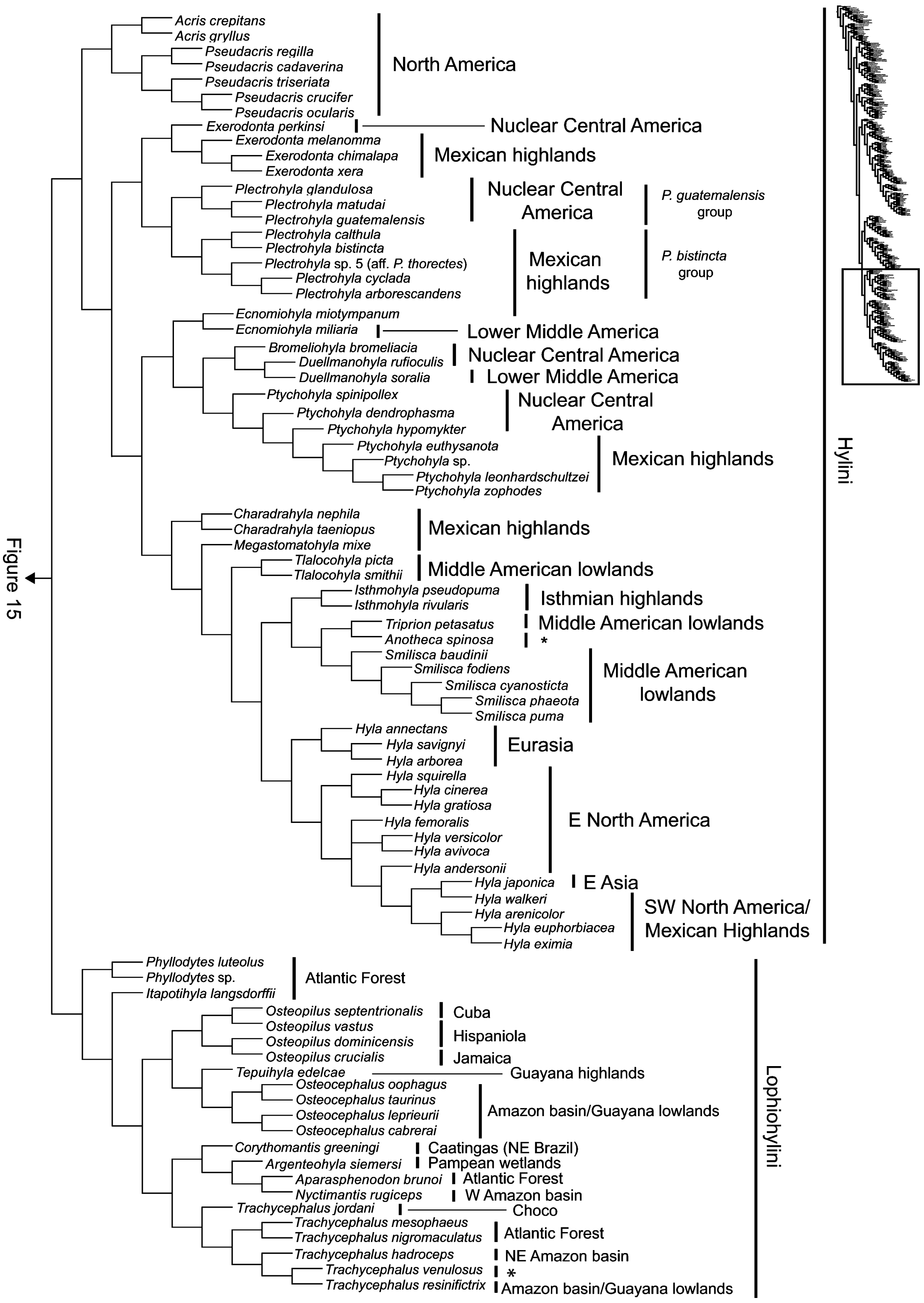
Fig. 15. Partial view of the strict consensus showing the geographic distribution of the components of Dendropsophini. Distributions, in general, are taken from Duellman (1999). Only collective groups referred in "Biogeographic Commentary" are shown. An asterisk (*) indicates the geographic distribution of *Scinax squalirostris* that includes the Atlantic forest, Cerrado, Chaco, and Pampean grasslands. Two asterisks (**) indicate the geographic distribution of *Scinax ruber* that includes the Amazonian and Guayana lowlands, Caribbean lowlands, and Llanos. Three asterisks (***) indicate the geographic distribution of *Pseudis paradoxa* that extends from the Chaco region to the Amazonian and Guayana lowlands, the Llanos, and the Caribbean lowlands.

event southward to explain the distribution of this lineage, as suggested by Duellman (2001).

A ROUGH TEMPORAL FRAMEWORK: CLUES FROM THE HYLID FOSSIL RECORD

The hylid fossil record is remarkably scant (Sanchiz, 1998a), and hylid remains, on most occasions, are represented by disarticulated ilia. The oldest fossil record tentatively assigned to Hylidae is remains of an ilium and a humerus from the Maastrichtian of Naskal, India (Prasad and Rage, 1995) tentatively assigned to Hylidae, although Sanchiz (1998a) considered the identification dubious. Hylids were mentioned from the Paleocene of Itaboraí (Brazil) by Estes (1970), Estes and Reig (1973), Estes and Baez (1985), and Baez (2001), but the material—also iliac remains—is stills unstudied.

The earliest known record for North America is *Hyla swanstoni*, from the Late


Acris crepitans
Acris gryllus
Pseudacris regilla
Pseudacris cadaverina
Pseudacris triseriata
Pseudacris crucifer
Pseudacris ocularis
North America
Exerodonta perkinsi
Nuclear Central America
Exerodonta melanomma
Exerodonta chimalapa
Exerodonta xera
Mexican highlands
Plectrohyla glandulosa
Plectrohyla matudai
Plectrohyla guatemalensis
Nuclear Central America
P. guatemalensis group
Plectrohyla calthula
Plectrohyla bistincta
Plectrohyla sp. 5 (aff. P. thorectes)
Plectrohyla cyclada
Plectrohyla arborescandens
Mexican highlands
P. bistincta group
Ecnomiohyla miotympanum
Ecnomiohyla miliaria
Lower Middle America
Bromeliohyla bromeliacia
Duellmanohyla rufioculis
Nuclear Central America
Duellmanohyla soralia
Lower Middle America
Ptychohyla spinipollex
Ptychohyla dendrophasma
Ptychohyla hypomykter
Nuclear Central America
Ptychohyla euthysanota
Ptychohyla sp.
Ptychohyla leonhardschultzei
Ptychohyla zophodes
Mexican highlands
Charadrahyla nephila
Charadrahyla taeniopus
Megastomatohyla mixe
Mexican highlands
Tlalocohyla picta
Tlalocohyla smithii
Middle American lowlands
Isthmohyla pseudopuma
Isthmohyla rivularis
Isthmian highlands
Triprion petasatus
Middle American lowlands
Anotheca spinosa
*
Smilisca baudinii
Smilisca fodiens
Smilisca cyanosticta
Smilisca phaeota
Smilisca puma
Middle American lowlands
Hyla annectans
Hyla savignyi
Hyla arborea
Eurasia
Hyla squirella
Hyla cinerea
Hyla gratiosa
Hyla femoralis
Hyla versicolor
Hyla avivoca
Hyla andersonii
E North America
Hyla japonica
E Asia
Hyla walkeri
Hyla arenicolor
Hyla euphorbiacea
Hyla eximia
SW North America/ Mexican Highlands
Hylini
Figure 15
Phyllodytes luteolus
Phyllodytes sp.
Itapotihyla langsdorffii
Atlantic Forest
Osteopilus septentrionalis
Cuba
Osteopilus vastus
Osteopilus dominicensis
Hispaniola
Osteopilus crucialis
Jamaica
Tepuihyla edelcae
Guayana highlands
Osteocephalus oophagus
Osteocephalus taurinus
Osteocephalus leprieurii
Osteocephalus cabrerai
Amazon basin/Guayana lowlands
Corythomantis greeningi
Caatingas (NE Brazil)
Argenteohyla siemersi
Pampean wetlands
Aparasphenodon brunoi
Atlantic Forest
Nyctimantis rugiceps
W Amazon basin
Trachycephalus jordani
Choco
Trachycephalus mesophaeus
Trachycephalus nigromaculatus
Atlantic Forest
Trachycephalus hadroceps
NE Amazon basin
Trachycephalus venulosus
*
Trachycephalus resinifictrix
Amazon basin/Guayana lowlands
Lophiohylini

Eocene of Cypress Hill Formation (Saskatchewan, Canada), described by Holman (1968) based on eroded iliac remains; Sanchiz (1998a) also considered this taxonomic assignment to be dubious. Other iliac remains from the mid-Miocene of North America (mostly from the Hemingfordian North American Land Mammal Age) were also referred to hylids (i.e., *Acris barbouri*, *Hyla miocenica*, *H. miofloridiana*, *Proacris mintoni*, *Pseudacris nordensis*), as well as several Pleistocene remains that were assigned to extant species (Holman, 2003).

The oldest known hylid record for Europe was reported by Sanchiz (1998b) from early Miocene lignite deposits of Austria. The remains consist of a fragmentary sacral vertebra and a scapula, which Sanchiz (1998b) found to be similar to *Hyla arborea* and *H. meridionalis*, and assigned to *Hyla* sp. Other remains from the late Miocene, as well as from the Pliocene to Holocene, were referred to *Hyla* sp., *H. arborea*, and the most recent ones to some extant species (see Sanchiz [1998a] for review).

The oldest fossil record of hylids in Australia dates to the Lower to Middle Miocene, where some species of *Litoria* were described on the basis of iliac remains (e.g., Tyler, 1991). Other Pleistocene and Holocene remains were assigned to extant species (see Sanchiz [1998a] for a review).

We are not inclined to construct far-reaching hypotheses based on such a sparse fossil record. Without taking into account *Hyla swanstoni*, already questioned by Sanchiz (1998a), we must consider the possibility that at least one of the North American iliac remains from the Miocene assigned to hylids is actually related to the extant groups of Holarctic hylids. If this were the case, it would imply a minimum age of approximately 15 mybp of hylid presence in North America. If we consider with the same leniency the Miocene remains from Europe, especially the approximately 17 mybp *Hyla* sp. reported by Sanchiz (1998b), we could consider an even earlier, though still unspecified, minimum age of hylid presence in North America. All the evidence regarding hylid fossil record and its minimum ages has been presented.

How this information could be used depends on how much we are willing to assume about the role of known geophysical data in dating cladogenetic events. In recent studies addressing phylogenetic studies of some frog groups, geophysical information was used for molecular clock calibrations (e.g., Bossuyt and Milinkovitch, 2000; Vences et al., 2003c). Leaving aside particular objections about molecular clock estimations, the use of clade-independent information as calibration points entails assumptions about the evolutionary process and about the primacy and precision of paleogeographic reconstructions that should be taken cautiously (Page and Lydeard, 1994). It has been this clade-independent information that has classically been used to date one of the important events of the hylid radiation: the origin of the Hylini.

Both Savage (1966, 1982, 2002a) and Duellman (1970, 2001) suggested an early colonization event of Middle America by Hylinae and Phyllomedusinae stocks in the late Cretaceous–Eocene; from these stocks, all remaining Middle American and North American elements differentiated due to several vicariant and dispersal events through the Tertiary. Considering that the evidence for the existence of a late mid-Miocene landbridge between North and South America (necessarily involving Central America) is ambiguous (Iturralde-Vinent and McPhee, 1999), a ‘‘classical’’ assumption of nonoverwater dispersal would imply that actually the minimum age of colonization of Middle America must have been at least about 75

←

Fig. 16. Partial view of the strict consensus showing the geographic distribution of the components of Hylini and Lophiohylini. Distributions were taken from Campbell (1999) and Duellman (1970, 2001). Only collective groups referred in ‘‘Biogeographic Commentary’’ are shown. An asterisk (*) indicates the distribution of *Anotheca spinosa* that is present in the Mexican, Nuclear Central American, and Isthmian highlands. Two asterisks (**) indicate the geographic distribution of *Trachycephalus venulosus*, which extends from central eastern Argentina to Southern Mexico.

mybp, during the existence of the so-called post-Cretaceous Arc landbridge (Iturralde-Vinent and McPhee, 1999). While this seems like a logical deduction, we find it to be unsupported by the available data pertaining to hylids. We only know (or better, assume) that hylids were present in North America 15 mybp and possibly in Europe 17 mybp. Accordingly, we are still uncomfortable in assigning 75 mybp as the minimum age of Hylini. Instead, this age should be the result of either a fossil record (still unknown) or a dating exercise.

FUTURE DIRECTIONS

In order to increase our knowledge of hylid phylogenetics, we see several lines of inquiry stemming from this project whose pursuit would be fruitful. These are:

1. Nonmolecular data set: As stated elsewhere in this paper, an extensive, well-researched nonmolecular data set is a major gap in our analysis. Every effort should be made to complete one and to combine it with the available molecular data.
2. Phylogeny of Pelodryadinae: By far the greatest deficiency in our knowledge of hylid relationships that still need to be solved is the relationships among Pelodryadinae. The combination of a densely sampled data set of Pelodryadinae with ours will be helpful for understanding Phyllomedusinae relationships.
3. Inclusion of unrepresented groups and denser taxon sampling of poorly represented groups of Hylinae: No exemplars of the *Bokermannohyla claresignata* and the *Dendropsophus garagoensis* groups were available for this analysis. Furthermore, several groups have been poorly represented; such is the case for *Ecnomiohyla*, *Exerodonta*, *Isthmohyla*, *Megastomatohyla*, *Plectrohyla*, and *Tlalocohyla*. A major task in the future will be to rigorously test all the tentative associations of species not included in the analysis with the various clades that we identified.
4. Relationships within smaller taxonomic units: Our results provide a general framework for the study of relationships within almost any of the genera or species groups of the species-rich genera of Hylidae. In particular, we think that the study of relationships through an increased taxon sampling within *Bokermannohyla*, *Dendropsophus*, *Ecnomiohyla*, *Hyloscirtus*, *Hypsiboas*, and *Plectrohyla* would result in important changes in our understanding of those groups.
5. Resolution of the taxa herein considered insertae sedis: A careful study of available material of the taxa that we could not associate with any of clades that we identify and, if available, the inclusion of molecular data derived from them would hopefully permit their inclusion in the phylogenetic context of hylids.

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APPENDIX 1

List of Valid Recent Species of Hylinae and Phyllomedusinae, Including, if Applicable, the Currently Assigned Species group and Its Status with the New Taxonomy

Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Acris crepitans Baird, 1854	—	*Acris crepitans*	—
Acris gryllus (LeConte, 1825)	—	*Acris gryllus*	—
Anotheca spinosa (Steindachner, 1864)	—	*Anotheca spinosa*	—
Aparasphenodon bokermanni Pombal, 1993	—	*Aparasphenodon bokermanni*	—
Aparasphenodon brunoi Miranda-Ribeiro, 1920	—	*Aparasphenodon brunoi*	—
Aparasphenodon venezolanus (Mertens, 1950)	—	*Aparasphenodon venezolanus*	—
Aplastodiscus cochranae (Mertens, 1952)	—	*Aplastodiscus cochranae*	*Aplastodiscus perviridis* group
Aplastodiscus perviridis A. Lutz, 1950	—	*Aplastodiscus perviridis*	*Aplastodiscus perviridis* group
Argenteohyla siemersi (Mertens, 1937)	—	*Argenteohyla siemersi*	—
Corythomantis greeningi Boulenger, 1896	—	*Corythomantis greeningi*	—
Duellmanohyla chamulae (Duellman, 1961)	—	*Duellmanohyla chamulae*	—
Duellmanohyla ignicolor (Duellman, 1961)	—	*Duellmanohyla ignicolor*	—
Duellmanohyla lythrodes (Savage, 1968)	—	*Duellmanohyla lythrodes*	—
Duellmanohyla rufioculis (Taylor, 1952)	—	*Duellmanohyla rufioculis*	—
Duellmanohyla salvavida (McCranie and Wilson, 1986)	—	*Duellmanohyla salvavida*	—
Duellmanohyla schmidtorum (Stuart, 1954)	—	*Duellmanohyla schmidtorum*	—
Duellmanohyla soralia (Wilson and McCranie, 1985)	—	*Duellmanohyla soralia*	—
Duellmanohyla uranochroa (Cope, 1875)	—	*Duellmanohyla uranochroa*	—
‘‘*Hyalinobatrachium estevesi*’’ (Rivero, 1968)	—	*Hyloscirtus estevesi*	*Hyloscirtus bogotensis* group
Hyla abdivita Campbell and Duellman, 2000	*H. miotympanum* group	*Exerodonta abdivita*	Unassigned
Hyla acreana Bokermann, 1964	*H. marmorata* group	*Dendropsophus acreanus*	*Dendropsophus marmoratus* group
Hyla ahenea Napoli and Caramaschi, 2004	*H. circumdata* group	*Bokermannohyla ahenea*	*Bokermannohyla circumdata* group
Hyla albofrenata A. Lutz, 1924	*H. albofrenata* complex, *H. albomarginata* group	*Aplastodiscus albofrenatus*	*Aplastodiscus albofrenatus* group
Hyla alboguttata Boulenger, 1882	Unassigned	*Incerta sedis*	—
Hyla albomarginata Spix, 1824	*H. albomarginata* complex, *H. albomarginata* group	*Hypsiboas albomarginatus*	*Hypsiboas faber* group
Hyla albonigra Nieden, 1923	*H. pulchella* group	*Hypsiboas alboniger*	*Hypsiboas pulchellus* group
Hyla albopunctata Spix, 1824	*H. albopunctata* group	*Hypsiboas albopunctatus*	*Hypsiboas albopunctatus* group
Hyla albopunctulata Boulenger, 1882	Unassigned	*Hyloscirtus albopunctulatus*	*Hyloscirtus bogotensis* group
Hyla albosignata A. Lutz and B. Lutz, 1938	*H. albosignata* complex, *H. albomarginata* group	*Aplastodiscus albosignatus*	*Aplastodiscus albosignatus* group
Hyla albovittata Lichtenstein and Martens, 1856	Unassigned	*Hypsiboas pulchellus*	*Hypsiboas pulchellus* group
Hyla alemani Rivero, 1964	*H. granosa* group	*Hypsiboas alemani*	*Hypsiboas punctatus* group

APPENDIX 1
(*Continued*)

Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Hyla allenorum Duellman and Trueb, 1989	*H. parviceps* group	*Dendropsophus allenorum*	*Dendropsophus parviceps* group
Hyla altipotens Duellman, 1968	*H. taeniopus* group	*Charadrahyla altipotens*	—
Hyla alvarengai Bokermann, 1956	Unassigned	*Bokermannohyla alvarengai*	*Bokermannohyla pseudopseudis* group
Hyla alytolylax Duellman, 1972	*H. bogotensis* group	*Hyloscirtus alytolylax*	*Hyloscirtus bogotensis* group
Hyla ameibothalame Canseco-Mŕquez, Mendelson, and Gutiérrez-Mayén, 2002	*H. bistincta* group	*Plectrohyla ameibothalame*	*Plectrohyla bistincta* group
Hyla americana (Duméril and Bibron, 1841)	Unassigned	*Nomen dubium*	—
Hyla amicorum Mijares-Urrutia, 1998	Unassigned	*Dendropsophus amicorum*	Unassigned
Hyla anataliasiasi Bokermann, 1972	*H. rubicundula* group	*Dendropsophus anataliasiasi*	*Dendropsophus microcephalus* group, *D. rubicundulus* clade
Hyla anceps A. Lutz, 1929	Unassigned	*Dendropsophus anceps*	*Dendropsophus leucophyllatus* group
Hyla andersonii Baird, 1854	*H. versicolor* group	*Hyla andersonii*	*Hyla eximia* group
Hyla andina Müller, 1924	*H. pulchella* group	*Hypsiboas andinus*	*Hypsiboas pulchellus* group
Hyla angustilineata Taylor, 1952	*H. pseudopuma* group	*Isthmohyla angustilineata*	*Isthmohyla pseudopuma* group
Hyla annectans (Jerdon, 1870)	*H. arborea* group	*Hyla annectans*	*Hyla arborea* group
Hyla aperomea Duellman, 1982	*H. minima* group	*Dendropsophus aperomeus*	*Dendropsophus minimus* group
Hyla araguaya Napoli and Caramaschi, 1998	*H. rubicundula* group	*Dendropsophus araguaya*	*Dendropsophus microcephalus* group, *D. rubicundulus* clade
Hyla arboricola Taylor, 1941	*H. eximia* group	*Hyla arboricola*	*H. eximia* group
Hyla arborea (Linnaeus, 1758)	*H. arborea* group	*Hyla arborea*	*Hyla arborea* group
Hyla arborescandens Taylor, 1939 ''1938''	*H. miotympanum* group	*Plectrohyla arborescandens*	*Plectrohyla bistincta* group
Hyla arenicolor Cope, 1866	*H. eximia* group	*Hyla arenicolor*	*Hyla eximia* group
Hyla arildae Cruz and Peixoto, 1987 ''1985''	*H. albofrenata* complex, *H. albomarginata* group	*Aplastodiscus arildae*	*Aplastodiscus albofrenatus* group
Hyla armata Boulenger, 1902	*H. armata* group	*Hyloscirtus armatus*	*Hyloscirtus armatus* group
Hyla aromatica Ayarzagaena and Señaris, 1994 ''1993''	*H. aromatica* group	*Myersiohyla aromatica*	—
Hyla astartea Bokermann, 1967	*H. circumdata* group	*Bokermannohyla astartea*	*Bokermannohyla circumdata* group
Hyla atlantica Caramaschi and Velosa, 1996	*H. punctata* group	*Hypsiboas atlanticus*	*Hypsiboas punctatus* group
Hyla auraria Peters, 1873	Unassigned	*Nomen dubium*	—
Hyla avivoca Viosca, 1928	*H. versicolor* group	*Hyla avivoca*	*Hyla versicolor* group
Hyla balzani Boulenger, 1898	*H. pulchella* group	*Hypsiboas balzani*	*Hypsiboas pulchellus* group
Hyla battersbyi Rivero, 1961	Unassigned	*Dendropsophus battersbyi*	*Dendropsophus microcephalus* group
Hyla beckeri Caramaschi and Cruz, 2004	*H. pulchella* group, *H. polytaenia* clade	*Hypsiboas beckeri*	*Hypsiboas pulchellus* group, *H. polytaenius* clade
Hyla benitezi Rivero, 1961	Unassigned	*Hypsiboas benitezi*	*Hypsiboas benitezi* group

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(*Continued*)

Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Hyla berthalutzae Bokermann, 1962	*Hyla decipiens* group	*Dendropsophus berthalutzae*	*Dendropsophus microcephalus* group, *D. decipiens* clade
Hyla bifurca Andersson, 1945	*H. leucophyllata* group	*Dendropsophus bifurcus*	*Dendropsophus leucophyllatus* group
Hyla bipunctata Spix, 1824	*H. microcephala* group	*Dendropsophus bipunctatus*	*Dendropsophus microcephalus* group
Hyla bischoffi Boulenger, 1887	*H. pulchella* group	*Hypsiboas bischoffi*	*Hypsiboas pulchellus* group
Hyla bistincta Cope, 1878 ‘‘1877’’	*H. bistincta* group	*Plectrohyla bistincta*	*Plectrohyla bistincta* group
Hyla bivocata Duellman and Hoyt, 1961	*H. miotympanum* group	*Exerodonta bivocata*	Unassigned
Hyla boans (Linnaeus, 1758)	*H. boans* group	*Hypsiboas boans*	*Hypsiboas semilineatus* group
Hyla bocourti Mocquard, 1899	*H. eximia* group	*Hyla bocourti*	*Hyla eximia* group
Hyla bogerti Cochran and Goin, 1970	*H. columbiana* group	*Dendropsophus bogerti*	*Dendropsophus columbianus* group
Hyla bogotensis (Peters, 1882)	*H. bogotensis* group	*Hyloscirtus bogotensis*	*Hyloscirtus bogotensis* group
Hyla bokermanni Goin, 1960	*H. parviceps* group	*Dendropsophus bokermanni*	*Dendropsophus parviceps* group
Hyla branneri Cochran, 1948	*H. microcephala* group	*Dendropsophus branneri*	*Dendropsophus microcephalus* group
Hyla brevifrons Duellman and Crump, 1974	*H. parviceps* group	*Dendropsophus brevifrons*	*Dendropsophus parviceps* group
Hyla bromeliacia Schmidt, 1933	*H. bromeliacia* group	*Bromeliohyla bromeliacia*	—
Hyla buriti Caramaschi and Cruz, 1999	*H. pulchella* group, *H. polytaenia* clade	*Hypsiboas buriti*	*Hypsiboas pulchellus* group, *H. polytaenius* clade
Hyla cachimbo Napoli and Caramaschi, 1999	*H. rubicundula* group	*Dendropsophus cachimbo*	*Dendropsophus microcephalus* group, *D. rubicundulus* clade
Hyla caingua Carrizo, 1991 ‘‘1990’’	*H. pulchella* group	*Hypsiboas caingua*	*Hypsiboas pulchellus* group
Hyla calcarata Troschel, 1848	*H. geographica* group	*Hypsiboas calcaratus*	*Hypsiboas albopunctatus* group
Hyla callipeza Duellman, 1989	*H. bogotensis* group	*Hyloscirtus callipeza*	*Hyloscirtus bogotensis* group
Hyla callipleura Boulenger, 1902	*H. pulchella* group	*Hypsiboas callipleura*	*Hypsiboas pulchellus* group
Hyla callipygia Cruz and Peixoto, 1985 1984	*H. albosignata* complex, *H. albomarginata* group	*Aplastodiscus callipygius*	*Aplastodiscus albosignatus* group
Hyla calthula Ustach, Mendelson, McDiarmid, and Campbell, 2000	*H. bistincta* group	*Plectrohyla calthula*	*Plectrohyla bistincta* group
Hyla calvicollina Toal, 1994	*H. bistincta* group	*Plectrohyla calvicollina*	*Plectrohyla bistincta* group
Hyla calypsa Lips, 1996	*H. pictipes* group	*Isthmohyla calypsa*	*Isthmohyla pictipes* group
Hyla caramaschii Napoli, 2005	*H. circumdata* group	*Bokermannohyla caramaschii*	*Bokermannohyla circumdata* group
Hyla carnifex Duellman, 1969	*H. columbiana* group	*Dendropsophus carnifex*	*Dendropsophus columbianus* group
Hyla carvalhoi Peixoto, 1981	*H. circumdata* group	*Bokermannohyla carvalhoi*	*Bokermannohyla circumdata* group
Hyla catracha Porras and Wilson, 1987	*H. miotympanum* group	*Exerodonta catracha*	Unassigned
Hyla caucana Ardila-Robayo, Ruiz-Carranza, and Roa-Trujillo, 1993	*H. larinopygion* group	*Hyloscirtus caucanus*	*Hyloscirtus larinopygion* group

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Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Hyla cavicola Cruz and Peixoto, 1985 ‘‘1984’’	*H. albosignata* complex, *H. albomarginata* group	*Aplastodiscus cavicola*	*Aplastodiscus albosignatus* group
Hyla celata Toal and Mendelson, 1995	*H. bistincta* group	*Plectrohyla celata*	*Plectrohyla bistincta* group
Hyla cembra Caldwell, 1974	*H. bistincta* group	*Plectrohyla cembra*	*Plectrohyla bistincta* group
Hyla cerradensis Napoli and Caramaschi, 1998	*H. rubicundula* group	*Dendropsophus cerradensis*	*Dendropsophus microcephalus* group, *D. rubicundulus* clade
Hyla chaneque Duellman, 1961	*H. taeniopus* group	*Charadrahyla chaneque*	—
Hyla charadricola Duellman, 1964	*H. bistincta* group	*Plectrohyla charadricola*	*Plectrohyla bistincta* group
Hyla charazani Vellard, 1970	*H. armata* group	*Hyloscirtus charazani*	*Hyloscirtus armatus* group
Hyla chimalapa Mendelson and Campbell, 1994	*H. sumichrasti* group	*Exerodonta chimalapa*	*Exerodonta sumichrasti* group
Hyla chinensis Günther, 1858	*H. arborea* group	*Hyla chinensis*	*Hyla arborea* group
Hyla chlorostea Reynolds and Foster, 1992	Unassigned	*Incerta sedis*	—
Hyla chryses Adler, 1965	*H. bistincta* group	*Plectrohyla chryses*	*Plectrohyla bistincta* group
Hyla chrysoscelis Cope, 1880	*H. versicolor* group	*Hyla chrysoscelis*	*Hyla versicolor* group
Hyla cinerea (Schneider, 1799)	*H. cinerea* group	*Hyla cinerea*	*Hyla cinerea* group
Hyla cipoensis B. Lutz, 1968	*H. pulchella* group, *H. polytaenia* clade	*Hypsiboas cipoensis*	*Hypsiboas pulchellus* group, *H. polytaenius* clade
Hyla circumdata (Cope, 1871)	*H. circumdata* group	*Bokermannohyla circumdata*	*Bokermannohyla circumdata* group
Hyla claresignata A. Lutz and B. Lutz, 1939	*H. claresignata* group	*Bokermannohyla claresignata*	*Bokermannohyla claresignata* group
Hyla clepsydra A. Lutz, 1925	*H. claresignata* group	*Bokermannohyla clepsydra*	*Bokermannohyla claresignata* group
Hyla columbiana Boettger, 1892	*H. columbiana* group	*Dendropsophus columbianus*	*Dendropsophus columbianus* group
Hyla colymba Dunn, 1931	*H. bogotensis* group	*Hyloscirtus colymba*	*Hyloscirtus bogotensis* group
Hyla cordobae Barrio, 1965	*H. pulchella* group	*Hypsiboas cordobae*	*Hypsiboas pulchellus* group
Hyla crassa (Brocchi, 1877)	*H. bistincta* group	*Plectrohyla crassa*	*Plectrohyla bistincta* group
Hyla crepitans Wied-Neuwied, 1824	*H. boans* group	*Hypsiboas crepitans*	*Hypsiboas faber* group
Hyla cruzi Pombal and Bastos, 1998	*H. microcephala* group	*Dendropsophus cruzi*	*Dendropsophus microcephalus* group
Hyla cyanomma Caldwell, 1974	*H. bistincta* group	*Plectrohyla cyanomma*	*Plectrohyla bistincta* group
Hyla cyclada Campbell and Duellman, 2000	*H. miotympanum* group	*Plectrohyla cyclada*	*Plectrohyla bistincta* group
Hyla cymbalum Bokermann, 1963	*H. pulchella* group	*Hypsiboas cymbalum*	*Hypsiboas pulchellus* group
Hyla debilis Taylor, 1952	*H. pictipes* group	*Isthmohyla debilis*	*Isthmohyla pictipes* group
Hyla decipiens A. Lutz, 1925	*H. decipiens* group	*Dendropsophus decipiens*	*Dendropsophus microcephalus* group, *D. decipiens* clade
Hyla delarivai Kḧler and Lẗters, 2001	*H. minuta* group	*Dendropsophus delarivai*	*Dendropsophus minutus* group
Hyla dendrophasma Campbell, Smith, and Acevedo, 2000	*H. miliaria* group	*Ptychohyla dendrophasma*	—
Hyla dendroscarta Taylor, 1940	*H. bromeliacia* group	*Bromeliohyla dendroscarta*	—

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Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Hyla dentei Bokermann, 1967	*H. geographica* group	*Hypsiboas dentei*	*Hypsiboas albopunctatus* group
Hyla denticulenta Duellman, 1972	*H. bogotensis* group	*Hyloscirtus denticulentus*	*Hyloscirtus bogotensis* group
Hyla dolloi Werner, 1903	Unassigned	*Scinax dolloi*	*Scinax ruber* clade
Hyla dutrai Gomes and Peixoto, 1996	*H. marmorata* group	*Dendropsophus dutrai*	*Dendropsophus marmoratus* group
Hyla ebraccata Cope, 1874	*H. leucophyllata* group	*Dendropsophus ebraccatus*	*Dendropsophus leucophyllatus* group
Hyla echinata Duellman, 1962	*H. tuberculosa* group	*Ecnomiohyla echinata*	—
Hyla ehrhardti Müller, 1924	*H. albofrenata* complex, *H. albomarginata* group	*Aplastodiscus ehrhardti*	*Aplastodiscus albofrenatus* group
Hyla elegans Wied-Neuwied, 1824	*H. leucophyllata* group	*Dendropsophus elegans*	*Dendropsophus leucophyllatus* group
Hyla elianeae Napoli and Caramaschi, 2000	*H. rubicundula* group	*Dendropsophus elianeae*	*Dendropsophus microcephalus* group, *D. rubicundulus* clade
Hyla ericae Caramaschi and Cruz, 2000	*H. pulchella* group	*Hypsiboas ericae*	*Hypsiboas pulchellus* group
Hyla euphorbiacea Günther, 1858	*H. eximia* group	*Hyla euphorbiacea*	*Hyla eximia* group
Hyla exastis Caramaschi and Rodrigues, 2003	*H. boans* group	*Hypsiboas exastis*	*Hypsiboas faber* group
Hyla eximia Baird, 1854	*H. eximia* group	*Hyla eximia*	*Hyla eximia* group
Hyla faber Wied-Neuwied, 1821	*H. boans* group	*Hypsiboas faber*	*Hypsiboas faber* group
Hyla fasciata Günther, 1858	*H. geographica* group	*Hypsiboas fasciatus*	*Hypsiboas albopunctatus* group
Hyla feioi Napoli and Caramaschi, 2004	*H. circumdata* group	*Bokermannohyla feioi*	*Bokermannohyla circumdata* group
Hyla femoralis Bosc, 1800	*H. cinerea* group	*Hyla femoralis*	Unassigned
Hyla fimbrimembra Taylor, 1948	*H. miliaria* group	*Ecnomiohyla fimbrimembra*	—
Hyla fluminea Cruz and Peixoto, 1985 ‘‘1984’’	*H. albofrenata* complex, *H. albomarginata* group	*Aplastodiscus flumineus*	*Aplastodiscus albofrenatus* group
Hyla freicanecae Carnaval and Peixoto, 2004	*H. pulchella* group	*Hypsiboas freicanecae*	*Hypsiboas pulchellus* group
Hyla fuentei C. Goin and O. Goin, 1968	Unassigned	*Hypsiboas fuentei*	Unassigned
Hyla fusca Laurenti, 1768	Unassigned	*Nomen dubium*	—
Hyla garagoensis Kaplan, 1991	*H. garagoensis* group	*Dendropsophus garagoensis*	*Dendropsophus garagoensis* group
Hyla gaucheri Lescure and Marty, 2000	*H. parviceps* group	*Dendropsophus gaucheri*	*Dendropsophus parviceps* group
Hyla geographica Spix, 1824	*H. geographica* group	*Hypsiboas geographicus*	*Hypsiboas semilineatus* group
Hyla giesleri Mertens, 1950	*H. parviceps* group	*Dendropsophus giesleri*	*Dendropsophus parviceps* group
Hyla godmani Günther, 1901	*H. godmani* group	*Tlalocohyla godmani*	—
Hyla goiana B. Lutz, 1968	*H. pulchella* group, *H. polytaenia* clade	*Hypsiboas goianus*	*Hypsiboas pulchellus* group
Hyla gouveai Peixoto and Cruz, 1992	*H. circumdata* group	*Bokermannohyla gouveai*	*Bokermannohyla circumdata* group
Hyla graceae Myers and Duellman, 1982	*H. pseudopuma* group	*Isthmohyla graceae*	*Isthmohyla pseudopuma* group
Hyla grandisonae Goin, 1966	*H. microcephala* group	*Dendropsophus grandisonae*	*Dendropsophus microcephalus* group
Hyla granosa Boulenger, 1882	*H. granosa* group	*Hypsiboas granosus*	*Hypsiboas punctatus* group

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Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Hyla gratiosa LeConte, 1857 ‘‘1856’’	*H. cinerea* group	*Hyla gratiosa*	*Hyla cinerea* group
Hyla gryllata Duellman, 1973	*H. microcephala* group	*Dendropsophus gryllatus*	*Dendropsophus microcephalus* group
Hyla guentheri Boulenger, 1886	*H. pulchella* group	*Hypsiboas guentheri*	*Hypsiboas pulchellus* group
Hyla haddadi Bastos and Pombal, 1996	*H. decipiens* group	*Dendropsophus haddadi*	*Dendropsophus microcephalus* group, *D. decipiens* clade
Hyla hallowellii Thompson, 1912	*H. arborea* group	*Hyla hallowellii*	*Hyla arborea* group
Hyla haraldschultzi Bokermann, 1962	Unassigned	*Dendropsophus haraldschultzi*	Unassigned
Hyla hazelae Taylor, 1940	*H. miotympanum* group	*Plectrohyla hazelae*	*Plectrohyla bistincta* group
Hyla heilprini Noble, 1923	Unassigned	*Hypsiboas heilprini*	*Hypsiboas albopunctatus* group
Hyla helenae Ruthven, 1919	Unassigned	*Incerta sedis*	—
Hyla hobbsi Cochran and Goin, 1970	*H. punctata* group	*Hypsiboas hobbsi*	*Hypsiboas punctatus* group
Hyla hutchinsi Pyburn and Hall, 1984	*H. geographica* group	*Hypsiboas hutchinsi*	*Hypsiboas benitezi* group
Hyla hylax Heyer, 1985	*H. circumdata* group	*Bokermannohyla hylax*	*Bokermannohyla circumdata* group
Hyla hypselops (Cope, 1871)	Unassigned	*Nomen dubium*	—
Hyla ibirapitanga Cruz, Pimenta and Silvano, 2003	*H. albosignata* complex, *H. albomarginata* group	*Aplastodiscus ibirapitanga*	*Aplastodiscus albosignatus* group
Hyla ibitiguara Cardoso, 1983	*H. pseudopseudis* group	*Bokermannohyla ibitiguara*	*Bokermannohyla pseudopseudis* group
Hyla ibitipoca Caramaschi and Feio, 1990	*H. circumdata* group	*Bokermannohyla ibitipoca*	*Bokermannohyla circumdata* group
Hyla imitator (Barbour and Dunn, 1921)	Unassigned	*Incerta sedis*	—
Hyla immaculata Boettger, 1888	*H. arborea* group	*Hyla immaculata*	*Hyla arborea* group
Hyla inframaculata Boulenger, 1882	Unassigned	*Incerta sedis*	—
Hyla infucata Duellman, 1968	*H. pseudopuma* group	*Isthmohyla infucata*	*Isthmohyla pseudopuma* group
Hyla inparquesi Ayarzagüena and Señaris, 1994 ‘‘1993’’	*H. aromatica* group	*Myersiohyla inparquesi*	—
Hyla insolita McCranie, Wilson, and Williams, 1993	*H. pictipes* group	*Isthmohyla insolita*	*Isthmohyla pictipes* group
Hyla intermedia Boulenger, 1882	*H. arborea* group	*Hyla intermedia*	*Hyla arborea* group
Hyla izecksohni Jim and Caramaschi, 1979	*H. circumdata* group	*Bokermannohyla izecksohni*	*Bokermannohyla circumdata* group
Hyla jahni Rivero, 1961	*H. bogotensis* group	*Hyloscirtus jahni*	*Hyloscirtus bogotensis* group
Hyla japonica Günther, 1859 ‘‘1858’’	*H. arborea* group	*Hyla japonica*	*Hyla eximia* group
Hyla jimi Napoli and Caramaschi, 1999	*H. rubicundula* group	*Dendropsophus jimi*	*Dendropsophus microcephalus* group, *D. rubicundulus* clade
Hyla joannae Köhler and Lötters, 2001	*H. microcephala* group	*Dendropsophus joannae*	*Dendropsophus microcephalus* group
Hyla joaquini B. Lutz, 1968	*H. pulchella* group	*Hypsiboas joaquini*	*Hypsiboas pulchellus* group
Hyla juanitae Snyder, 1972	*H. miotympanum* group	*Exerodonta juanitae*	—
Hyla kanaima Goin and Woodley, 1969	*H. geographica* group	*Myersiohyla kanaima*	—

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Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Hyla karenanneae Pyburn, 1993	Unassigned	*Scinax karenannae*	*Scinax ruber* clade
Hyla koechlini Duellman and Trueb, 1989	*H. parviceps* group	*Dendropsophus koechlini*	*Dendropsophus parviceps* group
Hyla labedactyla Mendelson and Toal, 1996	*H. bistincta* group	*Plectrohyla labedactyla*	*Plectrohyla bistincta* group
Hyla labialis Peters, 1863	*H. labialis* group	*Dendropsophus labialis*	*Dendropsophus labialis* group
Hyla lancasteri Barbour, 1928	*H. pictipes* group	*Isthmohyla lancasteri*	*Isthmohyla pictipes* group
Hyla lanciformis (Cope, 1871)	*H. albopunctata* group	*Hypsiboas lanciformis*	*Hypsiboas albopunctatus* group
Hyla langei Bokermann, 1965	*H. martinsi* group	*Bokermannohyla langei*	*Bokermannohyla martinsi* group
Hyla larinopygion Duellman, 1973	*H. larinopygion* group	*Hyloscirtus larinopygion*	*Hyloscirtus larinopygion* group
Hyla lascinia Rivero, 1969	*H. bogotensis* group	*Hyloscirtus lascinius*	*Hyloscirtus bogotensis* group
Hyla latistriata Caramaschi and Cruz, 2004	*H. pulchella* group, *H. polytaenia* clade	*Hypsiboas latistriatus*	*Hypsiboas pulchellus* group, *H. polytaenius* clade
Hyla leali Bokermann, 1964	*H. minima* group	*Dendropsophus leali*	*Dendropsophus minimus* group
Hyla lemai Rivero, 1971	Unassigned	*Hypsiboas lemai*	*Hypsiboas benitezi* group
Hyla leptolineata P. Braun and C. Braun, 1977	*H. pulchella* group, *H. polytaenia* clade	*Hypsiboas leptolineatus*	*Hypsiboas pulchellus* group, *H. polytaenius* clade
Hyla leucocheila Caramaschi and Niemeyer, 2003	*H. albopunctata* group	*Hypsiboas leucocheilus*	*Hypsiboas albopunctatus* group
Hyla leucophyllata (Beireis, 1783)	*H. leucophyllata* group	*Dendropsophus leucophyllatus*	*Dendropsophus leucophyllatus* group
Hyla leucopygia Cruz and Peixoto, 1985 1984.	*H. albosignata* complex, *H. albomarginata* group	*Aplastodiscus leucopygius*	*Aplastodiscus albosignatus* group
Hyla limai Bokermann, 1962	Unassigned	*Dendropsophus limai*	*Dendropsophus minutus* group
Hyla lindae Duellman and Altig, 1978	*H. larinopygion* group	*Hyloscirtus lindae*	*Hyloscirtus larinopygion* group
Hyla loquax Gaige and Stuart, 1934	*H. godmani* group	*Tlalocohyla loquax*	—
Hyla loveridgei Rivero, 1961	Unassigned	*Myersiohyla loveridgei*	—
Hyla lucianae Napoli and Pimenta, 2003	*H. circumdata* group	*Bokermannohyla lucianae*	*Bokermannohyla circumdata* group
Hyla luctuosa Pombal and Haddad, 1993	*H. circumdata* group	*Bokermannohyla luctuosa*	*Bokermannohyla circumdata* group
Hyla lundii Burmeister, 1856	*H. boans* group	*Hypsiboas lundii*	*Hypsiboas faber* group
Hyla luteoocellata Roux, 1927	*H. parviceps* group	*Dendropsophus luteoocellatus*	*Dendropsophus parviceps* group
Hyla lynchi Ruiz-Carranza and Ardila-Robayo, 1991	*H. bogotensis* group	*Hyloscirtus lynchi*	*Hyloscirtus bogotensis* group
Hyla marginata Boulenger, 1887	*H. pulchella* group	*Hypsiboas marginatus*	*Hypsiboas pulchellus* group
Hyla marianitae Carrizo, 1992	*H. pulchella* group	*Hypsiboas marianitae*	*Hypsiboas pulchellus* group
Hyla marmorata (Laurenti, 1768)	*H. marmorata* group	*Dendropsophus marmoratus*	*Dendropsophus marmoratus* group
Hyla martinsi Bokermann, 1964	*H. martinsi* group	*Bokermannohyla martinsi*	*Bokermannohyla martinsi* group
Hyla mathiassoni Cochran and Goin, 1970	*H. microcephala* group	*Dendropsophus mathiassoni*	*Dendropsophus microcephalus* group
Hyla melanargyrea Cope, 1887	*H. marmorata* group	*Dendropsophus melanargyreus*	*Dendropsophus marmoratus* group
Hyla melanomma Taylor, 1940	*H. miotympanum* group	*Exerodonta melanomma*	Unassigned

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Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Hyla melanopleura Boulenger, 1912	*H. pulchella* group	*Hypsiboas melanopleurus*	*Hypsiboas pulchellus* group
Hyla melanorabdota (Schneider, 1799)	Unassigned	*Nomen dubium*	—
Hyla meridensis Rivero, 1961	*H. labialis* group	*Dendropsophus meridensis*	*Dendropsophus labialis* group
Hyla meridiana B. Lutz, 1954	*H. microcephala* group	*Dendropsophus meridianus*	*Dendropsophus microcephalus* group
Hyla meridionalis Boettger, 1874	*H. arborea* group	*Hyla meridionalis*	*Hyla arborea* group
Hyla microcephala Cope, 1886	*H. microcephala* group	*Dendropsophus microcephalus*	*Dendropsophus microcephalus* group
Hyla microderma Pyburn, 1977	*H. geographica* group	*Hypsiboas microderma*	*Hypsiboas benitezi* group
Hyla microps Peters, 1872	*H. parviceps* group	*Dendropsophus microps*	*Dendropsophus parviceps* group
Hyla miliaria (Cope, 1886)	*H. tuberculosa* group	*Ecnomiohyla miliaria*	—
Hyla minera Wilson, McCranie, and Williams, 1985	*H. tuberculosa* group	*Ecnomiohyla minera*	—
Hyla minima Ahl, 1933	*H. minima* group	*Dendropsophus minimus*	*Dendropsophus minimus* group
Hyla minuscula Rivero, 1971	*H. microcephala* group	*Dendropsophus minusculus*	*Dendropsophus microcephalus* group
Hyla minuta Peters, 1872	*H. minuta* group	*Dendropsophus minutus*	*Dendropsophus minutus* group
Hyla miotympanum Cope, 1863	*H. miotympanum* group	*Ecnomiohyla miotympanum*	—
Hyla mixe Duellman, 1965	*H. mixomaculata* group	*Megastomatohyla mixe*	—
Hyla mixomaculata Taylor, 1950	*H. mixomaculata* group	*Megastomatohyla mixomaculata*	—
Hyla miyatai Vigle and Goberdhan-Vigle, 1990	*H. minima* group	*Dendropsophus miyatai*	*Dendropsophus minimus* group
Hyla molitor Schmidt, 1857	Unassigned	*Nomen dubium*	—
Hyla multifasciata Günther, 1859 ‘‘1858’’	*H. albopunctata* group	*Hypsiboas multifasciatus*	*Hypsiboas albopunctatus* group
Hyla musica B. Lutz, 1948	*H. albofrenata* complex, *H. albomarginata* group	*Aplastodiscus musicus*	*Aplastodiscus albofrenatus* group
Hyla mykter Adler and Dennis, 1972	*H. bistincta* group	*Plectrohyla mykter*	*Plectrohyla bistincta* group
Hyla nahdereri B. Lutz and Bokermann, 1963	*H. marmorata* group	*Dendropsophus nahdereri*	*Dendropsophus marmoratus* group
Hyla nana Boulenger, 1889	*H. microcephala* group	*Dendropsophus nanus*	*Dendropsophus microcephalus* group
Hyla nanuzae Bokermann and Sazima, 1973	*H. circumdata* group	*Bokermannohyla nanuzae*	*Bokermannohyla circumdata* group
Hyla nephila Mendelson and Campbell, 1999	*H. taeniopus* group	*Charadrahyla nephila*	—
Hyla novaisi Bokermann, 1968	*H. marmorata* group	*Dendropsophus novaisi*	*Dendropsophus marmoratus* group
Hyla nubicola Duellman, 1964 ‘‘1963’’	*H. mixomaculata* group	*Megastomatohyla nubicola*	—
Hyla oliveirai Bokermann, 1963	*H. decipiens* group	*Dendropsophus oliveirai*	*Dendropsophus microcephalus* group, *D. decipiens* clade
Hyla ornatissima Noble, 1923	*H. granosa* group	*Hypsiboas ornatissimus*	*Hypsiboas punctatus* group
Hyla pacha Duellman and Hillis, 1990	*H. larinopygion* group	*Hyloscirtus pacha*	*Hyloscirtus larinopygion* group
Hyla pachyderma Taylor, 1942	*H. bistincta* group	*Plectrohyla pachyderma*	*Plectrohyla bistincta* group
Hyla padreluna Kaplan and Ruiz, 1997	*H. garagoensis* group	*Dendropsophus padreluna*	*Dendropsophus garagoensis* group

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Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Hyla palaestes Duellman, De La Riva, and Wild, 1997	*H. pulchella* group	*Hypsiboas palaestes*	*Hypsiboas pulchellus* group
Hyla palliata Cope, 1863	Unassigned	*Nomen dubium*	—
Hyla palmeri Boulenger, 1908	*H. bogotensis* group	*Hyloscirtus palmeri*	*Hyloscirtus bogotensis* group
Hyla pantosticta Duellman and Berger, 1982	*H. larinopygion* group	*Hyloscirtus pantostictus*	*Hyloscirtus larinopygion* group
Hyla pardalis Spix, 1824	*H. boans* group	*Hypsiboas pardalis*	*Hypsiboas faber* group
Hyla parviceps Boulenger, 1882	*H. parviceps* group	*Dendropsophus parviceps*	*Dendropsophus parviceps* group
Hyla pauiniensis Heyer, 1977	*H. microcephala* group	*Dendropsophus pauiniensis*	*Dendropsophus parviceps* group
Hyla pelidna Duellman, 1989	*H. labialis* group	*Dendropsophus pelidna*	*Dendropsophus labialis* group
Hyla pellita Duellman, 1968	*H. mixomaculata* group	*Megastomatohyla pellita*	—
Hyla pellucens Werner, 1901	*H. albomarginata* complex, *H. albomarginata* group	*Hypsiboas pellucens*	*Hypsiboas pellucens* group
Hyla pentheter Adler, 1965	*H. bistincta* group	*Plectrohyla pentheter*	*Plectrohyla bistincta* group
Hyla perkinsi Campbell and Brodie, 1992	*H. miotympanum* group	*Exerodonta perkinsi*	Unassigned
Hyla phaeopleura Caramaschi and Cruz, 2000	*H. pulchella* group, *H. polytaenia* clade	*Hypsiboas phaeopleura*	*Hypsiboas pulchellus* group, *H. polytaenius* clade
Hyla phantasmagoria Dunn, 1943	*H. tuberculosa* group	*Ecnomiohyla phantasmagoria*	—
Hyla phlebodes Stejneger, 1906	*H. microcephala* group	*Dendropsophus phlebodes*	*Dendropsophus microcephalus* group
Hyla phyllognatha Melin, 1941	*H. bogotensis* group	*Hyloscirtus phyllognathus*	*Hyloscirtus bogotensis* group
Hyla picadoi Dunn, 1937	*H. pictipes* group	*Isthmohyla picadoi*	*Isthmohyla pictipes* group
Hyla piceigularis Ruiz-Carranza and Lynch, 1982	*H. bogotensis* group	*Hyloscirtus piceigularis*	*Hyloscirtus bogotensis* group
Hyla picta (Günther, 1901)	*H. godmani* group	*Tlalocohyla picta*	—
Hyla pictipes Cope, 1875 ‘‘1876’’	*H. pictipes* group	*Isthmohyla pictipes*	*Isthmohyla pictipes* group
Hyla picturata Boulenger, 1899	*H. geographica* group	*Hypsiboas picturatus*	*Hypsiboas punctatus* group
Hyla pinima Bokermann and Sazima, 1973	*H. uruguaya* group	*Scinax pinima*	*Scinax ruber* clade, *S. uruguayus* group
Hyla pinorum Taylor, 1937	*H. miotympanum* group	*Exerodonta pinorum*	Unassigned
Hyla platydactyla Boulenger, 1905	*H. bogotensis* group	*Hyloscirtus platydactylus*	*Hyloscirtus bogotensis* group
Hyla plicata Brocchi, 1877	*H. eximia* group	*Hyla plicata*	*Hyla eximia* group
Hyla polytaenia Cope, 1870 ‘‘1869’’	*H. pulchella* group, *H. polytaenia* clade	*Hypsiboas polytaenius*	*Hypsiboas pulchellus* group, *H. polytaenius* clade
Hyla pombali Caramaschi, Pimenta, and Feio, 2004	*H. geographica* group	*Hypsiboas pombali*	*Hypsiboas semilineatus* group
Hyla praestans Duellman and Trueb, 1983	Unassigned	*Dendropsophus praestans*	*Dendropsophus garagoensis* group
Hyla prasina Burmeister, 1856	*H. pulchella* group	*Hypsiboas prasinus*	*Hypsiboas pulchellus* group
Hyla psarolaima Duellman and Hillis, 1990	*H. larinopygion* group	*Hyloscirtus psarolaimus*	*Hyloscirtus larinopygion* group
Hyla psarosema Campbell and Duellman, 2000	*H. bistincta* group	*Plectrohyla psarosema*	*Plectrohyla bistincta* group

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Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Hyla pseudomeridiana Cruz, Caramaschi, and Dias, 2000	*H. microcephala* group	*Dendropsophus pseudomeridianus*	*Dendropsophus microcephalus* group
Hyla pseudopseudis Miranda-Ribeiro, 1937	*H. pseudopseudis* group	*Bokermannohyla pseudopseudis*	*Bokermannohyla pseudopseudis* group
Hyla pseudopuma Günther, 1901	*H. pseudopuma* group	*Isthmohyla pseudopuma*	*Isthmohyla pseudopuma* group
Hyla ptychodactyla Duellman and Hillis, 1990	*H. larinopygion* group	*Hyloscirtus ptychodactylus*	*Hyloscirtus larinopygion* group
Hyla pugnax Schmidt, 1857	*H. boans* group	*Hypsiboas pugnax*	*Hypsiboas faber* group
Hyla pulchella Duméril and Bibron, 1841	*H. pulchella* group	*Hypsiboas pulchellus*	*Hypsiboas pulchellus* group
Hyla pulidoi (Rivero, 1961)	Unassigned	*Hypsiboas pulidoi*	*Hypsiboas benitezi* group
Hyla punctata (Schneider, 1799)	*H. punctata* group	*Hypsiboas punctatus*	*Hypsiboas punctatus* group
Hyla quadrilineata (Schneider, 1799)	Unassigned	*Nomen dubium*	—
Hyla raniceps (Cope, 1862)	*H. albopunctata* group	*Hypsiboas raniceps*	*Hypsiboas albopunctatus* group
Hyla ravida Caramaschi, Napoli, and Bernardes, 2001	*H. circumdata* group	*Bokermannohyla ravida*	*Bokermannohyla circumdata* group
Hyla rhea Napoli and Caramaschi, 1999	*H. rubicundula* group	*Dendropsophus rhea*	*Dendropsophus microcephalus* group, *D. rubicundulus* clade
Hyla rhodopepla Günther, 1858	*H. microcephala* group	*Dendropsophus rhodopeplus*	*Dendropsophus microcephalus* group
Hyla rhythmicus Señaris, and Ayarzagüena. 2002	Unassigned	*Hypsiboas rhythmicus*	*Hypsiboas benitezi* group
Hyla riojana Koslowsky, 1895	*H. pulchella* group	*Hypsiboas riojanus*	*Hypsibioas pulchellus* group
Hyla riveroi Cochran and Goin, 1970	*H. minima* group	*Dendropsophus riveroi*	*Dendropsophus minimus* group
Hyla rivularis Taylor, 1952	*H. pictipes* group	*Isthmohyla rivularis*	*Isthmohyla pictipes* group
Hyla robertmertensi Taylor, 1937	*H. microcephala* group	*Dendropsophus robertmertensi*	*Dendropsophus microcephalus* group
Hyla robertsorum Taylor, 1940	*H. bistincta* group	*Plectrohyla robertsorum*	*Plectrohyla bistincta* group
Hyla roeschmanni DeGrys, 1938	Unassigned	*Nomen dubium*	—
Hyla roraima Duellman and Hoogmoed, 1992	*H. geographica* group	*Hypsiboas roraima*	*Hypsiboas benitezi* group
Hyla rosenbergi Boulenger, 1898	*H. boans* group	*Hypsiboas rosenbergi*	*Hypsiboas faber* group
Hyla rossalleni Goin, 1959	*H. leucophyllata* group	*Dendropsophus rossalleni*	*Dendropsophus leucophyllatus* group
Hyla rubicundula Reinhardt and Lütken, 1862 ‘‘1861’’	*H. rubicundula* group	*Dendropsophus rubicundulus*	*Dendropsophus microcephalus* group, *D. rubicundulus* clade
Hyla rubracyla Cochran and Goin, 1970	*H. albomarginata* complex, *H. albomarginata* group	*Hypsiboas rubracylus*	*Hypsiboas pellucens* group
Hyla rufitela Fouquette, 1961	*H. albomarginata* complex, *H. albomarginata* group	*Hypsiboas rufitelus*	*Hypsiboas pellucens* group
Hyla ruschii Weygoldt and Peixoto, 1987	*H. parviceps* group	*Dendropsophus ruschii*	*Dendropsophus parviceps* group
Hyla sabrina Caldwell, 1974	*H. bistincta* group	*Plectrohyla sabrina*	*Plectrohyla bistincta* group
Hyla salvaje Wilson, McCranie, and Williams, 1985	*H. tuberculosa* group	*Ecnomiohyla salvaje*	—

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Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Hyla sanborni Schmidt, 1944	*H. microcephala* group	*Dendropsophus sanborni*	*Dendropsophus microcephalus* group
Hyla sanchiangensis Pope, 1929	*H. arborea* group	*Hyla sanchiangensis*	*Hyla arborea* group
Hyla sarampiona Ruiz-Carranza and Lynch, 1982	*H. larinopygion* group	*Hyloscirtus sarampiona*	*Hyloscirtus larinopygion* group
Hyla sarayacuensis Shreve, 1935	*H. leucophyllata* group	*Dendropsophus sarayacuensis*	*Dendropsophus leucophyllatus* group
Hyla sarda (De Betta, 1853)	*H. arborea* group	*Hyla sarda*	*Hyla arborea* group
Hyla sartori Smith, 1951	*H. microcephala* group	*Dendropsophus sartori*	*Dendropsophus microcephalus* group
Hyla savignyi Audouin, 1827	*H. arborea* group	*Hyla savignyi*	*Hyla arborea* group
Hyla saxicola Bokermann, 1964	*H. pseudopseudis* group	*Bokermannohyla saxicola*	*Bokermannohyla pseudopseudis* group
Hyla sazimai Cardoso and Andrade, 1983 ‘‘1982’’	*H. circumdata* group	*Bokermannohyla sazimai*	*Bokermannohyla circumdata* group
Hyla schubarti Bokermann, 1963	*H. minima* group	*Dendropsophus schubarti*	*Dendropsophus microcephalus* group
Hyla secedens B. Lutz, 1963	*H. pulchella* group	*Hypsiboas secedens*	*Hypsiboas pulchellus* group
Hyla semiguttata A. Lutz, 1925	*H. pulchella* group	*Hypsiboas semiguttatus*	*Hypsiboas pulchellus* group
Hyla semilineata Spix, 1824	*H. geographica* group	*Hypsiboas semilineatus*	*Hypsiboas semilineatus* group
Hyla senicula Cope, 1868	*H. marmorata* group	*Dendropsophus seniculus*	*Dendropsophus marmoratus* group
Hyla sibilata Cruz, Pimenta, and Silvano, 2003	*H. albosignata* complex, *H. albomarginata* group	*Aplastodiscus sibilatus*	*Aplastodiscus albosignatus* group
Hyla sibleszi Rivero, 1971	*H. granosa* group	*Hypsiboas sibleszi*	*Hypsiboas punctatus* group
Hyla simmonsi Duellman, 1989	*H. bogotensis* group	*Hyloscirtus simmonsi*	*Hyloscirtus bogotensis* group
Hyla simplex Boettger, 1901	*H. arborea* group	*Hyla simplex*	*Hyla arborea* group
Hyla siopela Duellman, 1968	*H. bistincta* group	*Plectrohyla siopela*	*Plectrohyla bistincta* group
Hyla smaragdina Taylor, 1940	*H. sumichrasti* group	*Exerodonta smaragdina*	*Exerodonta sumichrasti* group
Hyla smithii Boulenger, 1901	*H. godmani* group	*Tlalocohyla smithii*	—
Hyla soaresi Caramaschi and Jim, 1983	*H. marmorata* group	*Dendropsophus soaresi*	*Dendropsophus marmoratus* group
Hyla squirella Bosc, 1800	*H. cinerea* group	*Hyla squirella*	*Hyla cinerea* group
Hyla staufferorum Duellman and Coloma, 1993	*H. larinopygion* group	*Hyloscirtus staufferorum*	*Hyloscirtus larinopygion* group
Hyla stenocephala Caramaschi and Cruz, 1999	*H. pulchella* group, *H. polytaenia* clade	*Hypsiboas stenocephalus*	*Hypsiboas pulchellus* group, *H. polytaenius* clade
Hyla stingi Kaplan, 1994	Unassigned	*Dendropsophus stingi*	Unassigned
Hyla studerae Carvalho e Silva, Carvalho e Silva, and Izecksohn, 2003	*H. microcephala* group	*Dendropsophus studerae*	*Dendropsophus microcephalus* group
Hyla subocularis Dunn, 1934	*H. parviceps* group	*Dendropsophus subocularis*	*Dendropsophus parviceps* group
Hyla sumichrasti (Brocchi, 1879)	*H. sumichrasti* group	*Exerodonta sumichrasti*	*Exerodonta sumichrasti* group
Hyla surinamensis Daudin, 1802	Unassigned	*Nomen dubium*	—
Hyla suweonensis Kuramoto, 1980	*H. arborea* group	*Hyla suweonensis*	*Hyla eximia* group
Hyla taeniopus Günther, 1901	*H. taeniopus* group	*Charadrahyla taeniopus*	—

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Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Hyla tapichalaca Kizirian, Coloma, and Paredes-Recalde, 2003	*H. larinopygion* group	*Hyloscirtus tapichalaca*	*Hyloscirtus larinopygion* group
Hyla thorectes Adler, 1965	*H. pictipes* group	*Plectrohyla thorectes*	*Plectrohyla bistincta* group
Hyla thysanota Duellman, 1966	*H. tuberculosa* group	*Ecnomiohyla thysanota*	—
Hyla tica Starrett, 1966	*H. pictipes* group	*Isthmohyla tica*	*Isthmohyla pictipes* group
Hyla timbeba Martins and Cardoso, 1987	*H. parviceps* group	*Dendropsophus timbeba*	*Dendropsophus parviceps* group
Hyla tintinnabulum Melin, 1941	Unassigned	*Dendropsophus tintinnabulum*	Unassigned
Hyla torrenticola Duellman and Altig, 1978	*H. bogotensis* group	*Hyloscirtus torrenticola*	*Hyloscirtus bogotensis* group
Hyla triangulum Günther, 1869 ‘‘1868’’	*H. leucophyllata* group	*Dendropsophus triangulum*	*Dendropsophus leucophyllatus* group
Hyla tritaeniata Bokermann, 1965	*H. rubicundula* group	*Dendropsophus tritaeniatus*	*Dendropsophus microcephalus* group, *D. rubicundulus* clade
Hyla trux Adler and Dennis, 1972	*H. taeniopus* group	*Charadrahyla trux*	—
Hyla tsinlingensis Liu and Hu, 1966	*H. arborea* group	*Hyla tsinlingensis*	*Hyla arborea* group
Hyla tuberculosa Boulenger, 1882	*H. tuberculosa* group	*Ecnomiohyla tuberculosa*	—
Hyla uruguaya Schmidt, 1944	*H. uruguaya* group	*Scinax uruguayus*	*Scinax ruber* clade, *S. uruguayus* group
Hyla ussuriensis Nikolsky, 1918	*H. arborea* group	*Hyla ussuriensis*	*Hyla arborea* group
Hyla valancifer Firschein and Smith, 1956	*H. tuberculosa* group	*Ecnomiohyla valancifer*	—
Hyla varelae Carrizo, 1992	Unassigned	*Hypsiboas varelae*	Unassigned
Hyla versicolor LeConte, 1825	*H. versicolor* group	*Hyla versicolor*	*Hyla versicolor* group
Hyla vigilans Solano, 1971	Unassigned	*Incerta sedis*	—
Hyla virolinensis Kaplan and Ruiz, 1997	*H. garagoensis* group	*Dendropsophus virolinensis*	*Dendropsophus garagoensis* group
Hyla walfordi Bokermann, 1962	*H. microcephala* group	*Dendropsophus walfordi*	*Dendropsophus microcephalus* group
Hyla walkeri Stuart, 1954	*H. eximia* group	*Hyla walkeri*	*Hyla eximia* group
Hyla warreni Duellman and Hoogmoed, 1992	Unassigned	*Incertae sedis*	—
Hyla wavrini Parker, 1936	*H. boans* group	*Hypsiboas wavrini*	*Hypsiboas semilineatus* group
Hyla werneri Cochran, 1952	*H. microcephala* group	*Dendropsophus werneri*	*Dendropsophus microcephalus* group
Hyla weygoldti Cruz and Peixoto, 1987 ‘‘1985’’.	*H. albofrenata* complex, *H. albomarginata* group	*Aplastodiscus weygoldti*	*Aplastodiscus albofrenatus* group
Hyla wrightorum Taylor, 1939 ‘‘1938’’	*H. eximia* group	*Hyla wrightorum*	*Hyla eximia* group
Hyla xanthosticta Duellman, 1968	*H. pictipes* group	*Isthmohyla xanthosticta*	*Isthmohyla pictipes* group
Hyla xapuriensis Martins and Cardoso, 1987	*H. minuta* group	*Dendropsophus xapuriensis*	*Dendropsophus minutus* group
Hyla xera Mendelson and Campbell, 1994	*H. sumichrasti* group	*Exerodonta xera*	*Exerodonta sumichrasti* group
Hyla yaracuyana Mijares-Urrutia and Rivero, 2000	Unassigned	*Dendropsophus yaracuyanus*	Unassigned
Hyla zeteki Gaige, 1929	*H. pictipes* group	*Isthmohyla zeteki*	*Isthmohyla pictipes* group
Hyla zhaopingensis Tang and Zhang, 1984	*H. arborea* group	*Hyla zhaopingensis*	*Hyla arborea* group
Lysapsus caraya Gallardo, 1964	—	*Lysapsus caraya*	—

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Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Lysapsus laevis Parker, 1935	—	*Lysapsus laevis*	—
Lysapsus limellum Cope, 1862	—	*Lysapsus limellum*	—
Nyctimantis rugiceps Boulenger, 1882	—	*Nyctimantis rugiceps*	—
Osteocephalus buckleyi (Boulenger, 1882)	—	*Osteocephalus buckleyi*	—
Osteocephalus cabrerai (Cochran and Goin, 1970)	—	*Osteocephalus cabrerai*	—
Osteocephalus deridens Jungfer, Ron, Seipp, and Almendáriz, 2000	—	*Osteocephalus deridens*	—
Osteocephalus elkejungingerae (Henle, 1981)	—	*Osteocephalus elkejungingerae*	—
Osteocephalus exophthalmus Smith and Noonan, 2001	—	*Osteocephalus exophthalmus*	—
Osteocephalus fuscifacies Jungfer, Ron, Seipp, and Almendáriz, 2000	—	*Osteocephalus fuscifacies*	—
Osteocephalus heyeri Lynch, 2002	—	*Osteocephalus heyeri*	—
Osteocephalus langsdorffii (Duméril and Bibron, 1841)	—	*Itapotihyla langsdorffii*	—
Osteocephalus leoniae Jungfer and Lehr, 2001	—	*Osteocephalus leoniae*	—
Osteocephalus leprieurii (Dumláril and Bibron, 1841)	—	*Osteocephalus leprieurii*	—
Osteocephalus mutabor Jungfer and Hödl, 2002	—	*Osteocephalus mutabor*	—
Osteocephalus oophagus Jungfer and Schiesari, 1995	—	*Osteocephalus oophagus*	—
Osteocephalus pearsoni (Gaige, 1929)	—	*Osteocephalus pearsoni*	—
Osteocephalus planiceps Cope, 1874	—	*Osteocephalus planiceps*	—
Osteocephalus subtilis Martins and Cardoso, 1987	—	*Osteocephalus subtilis*	—
Osteocephalus taurinus Steindachner, 1862	—	*Osteocephalus taurinus*	—
Osteocephalus verruciger (Werner, 1901)	—	*Osteocephalus verruciger*	—
Osteocephalus yasuni Ron and Pramuk, 1999	—	*Osteocephalus yasuni*	—
Osteopilus brunneus (Gosse, 1851)	—	*Osteopilus brunneus*	—
Osteopilus crucialis (Harlan, 1826)	—	*Osteopilus crucialis*	—
Osteopilus dominicensis (Tschudi, 1838)	—	*Osteopilus dominicensis*	—
Osteopilus marianae (Dunn, 1926)	—	*Osteopilus marianae*	—
Osteopilus pulchrilineatus Cope, 1870 ‘‘1869’’	—	*Osteopilus pulchrilineatus*	—
Osteopilus septentrionalis (Duméril and Bibron, 1841)	—	*Osteopilus septentrionalis*	—
Osteopilus vastus (Cope, 1871)	—	*Osteopilus vastus*	—
Osteopilus wilderi (Dunn, 1925)	—	*Osteopilus wilderi*	—

APPENDIX 1
(*Continued*)

Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Phrynohyas coriacea (Peters, 1867)	—	*Trachycephalus coriaceus*	—
Phrynohyas hadroceps (Duellman and Hoogmoed, 1992)	—	*Trachycephalus hadroceps*	—
Phrynohyas imitatrix (Miranda-Ribeiro, 1926)	—	*Trachycephalus imitatrix*	—
Phrynohyas mesophaea (Hensel, 1867)	—	*Trachycephalus mesophaeus*	—
Phrynohyas resinifictrix (Goeldi, 1907)	—	*Trachycephalus resinifictrix*	—
Phrynohyas venulosa (Laurenti, 1768)	—	*Trachycephalus venulosus*	—
Phyllodytes acuminatus Bokermann, 1966	*Phyllodytes luteolus* group	*Phyllodytes acuminatus*	*Phyllodytes luteolus* group
Phyllodytes auratus (Boulenger, 1917)	*P. auratus* group	*Phyllodytes auratus*	*P. auratus* group
Phyllodytes brevirostris Peixoto and Cruz, 1988	*P. luteolus* group	*Phyllodytes brevirostris*	*P. luteolus* group
Phyllodytes edelmoi Peixoto, Caramaschi, and Freire, 2003	*P. luteolus* group	*Phyllodytes edelmoi*	*P. luteolus* group
Phyllodytes gyrinaethes Peixoto, Caramaschi and Freire, 2003	*P. gyrinaethes* group	*Phyllodytes gyrinaethes*	*P. gyrinaethes* group
Phyllodytes kautskyi Peixoto and Cruz, 1988	*P. luteolus* group	*Phyllodytes kautskyi*	*P. luteolus* group
Phyllodytes luteolus (Wied-Neuwied, 1824)	*P. luteolus* group	*Phyllodytes luteolus*	*P. luteolus* group
Phyllodytes melanomystax Caramaschi, da Silva, and Britto-Pereira, 1992	*P. luteolus* group	*Phyllodytes melanomystax*	*P. luteolus* group
Phyllodytes punctatus Caramaschi and Peixoto, 2004	*P. tuberculosus* group	*Phyllodytes punctatus*	*P. tuberculosus* group
Phyllodytes tuberculosus Bokermann, 1966	*P. tuberculosus* group	*Phyllodytes tuberculosus*	*P. tuberculosus* group
Phyllodytes wuchereri (Peters, 1873)	*P. auratus* group	*Phyllodytes wuchereri*	*P. auratus* group
Plectrohyla acanthodes Duellman and Campbell, 1992	—	*Plectrohyla acanthodes*	*Plectrohyla guatemalensis* group
Plectrohyla avia Stuart, 1952	—	*Plectrohyla avia*	*Plectrohyla guatemalensis* group
Plectrohyla chrysopleura Wilson, McCranie, and Cruz, 1994	—	*Plectrohyla chrysopleura*	*Plectrohyla guatemalensis* group
Plectrohyla dasypus McCranie and Wilson, 1981	—	*Plectrohyla dasypus*	*Plectrohyla guatemalensis* group
Plectrohyla exquisita McCranie and Wilson, 1998	—	*Plectrohyla exquisita*	*Plectrohyla guatemalensis* group
Plectrohyla glandulosa (Boulenger, 1883)	—	*Plectrohyla glandulosa*	*Plectrohyla guatemalensis* group
Plectrohyla guatemalensis Brocchi, 1877	—	*Plectrohyla guatemalensis*	*Plectrohyla guatemalensis* group
Plectrohyla hartwegi Duellman, 1968	—	*Plectrohyla hartwegi*	*Plectrohyla guatemalensis* group
Plectrohyla ixil Stuart, 1942	—	*Plectrohyla ixil*	*Plectrohyla guatemalensis* group
Plectrohyla lacertosa Bumzahem and Smith, 1954	—	*Plectrohyla lacertosa*	*Plectrohyla guatemalensis* group
Plectrohyla matudai Hartweg, 1941	—	*Plectrohyla matudai*	*Plectrohyla guatemalensis* group

APPENDIX 1
(*Continued*)

Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Plectrohyla pokomchi Duellman and Campbell, 1984	—	*Plectrohyla pokomchi*	*Plectrohyla guatemalensis* group
Plectrohyla psiloderma McCranie and Wilson, 1999	—	*Plectrohyla psiloderma*	*Plectrohyla guatemalensis* group
Plectrohyla pycnochila Rabb, 1959	—	*Plectrohyla pycnochila*	*Plectrohyla guatemalensis* group
Plectrohyla quecchi Stuart, 1942	—	*Plectrohyla quecchi*	*Plectrohyla guatemalensis* group
Plectrohyla sagorum Hartweg, 1941	—	*Plectrohyla sagorum*	*Plectrohyla guatemalensis* group
Plectrohyla tecunumani Duellman and Campbell, 1984	—	*Plectrohyla tecunumani*	*Plectrohyla guatemalensis* group
Plectrohyla teuchestes Duellman and Campbell, 1992	—	*Plectrohyla teuchestes*	*Plectrohyla guatemalensis* group
Pseudacris brachyphona (Cope, 1889)	*Pseudacris nigrita* clade	*Pseudacris brachyphona*	*Pseudacris nigrita* clade
Pseudacris brimleyi Brandt and Walker, 1933	*P. nigrita* clade	*Pseudacris brimleyi*	*P. nigrita* clade
Pseudacris cadaverina (Cope, 1866)	*P. regilla* clade	*Pseudacris cadaverina*	*P. regilla* clade
Pseudacris clarkii (Baird, 1854)	*P. nigrita* clade	*Pseudacris clarkii*	*P. nigrita* clade
Pseudacris crucifer (Wied-Neuwied, 1838)	*P. crucifer* clade	*Pseudacris crucifer*	*P. crucifer* clade
Pseudacris feriarum (Baird, 1854)	*P. nigrita* clade	*Pseudacris feriarum*	*P. nigrita* clade
Pseudacris illinoensis Smith, 1951	*P. ornata* clade	*Pseudacris illinoensis*	*P. ornata* clade
Pseudacris maculata (Agassiz, 1850)	*P. nigrita* clade	*Pseudacris maculata*	*P. nigrita* clade
Pseudacris nigrita (LeConte, 1825)	*P. nigrita* clade	*Pseudacris nigrita*	*P. nigrita* clade
Pseudacris ocularis (Bosc and Daudin, 1801)	*P. crucifer* clade	*Pseudacris ocularis*	*P. crucifer* clade
Pseudacris ornata (Holbrook, 1836)	*P. ornata* clade	*Pseudacris ornata*	*P. ornata* clade
Pseudacris regilla (Baird and Girard, 1852)	*P. regilla* clade	*Pseudacris regilla*	*P. regilla* clade
Pseudacris streckeri A. A. Wright and A. H. Wright, 1933	*P. ornata* clade	*Pseudacris streckeri*	*P. ornata* clade
Pseudacris triseriata (Wied-Neuwied, 1838)	*P. nigrita* clade	*Pseudacris triseriata*	*P. nigrita* clade
Pseudis bolbodactyla A. Lutz, 1925	—	*Pseudis bolbodactyla*	—
Pseudis cardosoi Kwet, 2000	—	*Pseudis cardosoi*	—
Pseudis fusca Garman, 1883	—	*Pseudis fusca*	—
Pseudis minuta Günther, 1858	—	*Pseudis minuta*	—
Pseudis paradoxa (Linnaeus, 1758)	—	*Pseudis paradoxa*	—
Pseudis tocantins Caramaschi and Cruz, 1998	—	*Pseudis tocantins*	—
Pternohyla dentata Smith, 1957	—	*Smilisca dentata*	—
Pternohyla fodiens Boulenger, 1882	—	*Smilisca fodiens*	—
Ptychohyla acrochorda Campbell and Duellman, 2000	—	*Ptychohyla acrochorda*	—

APPENDIX 1
(*Continued*)

Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Ptychohyla erythromma (Taylor, 1937)	—	*Ptychohyla erythromma*	—
Ptychohyla euthysanota (Kellogg, 1928)	—	*Ptychohyla euthysanota*	—
Ptychohyla hypomykter McCranie and Wilson, 1993	—	*Ptychohyla hypomykter*	—
Ptychohyla legleri (Taylor, 1958)	—	*Ptychohyla legleri*	—
Ptychohyla leonhardschultzei (Ahl, 1934)	—	*Ptychohyla leonhardschultzei*	—
Ptychohyla macrotympanum (Tanner, 1957)	—	*Ptychohyla macrotympanum*	—
Ptychohyla panchoi Duellman and Campbell, 1982	—	*Ptychohyla panchoi*	—
Ptychohyla salvadorensis (Mertens, 1952)	—	*Ptychohyla salvadorensis*	—
Ptychohyla sanctaecrucis Campbell and Smith, 1992	—	*Ptychohyla sanctaecrucis*	—
Ptychohyla spinipollex (Schmidt, 1936)	—	*Ptychohyla spinipollex*	—
Ptychohyla zophodes Campbell and Duellman, 2000	—	*Ptychohyla zophodes*	—
Scarthyla goinorum (Bokermann, 1964)	—	*Scarthyla goinorum*	—
Scinax acuminatus (Cope, 1862)	*S. ruber* clade	*Scinax acuminatus*	*S. ruber* clade
Scinax agilis (Cruz & Peixoto, 1983)	*S. catharinae* clade	*Scinax agilis*	*S. catharinae* clade, *S. catharinae* group.
Scinax albicans (Bokermann,1967)	*S. catharinae* clade	*Scinax albicans*	*S. catharinae* clade, *S. catharinae* group
Scinax alcatraz (B. Lutz, 1973)	*S. catharinae* clade, *S. perpusillus* group	*Scinax alcatraz*	*S. catharinae* clade, *S. perpusillus* group
Scinax altae (Dunn, 1933)	*S. ruber* clade	*Scinax altae*	*S. ruber* clade
Scinax alter (B. Lutz, 1973)	*S. ruber* clade	*Scinax alter*	*S. ruber* clade
Scinax angrensis (B. Lutz, 1973)	*S. catharinae* clade, *S. catharinae* group	*Scinax angrensis*	*S. catharinae* clade, *S. catharinae* group
Scinax arduous (Peixoto, 2001)	*S. catharinae* clade, *S. perpusillus* group	*Scinax arduous*	*S. catharinae* clade, *S. perpusillus* group
Scinax argyreornatus (Miranda-Ribeiro, 1926)	*S. catharinae* clade, *S. catharinae* group	*Scinax argyreornatus*	*S. catharinae* clade, *S. catharinae* group
Scinax ariadne (Bokermann, 1967)	*S. catharinae* clade, *S. catharinae* group	*Scinax ariadne*	*S. catharinae* clade, *S. catharinae* group
Scinax aromothyella Faivovich, 2005	*S. catharinae* clade, *S. catharinae* group	*Scinax aromothyella*	*S. catharinae* clade, *S. catharinae* group
Scinax atratus (Peixoto, ‘‘1988’’ 1989)	*S. catharinae* clade, *S. perpusillus* group	*Scinax atratus*	*S. catharinae* clade, *S. perpusillus* group

APPENDIX 1
(*Continued*)

Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Scinax auratus (Wied, 1821)	*S. ruber* clade	*Scinax auratus*	*S. ruber* clade
Scinax baumgardneri (Rivero, 1961)	*S. ruber* clade	*Scinax baumgardneri*	*S. ruber* clade
Scinax berthae (Barrio, 1962)	*S. catharinae* clade, *S. catharinae* group	*Scinax berthae*	*S. catharinae* clade, *S. catharinae* group
Scinax blairi (Fouquette and Pyburn, 1972)	*S. ruber* clade	*Scinax blairi*	*S. ruber* clade
Scinax boesemani (Goin, 1966)	*S. ruber* clade	*Scinax boesemani*	*S. ruber* clade
Scinax boulengeri (Cope, 1887)	*S. ruber* clade, *S. rostratus* group	*Scinax boulengeri*	*S. ruber* clade, *S. rostratus* group
Scinax brieni (De Witte, 1930)	*S. catharinae* clade, *S. catharinae* group	*Scinax brieni*	*S. catharinae* clade, *S. catharinae* group
Scinax caldarum (B. Lutz, 1968)	*S. ruber* clade	*Scinax caldarum*	*S. ruber* clade
Scinax canastrensis (Cardoso and Haddad, 1982)	*S. catharinae* clade, *S. catharinae* group	*Scinax canastrensis*	*S. catharinae* clade, *S. catharinae* group
Scinax cardosoi (Carvalho e Silva and Peixoto, 1991)	*S. ruber* clade	*Scinax cardosoi*	*S. ruber* clade
Scinax carnevallii (Caramaschi and Kisteumacher, 1989)	*S. catharinae* clade, *S. catharinae* group	*Scinax carnevalli*	*S. catharinae* clade, *S. catharinae* group
Scinax castroviejoi De La Riva, 1993	*S. ruber* clade	*Scinax castroviejoi*	*S. ruber* clade
Scinax catharinae (Boulenger, 1888)	*S. catharinae* clade, *S. catharinae* group	*Scinax catharinae*	*S. catharinae* clade, *S. catharinae* group
Scinax centralis Pombal and Bastos, 1996	*S. catharinae* clade, *S. catharinae* group	*Scinax centralis*	*S. catharinae* clade, *S. catharinae* group
Scinax chiquitanus (De La Riva, 1990)	*S. ruber* clade	*Scinax chiquitanus*	*S. ruber* clade
Scinax crospedospilus (A. Lutz, 1925)	*S. ruber* clade	*Scinax crospedospilus*	*S. ruber* clade
Scinax cruentommus (Duellman, 1972)	*S. ruber* clade	*Scinax cruentommus*	*S. ruber* clade
Scinax curicica Pugliese, Pombal, and Sazima, 2004	*S. ruber* clade	*Scinax curicica*	*S. ruber* clade
Scinax cuspidatus (A. Lutz, 1925)	*S. ruber* clade	*Scinax cuspidatus*	*S. ruber* clade
Scinax danae (Duellman, 1986)	*S. ruber* clade	*Scinax danae*	*S. ruber* clade
Scinax duartei (B. Lutz, 1951)	*S. ruber* clade	*Scinax duartei*	*S. ruber* clade
Scinax elaeochrous (Cope, 1875)	*S. ruber* clade	*Scinax elaeochrous*	*S. ruber* clade
Scinax eurydice (Bokermann, 1968)	*S. ruber* clade	*Scinax eurydice*	*S. ruber* clade
Scinax exiguus (Duellman, 1986)	*S. ruber* clade	*Scinax exiguus*	*S. ruber* clade
Scinax flavidus La Marca, 2004	*S. ruber* clade	*Scinax flavidus*	*S. ruber* clade
Scinax flavoguttatus (A. Lutz and B. Lutz, 1939)	*S. catharinae* clade, *S. catharinae* group	*Scinax flavoguttatus*	*S. catharinae* clade, *S. catharinae* group

APPENDIX 1
(*Continued*)

Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Scinax funereus (Cope, 1874)	*S. ruber* clade	*Scinax funereus*	*S. ruber* clade
Scinax fuscomarginatus (A. Lutz, 1925)	*S. ruber* clade	*Scinax fuscomarginatus*	*S. ruber* clade
Scinax fuscovarius (A. Lutz, 1925)	*S. ruber* clade	*Scinax fuscovarius*	*S. ruber* clade
Scinax garbei (Miranda-Ribeiro, 1926)	*S. ruber* clade, *S. rostratus* group	*Scinax garbei*	*S. ruber* clade, *S. rostratus* group
Scinax granulatus (Peters, 1871)	*S. ruber* clade	*Scinax granulatus*	*S. ruber* clade
Scinax hayii (Barbour, 1909)	*S. ruber* clade	*Scinax hayii*	*S. ruber* clade
Scinax heyeri (Peixoto and Weygoldt, 1986)	*S. catharinae* clade, *S. catharinae* group	*Scinax heyeri*	*S. catharinae* clade, *S. catharinae* group
Scinax hiemalis (Haddad and Pombal, 1987)	*S. catharinae* clade, *S. catharinae* group	*Scinax hiemalis*	*S. catharinae* clade, *S. catharinae* group
Scinax humilis (B. Lutz, 1954)	*S. catharinae* clade, *S. catharinae* group	*Scinax humilis*	*S. catharinae* clade, *S. catharinae* group
Scinax ictericus Duellman and Wiens, 1993	*S. ruber* clade	*Scinax ictericus*	*S. ruber* clade
Scinax jolyi Lescure and Marty, 2000	*S. ruber* clade, *S. rostratus* group	*Scinax jolyi*	*S. ruber* clade, *S. rostratus* group
Scinax jureia (Pombal and Gordo, 1991)	*S. catharinae* clade, *S. catharinae* group	*Scinax jureia*	*S. catharinae* clade, *S. catharinae* group
Scinax kautskyi (Carvalho e Silva and Peixoto, 1991)	*S. catharinae* clade, *S. catharinae* group	*Scinax kautskyi*	*S. catharinae*
Scinax kennedyi (Pyburn 1973)	*S. ruber* clade, *S. rostratus* group	*Scinax kennedyi*	*S. ruber* clade, *S. rostratus* group
Scinax lindsayi Pyburn, 1992	*S. ruber* clade	*Scinax lindsayi*	*S. ruber* clade
Scinax littoralis (Pombal and Gordo, 1991)	*S. catharinae* clade, *S. catharinae* group	*Scinax littoralis*	*S. catharinae* clade, *S. catharinae* group
Scinax littoreus (Pexoto, 1988)	*S. catharinae* clade, *S. perpusillus* group	*Scinax littoreus*	*S. catharinae* clade, *S. perpusillus* group
Scinax longilineus (B. Lutz, 1968)	*S. catharinae* clade, *S. catharinae* group	*Scinax longilineus*	*S. catharinae* clade, *S. catharinae* group
Scinax luizotavioi (Caramaschi and Kisteumacher, 1989)	*S. catharinae* clade, *S. catharinae* group	*Scinax luizotavioi*	*S. catharinae* clade, *S. catharinae* group
Scinax machadoi (Bokermann and Sazima, 1973)	*S. catharinae* clade, *S. catharinae* group	*Scinax machadoi*	*S. catharinae* clade, *S. catharinae* group
Scinax manriquei Barrio-Amorós, Orellana, and Chacon, 2004	*S. ruber* clade	*Scinax manriquei*	*S. ruber* clade
Scinax maracaya (Cardoso and Sazima, 1980)	*S. ruber* clade	*Scinax maracaya*	*S. ruber* clade

APPENDIX 1
(*Continued*)

Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Scinax megapodius (Miranda-Ribeiro, 1926)	*S. ruber* clade	*Scinax fuscovarius*	*S. ruber* clade
Scinax melloi (Peixoto, 1989)	*S. catharinae* clade, *S. perpusillus* group	*Scinax melloi*	*S. catharinae* clade, *S. perpusillus* group
Scinax nasicus (Cope, 1862)	*S. ruber* clade	*Scinax nasicus*	*S. ruber* clade
Scinax nebulosus (Spix, 1824)	*S. ruber* clade, *S. rostratus* group	*Scinax nebulosus*	*S. ruber* clade, *S. rostratus* group
Scinax obtriangulatus (B. Lutz, 1973)	*S. catharinae* clade, *S. catharinae* group	*Scinax obtriangulatus*	*S. catharinae* clade, *S. catharinae* group
Scinax oreites Duellman and Wiens, 1993	*S. ruber* clade	*Scinax oreites*	*S. ruber* clade
Scinax pachycrus (Miranda-Ribeiro, 1937)	*S. ruber* clade	*Scinax pachycrus*	*S. ruber* clade
Scinax parkeri (Gaige, 1926)	*S. ruber* clade	*Scinax parkeri*	*S. ruber* clade
Scinax pedromedinae (Henle, 1991)	*S. ruber* clade, *S. rostratus* group	*Scinax pedromedinae*	*S. ruber* clade, *S. rostratus* group
Scinax perereca Pombal, Haddad, and Kasahara, 1995	*S. ruber* clade	*Scinax perereca*	*S. ruber* clade
Scinax perpusillus (A. Lutz and B. Lutz, 1939)	*S. catharinae* clade, *S. perpusillus* group	*Scinax perpusillus*	*S. catharinae* clade, *S. perpusillus* group
Scinax proboscideus (Brongersma, 1933)	*S. ruber* clade, *S. rostratus* group	*Scinax proboscideus*	*S. ruber* clade, *S. rostratus* group
Scinax quinquefasciatus (Fowler, 1913)	*S. ruber* clade	*Scinax quinquefasciatus*	*S. ruber* clade
Scinax ranki (Andrade and Cardoso, 1987)	*S. catharinae* clade, *S. catharinae* group	*Scinax ranki*	*S. catharinae* clade, *S. catharinae* group
Scinax rizibilis (Bokermann, 1964)	*S. catharinae* clade, *S. catharinae* group	*Scinax rizibilis*	*S. catharinae* clade, *S. catharinae* group
Scinax rostratus (Peters, 1863)	*S. ruber* clade, *S. rostratus* group	*Scinax rostratus*	*S. ruber* clade, *S. rostratus* group
Scinax ruber (Laurenti, 1768)	*S. ruber* clade	*Scinax ruber*	*S. ruber* clade
Scinax similis (Cochran, 1952)	*S. ruber* clade	*Scinax similis*	*S. ruber* clade
Scinax squalirostris (A. Lutz, 1926)	*S. ruber* clade	*Scinax squalirostris*	*S. ruber* clade
Scinax staufferi (Cope, 1865)	*S. ruber* clade	*Scinax staufferi*	*S. ruber* clade
Scinax strigilatus (Spix, 1824)	*S. catharinae* clade	*Scinax strigilatus*	*S. catharinae* clade
Scinax sugillatus (Duellman, 1973)	*S. ruber* clade, *S. rostratus* group	*Scinax sugillatus*	*S. ruber* clade, *S. rostratus* group
Scinax trachythorax (Müller and Hellmich, 1936)	*S. ruber* clade	*Scinax fuscovarius*	*S. ruber* clade
Scinax trapicheiroi (B. Lutz, 1954)	*S. catharinae* clade, *S. catharinae* group	*Scinax trapicheiroi*	*S. catharinae* clade, *S. catharinae* group

APPENDIX 1
(*Continued*)

Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Scinax trilineatus (Hoogmoed and Gorzula, 1977)	*S. ruber* clade	*Scinax trilineatus*	*S. ruber* clade
Scinax v-signatus (B. Lutz, 1968)	*S. catharinae* clade, *S. perpusillus* group	*Scinax v-signatus*	*S. catharinae* clade, *S. perpusillus* group
Scinax wandae (Pyburn and Fouquette, 1971)	*S. ruber* clade	*Scinax wandae*	*S. ruber* clade
Scinax x-signatus (Spix, 1824)	*S. ruber* clade	*Scinax x-signatus*	*S. ruber* clade
Smilisca baudinii (Duméril and Bibron, 1841)	—	*Smilisca baudinii*	—
Smilisca cyanosticta (Smith, 1953)	—	*Smilisca cyanosticta*	—
Smilisca phaeota (Cope, 1862)	—	*Smilisca phaeota*	—
Smilisca puma (Cope, 1885)	—	*Smilisca puma*	—
Smilisca sila Duellman and Trueb, 1966	—	*Smilisca sila*	—
Smilisca sordida (Peters, 1863)	—	*Smilisca sordida*	—
Sphaenorhynchus bromelicola Bokermann, 1966	—	*Sphaenorhynchus bromelicola*	—
Sphaenorhynchus carneus (Cope, 1868)	—	*Sphaenorhynchus carneus*	—
Sphaenorhynchus dorisae (Goin, 1957)	—	*Sphaenorhynchus dorisae*	—
Sphaenorhynchus lacteus (Daudin, 1801)	—	*Sphaenorhynchus lacteus*	—
Sphaenorhynchus orophilus (A. Lutz and B. Lutz, 1938)	—	*Sphaenorhynchus orophilus*	—
Sphaenorhynchus palustris Bokermann, 1966	—	*Sphaenorhynchus palustris*	—
Sphaenorhynchus pauloalvini Bokermann, 1973	—	*Sphaenorhynchus pauloalvini*	—
Sphaenorhynchus planicola (A. Lutz and B. Lutz, 1938)	—	*Sphaenorhynchus planicola*	—
Sphaenorhynchus platycephalus (Werner, 1894)	—	*Sphaenorhynchus platycephalus*	—
Sphaenorhynchus prasinus Bokermann, 1973	—	*Sphaenorhynchus prasinus*	—
Sphaenorhynchus surdus (Cochran, 1953)	—	*Sphaenorhynchus surdus*	—
Tepuihyla aecii (Ayarzagüena, Señaris, and Gorzula, 1993)	—	*Tepuihyla aecii*	—
Tepuihyla celsae Mijares-Urrutia, Manzanilla-Puppo, and La Marca, 1999	—	*Tepuihyla celsae*	—
Tepuihyla edelcae (Ayarzagüena, Señaris, and Gorzula, 1993)	—	*Tepuihyla edelcae*	—
Tepuihyla galani (Ayarzagüena, Señaris, and Gorzula, 1993)	—	*Tepuihyla galani*	—
Tepuihyla luteolabris (Ayarzagüena, Señaris, and Gorzula, 1993)	—	*Tepuihyla luteolabris*	—
Tepuihyla rimarum (Ayarzagüena, Señaris, and Gorzula, 1993)	—	*Tepuihyla rimarum*	—

APPENDIX 1
(*Continued*)

Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Tepuihyla rodriguezi (Rivero, 1968)	—	*Tepuihyla rodriguezi*	—
Tepuihyla talbergae Duellman and Yoshpa, 1996	—	*Tepuihyla talbergae*	—
Trachycephalus atlas Bokermann, 1966	—	*Trachycephalus atlas*	—
Trachycephalus jordani (Stejneger and Test, 1891)	—	*Trachycephalus jordani*	—
Trachycephalus nigromaculatus Tschudi, 1838	—	*Trachycephalus nigromaculatus*	—
Triprion petasatus (Cope, 1865)	—	*Triprion petasatus*	—
Triprion spatulatus Günther, 1882	—	*Triprion spatulatus*	—
Xenohyla eugenioi Caramaschi, 1998	—	*Xenohyla eugenioi*	—
Xenohyla truncata (Izecksohn, 1959)	—	*Xenohyla truncata*	—
Phyllomedusinae			
Agalychnis annae (Duellman, 1963)	—	*Agalychnis annae*	—
Agalychnis calcarifer Boulenger, 1902	—	*Cruziohyla calcarifer*	—
Agalychnis callidryas (Cope, 1862)	—	*Agalychnis callidryas*	—
Agalychnis craspedopus (Funkhouser, 1957)	—	*Cruziohyla craspedopus*	—
Agalychnis litodryas (Duellman and Trueb, 1967)	—	*Agalychnis litodryas*	—
Agalychnis moreletii (Duméril, 1853)	—	*Agalychnis moreletii*	—
Agalychnis saltator Taylor, 1955	—	*Agalychnis saltator*	—
Agalychnis spurrelli Boulenger, 1914 ‘‘1913’’	—	*Agalychnis spurrelli*	—
Hylomantis aspera Peters, 1873 ‘‘1872’’	—	*Hylomantis aspera*	*Hylomantis aspera* group
Hylomantis granulosa (Cruz, 1989)	—	*Hylomantis granulosa*	*Hylomantis aspera* group
Pachymedusa dacnicolor (Cope, 1864)	—	*Pachymedusa dacnicolor*	—
Phasmahyla cochranae (Bokermann, 1966)	—	*Phasmahyla cochranae*	—
Phasmahyla exilis (Cruz, 1980)	—	*Phasmahyla exilis*	—
Phasmahyla guttata (A. Lutz, 1925)	—	*Phasmahyla guttata*	—
Phasmahyla jandaia (Bokermann and Sazima, 1978)	—	*Phasmahyla jandaia*	—
Phrynomedusa appendiculata (A. Lutz, 1925)	—	*Phrynomedusa appendiculata*	—
Phrynomedusa bokermanni Cruz, 1991	—	*Phrynomedusa bokermanni*	—
Phrynomedusa fimbriata Miranda-Ribeiro, 1923	—	*Phrynomedusa fimbriata*	—
Phrynomedusa marginata (Izecksohn and Cruz, 1976)	—	*Phrynomedusa marginata*	—
Phrynomedusa vanzolinii Cruz, 1991	—	*Phrynomedusa vanzolinii*	—
Phyllomedusa atelopoides Duellman, Cadle, and Cannatella, 1988	Unassigned	*Phyllomedusa atelopoides*	Unassigned
Phyllomedusa ayeaye (B. Lutz, 1966)	*P. hypochondrialis* group	*Phyllomedusa ayeaye*	*P. hypochondrialis* group

APPENDIX 1
(*Continued*)

Current taxonomy	Species group in current taxonomy	New taxonomy	Species group in new taxonomy
Phyllomedusa baltea Duellman and Toft, 1979	*P. perinesos* group	*Phyllomedusa baltea*	*P. perinesos* group
Phyllomedusa bicolor (Boddaert, 1772)	Unassigned	*Phyllomedusa bicolor*	Unassigned
Phyllomedusa boliviana Boulenger, 1902	*P. tarsius* group	*Phyllomedusa boliviana*	*P. tarsius* group
Phyllomedusa buckleyi Boulenger, 1882	*P. buckleyi* group	*Hylomantis buckleyi*	*Hylomantis buckleyi* group
Phyllomedusa burmeisteri Boulenger, 1882	*P. burmeisteri* group	*Phyllomedusa burmeisteri*	*P. burmeisteri* group
Phyllomedusa camba De La Riva, 2000	*P. tarsius* group	*Phyllomedusa camba*	*P. tarsius* group
Phyllomedusa centralis Bokermann, 1965	*P. hypochondrialis* group	*Phyllomedusa centralis*	*P. hypochondrialis* group
Phyllomedusa coelestis (Cope, 1874)	Unassigned	*Phyllomedusa coelestis*	Unassigned
Phyllomedusa danieli Ruiz-Carranza, Hernandez-Camacho, and Rueda-Almonacid, 1988	*P. buckleyi* group	*Hylomantis danieli*	*Hylomantis buckleyi* group
Phyllomedusa distincta B. Lutz, 1950	*P. burmeisteri* group	*Phyllomedusa distincta*	*P. burmeisteri* group
Phyllomedusa duellmani Cannatella, 1982	*P. perinesos* group	*Phyllomedusa duellmani*	*P. perinesos* group
Phyllomedusa ecuatoriana Cannatella, 1982	*P. perinesos* group	*Phyllomedusa ecuatoriana*	*P. perinesos* group
Phyllomedusa hulli Duellman and Mendelson, 1995	*P. buckleyi* group	*Hylomantis hulli*	*Hylomantis buckleyi* group
Phyllomedusa hypochondrialis (Daudin, 1800)	*P. hypochondrialis* group	*Phyllomedusa hypochondrialis*	*P. hypochondrialis* group
Phyllomedusa iheringii Boulenger, 1885	*P. burmeisteri* group	*Phyllomedusa iheringii*	*P. burmeisteri* group
Phyllomedusa lemur Boulenger, 1882	*P. buckleyi* group	*Hylomantis lemur*	*Hylomantis buckleyi* group
Phyllomedusa megacephala (Miranda-Ribeiro, 1926)	*P. hypochondrialis* group	*Phyllomedusa megacephala*	*P. hypochondrialis* group
Phyllomedusa medinai Funkhouser, 1962	*P. buckleyi* group	*Hylomantis medinai*	*Hylomantis buckleyi* group
Phyllomedusa oreades Brandao, 2002	*P. hypochondrialis* group	*Phyllomedusa oreades*	*P. hypochondrialis* group
Phyllomedusa palliata Peters, 1873 ‘‘1872’’	Unassigned	*Phyllomedusa palliata*	Unassigned
Phyllomedusa perinesos Duellman, 1973	*P. perinesos* group	*Phyllomedusa perinesos*	*P. perinesos* group
Phyllomedusa psilopygion Cannatella, 1980	*P. buckleyi* group	*Hylomantis psilopygion*	*Hylomantis buckleyi* group
Phyllomedusa rohdei Mertens, 1926	*P. hypochondrialis* group	*Phyllomedusa rohdei*	*P. hypochondrialis* group
Phyllomedusa sauvagii Boulenger, 1882	*P. tarsius* group	*Phyllomedusa sauvagii*	*P. tarsius* group
Phyllomedusa tarsius (Cope, 1868)	*P. tarsius* group	*Phyllomedusa tarsius*	*P. tarsius* group
Phyllomedusa tetraploidea Pombal and Haddad, 1992	*P. burmeisteri* group	*Phyllomedusa tetraploidea*	*P. burmeisteri* group
Phyllomedusa tomopterna (Cope, 1868)	Unassigned	*Phyllomedusa tomopterna*	Unassigned
Phyllomedusa trinitatis Mertens, 1926	Unassigned	*Phyllomedusa trinitatis*	Unassigned
Phyllomedusa vaillantii Boulenger, 1882	Unassigned	*Phyllomedusa vaillantii*	Unassigned
Phyllomedusa venusta Duellman and Trueb, 1967	Unassigned	*Phyllomedusa venusta*	Unassigned

APPENDIX 2

LOCALITY DATA AND GENBANK ACCESSIONS

The table on the following pages lists all specimens, collection numbers, localities, and GenBank accessions of the sequences included in this analysis. **The current taxonomy of hylids is used here, as these names were used for the GenBank submission; see appendix 1 for the new taxonomy.** All species followed by an asterisk (*) correspond to sequences retrieved from GenBank. In a few cases, the tissues have separate numbers of official tissue collections. These are given as footnotes. The list includes collection abbreviations for (1) vouchers and or tissues employed in this project, (2) preserved specimens referred to in this paper, and (3) vouchers from sequences retrieved from GenBank, followed by an asterisk (*), with their locality data taken from Darst and Cannatella (2004).

Collection abbreviations are as follows: **AF,** Laboratório de Citogenética de Vertebrados, Instituto de Biociências, Universidade de São Paulo (to be accesioned in MZUSP); **AM,** Australian Museum, Sidney, Australia; **AM-CC,** Ambrose Monell Cryo Collection; **AMNH,** American Museum of Natural History, New York; **BMNH,** British Museum (Natural History), London; **CFBH,** Collection Célio F.B. Haddad, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil; **CWM,** Field number of Charles W. Myers (to be accessioned in AMNH); **DFCH-USFQ,** Universidad San Francisco de Quito, Quito, Ecuador; **DLR,** field numbers of Ignacio De la Riva (to be accessioned in the Museo Nacional de Ciencias Naturales, Madrid, Spain); **IRSNB,** Institut Royal des Sciences Naturelles de Belgique, Bruxelles; **ITH,** field numbers used in the project Levantamento da Fauna de Vertebrados Terrestres do área sob influência da Linha de Transmissão (LT) Itaberá-Tijuco Preto III (to be accessioned in MZUSP); **IWK,** field numbers used by Maureen A. Donnelly (to be accessioned in the Herpetological Collection of the Florida International University); **JF,** field numbers of Julian Faivovich (to be accessioned in MACN); **JPC,** field numbers of Janalee P. Caldwell; **KRL,** field numbers of Karen Lips; **KU,** University of Kansas, Museum of Natural History, Lawrence, KS; **LSUMZ H,** tissue collection, Louisiana State University Museum of Zoology, Baton Rouge, LA; **MACN,** Museo Argentino de Ciencias Naturales ‘‘Bernardino Rivadavia’’, Buenos Aires, Argentina; **MAD,** field numbers of Maureen Donnelly; **MCN,** Museo de Ciencias Naturales de la Universidad Nacional de Salta, Salta, Argentina; **MCP,** Museu de Ciências e Tecnologia da Pontificia Universidade Católica de Rio Grande do Sul, Brazil; **MCZ,** Museum of Comparative Zoology, Harvard University, Cambridge, MA; **MJH,** field numbers of Martin J. Henzl; **MLP-A,** Museo de La Plata, La Plata, Argentina; **MLP-DB,** Collection Diego Baldo, at MLP; **MNCN ADN,** collection of DNA samples of the Museo Nacional de Ciencias Naturales, Madrid, Spain; **MNHN.** Museum National d’Histoire Naturelle, Paris; **MNK,** Museo ‘‘Noel Kempf Mercado’’, Santa Cruz, Bolivia; **MRT,** field numbers of Miguel Trefaut Rodrigues (to be accesioned in MZUSP); **MVZ,** Museum of Vertebrate Zoology, University of California, Berkeley, CA; **MVZFC,** MVZ frozen tissue collection; **MZFC,** Museo de Zoología de la Facultad de Ciencias, Universidad Nacional Autónoma de Mexico; **MZUSP,** Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; **NHMG,** Naturhistoriska Museet, Göteborg, Sweden; **NMP6V,** National Museum, Prague, Czech Republic; **QCAZ,** Museo de Zoología de la Pontificia Universidad Católica del Ecuador; **QULC,** Queen’s University Laboratory Collection, Kingston, Canada; **RdS,** field numbers of Rafael de Sá; **RNF,** field numbers of Robert N. Fisher; **ROM,** Royal Ontario Museum, Toronto, Canada; **RWM,** field numbers of Roy W. McDiarmid (specimens to be accessioned in USNM); **SAMA,** South Australia Museum, Adelaide, South Australia; **SIUC-H,** Department of Zoology and Center for Systematic Biology, Southern Illinois University at Carbondale, IL; **TMSA,** Transvaal Museum, Pretoria, South Africa; **TNHC,** Texas Memorial Museum, Texas Natural History Collection, Austin, TX; **UMMZ,** University of Michigan, Museum of Zoology, Ann Arbor, MI; **USNM,** National Museum of Natural History, Smithsonian Institution, Washington DC; **UTA,** University of Texas at Arlington, TX; **ZFMK-H,** tissue collection of the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany; **ZMB,** Zoologisches Museum–Universität Humboldt, Berlin; **ZSM,** Zoologisches Staatssammlung, Munich, Germany; **ZUEC,** Museu de História Natural, Universidade de Campinas, Campinas, São Paulo, Brazil; **ZUFRJ,** Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

LIST OF SPECIMENS, COLLECTION NUMBERS, LOCALITIES, AND GENBANK ACCESSIONS OF SEQUENCES

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
LSUMZ H-2164	*Acris crepitans*	AY843559	AY843782	AY844533	AY844358	AY844019	AY844762	AY844194	USA: Alabama: De Kalb Co.: powerline access, 0.1 mi W of Lookout Mt. Boys Camp Rd.
AMNH A-168422	*Acris gryllus*	AY843560	AY843783	AY844534	AY844359	AY844020	AY844763	—	USA: Florida: Okaloosa Co.: Eglin AFB, J.R. Walton Pond. 30°41.59′N, 86°28.36′W
ENS 10039	*Anotheca spinosa*	AY843566	AY843788	AY844540	AY844363	AY844022	AY844768	AY844198	Mexico: Oaxaca: Ixtlan de Juarez: Santiago Comaltepec, Vista Hermosa
CFBH 2715	*Aparasphenodon brunoi*	AY843567	AY843789	AY844541	AY844364	AY844023	AY844769	AY844199	Brazil: Espírito Santo: Aracruz
CFBH 3001	*Aplastodiscus cochranae*	AY843568	AY843790	AY844542	AY844365	AY844024	AY844770	AY844200	Brazil: Santa Catarina: Rancho Queimado
MACN 37791	*Aplastodiscus perviridis*	AY843569	AY843791	AY844543	AY844366	AY844025	AY844771	AY844201	Argentina: Misiones: Guarani: San Vicente: Campo Anexo INTA ‘‘Cuartel Rio Victoria’’
MACN 38644	*Argenteohyla siemersi*	AY843570	AY843792	AY844544	AY844367	AY844026	AY844772	AY844202	Argentina: Corrientes: Bella Vista: Intersección R.N. 12 y Rio Santa Lucia
CFBH 2968	*Corythomantis greeningi*	AY843578	AY843800	AY844551	AY844374	AY844030	AY844779	AY844209	Brazil: Alagoas: Represa de Xingó, Piranhas
MVZ 207193[a]	*Duellmanohyla rufioculis*	AY549315	AY549368	AY844556	AY844377	AY844033	AY844782	AY844212	Costa Rica: Guanacaste: Volcan Cacao
UTA A-50812	*Duellmanohyla soralia*	AY843584	AY843806	AY844557	AY844378	AY844034	AY844783	—	Guatemala: Izabal: Morales, Sierra de Caral, Finca Quebradas–Cerro Pozo de Agua
CFBH 5915	*Hyla* sp. 1 (af. *H. ehrhardti*)	AY843669	AY843913	AY844660	AY844456	—	AY844875	—	Brazil: São Paulo: Ubatuba (Picinguaba)

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
USNM 303022	*Hyla arildae*	AY843604	AY843825	AY844578	AY844392	AY844049	AY844803	AY844223	Brazil: São Paulo: Near Salesópolis, Estaço Biologica de Boraceia
AF 0068	*Hyla weygoldti*	AY843685	AY843931	AY844678	AY844467	—	AY844887	—	Brazil: Espírito Santo: Domingos Martins: São Paulo do Aracã
USNM 284519	*Hyla albomarginata*	AY549316	AY549369	AY844568	AY844384	—	AY844794	AY844218	Brazil: Pernambuco: Near Carauruçu, on way to Serra dos Cavalos
KU 202734	*Hyla pellucens**	AY326058	—	—	—	—	—	—	Ecuador: Pichincha: 1.8 km SSE San Juan, 3420 m
KRL 798	*Hyla rufitela*	AY843662	AY843905	AY844652	—	AY844105	AY844867	AY844282	Panama: Coclé: El Copé: Parque Nacional ‘‘Omar Torrijos’’
CFBH 3184	*Hyla albosignata*	AY843596	AY843817	AY844570	AY844385	AY844042	AY844796	AY844219	Brazil: Santa Catarina: São Bento do Sul (Rio Vermelho)
CFBH 3909	*Hyla callipygia*	AY843614	AY843840	AY844592	AY844402	AY844058	AY844813	AY844236	Brazil: Minas Gerais: Monte Verde
AF 0070	*Hyla cavicola*	AY843617	AY843843	AY844594	AY844405	—	AY844814	—	Brazil: Espírito Santo: Domingos Martins
USNM 303038	*Hyla leucopygia*	AY843638	AY843873	AY844622	AY844425	AY844084	AY844840	AY844261	Brazil: São Paulo: Near Salesópolis, Estação Biologica de Boraceia
ZUEC 12053	*Hyla albopunctata*	AY549317	AY549370	AY844569	—	AY844041	AY844795	—	Brazil: São Paulo: Campinas
MJH 564	*Hyla lanciformis*	AY843636	AY843870	AY844619	—	AY844081	AY844837	AY844258	Peru: Loreto: Alpahuayo
AMNH A-141040[b]	*Hyla multifasciata*	AY843648	AY843887	AY844633	AY844436	AY844093	AY844851	AY844270	Guyana: Demerara: Ceiba Station, Madewini River, ca. 3 mi (linear) E Timehri Airport

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
MACN 37795	*Hyla raniceps*	AY843657	AY843900	AY844646	—	AY844103	AY844863	—	Argentina: Santa Fe: Vera: Ea. ‘‘Las Gamas’’
ROM 40304	*Hyla annectans*	AY843600	AY843821	AY844574	AY844388	AY844045	AY844800	—	Vietnam: Lao Cai: Sa Pa
N/A	*Hyla arborea*	AY843601	AY843822	AY844575	AY844389	AY844046	—	AY844221	Pet trade
LSUMZ H-230	*Hyla japonica*	AY843633	AY843866	AY844615	AY844420	AY844078	AY844833	AY844255	Japan: Hiroshima Prefecture: Hiroshima city Yasufutuichi-cho, Aita
N/A[c]	*Hyla savignyi*	AY843665	AY843907	AY844654	—	AY844107	—	AY844284	Yemen: Yarim (2813 m)
AMNH A-165163	*Hyla armata*	AY549321	AY549374	AY844579	AY844393	AY844050	AY844804	AY844224	Bolivia: Santa Cruz: Caballero: Canton San Juan: Amboro National Park
AMNH-A 165132[d]	*Hyla charazani*	AY843618	AY843844	AY844595	AY844406	AY844061	—	AY844239	Bolivia: La Paz: Bautista Saavedra: Canton Charazani, stream 2
RWM 17688	*Hyla inparquesi*	AY843672	—	AY844663	—	AY844114	AY844876	AY844291	Venezuela: Amazonas: Cerro de la Neblina
JAC 22650	*Hyla bistincta*	AY843609	AY843834	AY844587	AY844399	AY844054	—	AY844230	Mexico: Oaxaca: Mpo. Cuicatlan, Tutepetongo, 1619 m
JAC 21167	*Hyla calthula*	AY843615	AY843841	AY844593	AY844403	AY844059	—	AY844237	Mexico: Oaxaca: Carretera Coconales-Zacatepec, 1360 m
RWM 17746	*Hyla boans*	AY843610	AY843835	AY844588	—	AY844055	AY844809	AY844231	Venezuela: Amazonas: Caño Agua Blanca: 3.5 km SE Neblina base camp on Rio Baria
CFBH 2966	*Hyla crepitans*	AY843621	AY843850	AY844601	AY844412	AY844067	—	—	Brazil: Alagoas: Município de Piranhas: Represa de Xingó

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
MACN 37000	*Hyla faber*	AY549334	AY549387	AY844607	—	—	AY844825	—	Argentina: Misiones: Guarani: San Vicente: Campo Anexo INTA ‘‘Cuartel Rio Victoria’’
CFBH 4000	*Hyla lundii*	AY843639	AY843874	AY844623	—	AY844085	AY844841	AY844262	Brazil: São Paulo: Rio Claro (Itapé)
USNM 303046	*Hyla pardalis*	AY843651	AY843891	AY844637	—	AY844096	AY844855	—	Brazil: São Paulo: near Salesópolis, Estação Biologica de Boraceia
SIUC H-7079	*Hyla colymba*	AY843620	AY843848	AY844599	AY844410	AY844065	AY844818	AY844243	Panama: Coclé: Parque Nacional El Copé
SIUC H-6924	*Hyla palmeri*	AY843650	AY843890	AY844636	AY844439	AY844095	AY844854	AY844273	Panama: El Copé: Parque Nacional ‘‘Omar Torrijos’’
UTA A-50771	*Hyla bromeliacia*	AY843612	AY843837	AY844590	AY844401	AY844056	AY844811	AY844233	Guatemala: Huehuetenango: Sierra de los Cuchumatanes: Finca Chiblac (now Aldea Buenos Aires)
N/A (AMCC 125627)	*Hyla andersonii*	AY843598	AY843819	AY844572	—	AY844044	AY844798	—	USA: Florida: Santa Rosa Co.: Co. Rd. 191 N of Munson
MVZ 145385[e]	*Hyla cinerea*	AY549327	AY549380	AY844597	AY844408	AY844063	AY844816	AY844241	USA: Texas: Travis Co. Austin, Municipal Golf Course
AMNH A-168404	*Hyla gratiosa*	AY843630	AY843862	AY844611	AY844418	AY844076	AY844829	AY844252	USA: Florida: Santa Rosa Co.: Co. Rd. 191 N of Munson. 30°53.28′N, 86°53.26′W
AMNH A-168427	*Hyla squirella*	AY843678	AY843923	AY844670	AY844462	AY844119	AY844882	AY844295	USA: Florida: Alachua Co.: Co. Rd. 346 1.2 mi 121, 29°30.11′N, 82°25.62′W

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
USNM 303032	*Hyla astartea*	AY549322	AY549375	AY844580	—	—	—	AY844225	Brazil: São Paulo: near Salesópolis, Estação Biológica de Boracéia
CFBH 3621	*Hyla circumdata*	AY549328	AY549381	AY844598	AY844409	AY844064	AY844817	AY844242	Brazil: Santa Catarina: São Bento do Sul
USNM 303036	*Hyla hylax*	AY549338	AY549391	AY844614	AY844419	AY844077	AY844832	AY844254	Brazil: São Paulo: near Salesópolis, Estação Biológica de Boracéia
CFBH 5766	*Hyla* sp. 3	AY843673	AY843916	AY844664	—	AY844115	—	—	Brazil: Rio de Janeiro: Angra dos Reis
CFBH 5917	*Hyla* sp. 4	AY843674	AY843917	AY844665	AY844458	AY844116	AY844877	—	Brazil: São Paulo: Ubatuba: Picinguaba
DFCH-USFQ 899	*Hyla carnifex*	AY843616	AY843842	—	AY844404	AY844060	—	AY844238	Ecuador: Pichincha: Tandayapa
CFBH 5418	*Hyla berthalutzae*	AY843607	AY843831	AY844584	AY844397	AY844052	AY844807	AY844228	Brazil: Rio de Janeiro: Duque de Caxias
UMMZ 7755	*Hyla arenicolor*	AY843603	AY843824	AY844577	AY844391	AY844048	AY844802	—	USA: Arizona: Gila Co.: Houston creek just N Hwy 260, approx. 4 mi E of Payson
UTA A-54763	*Hyla euphorbiacea*	AY843625	AY843855	AY844606	—	AY844072	AY844823	AY844248	Mexico: Oaxaca: Carretera Mitla-Ayutla, 1950 m
MZFC 4814	*Hyla eximia*	AY843626	AY843856	—	—	AY844073	AY844824	AY844249	Mexico: Puebla: Chignahuapan, 20 km S
AMNH A-168406	*Hyla walkeri*	AY843684	AY843930	AY844677	AY844466	AY844125	—	—	Pet trade
NMP6V 71250	*Hyla calcarata*	AY843613	AY843839	—	—	—	—	AY844235	Peru: Anguilla, 50 km W of Iquitos
MAD 440	*Hyla fasciata*	AY549335	AY549388	AY844608	—	—	—	—	Guyana: Iwokrama: Cowfly camp, 80 m
AMNH-A 141054[f]	*Hyla geographica*	AY843628	—	—	—	—	—	—	Guyana: Warniabo Creek, 4 mi (by rd) SW Dubulay Ranch house
ROM 39582	*Hyla kanaima*	AY843634	AY843868	AY844617	AY844422	AY844079	AY844835	—	Guyana: Mount Ayanganna

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
NMP6V 71258/1	*Hyla microderma*	AY843644	AY843881	—	—	—	—	AY844267	Peru: Anguilla, 50 km W of Iquitos
KU 202737	*Hyla picturata**	AY326055	—	—	—	—	—	—	Ecuador: Pichincha: Tinalandia: 15.5 km SE Santo Domingo de los Colorados, 700 m
ROM 39624	*Hyla roraima*	AY843660	AY843903	AY844650	AY844448	AY844104	AY844866	AY844280	Guyana: Mount Ayanganna
CFBH 5424	*Hyla semilineata*	AY843778 AY843779	AY843909	AY844656	AY844453	AY844108	AY844871	AY844286	Brazil: Rio de Janeiro: Duque de Caxias
RdS 606	*Hyla picta*	AY843654	AY843894	AY844640	AY844442	AY844099	AY844858	AY844276	Belize: Stann Creek District: Cokscomb Basin Wildlife Santuary
UTA A-54773	*Hyla smithii*	AY843668	AY843912	AY844659	—	AY844111	AY844874	—	Mexico: Oaxaca: Sierra Madre del Sur; Carretera Pochutla, 288 m
MAD 085	*Hyla granosa*	AY549336	AY843861	AY844610	—	—	AY844828	—	Guyana: Iwokrama: Muri Scrub camp, 80 m
ROM 39570	*Hyla lemai*	AY843637	AY843871	AY844620	AY844423	AY844082	AY844838	AY844259	Guyana: Mount Ayanganna
ROM 39561	*Hyla sibleszi*	AY843667	AY843911	AY844658	AY844455	AY844110	AY844873	AY844288	Guyana: Mount Ayanganna
QULC 97005	*Hyla labialis*	AY843635	AY843869	AY844618	—	AY844080	AY844836	AY844257	Colombia: Parque Natural Nacional Chingaza
KU 202760	*Hyla pacha**	AY326057	—	—	—	—	—	—	Ecuador: Azuay: 2 km SSE Palmas, 2340 m
KU 202732	*Hyla pantosticta**	AY326052	—	—	—	—	—	—	Ecuador: Napo: 18 km E Santa Barbara
QCAZ 16704	*Hyla tapichalaca*	AY563625	AY843925	AY844672	—	AY844121	—	AY844297	Ecuador: Zamora-Chinchipe: Reserva Tapichalaca: road between Yangana and Valladolid

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
RdS 790	*Hyla ebraccata*	AY843624	AY843853	AY844604	AY844415	AY844070	AY844822	AY844247	Belize: Stann Creek District: Cokscomb Basin Wildlife Santuary (captive-raised tadpoles from adults collected in this locality)
MJH 7143	*Hyla sarayacuensis*	AY843664	—	—	AY844451	—	AY844869	—	Peru: Huanuco: Rio Llullapichis: Panguana
MJH 3844	*Hyla triangulum*	AY843680	AY843926	AY844673	AY844464	AY844122	—	AY844298	Brazil: Acre: Lago Catalão: Ilha Xiborena
AF 414	*Hyla martinsi*	AY843641	AY843878	AY844626	—	AY844086	AY844844	AY844264	Brazil: Minas Gerais: Santa Bárbara
MJH 7116	*Hyla marmorata*	AY843640	AY843877	—	AY844428	—	—	—	Peru: Huanuco: Rio Llullapichis: Panguana
CFBH 5761	*Hyla senicula*	AY843666	AY843910	AY844657	AY844454	AY844109	AY844872	AY844287	Brazil: Rio de Janeiro: Angra dos Reis
MRT5946	*Hyla bipunctata*	AY843608	AY843832	AY844585	—	AY844053	AY844808	AY844229	Brazil: Bahia: Jussari: Serra do Teimoso
UTA A-50632	*Hyla microcephala*	AY843643	AY843880	AY844628	AY844430	—	AY844846	AY844266	Honduras: Atlantida: Cordillera Nombre de Dios, Aldea Rio Viejo
MACN 37785	*Hyla nana*	AY549346	AY843888	AY844634	AY844437	—	AY844852	AY844271	Argentina: Entre Rios: Depto. Islas del Ibicuy
MHZ 462	*Hyla rhodopepla*	AY843658	—	AY844647	AY844446	—	AY844864	—	Peru: Loreto: Jenaro Herrera
MACN 38638	*Hyla sanborni*	AY843663	AY843906	AY844653	AY844450	AY844106	AY844868	AY844283	Argentina: Entre Rios: Depto. Islas del Ibicuy: Ruta 12 vieja, entre Brazo Largo y Arroyo Luciano
MJH 129	*Hyla walfordi*	AY843683	AY843929	AY844676	—	—	AY844886	—	Brazil: Unknown
JPC 10772[g]	*Hyla miyatai*	AY843647	AY843886	AY844632	AY844435	AY844092	AY844850	—	Ecuador: Sucumbios

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
MACN 33799	*Hyla minuta*	AY549345	AY549398	—	AY844432	AY844089	—	—	Argentina: Misiones: Guarani: San Vicente: Campo Anexo INTA ‘‘Cuartel Rio Victoria’’
UTA A-56283	*Hyla arborescandens*	AY843602	AY843823	AY844576	AY844390	AY844047	AY844801	AY844222	Mexico: Puebla: Sierra Negra, 1833 m
UTA A-54762	*Hyla cyclada*	AY843622	AY843851	AY844602	AY844413	AY844068	AY844820	AY844245	Mexico: Oaxaca: Sierra Mixe, 2.0 mi W Totontepec, 2045 m
UTA A-54766	*Hyla melonomma*	AY843642	AY843879	AY844627	AY844429	AY844087	AY844845	AY844265	Mexico: Oaxaca: Sierra Madre del Sur; Carretera Pochutla, 681m
JAC 22438	*Hyla miotympanum*	AY843645	AY843884	AY844630	AY844433	AY844090	AY844848	—	Mexico: Puebla: Sierra Norte, Cuetzalan, Hotel Villas Cuetzalan, 1250 m
UTA A-54721	*Hyla perkinsi*	AY843653	AY843893	AY844639	AY844441	AY844098	AY844857	AY844275	Guatemala: Huehuetenango: Barillas, Aldea Nucaquexis
JAC 21583	*Hyla mixe*	AY843646	AY843885	AY844631	AY844434	AY844091	AY844849	AY844269	Mexico: Oaxaca: Sierra Mixe; Mun. Santiago Zacatepec: carretera Zacatepec-Jesus Carranza, 28 mi de entronque con carretera a Totontepec, 803 m
MJH 7101	*Hyla brevifrons*	AY843611	AY843836	AY844589	AY844400	—	AY844810	AY844232	Peru: Huanuco: Rio Llullapichis: anguana
CFBH S/N	*Hyla giesleri*	AY843629	AY843860	—	AY844417	AY844075	AY844827	AY844251	Brazil: São Paulo: Ubatuba: Picinguaba

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
AMNH A-139315	*Hyla parviceps*	AY843652	AY843892	AY844638	AY844440	AY844097	AY844856	AY844274	Brazil: Acre: Centro Experimental da Universidade do Acre at km 23 on Rio Branco-Porto Velho Road
MVZ 149750[h]	*Hyla rivularis*	AY843659	AY843902	AY844649	—	AY844117	—	—	Costa Rica: Heredia: ''Chompipe'' vicinity of Volcan Banba
JAC 2224	*Hyla* sp. 5 (aff. *H. thorectes*)	AY843675	AY843918	AY844666	AY844459	AY844118	AY844878	—	Mexico: Guerrero: Carretera Nueva Delhi-La Guitarra, 1900 m
CFBH 5642	*Hyla* sp. 6 (aff. *H. pseudopseudis*)	AY843676	AY843919	AY844667	AY844460	AY844101	AY844879	AY844292	Brazil: Bahia: Município de Lençois: Rio Grisante, Serra do Sincorá, Chapada Diamantina
MVZ 149764	*Hyla pseudopuma*	AY843656	AY843897	AY844643	AY844444	AY844075	AY844861	AY844277	Costa Rica: Punta Arenas: Monteverde
MLPA 2138	*Hyla andina*	AY549319	AY549372	AY844573	AY844387	—	AY844799	—	Argentina: Tucuman: Tafi del Valle
DLR 4119	*Hyla balzani*	AY549323	AY549376	AY844582	AY844395	—	AY844806	AY844226	Bolivia: Depto. La Paz: Prov. Noryungas: Serrania Bellavista
CFBH 3356	*Hyla bischoffi*	AY549324	AY549377	AY844586	AY844398	—	—	—	Brazil: Santa Catarina: Rancho Queimado
MLP-DB 1084	*Hyla caingua*	AY549326	AY549379	AY844591	—	AY844057	AY844812	AY844234	Argentina: Misiones: Posadas
MACN 37692	*Hyla cordobae*	AY549330	AY549383	AY844600	AY844411	AY844066	AY844819	AY844244	Argentina: San Luis: Depto. Chacabuco: Villa Elena: Arroyo ''La calera''
MACN 37794	*Hyla* sp. 7 (aff. *H. semiguttata*)	AY549359	AY549412	—	—	—	AY844880	—	Argentina: Misiones: San Vicente: Campo Anexo INTA ''Cuartel Rio Victoria''

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
MZUSP 111556	*Hyla latistriata*	AY549360	AY549413	AY844668	—	—	—	AY844293	Brazil: Minas Gerais: Município Itamontes
CFBH 3599	*Hyla ericae*	AY549332	AY549385	AY844605	AY844416	AY844071	—	—	Brazil: Goiás: Alto Paraiso de Goiás
CFBH 3386	*Hyla guentheri*	AY843631	AY549390	AY844612	—	—	AY844830	AY844253	Brazil: Rio Grande do Sul: Terra de Areia
CFBH 3625	*Hyla joaquini*	AY549339	AY549392	AY844616	AY844421	—	AY844834	AY844256	Brazil: Santa Catarina: Urubici
CFBH 3848	*Hyla leptolineata*	AY549341	AY549394	AY844621	AY844424	AY844083	AY844839	AY844260	Brazil: Santa Catarina: Municipio de São Domingos
CFBH 3098	*Hyla marginata*	AY549342	AY549395	AY844624	AY844426	—	AY844842	AY844263	Brazil: Rio Grande do Sul: São Francisco de Paula
MV 0249	*Hyla marianitae*	AY549344	AY549397	AY844625	AY844427	—	AY844843	—	Argentina: Salta: Baritu
CFBH 5752	*Hyla polytaenia*	AY843655	AY843895	AY844641	AY844443	—	AY844859	—	Brazil: Rio de Janeiro: Itatiaia: Maringá
CFBH 3388	*Hyla prasina*	AY549347	AY549400	AY844642	—	AY844100	AY844860	—	Brazil: Santa Catarina: Rio Vermelho
MACN 37788	*Hyla pulchella*	AY549352	AY549405	AY844644	AY844445	AY844102	AY844862	AY844278	Argentina: Buenos Aires: Cariló
MACN 37509	*Hyla riojana*	AY549355	AY549408	AY844648	AY844447	—	AY844865	AY844279	Argentina: La Rioja: Sanogasta: El Huaco de Arriba
CFBH 3579	*Hyla semiguttata*	AY549357	AY549410	AY844655	AY844452	—	AY844870	AY844285	Brazil: Paraná: Piraquara
MACN 37792	*Hyla punctata*	AY549353	AY549406	AY844645	—	—	—	—	Argentina: Chaco: Resistencia: Camino a Isla del Cerrito, altura Peaje Gral. Belgrano
IT-H 0653	*Hyla rubicundula*	AY843661	AY843904	AY844651	AY844449	—	—	AY844281	Brazil: São Paulo: Buri
JAC 21736	*Hyla chimalapa*	AY843619	AY843845	AY844596	AY844407	AY844062	AY844815	AY844240	Mexico: Chiapas: Colonia Rodulfo Figueroa, El Carrizal, 1475 m

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
JAC 22371	*Hyla xera*	AY843686	AY843932	AY844679	AY844468	AY844126	AY844888	AY844300	Mexico: Puebla: Carretera Texcala-Zapotitlan Salinas, 5227 ft
JAC 21531	*Hyla nephila*	AY843649	AY843889	AY844635	AY844438	AY844094	AY844853	AY844272	Mexico: Oaxaca: Colonia Rodulfo Figueroa, El Carrizal, 1475 m
JAC 24443	*Hyla taeniopus*	AY843679	AY843924	AY844671	AY844463	AY844120	AY844883	AY844296	Mexico: Puebla: Sierra Norte, Cuetzalan, Hotel Villas Cuetzalan, 1250 m
UTA A-51838	*Hyla dendrophasma*	AY843623	AY843852	AY844603	AY844414	AY844069	AY844821	AY844246	Guatemala: Huehuetenango: Finca San Francisco, near Aldea Yalambojoch
SIUC H-06998	*Hyla miliaria*	AY843776 AY843777	AY843882	AY844629	AY844431	AY844088	AY844847	AY844268	Panama: Coclé: El Copé: Parque Nacional Omar Torrijos
CFBH 5788	*Hyla uruguaya*	AY843681	AY843927	AY844674	—	AY844123	AY844884	AY844299	Brazil: Rio Grande do Sul: Cambará do Sul
AMNH A-168423	*Hyla avivoca*	AY843605	AY843828	AY844581	AY844394	AY844051	AY844805	—	USA: Florida: Alachua Co.: Lochloosa Wildlife Mgmt area near River Styx. 29°31.25′N, 82°13.04′
AMNH A-168425	*Hyla femoralis*	AY843627	AY843859	AY844609	—	AY844074	AY844826	AY844250	USA: Florida: Okaloosa Co.: US Hwy 90 at Yellow River floodplain
UMFS 5545	*Hyla versicolor*	AY843682	AY843928	AY844675	AY844465	AY844124	AY844885	—	Pet trade
CWM 19512	*Hyla* sp. 8	AY843671	AY843915	AY844662	—	AY844113	—	AY844290	Venezuela: Bolivar: Cerro Guanay

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
CFBH 5652	*Hyla* sp. 9 (aff. *H. alvarengai*)	AY843677	AY843922	AY844669	AY844461	—	AY844881	AY844294	Brazil: Bahia: Município de Lençois: Rio Grisante, Serra do Sincorá, Chapada Diamantina
CFBH 5797	*Hyla anceps*	AY843597	AY843818	AY844571	AY844386	AY844043	AY844797	AY844220	Brazil: Espírito Santo: Linhares (Povoação)
USNM 302435	*Hyla benitezi*	AY843606	AY843830	AY844583	AY844396	—	—	AY844227	Brazil: Roraima: Villa Pacaraima, border marker BV (Brazil–Venezuela) 8
AMNH A-168405	*Hyla heilprini*	AY843632	AY843864	AY844613	—	—	AY844831	—	Pet trade
NMP6V 71202/2	*Hyla* sp. 2	AY843670	AY843914	AY844661	AY844457	AY844112	—	AY844289	Peru: 50 km W of Iquitos
N/A[i]	*Lysapsus laevis*	AY843696	AY843941	AY844689	AY844476	AY844133	AY844896	AY844305	Guyana: Southern Rupununi Savanah: Aishalton (on Kubanawan Creek)
MACN 38645	*Lysapsus limellum*	AY843697	AY843942	AY844690	AY844477	—	AY844897	—	Argentina: Corrientes: Bella Vista: Intersección R.N. 12 y Rio Santa Lucia
N/A	*Nyctimantis rugiceps*	AY843780 AY843781	AY843945	—	—	—	—	—	Ecuador: Napo: Jatun Sacha (eggs laid in captivity from adults collected there)
JPC 13178[j]	*Osteocephalus cabrerai*	AY843705	AY843950	AY844696	AY844481	AY844136	AY844902	AY844310	Brazil: Acre: 5 km N Porto Walter, inland from Rio Jurua
MACN 38643	*Osteocephalus langsdorffii*	AY843706	AY843951	AY844697	AY844482	AY844137	AY844903	AY844311	Argentina: Misiones: General Belgrano: 10 km N Bernardo de Irigoyen: Salto Andresito

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
AMNH A-131254	*Osteocephalus leprieurii*	AY549361	AY843952	AY844698	AY844483	AY844138	AY844904	AY844312	Venezuela: Amazonas: Neblina Base Camp on Rio Mawarinuma (= Rio Baria), 140 m
MNHN 2001.0828	*Osteocephalus oophagus*	AY843708	AY843953	AY844699	AY844484	AY844139	—	—	French Guyana: Kaw road: 04°42N/52°18W
AMNH-A 131245	*Osteocephalus taurinus*	AY843709	AY843954	AY844700	AY844485	AY844140	AY844905	AY844313	Venezuela: Amazonas: Neblina Base Camp on Rio Mawarinuma (=Rio Baria), 140 M
N/A	*Osteopilus crucialis*	AY843710	AY843955	—	—	—	—	AY844314	Jamaica: Manchester Parish: Mandeville (eggs laid in captivity from adults collected there)
AMNH A-168410	*Osteopilus dominicensis*	AY843711	AY843956	AY844701	AY844486	AY844141	—	AY844315	Pet trade
USNM 317830	*Osteopilus septentrionalis*	AY843712	AY843957	—	AY844487	AY844142	AY844906	AY844316	Cuba: Guantanamo: Guantanamo Bay
AMNH A-168415	*Osteopilus vastus*	AY843713	AY843958	—	—	AY844143	AY844907	AY844317	Pet trade
MNHN 2001.0814	*Phrynohyas hadroceps*	AY843717	AY843962	AY844704	AY844490	AY844146	—	AY844319	French Guyana: Kaw road: 04°42′N, 52°18′W
CFBH 5780	*Phrynohyas mesophaea*	AY843718	AY843963	AY844705	AY844491	AY844147	AY844910	AY844320	Brazil: Rio de Janeiro: Parati
AMNH-A 131201[k]	*Phrynohyas resinifrictix*	AY843719	AY843964	AY844706	AY844492	AY844148	AY844911	AY844321	Venezuela: Amazonas: Neblina base camp on Rio Mawarinuma, 140 m
AMNH-A 141142	*Phrynohyas venulosa*	AY549362	AY549415	AY844707	AY844493	AY844149	AY844912	AY844322	Guyana: Dubulay Ranch on the Berbice River, 200 ft
N/A[l]	*Phyllodytes luteolus*	AY843721	AY843965	AY844708	AY844494	AY844150	AY844913	AY844324	Brazil: Espírito Santo: Setiba, Guarapari
MRT 6144	*Phyllodytes* sp.	AY843722	AY843966	AY844709	—	AY844151	AY844914	AY844325	Brazil: Bahia: Uruci-Una

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
MVZ 149403	*Plectrohyla glandulosa*	AY843730	AY843967	AY844718	AY844500	AY844159	AY844923	AY844331	Guatemala: San Marcos: ridge above El Rincon
UTA A-55140	*Plectrohyla guatemalensis*	AY843731	AY843976	AY844719	AY844501	AY844160	AY844924	AY844332	Guatemala: Guatemala: Don Justo: Santa Rosalia: km 12.5 carretera a El Salvador
JAC 21707	*Plectrohyla matudai*	AY843732	AY843977	AY844720	AY844502	AY844161	AY844925	AY844333	Mexico: Chiapas: camino Colonia Rodulfo Figueroa, Diaz Ordaz–1.4 mi de Rodulfo Figueroa
RNF 2424	*Pseudacris cadaverina*	AY843734	AY843978	AY844722	—	AY844162	—	AY844334	USA: California: San Diego Co: Anza Borrego
N/A	*Pseudacris crucifer*	AY843735	AY843980	AY844723	—	AY844163	AY844927	—	Pet trade
AMNH A-168472	*Pseudacris ocularis*	AY843736	AY843981	AY844724	—	AY844164	—	—	USA: Florida: Columbia Co., SR 250 2 mi W I-10
RNF 3255	*Pseudacris regilla*	AY843737	AY843982	AY844725	AY844504	AY844165	—	—	USA: California: San Diego Co.: Bowden Canyon
AMNH A-168468	*Pseudacris triseriata*	AY843738	AY843983	AY844726	—	AY844166	AY844928	AY844335	USA: Utah: Cache: Amalga
MACN 37786	*Pseudis minuta*	AY843739	AY843984	—	AY844505	—	AY844929	AY844336	Argentina: Entre Rios: Depto. Islas del Ibicuy: Ruta 12 vieja
MACN 38642	*Pseudis paradoxa*	AY843740	AY843985	AY844727	AY844506	AY844167	—	AY844337	Argentina: Corrientes: Depto. Bellavista: Camino San Roque-Bellavista
MVZ 132995	*Pternohyla fodiens*	AY843743	AY843986	AY844730	AY844508	AY844169	AY844932	AY844339	Mexico: Sonora: Vicinity Alamos
UTA A-54786	*Ptychohyla euthysanota*	AY843744	AY843989	AY844731	AY844509	AY844170	AY844933	AY844340	Mexico: Chiapas: Cerro El Baul, Colonia Rodulfo Figueroa, 1307 m

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
ENS 8486	*Ptychohyla hypomykter*	AY843745	AY843990	AY844732	—	—	—	—	Guatemala: Izabal
UTA A-54782	*Ptychohyla leonhardschultzei*	AY843746	AY843991	AY844733	AY844510	AY844171	AY844934	AY844341	Mexico: Oaxaca: Sierra Madre del Sur; Carretera Pochutla, 681 m
USNM 514381	*Ptychohyla spinipollex*	AY843748	AY843992	AY844735	AY844512	AY844173	AY844936	AY844343	Honduras: Atlantida: Parque Nacional Pico Bonito, Quebrada de Oro (tributary of Rio Viejo)
UTA A-54784	*Ptychohyla zophodes*	AY843749	AY843994	AY844736	AY844513	AY844174	AY844937	AY844344	Mexico: Oaxaca: Sierra Mixe; Mun. Santiago Zacatepec, carretera Zacatepec–Jesus Carranza, 1182 m
JAC 21606	*Ptychohyla* sp.	AY843747	AY843993	AY844734	AY844511	AY844172	AY844935	AY844342	Mexico: Oaxaca: Sierra Mixe
QULC 2340	*Scarthyla goinorum*	AY843752	AY843997	AY844738	AY844514	—	AY844938	—	Brazil: Amazonas: Igarapé Nova Empresa
MACN 38649	*Scinax acuminatus*	AY843753	AY843998	AY844739	AY844515	AY844176	AY844939	—	Argentina: Corrientes: Paso de la Patria
MLPA 2137	*Scinax berthae*	AY843754	AY843999	AY844740	—	—	AY844940	AY844345	Argentina: Buenos Aires: Atalaya
MVZ 207215[m]	*Scinax boulengeri*	AY843755	AY844000	AY844741	AY844516	AY844177	—	—	Costa Rica: Guanacaste: ca. 0.2 km W Costa Rica Hwy 1 on first paved road 10 km N entrance Santa Rosa National Park along Hwy 1
MCP3734	*Scinax catharinae*	AY843756	AY844001	AY844742	AY844517	—	AY844941	AY844346	Brazil: Rio Grande Do Sul: Pro-Mata

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
MVZ 203919[n]	*Scinax elaeochrous*	AY843757	AY844002	AY844743	AY844518	AY844178	AY844942	—	Costa Rica: Heredia: Starkey′s Woods, 1.5–3.0 km E Rio Frio Rd., at 1 km NW entrance Estacion Biologica La Selva
JF1973	*Scinax fuscovarius*	AY843758	AY844003	AY844744	AY844519	AY844179	AY844943	AY844347	Argentina: Misiones: Guarani: San Vicente: Campo Anexo INTA ‘‘Cuartel Rio Victoria’’
MACN 38650	*Scinax nasicus*	AY843759	AY844004	AY844745	AY844520	AY844180	—	AY844348	Argentina: Buenos Aires: Baradero: Estancia ‘‘El Retoño’’
IWK 109	*Scinax ruber*	AY549365	AY549418	AY844746	AY844521	AY844181	AY844944	—	Guyana: Iwokrama: Muri Scrub camp
MACN 38241	*Scinax squalirostris*	AY843760	—	AY844747	AY844522	AY844182	AY844945	AY844349	Argentina: Entre Rios: Depto. Islas del Ibicuy: Ruta 12 vieja, entre Brazo Largo y Arroyo Luciano
UTA A-50749	*Scinax staufferi*	AY843761	AY844006	AY844748	AY844523	AY844183	—	—	Guatemala: Zacapa: 2.9 km S Teculutan, on road to Huit
MVZ 133014[o]	*Smilisca baudinii*	AY549366	AY844007	AY844749	—	—	AY844946	—	Mexico: Sonora: 10.6 mi W (by road) Alamos
JAC 22624	*Smilisca cyanosticta*	AY843763	AY844008	AY844750	AY844524	AY844184	AY844947	AY844350	Mexico: Veracruz: Mpo. San Andres Tuxtla, Volcan San Martin, Martires de Chicago
RdS 786	*Smilisca phaeota*	AY843764	AY844009	AY844751	—	AY844185	AY844948	AY844351	Captive raised from breeding adults at Baltimore National Aquarium

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
VCR 179	*Smilisca puma*	AY843765	AY844010	AY844752	AY844525	AY844186	AY844949	—	Costa Rica: Provincia Heredia: Chilamate (15 km W Puerto Viejo): Reserva ‘‘El Vejuco’’
MJH 46	*Sphaenorhynchus dorisae*	AY843766	AY844011	AY844753	AY844526	AY844187	—	—	Brazil: Amazonas: Manaus: Lago Janauri
USNM 152136	*Sphaenorhynchus lacteus*	AY549367	AY844012	AY844754	AY844527	AY844188	—	AY844352	Peru: Madre de Dios: 30 km (airline) SSW Puerto Maldonado, Tambopata Reserve
MNHNP 1998-311	*Tepuihyla edelcae*	AY843770	—	—	AY844530	—	—	—	Venezuela: Estado Bolivar: Auyantepui, 2015 m
UMMZ 218914	*Trachycephalus jordani*	AY843771	AY844015	AY844758	AY844531	AY844190	AY844953	AY844356	No data
N/A[1]	*Trachycephalus nigromaculatus*	AY843772	AY844016	AY844759	—	AY844191	—	—	Brazil: Espírito Santo: Setiba, Guarapari
RdS 749	*Triprion petasatus*	AY843774	AY844017	AY844761	AY844532	AY844193	AY844955	AY844357	Belize: Hummingbird Hwy, 9.5 km from Western Highway turnpoint (captive-raised tadpoles, from adults collected in this locality)
N/A[1]	*Xenohyla truncata*	AY843775	AY844018	—	—	—	—	—	Brazil: Rio de Janeiro: Restinga de Maricá
	Hylidae, Hemiphractinae								
	Cryptobatrachus sp.*	AY326050	—	—	—	—	—	—	Colombia: Santander: Municipio San Gil: 7 km by road SW San Gil
CFBH 5720	*Flectonotus* sp.	AY843589	AY843809	AY844562	AY844379	AY844038	AY844788	AY844215	Brazil: Santa Catarina: Santo Amaro da Imperatriz

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
KRL 799	*Gastrotheca cornuta*	AY843591	AY843811	—	—	AY844040	—	—	Panama: Coclé: El Copé: Parque Nacional ‘‘Omar Torrijos’’
JLG90	*Gastrotheca fissipes*	AY843592	—	AY844564	AY844381	—	AY844790	—	Brazil: Espírito Santo: Setiba, Guarapari
MNK 5286	*Gastrotheca* cf. *marsupiata*	AY843590	AY843810	AY844563	AY844380	AY844039	AY844789	—	Bolivia: Santa Cruz: Caballero: Canton San Juan: Amboro Narional Park
TNHC 62492	*Gastrotheca pseustes**	AY326051	—	—	—	—	—	—	Ecuador: Chimborazo: 3.3 km S Tix an, 2990 m
MJH 3689	*Hemiphractus helioi*	AY843594	AY843813	AY844566	AY844382	—	AY844792	—	Peru: Ucayali: 3 km S km 65 on Carretera Federico Basadre at Ivita
AMNH A-164211	*Stefania evansi*	AY843767	—	AY844755	—	AY844189	AY844950	AY844353	Guyana: Iwokrama: Pakatau Creek (85 m, 4°45′N, 59°01′W)
MNHN 2002.692	*Stefania schuberti*	AY843768	AY844013	AY844756	AY844528	—	AY844951	AY844354	Venezuela: Estado Bolivar: Auyantepui, 2325 m
	Hylidae, Phyllomedusinae								
KRL 800	*Agalychnis calcarifer*	AY843562	AY843785	AY844536	—	—	—	AY844196	Panama: Coclé: El Copé: Parque Nacional ‘‘Omar Torrijos’’
RdS 537	*Agalychnis callidryas*	AY843563	—	AY844537	—	—	AY844765	—	Belize: Stann Creek District: Cokscomb Basin Wildlife Santuary
QCAZ 13217	*Agalychnis litodryas**	AY326043	—	—	—	—	—	—	Ecuador: Unknown

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
MVZ 203768	*Agalychnis saltator**	AY326044	—	—	—	—	—	—	Costa Rica: Heredia: Starkey's Woods: 1.5–3.0 km E Rio Frio Rd at 1 km NW entrance to Estacion Biologica La Selva
ZUFRJ 7926	*Hylomantis granulosa*	AY843687	AY843933	AY844680	AY844469	AY844127	AY844889	AY844301	Brazil: Pernambuco: Jaqueira
JAC 22009	*Pachymedusa dacnicolor*	AY843714	AY843959	AY844702	AY844488	AY844144	AY844908	AY844318	Mexico: Guerrero: Carretera Tierra Colorada-Ayutla, 187 m
CFBH 7307	*Phasmahyla cochranae*	AY843715	AY843960	—	—	—	—	—	Brazil: Minas Gerais: Poços de Caldas
CFBH 5756	*Phasmahyla guttata*	AY843716	AY843961	AY844703	AY844489	AY844145	AY844909	—	Brazil: São Paulo: Ubatuba: Picinguaba
AMNH A 168459	*Phyllomedusa bicolor*	AY843723	AY843968	AY844710	AY844495	AY844152	AY844915	—	Pet trade
AMNH-A 141109[p]	*Phyllomedusa hypochondrialis*	AY843724	AY843969	AY844711	AY844496	AY844153	AY844916	—	Guyana: Dubulay Ranch on the Berbice River
KRL 955	*Phyllomedusa lemur*	AY843687	AY843970	AY844712	—	AY844154	AY844917	—	Panama: Coclé: El Copé: Parque Nacional "Omar Torrijos"
KU 205420	*Phyllomedusa palliata**	AY326046	—	—	—	—	—	—	Peru: Madre de Dios: Cuzco Amazonico
MJH 67	*Phyllomedusa tarsius*	AY843726	AY843971	AY844713	—	AY844155	AY844918	AY844326	Brazil: Amazonas: Manaus: Reserva Duke
MACN 37796	*Phyllomedusa tetraploidea*	AY843727	AY843972	AY844714	—	AY844156	AY844919	AY844327	Argentina: Misiones: Guarani: San Vicente: Campo Anexo INTA "Cuartel Rio Victoria"
MJH 7076	*Phyllomedusa tomopterna*	AY843728	AY843973	AY844715	AY844497	AY844157	AY844920	AY844328	Peru: Huanuco: Rio Llullapichis: Panguana

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
AMNH-A 166288[q]	*Phyllomedusa vaillanti*	AY549363	AY549416	AY844716	AY844498	AY844158	AY844921	AY844329	Guyana: Berbice River camp at ca. 18 mi (linear) SW Kwakwani (ca. 2 mi downriver from Kurundi River) confluence), 200 ft
	Hylidae, Pelodryadinae								
SAM 16906	*Cyclorana australis*	AY843580	AY843802	AY844553	AY844376	—	—	—	Australia: No data
TNHC 51936	*Litoria arfakiana**	AY326039	—	—	—	—	—	—	Papua New Guinea: Madang: ca. 10 km NW Simbai, Kaironk Village, 2000 m
AM 52744	*Litoria aurea*	AY843691	AY843937	AY844684	—	AY844130	AY844892	—	New Caledonia: Province Nord: Valle Phaaye, Nomac River, 8 km E Poum
AMNH A-168409	*Litoria caerulea*	AY843692	AY843938	AY844685	—	AY844131	AY844893	—	Pet trade
SAMA 12260	*Litoria freicyneti*	AY843693	AY843939	AY844686	AY844473	—	AY844894	—	Australia: New South Wales: 16 km E Retreat
N/A	*Litoria infrafrenata*	AY843694	AY843940	AY844687	AY844474	—	—	AY844304	Pet trade
SAMA 17215	*Litoria meiriana*	AY843695	—	AY844688	AY844475	AY844132	AY844895	—	Australia: Western Australia: Black Rock, near Kununurra
SAMA 45336	*Nyctimistes pulcher*	AY843701	AY843946	AY844692	—	AY844134	—	—	Papua New Guinea: Magidobo, SHP
AMNH A-82822[r]	*Nyctimystes kubori*	AY843702	AY843947	AY844693	AY844479	—	—	—	Papua New Guinea: Moroba: Wau
AMNH A-82845[s]	*Nyctimystes narinosus*	AY843703	AY843948	AY844694	—	AY844135	—	AY844308	Papua New Guinea: Tambul
	Allophrynidae								
MAD 1512	*Allophryne ruthveni*	AY843564	AY843786	AY844538	AY844361	—	AY844766	—	Guyana: Kabocali camp (101 m, 4°17.10′N, 58°30.56′W)

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
	Astylosternidae								
DPL 3932[t]	*Trichobatrachus robustus*	AY843773	—	AY844760	—	AY844192	AY844954	—	Cameroon: Southwest Province: nn hill south of Manyemen
	Bufonidae								
MVZ 223279	*Atelopus varius**	AY325996	—	—	—	—	—	—	Costa Rica: South of Las Alturas
MACN 38639	*Bufo arenarum*	AY843573	AY843795	AY844547	AY844370	—	AY844775	AY844205	Argentina: San Luis, ruta 20 entre Bardas Blancas y km 330
MJH 7095	*Dendrophryniscus minutus*	AY843582	AY843804	AY844555	—	—	—	—	Peru: Huanuco: Rio Llullapichis: Panguana
N/A	*Dydinamipus sjoestedti**	AY325991	—	—	—	—	—	—	Cameroon: Unknown
MACN 38531	*Melanophryniscus klappenbachi*	AY843699	AY843944	—	AY844478	—	AY844899	AY844306	Argentina: Chaco: proximidades de Resistencia
QCAZ 4580	*Osornophryne guacamayo**	AY326036	—	—	—	—	—	—	Ecuador: Napo: Lago Sumaco, Volcan Sumaco
N/A	*Pedostibes hossi**	AY325993	—	—	—	—	—	—	Malaysia: Pahang: Krau Wildlife Reserve, Pehang main research field station, ca. 13 km NW Kuala Krau at confluence Krau and Lompat Rivers
TNHC 62001	*Schismaderma carens**	AY325997	—	—	—	—	—	—	Tanzania: Dodoman
	Brachycephalidae								
N/A	*Brachycephalus ephippium**	AY326008	—	—	—	—	—	—	Brazil: no data
	Centrolenidae								
SIUC H-7053	*Centrolene prosoblepon*	AY843574	AY843796	AY844548	AY844371	—	AY844776	AY844206	Panama: Coclé: El Copé: Parque Nacional ‘‘Omar Torrijos’’

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
MNK 5242	*Cochranella bejaranoi*	AY843576	AY843798	AY844549	AY844372	AY844029	AY844777	AY844208	Bolivia: Santa Cruz: Caballero: Canton San Juan: Amboro National Park
CFBH 5729	*Hyalinobatrachium eurygnathum*	AY843595	AY843814	AY844567	AY844383	—	AY844793	AY844217	Brazil: Minas Gerais: Itamontes
	Dendrobatidae								
USNM-FS 52055	*Colostethus talamancae*	AY843577	AY843799	AY844550	AY844373	—	AY844778	—	Panama: Bocas del Toro
USNM 31318	*Dendrobates auratus*	AY843581	AY843803	AY844554	—	AY844032	AY844781	AY844211	Panama: Bocas del Toro
TNHC 62488	*Phyllobates bicolor**	AY326031	—	—	—	—	—	—	No data
	Heleophrynidae								
TMSA 84157	*Heleophryne purcelli*	AY843593	AY843812	AY844565	—	—	AY844791	AY844216	South Africa: Western Cape Province: Cedarberg Mountain Range: head of Krom River
	Hemisotidae								
TNHC 62489	*Hemisus marmoratum**	AY326070	—	AY364397	—	—	—	—	See Darst and Cannatella (2004) and Biju and Bossuyt (2003)
Leptodactylidae, Ceratophryinae									
JF 929	*Ceratophrys cranwelli*	AY843575	AY843797	—	—	—	—	AY844207	Argentina: Santa Fe: Vera: Ea. ‘‘Las Gamas’’
JF 1891	*Odontophrynus americanus*	AY843704	AY843949	AY844695	AY844480	—	AY844901	AY844309	Argentina: Buenos Aires: Escobar: Loma Verde: Ea. ‘‘Los Cipreses’’
	Leptodactylidae, Cycloramphinae								
MLPA 1414	*Crossodactylus schmidti*	AY843579	AY843801	AY844552	AY844375	AY844031	AY844780	AY844210	Argentina: Misiones: Aristobulo del Valle: Balneario Cuñapirú

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
	Leptodactylidae, Eleutherodactylinae								
AMNH-A 165195	*Eleutherodactylus pluvicanorus*	AY843586	—	AY844559	—	AY844035	AY844785	AY844213	Bolivia: Santa Cruz: Caballero: Canton San Juan: Amboro National Park
KU 202519	*Eleutherodactylus thymelensis**	AY326009	—	—	—	—	—	—	Ecuador: Carchi: 12 km W Tufino, 3520 m
AMNH-A 165108	*Phrynopus* sp.	AY843720	—	—	—	—	—	AY844323	Bolivia: La Paz: Bautista Saavedra: Canton Charazani
	Leptodactylidae, Leptodactylinae								
AMNH-A 166312	*Adenomera* sp.	AY843561	AY843784	AY844535	AY844360	AY844021	—	AY844195	Guyana: Berebice River camp at ca. 18 mi (linear) SW Kwakwani (ca. 2 mi downriver from Kurundi River confluence)
MJH 7082	*Edalorhina perezi*	AY843585	AY843807	AY844558	—	—	AY844764	—	Peru: Huanuco: Rio Llullapichis: Panguana
MACN 38648	*Leptodactylus ocellatus*	AY843688	AY843934	AY844681	AY844470	—	AY844784	AY844302	Argentina: Buenos Aires: Escobar: Loma Verde: Establecimiento ‘‘Los Cipreses’’
MACN 38641	*Limnomedusa macroglossa*	AY843689	AY843935	AY844682	AY844471	AY844128	AY844890	—	Argentina: Misiones: Aristobulo del Valle: Balneario Cuñapirú
AMNH-A 166426	*Lithodytes lineatus*	AY843690	AY843936	AY844683	AY844472	AY844129	—	AY844303	Guyana: Berebice River camp at ca. 18 mi (linear) SW Kwakwani (ca 2. mi downriver from Kurundi River confluence)

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
MACN 38640	*Physalaemus cuvieri*	AY843729	AY843975	AY844717	AY844499	—	AY844922	AY844330	Argentina: Misiones: Guarani: San Vicente: Campo Anexo INTA ‘‘Cuartel Rio Victoria’’
AMNH-A 139118	*Pleurodema brachyops*	AY843733	AY843979	AY844721	AY844503	—	AY844926	—	Guyana: Southern Rupununi Savanna, Aishalton (on Kubanawau Creek)
MACN 38647	*Pseudopaludicola falcipes*	AY843741	AY843987	AY844728	AY844507	AY844168	AY844930	—	Argentina: Corrientes: Yapeyu
	Leptodactylidae, Telmatobiinae								
MACN 37942	*Alsodes gargola*	AY843565	AY843787	AY844539	AY844362	—	AY844767	AY844197	Argentina: Neuquén: Aluminé: Stream 10 km W Primeros Pinos
MACN 37905	*Atelognathus patagonicus*	AY843571	AY843793	AY844545	AY844368	AY844027	AY844773	AY844203	Argentina: Neuquén: Catan Lil: Laguna del Burro
MACN 38008	*Batrachyla leptopus*	AY843572	AY843794	AY844546	AY844369	AY844028	AY844774	AY844204	Argentina: Chubut: Cushamen: Lago Puelo
MACN 37980	*Eupsophus calcaratus*	AY843587	AY843808	AY844560	—	AY844036	AY844786	AY844214	Argentina: Neuquén: Huiliches: Termas de Epulafquen
AMNH-A 165114	*Telmatobius* sp.	AY843769	AY844014	AY844757	AY844529	—	AY844952	AY844355	Bolivia: La Paz: Bautista Saavedra: Canton Charazani
	Mantellidae								
AMNH A-167581	*Mantidactylus femoralis*	AY843698	AY843943	—	—	—	AY844898	—	Madagascar: Antsiranana: Ambanja: Ramena River camp, Tsaratanana Reserve (730 m)
	Microhylidae								
AMNH A-167395	*Scaphiophryne marmorata*	AY843751	—	AY364390	—	AY844175	—	—	Madagascar: Antsiranana: Vohemnar: Sorata Mountain (1320 m)

APPENDIX 2
(*Continued*)

Voucher	Species	12S-tRNA valine-16S	Cytochrome *b*	Rhodopsin exon 1	RAG-1	Tyrosinase	Seventh in absentia	28S	Locality
N/A	*Kaloula conjuncta**	AY326064	—	—	—	—	—	—	Philippines: Negros Island: City of Dumaguete
	Myobatrachidae, Limnodynastinae								
TNHC 61075	*Limnodynastes salmini**	AY326071	—	—	—	—	—	—	No data
SAMA 12391	*Neobatrachus sudelli*	AY843700	—	AY844691	—	—	AY844900	AY844307	Australia: New South Wales: 30 km N Kenmore
	Myobatrachidae, Myobatrachinae								
SAMA 73293	*Pseudophryne bibroni*	AY843742	AY843988	AY844729	—	—	AY844931	AY844338	Australia: South Australia: S of Para Reservoir Reserve
	Ranidae								
AMNH A-161230	*Fejervarya limnocharis*	AY843588	—	AY844561	—	AY844037	AY844787	—	Vietnam: Nghe An Province: Con Cuong District: Bong Khe Commune
N/A	*Platymantis* sp.*	AY326061	—	—	—	—	—	—	Solomon Islands
N/A	*Rana temporaria**	AY326063	—	—	—	—	—	—	No data
	Rhacophoridae								
AMNH-A 161418	*Rhacophorus bipunctatus*	AY843750	AY843996	AY844737	—	—	—	—	Vietnam: Ha Tinh: Huong Son District: Huon Son Reserve (Rao An region): top of Po-Mu mountain

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[a] VZFC 14248.
[b] AMCC 101446.
[c] ZFMK H-074.
[d] AMCC 107369.
[e] MVZ 11676.
[f] AMCC 101481.
[g] LSUMZ H-12939.
[h] MVZFC 11248.
[i] AMCC 101720.
[j] LSUMZ H-13720.
[k] AMCC 101463.
[l] To be accessioned in CFBH collection.
[m] MVZFC 14296.
[n] MVZFC 14457.
[o] MVZFC 12876.
[p] AMCC 101463.
[q] AMCC 107020.
[r] LSUMZ H-10864.
[s] LSUMZ H-9970.
[t] AMCC 124743.
[u] Obtained by Biju and Bossuyt (2003); voucher of unknown provenance.

APPENDIX 3

MORPHOLOGICAL CHARACTERS

Based on Burton's (2004) collection of observations on hylid foot musculature, we built a data set. Burton (2004) included two appendices, A and B, with the taxa he examined for the different characters. In the text, however, it is not immediately clear which of the appendices he refers to in some cases. Burton (personal commun.) graciously provided us with a precise list of the appendix to which each character refers. This information is reproduced below in a character list that includes a brief discussion when relevant. Burton (2004) numbered his characters as a continuation of Duellman's (2001) character list. We are not incorporating Duellman's (2001) characters because he only summarized character states for the hylid subfamilies without any reference to the individual taxa, therefore assuming monophyly.

Character List

0 (Burton's char. 25): Insertions of the m. flexor digitorum brevis superficialis. (0) Three insertions. (1) Two insertions.

1 (Burton's char. 26): Structure of the tendon of the m. flexor digitorum brevis superficialis. (0) Undivided. (1) Divided along its length into a medial tendon, from which arises tendo superficialis IV, and a lateral tendon from which arise tendines superficiales III and V, with cross tendons between the divisions. (2) Divided along its length into a medial tendon, from which arise tendo superficialis IV and m. lumbricalis longus digiti V, and a lateral tendon from which arise tendo superficialis V and m. lumbricalis longus digiti IV.

2 (Burton's char. 27): Structure of the termini of tendines superficiales. (0) Tendon neither expanded nor bifurcated. (1) Tendon bifid.

3 (Burton's char. 28): Origin of the tendo superficialis hallucis. (0) Tendo superficialis hallucis arises from the mediodistal corner of the aponeurosis plantaris. (1) (Burton's char. 28.2). The tendo superficialis hallucis tapers from an expanded corner of the aponeurosis plantaris; fibers of the m. transversus plantae distalis originating on distal tarsal 2–3 insert on the lateral side of the tendon. (2) (Burton's char. 28.3). The tendo superficialis hallucis arises from the aponeurosis, but the origin is proximal to that of the m. lumbricalis brevis hallucis, so that the tendo passes at an angle across that muscle as it passes along the toe, neither along its marginor straight along the muscle. (3) (Burton's char. 28.4). The tendo superficialis hallucis comes from a massive muscle that arises from distal tarsal 2–3. COMMENT: Burton (2004: 218) included within this character a state (1) pertaining to the morphology of the tendo superficialis hallucis, not to its origin. For this reason, we consider it to be a different character and that is why we excluded it here.

4 (Burton's char. A): Structure of m. contrahentis hallucis. (0) Present and conspicuous. (1) Absent or reduced.

5 (Burton's char. B): Origin of m. contrahentis hallucis (if present). (0) Origin on distal tarsal 1. (1) Origin on distal tarsal 2–3.

6 (Burton's char. 29): Presence or absence of m. flexor teres hallucis. (0) Absent. (1) Present.

7 (Burton's char. 30): Presence or absence of m. abductor brevis plantae hallucis. (0) Present. (1) Absent. COMMENT: Burton (2004: 219) included states pertaining to presence or absence, as well as structure, in the same character. Following Hawkins et al. (1997) and Strong and Lipscomb (1999), we consider them as two different characters.

8 (Burton's char. 30): Structure of the m. abductor brevis plantae hallucis. (0) Narrow. (1) Broad.

9 (Burton's char. 31): Origin of tendo superficialis pro digiti II. (0) Tendon arising from the distal edge of the aponeurosis plantaris. (1) Tendon arising from a deep, triangular muscle, which originates on the distal tarsal 2–3. (2) Tendon broad at the base, acting as a point of insertion of a portion of the m. transversus plantae distalis, so that the tendo superficialis pro digiti II appears to be the tendon of insertion of the m. transversus plantae distalis.

10 (Burton's char. 32): Origin of tendo superficialis pro digiti III. (0) Tendo superficialis pro digiti III arising from the m. flexor digitorum brevis superficialis, but with the distal margin of the aponeurosis wrapped around the tendon. (1) Tendo superficialis pro digiti III arising from the. flexor digitorum brevis superficialis, with no contribution from the aponeurosis plantaris. (2) Tendo superficialis pro digiti III arising in part from m. flexor digitorum brevis superficialis or the tendo superficialis pro digiti IV, and in part by a superficial tendon (from which also cutaneous tendons arise) that emerges from centrally on the plantar surface of the aponeurosis plantaris. (3) Tendo superficialis pro digiti III arising entirely from the margin of the aponeurosis plantaris. (4) Tendo superficialis pro digiti III arising entirely from the superficial tendon.

11 (Burton's char. 33): Origin of m. flexor ossis metatarsi II. (0) Tendon arising from the condyle of the fibulare alone, in common with the tendon of origin of the m. flexor ossis metatarsi III. (1) Tendon arising from distal tarsal 2–3 only. (2) Muscle with two origins—a long distal section arising from a tendon on the distal condyle of the fibulare, and a short proximal section arising from distal tarsal 2–3.

12 (Burton's char. D): Accessory tendon of origin of the m. lumbricalis longus digiti III. (0) Absent. (1) Present.

13 (Burton's char. 34): Number of tendons of insertion of m. lumbricalis longissimus digiti IV. (0) Two tendons. (1) One tendon.

14 (Burton's char. 35, refers to taxa listed on his appendix B): Relationship between the origin of m. flexor ossis metatarsi IV and the joint tendon of origin of m. flexores ossum metatarsorum II and III varies. (0) The tendons are adjacent at their origins. (1) The tendons cross each other. COMMENT: Burton (2004: 222) included a third state in this character, whose taxonomic distribution does not match any of the taxa included in this study.

15 (Burton's char. F): Structure of m. flexor ossis metatarsi IV. (0) Inserting on metatarsus IV only. (1) Inserting on both metatarsi IV and V.

16 (Burton's char. 36): Length variation of the m. flexor ossis metatarsi IV. (0) Very short, inserting on the proximal two thirds of metatarsal IV or less only. (1) Extending the entire length of Metatarsal IV.

17 (Burton's char. 37, refers to taxa listed in his appendix A): Tendons of insertion of m. lumbricalis longus digiti V. (0) One tendon. (1) Two tendons arising equally from both sides of an undivided muscle. (2) Two tendons arising from two equal muscle slips. (3) (Burton's char. 37.4). Two tendons, the medial of which arises from a small, distal slip. COMMENT: The state 3 of this character described by Burton is present only in *Cochranella siren*, a taxon not included in this analysis.

18 (Burton's char. 38, refers to taxa listed in his appendix A): Number of slips of the medial m. lumbricalis brevis digiti V. (0) Two slips. (1) One slip. COMMENT: Burton included a third state that is present in *Gastrophryne*, a taxon not included in this analysis.

19 (Burton's char. 39, refers to taxa listed in both appendices): Presence or absence of a tendon from the m. flexor digitorum brevis superficialis to the medial slip of the medial m. lumbricalis brevis digiti V. (0) Absent. (1) Present.

20 (Burton's char. 40): Insertion of the lateral slip of the medial m. lumbricalis brevis digiti V. (0) Insertion by tendon onto the basal phalanx. (1) Insertion pennate.

21 (Burton's char. 41, refers to taxa listed in his appendix A): Width and orientation of the m. transversus metatarsus II. (0) Narrow, occupying less than 80% of the length of metatarsus II. (1) Broad, occupying the entire length of metatarsus II. (2) Oblique, with a narrow, proximal connection onto metatarsus III, and a broad, distal connection to metatarsus II. COMMENT: Burton (in litt., 19 July 2004) warned us that the numbers of the metatarsals in the description of state 2 of chars. 41 and 42 were accidentally reversed in his paper; this reversal is corrected here.

22 (Burton's char. 42): Position of m. transversus metatarsus III. (0) Relatively distal, not occupying the proximal 15% of either metatarsus. (1) Proximal. (2) Oblique, with a narrow, proximal connection onto metatarsus IV, and a broad, distal connection to metatarsus III.

23 (Burton's char. 43, refers to taxa listed in his appendix A): Breadth of m. transversus metatarsus III. (0) Narrow, extending less than 70% of the length of metatarsus III. (1) Broad, occupying more than 75% of the length of metatarsus III.

24 (Burton's char. 44): Presence or absence of m. transversus metatarsus IV. (0) Present. (1) Absent. COMMENTS: Burton included presence, absence, and several modifications within a single character. We are unsure as to the definitions and limits of the states describing the different origins and insertions of the muscle when present, and thus we only score its presence or absence.

25 (Burton's char. 45): Relationship of the m. flexor ossis metatarsi IV with m. transversus metatarsus IV, if present. (0) M. flexor ossis metatarsi IV dorsal to m. transversus metatarsus IV. (1) M. flexor ossis metatarsi IV ventral to m. transversus metatarsus IV.

26 (Burton's char. 46, refers to taxa listed in his appendix A): Nature of origin of m. extensor digitorum comunis longus. (0) Fibrous origin from the medial surface of the m. tarsalis anticus. (1) A long, straplike tendon arising on the lateral side of the distal end of the tibiofibula, close to the origin of the m. tarsalis anticus.

27 (Burton's char. 47, refers to taxa listed in his appendix A): Nature of insertion of m. extensor digitorum comunis longus. (0) Flat tendon onto the fascia of one or more dorsal superficial muscles. (1) Strong tendon(s) directly to the dorsa of one or more metatarsi.

28 (Burton's char. 48): Insertion of m. extensor digitorum comunis longus on metatarsal II. (0) Present. (1) Absent. COMMENTS: Burton defined the states of character 48 in a complex way, combining the different points of insertions into single states. We consider it more informative and less redundant to consider the different points of insertion as different characters. The insertion on metatarsal III is uninformative in the present context, since it is reported absent only in *Stefania scalae*, a taxon not included in the analysis.

29 (Burton's char. 48): Insertion of m. extensor digitorum comunis longus on metatarsal IV. (0) Present. (1) Absent.

30 (Burton's char. 49): Origins of the m. extensor brevis medius hallucis and m. extensor brevis medius digiti II. (0) Separate origins. (1) Adjacent origins.

31 (Burton's char. G): Insertion of the m. extensor brevis medius hallucis. (0) Insertion in the basal phalanx of digit I only. (1) Insertion by a flat tendon onto the base of the basal phalanx of digit I, plus a strong, narrow tendon that passes along the medial margin of digit II, inserting on the basal phalanx.

32 (Burton's char. 50, refers to taxa listed in his appendix A): Position and nature of insertions of m. abductor brevis dorsalis digiti V. (0) Insertion pennate, along the proximal half of the lateral margin of metatarsal V, displacing the origins of mm. extensores breves profundi digiti V, so that the lateral m. extensor brevis profundus originates on the mediodorsal surface of the metatarsal V. (1) Insertion by a short tendon to the dorsum of the metatarsal V. COMMENT: Burton described a third state that is present in *Hyperolius*, a taxon not included in this analysis.

33 (Burton's char. 51, refers to taxa listed on his appendix A): Nature of the origin of the m. extensor brevis superficialis digiti III on the distal end of the fibulare. (0) Fibrous origin. (1) Origin by a flat tendon.

34 (Burton's char. 52, refers to taxa listed in his appendix A): Number of insertions of m. extensor brevis superficialis digiti III. (0) Single insertion onto the dorsum of the m. extensor brevis medius digiti III. (1) Single insertion via a long tendon proximally on the dorsum of basal phalanx III. (2) Two insertions, a flat tendon onto basal phalanx III, as state 1, and a pennate insertion on metatarsus III.

35 (Burton's char. 53, refers to taxa listed in his appendix A): Presence or absence of m. extensor brevis medius digiti III. (0) Present. (1) Absent.

36 (Burton's char. 54): Number of slips in the m. extensor brevis superficialis digiti IV. (0) Two origins, two separate muscles. (1) One origin, belly undivided.

37 (Burton's char. 55, refers to taxa listed in his appendix A): Nature of the origin of the mm. extensores breves superficiales digiti IV. (0) Both origins pennate. (1) (Burton's char. 55.2): Both origins from long, flat tendons. COMMENT: Burton described a third state present in *Rhacophorus maculatus*, a taxon not included here.

Characters C and E were not included because the taxonomic distribution of their states is irrelevant for hylids. Character 56 was excluded because it actually includes several characters (presence or absence of mm. extensores breves distales in each digit), and there is no information as to which of the slips (medial or lateral) is present.

Morphological Synapomorphies Common to All Trees
(node numbers as in figs. 2–5)

Allophryne ruthveni, 10: 2 → 4. *Anotheca spinosa*, 3: 0 → 1. *Cyclorana australis*, 17: 3 → 0. *Dendropsophus sarayacuensis*, 6: 1 → 0. *Hyla euphorbiacea*, 28: 1 → 0. *Hypsiboas calcaratus*, 3: 1 → 0. *Hypsiboas granosus*, 9: 2 → 0. *Hypsiboas pellucens*, 3: 1 → 0, 9: 2 → 0. *Hypsiboas picturatus*, 6: 0 → 1. *Hypsiboas punctatus*, 3: 1 → 0. *Hypsiboas raniceps*, 5: 0 → 1. *Hypsiboas rufitelus*, 6: 0 → 1. *Litoria aurea*, 21: 0 → 1. *Litoria freycineti*, 18: 0 → 1, 28: 1 → 0. *Osteopilus septentrionalis*, 6: 0 → 1, 29: 1 → 0. *Osteopilus vastus*, 31: 1 → 0. *Plectrohyla guatemalensis*, 12: 0 → 1. *Scarthyla goinorum*, 25: 0 → 1. Node 289, 1: 0 → 1, 10: 2 → 1. Node 337, 21: 0 → 2. Node 338, 1: 1 → 0. Node 352, 11: 0 → 1. Node 372, 3: 0 → 1. Node 375, 1: 1 → 0. Node 390, 28: 1 → 0. Node 422, 10: 1 → 0, 14: 1 → 0, 16: 1 → 0, 19: 1 → 0. 22: 1 → 2. Node 462, 28: 1 → 0. Node 465, 33: 1 → 0. Node 498, 21: 0 → 1. Node 507, 7: 0 → 1.

APPENDIX 4

ADDITIONAL COMMENTS ON SOME SPECIES

Hyla albovittata Lichtenstein and Martens, 1856: Lichtenstein and Martens (1856) described this species from ''Brazil'', without further data. Subsequently, it was not included in Nieden's (1923) catalog; Duellman (1977) stated that the holotype was unknown; however, the holotype is housed at the Zoologisches Museum–Universität Humboldt, Berlin. The specimen (ZMB 3140), an adult male, is in a remarkably good state of preservation, retaining details of pattern and coloration. On study, it is evident that it is a junior synonym of *Hyla pulchella* Duméril and Bibron, 1841.

Hyla auraria Peters, 1873: This species was described in detail based on a single specimen reported as coming from ‘‘angeblich aus Sudamerika’’ (Peters, 1873). Subsequently, Boulenger (1882) presented a brief description without further comment. Duellman (1977) reported that the holotype was ‘‘formerly at ZSM, now lost.’’ Duellman (*in* Frost 1985) stated that the name has never been associated with a population of anurans. However, the holotype is extant. The holotype of *H. auraria* (ZSM 1175/0), presumably a female (it lacks vocal slits), is in relatively good state of preservation, but it is very faded. We could not associate it with any known species of Hylinae nor could we associate it with any of the genera recognized in this work.

Hyla palliata Cope, 1863: Cope (1863) described this species, stating that it was a specimen from the Page collection, with provenance ‘‘Paraguay’’.[32] He also provided the Smithsonian Museum number 6225. The species was not included in the list of type specimens of the USNM (Cochran, 1961). According to Heyer (personal commun. to J.F., 21 Jan. 2004), the USNM catalog entry indicates that there were originally two specimens cataloged as 6225, and in a card file initiated by Cochran of missing type specimens, there is a card indicating that the specimens could not be found in 1957. Because the specimens had not been found since, Heyer noted, ‘‘the most reasonable conclusion is that the specimens are indeed lost.’’ The description provided by Cope indicates a character combination that could be indicative of a species of *Hypsiboas* (no species of *Bokermannohyla* are known for the area surveyed by the Page expedition): ‘‘All the digits of posterior extremity palmate to penultimate phalanx; of the anterior the three external are one third webbed. Metacarpus of inner digit with a large tubercle.’’ Nevertheless, in the absence of other evidence, we prefer to consider this species as a nomen dubium.

Hyloscirtus estevesi (Rivero, 1968): This species was originally described as a member of the Centrolenidae by Rivero (1968), and was later (Rivero, 1985) included in the *Centrolenella pulidoi* species group. Savage (*in* Frost, 1985) considered this species to be a member of the Hylidae, and it was not included in the taxonomic rearrangement of Centrolenidae by Ruiz-Carranza and Lynch (1991). Myers and Donnelly (1997) and Frost (2002) considered it as incerta sedis. However, La Marca (1992) listed it as a centrolenid, and later (La Marca, 1997; 1998) employed the combination *Hyalinobatrachium estevesi*, mistakenly attributing it to Ruiz-Carranza and Lynch (1991). The study of its holotype (MCZ 72498) indicates that it is a juvenile of an unidentified species that we associate with the *Hyloscirtus bogotensis* species group. While it could well be a juvenile of either *H. jahni* or *H. platydactylus*, and therefore a potential junior synonym of either of these species, we tentatively recognize it as a valid species pending additional work.

Hypsiboas pulidoi (Rivero, 1968): This species was described from ‘‘Monte Duida, 2000 pies, Territorio Amazonas, Venezuela’’ as a Centrolenidae by Rivero (1968). Later Rivero (1985) included in its own species group, the *Centrolenella pulidoi* group. Savage (*in* Frost, 1985) considered this species to be a hylid. Furthermore, Rivero (1985: 361) stated that ‘‘the resemblance of *C. pulidoi* with some specimens with the same coloration of *H. benitezi* (with which it is syntopic) is so remarkable that for some time it was thought to consider them synonyms, but *C. pulidoi* has fused tarsal bones, a different coloration, and the eyes are red in living specimens’’ (freely translated from the Spanish). This species was not included in the taxonomic rearrangement of Centrolenidae by Ruiz-Carranza and Lynch (1991), but Ayarzagüena (1992) and La Marca (1992) still listed it as a centrolenid, and Gorzula and Señaris (1999) referred to it as ‘‘*Centrolenella*’’ *pulidoi*. Duellman (1999) employed the combination *Hyla pulidoi* without further comment; Myers and Donnelly (1997) and Frost (2002) considered it as incertae sedis. The study of the holotype (MCZ 72499), a female according to Rivero (1968), indicates that it is a species close to *Hypsiboas benitezi*. The specimen has a slightly enlarged prepollex, similar to the situation seen in females of *H. benitezi*. Considering its small size (20.3 mm), we are unsure as to whether it is an adult female or a juvenile. We tentatively consider this species as valid, pending a careful comparison with juveniles of *Hypsiboas benitezi*. The only apparent difference between *Hypsiboas benitezi* and *H. pulidoi* is that the latter has a red iris (Rivero, 1968), whereas the iris of the former was described by Myers and Donnelly (1997) as ‘‘light bronzy brown with fine balck venation.’’ However, this issue should be addressed cautiously, because as noted by Myers and Donnelly (1997), at least two species are probably confounded under the name *H. benitezi*, and these authors described specimens from Tamacuari, that they considered morphologically different from the topotypes, and iris coloration in topotypic material remains undescribed.

Scinax dolloi (Werner, 1903): Werner (1903)

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[32] Although the provenance is ‘‘Paraguay’’, this should be taken in a very wide sense, since the Page expedition travelled from Buenos Aires, through the Parana river up to Corumba, State of Matto Grosso, Brazil (Page, 1859).

described *H. dolloi*, based on two specimens, whose provenance was stated as Brazil, adding ‘‘unfortunately it is unknown with more precision’’ (from the German). The species was included in Nieden (1923) with a brief description, and without additional comments by Bokermann (1966b), Gorham (1974), and Duellman (1977). B. Lutz (1973) included it as a ‘‘doubtful species’’. Duellman (*in* Frost, 1985, 2002) stated that the name had not been associated with any known population.

Lang (1990) included it on the list of type specimens housed at the Institut Royal des Sciences Naturelles in Brussels, Belgium, commenting that ‘‘although the original type-description lists specifically that no specific locality is know the register has ‘Haut Maringa, Brésil’ as locality data’’. The two syntypes (IRSNB 6481) are in a fairly good state of preservation, and their study shows that they clearly belong to the genus *Scinax*, and, within it, they seem to be related to the *ruber* clade (Faivovich, 2002). *Scinax dolloi* is morphologically close to *Scinax hayii* and *S. perereca*. While its exact status remains to be elucidated, in the meantime we consider it a valid species of *Scinax*.

Scinax karenanneae Pyburn, 1993: Pyburn (1993) described this species from ‘‘near Timbó, Department of Vaupés, Colombia’’. Although the original description and accompanying figures suggest that the species is superficially very similar to many species of *Scinax*, Pyburn (1993) ruled out the possibility that this species belonged to *Scinax* due to the sperm with a single tail filament. Problems with the interpretation of sperm morphology data have been discussed earlier, and in this particular case the poorly known taxonomic distribution of this character state in Hylinae precludes any interpretation of polarity.

The paratypes of *Hyla karenanneae* (UTA A-3768–79) show the synapomorphies of *Scinax* listed by Faivovich (2002) that can be seen without deep dissections. Therefore, we propose its inclusion in *Scinax*. This species has a large subgular vocal sac, which in the phylogenetic analysis of *Scinax* of Faivovich (2002) optimized as a synapomorphy of a clade composed by *S. staufferi*, *S. cruentommus*, *S. fuscomarginatus*, and an undescribed species from northern Brazil.

Scinax megapodius: This species was figured by Miranda-Ribeiro (1926), but formally described only later (Miranda-Ribeiro, 1937). Originally described from the localities of São Luiz de Cáceres and Porto Esperidião, Matto Grosso (Miranda-Ribeiro, 1937), this species was considered a synonym of *Hyla fuscovaria* by Lutz (1973). However, Fouquette and Delahoussaye (1977) consider it a valid species, based on differences in sperm morphology from *H. fuscovaria*. On that basis, they included it in their *Ololygon catharinae* group. Almeida and Cardoso (1985) presented an analysis of intraspecific variation among spermatozoa of *O. fuscovaria*, and suggested that the differences observed among *O. fuscovaria* and *O. megapodia* were the same as those seen among different specimens of the same population of *O. fuscovarius*. Without comment, Duellman and Wiens (1992) considered *Hyla megapodia* to be a synonym of *Scinax fuscovarius*, as did Lavilla (1992). Based on the lack of comments by these authors, Frost (2002) continued recognition of *Scinax megapodius* as a valid species. Based on the results of Almeida and Cardoso (1985), and considering that there is no published evidence that *Scinax megapodius* is different from *S. fuscovarius*, following Lutz (1973), we treat it as a junior synonym of the latter.

Scinax trachythorax: This species was described by Müller and Hellmich (1936) from the locality of ‘‘Apa-Bergland (San Luis)’’, Paraguay, also referred as ‘‘Estancia San Luis de la Sierra, Apa-Bergland’’ (Müller and Hellmich, 1936: 114). Lutz (1973) considered this species a junior synonym of *Hyla fuscovaria*. Fouquette and Delahoussaye (1977) considered it a valid species, based on differences in sperm morphology from *H. fuscovaria*, and recognized it as *Ololygon trachthorax*. Almeida and Cardoso (1985) presented an analysis of intraspecific variation in spermatozoa of *O. fuscovaria*, and suggested that the differences observed among *O. fuscovaria* and *O. trachythorax* were the same as those seen among different specimens within the same population of *O. fuscovaria*. However, *O. trachythorax* was recognized as a valid species by Duellman and Wiens (1992), who employed the combination *Scinax trachythorax*. Lavilla (1992) considered it a synonym of *S. fuscovarius*, as did De la Riva et al. (2000), who explicitly followed Lutz (1973) and Cei (1980). (This publication did not incorporate changes introduced by Fouquette and Delahoussaye [1977]; Cei [1987] later recognized *S. trachythorax* as a valid species.) Considering the comments of Almeida and Cardoso (1985), and in light of the absence of any published diagnostic character state between *S. fuscovarius* and *S. trachythorax*, following Lutz (1973), we tentatively consider the latter a junior synonym of the former.

APPENDIX 5

Synapomorphies Involving DNA Sequences, for All Taxonomic Groups of Hylidae With the Exception of Species Groups Whose Monophyly Was Not Tested in this Analysis

Hylidae

Cytochrome *b*
Pos. 14: T → A
12S
Pos. 646: A → T
Pos. 1270: G → A
Pos. 1423: T → A
tRNA valine
Pos. 6: A → G
Pos. 105: T → C
16S
Pos. 162: T → C
Pos. 172: T → A
Pos. 369: C → Gap
Pos. 399: A → T
Pos. 483: C → A
Pos. 1458: Gap → A
Pos. 1649: Gap → T
Pos. 1842: CT → A
Pos. 1883: G → C
Pos. 1948: A → T
Pos. 1951: T → A
Pos. 2381: Gap → T
Pos. 2844: C → A
Pos. 2866: Gap → A
Pos. 3032: C → T
Pos. 3230: C → T
Pos. 3234: T → A
28S
Pos. 249: Gap → C
Pos. 505: Gap → G
Pos. 783: Gap → C
Pos. 1049: C → G
RAG-1
Pos. 6 A → T
Pos. 65 T → C
Rhodopsin
Pos. 281: C → T
Pos. 296: C → T
Pos. 316: T → A
SIA
Pos. 331: G → A
Tyrosinase
Pos. 160: C → T
Pos. 470: T → A
Pos. 483: A → T

Hylinae

12S
Pos. 733: T → A
Pos. 1296: T → C
Pos. 1409: A → G
Pos. 1426: T → C
16S
Pos. 392: C → A
Pos. 665: T → A
Pos. 1237: A → Gap
Pos. 1705: T → C
Pos. 1718: A → C
Pos. 2058: C → A
Pos. 2875: A → T
Pos. 3173: A → G
Pos. 3239: T → A
Pos. 3274: A → G
Pos. 3301: T → C
28S
Pos. 863: Gap → G
RAG-1
Pos. 2: A → C
Pos. 53: G → A
Pos. 341: T → C
Pos. 410: C → A
Rhodopsin
Pos. 194: T → C
SIA
Pos. 169: A → T
Tyrosinase
Pos. 73: T → A
Pos. 150: T → C
Pos. 270: A → G
Pos. 300: C → A
Pos. 324: A → G
Pos. 348: T → C
Pos. 376: G → T
Pos. 511: A → G

Cophomantini

Cytochrome *b*
Pos. 13: A → T
Pos. 153: C → T
Pos. 238: T → A
12S
Pos. 159: C → A
Pos. 297: T → C
Pos. 379: A → G
Pos. 436: T → C
Pos. 571: A → CT
Pos. 622: C → T
Pos. 636: G → A
Pos. 716: A → CT
Pos. 729: T → C
Pos. 838: A → T
Pos. 1002: C → T
Pos. 1066: C → T
Pos. 1203: Gap → T
Pos. 1264: G → A
Pos. 1266: A → T
Pos. 1332: G → A
Pos. 1343: CT → Gap
Pos. 1374: C → T
Pos. 1412: C → T
Pos. 1509: A → G
16S
Pos. 294: A → C
Pos. 498: T → C
Pos. 876: A → G
Pos. 877: G → A
Pos. 1049: T → C
Pos. 1228: A → C
Pos. 1402: A → Gap
Pos. 1530: A → C
Pos. 1616: Gap → C
Pos. 1795: T → A
Pos. 1874: T → C
Pos. 1925: A → C
Pos. 1998: A → C
Pos. 2605: G → A
Pos. 2711: C → Gap
Pos. 2736: A → Gap
Pos. 2802: T → C
Pos. 2866: A → C
Pos. 3018: T → A
Pos. 3027: T → G
Pos. 3328: A → T
28S
Pos. 150: A → C
Pos. 152: C → T
Pos. 153: T → G
Pos. 178: G → A
Pos. 211: Gap → C
Pos. 212: Gap → T
Pos. 230: Gap → A
Pos. 302: G → A
Pos. 343: Gap → A
Pos. 344: Gap → G
Pos. 654: Gap → T
Pos. 1032: C → G
RAG-1
Pos. 357 C → T
Rhodopdsin
Pos. 93: C → T
Pos. 163: C → T
SIA
Pos. 112: C → T
Pos. 304: T → C
Tyrosinase
Pos. 174: G → A
Pos. 258: A → T
Pos. 508: T → G
Pos. 532: T → C

Aplastodiscus

Cytochrome *b*
Pos. 31: A → G
Pos. 79: A → C
Pos. 137: C → A
Pos. 220: T → C
Pos. 310: C → A
12S
Pos. 117: A → T
Pos. 152: A → Gap
Pos. 174: G → A
Pos. 206: A → T
Pos. 392: T → C
Pos. 414: C → T
Pos. 558: C → A
Pos. 571: CT → A
Pos. 655: Gap → A
Pos. 823: A → T
Pos. 880: A → C
Pos. 1116: A → T
Pos. 1187: T → C
Pos. 1330: A → G
Pos. 1397: A → Gap
Pos. 1408: A → G
Pos. 1427: T → C
Pos. 1431: T → C
Pos. 1539: C → T
Pos. 1573: A → G
Pos. 1590: Gap → A
tRNA valine
Pos. 6: G → A
Pos. 105: C → T
16S
Pos. 376: A → T
Pos. 399: T → C
Pos. 664: A → T
Pos. 800: C → T
Pos. 803: C → T
Pos. 974: A → C
Pos. 984: T → A
Pos. 1298: C → T
Pos. 1403: Gap → C
Pos. 1710: T → G
Pos. 1788: Gap → T
Pos. 1842: A → Gap
Pos. 2019: A → T
Pos. 2030: A → G
Pos. 2105: A → C
Pos. 2130: C → T
Pos. 2240: A → G
Pos. 2280: A → T
Pos. 2289: A → G
Pos. 2301: G → A
Pos. 2313: T → C
Pos. 2392: A → Gap
Pos. 2398: A → T
Pos. 2551: A → G
Pos. 2563: T → C
Pos. 2820: A → C
Pos. 3032: T → C
Pos. 3148: G → A
Pos. 3287: T → C
Pos. 3322: C → T
Pos. 3330: A → C
Pos. 3486: A → G
28S
Pos. 390: C → T
RAG-1
Pos. 125 A → G
Pos. 284 A → G
Pos. 419 C → T
SIA
Pos. 391: C → T
Tyrosinase
Pos. 6: G → A
Pos. 130: C → T
Pos. 157: C → G
Pos. 233: C → T
Pos. 315: C → A
Pos. 330: T → C
Pos. 513: G → A

***Aplastodiscus albofrenatus* group**

Cytochrome *b*
Pos. 10: A → T
Pos. 23: T → C
Pos. 101: C → T
Pos. 109: A → G
Pos. 111: C → G
Pos. 132: A → G
Pos. 135: G → C
Pos. 239: C → T
Pos. 250: T → C
Pos. 259: C → T
Pos. 268: T → C
Pos. 290: C → T
Pos. 322: C → A
Pos. 334: A → G
12S
Pos. 37: T → C
Pos. 94: Gap → T
Pos. 218: Gap → T
Pos. 251: G → A
Pos. 264: C → T
Pos. 333: C → T
Pos. 460: T → A
Pos. 462: T → C
Pos. 484: A → T
Pos. 550: T → C
Pos. 587: T → C
Pos. 625: G → A
Pos. 641: A → G
Pos. 654: T → C
Pos. 692: T → C
Pos. 696: A → G
Pos. 788: A → G
Pos. 802: T → C
Pos. 830: A → G
Pos. 835: T → C
Pos. 943: A → G

APPENDIX 5
(*Continued*)

Pos. 1036: C → Gap
Pos. 1094: A → G
Pos. 1105: A → C
Pos. 1128: T → A
Pos. 1141: T → C
Pos. 1211: T → C
Pos. 1217: T → C
Pos. 1402: A → C
Pos. 1413: C → A
Pos. 1417: G → T
Pos. 1441: C → A
Pos. 1496: T → C
Pos. 1674: A → T
Pos. 1688: A → G
Pos. 1762: A → G
Pos. 1763: T → C
Pos. 1775: T → C
tRNA valine
Pos. 55: A → C
Pos. 56: T → C
16S
Pos. 74: Gap → A
Pos. 234: T → A
Pos. 355: C → T
Pos. 483: A → T
Pos. 517: A → T
Pos. 566: A → T
Pos. 702: A → G
Pos. 763: G → A
Pos. 808: T → C
Pos. 839: C → T
Pos. 864: C → T
Pos. 908: T → A
Pos. 1021: T → A
Pos. 1092: A → T
Pos. 1203: A → Gap
Pos. 1211: A → Gap
Pos. 1360: A → C
Pos. 1574: A → T
Pos. 1643: A → G
Pos. 1654: T → Gap
Pos. 1688: T → C
Pos. 1799: C → A
Pos. 1823: A → T
Pos. 1888: C → T
Pos. 1900: C → T
Pos. 1945: G → A
Pos. 1962: A → G
Pos. 1981: Gap → T
Pos. 2059: A → C
Pos. 2285: A → T
Pos. 2308: C → T
Pos. 2406: T → A
Pos. 2457: G → A
Pos. 2515: A → T
Pos. 2545: G → A
Pos. 2663: A → Gap
Pos. 2664: A → Gap
Pos. 2672: T → Gap
Pos. 2685: A → Gap
Pos. 2704: G → Gap
Pos. 2742: T → Gap
Pos. 2780: A → Gap
Pos. 2844: A → G
Pos. 2875: A → Gap
Pos. 2901: T → Gap
Pos. 2906: T → Gap
Pos. 2929: C → Gap
Pos. 2946: G → T
Pos. 3010: A → T
Pos. 3054: CT → G
Pos. 3056: T → G
Pos. 3071: A → T
Pos. 3088: A → T
Pos. 3118: T → C
Pos. 3145: C → A
Pos. 3310: A → T
Pos. 3516: T → G
RAG-1
Pos. 428 A → T
SIA
Pos. 280: C → T
Pos. 349: T → A

Aplastodiscus albosignatus group

Cytochrome *b*
Pos. 49: A → C
Pos. 339: A → C
Pos. 376: T → A
Pos. 405: CG → T
12S
Pos. 227: T → C
Pos. 452: T → A
Pos. 521: A → T
Pos. 611: A → G
Pos. 875: C → A
Pos. 908: A → T
Pos. 958: A → G
Pos. 1048: T → A
Pos. 1579: C → T
Pos. 1589: C → A
Pos. 1645: C → T
Pos. 1674: A → C
16S
Pos. 94: C → T
Pos. 308: A → Gap
Pos. 378: Gap → C
Pos. 419: Gap → A
Pos. 648: G → T
Pos. 667: A → C
Pos. 668: CT → A
Pos. 780: A → G
Pos. 887: C → T
Pos. 985: G → A
Pos. 1049: C → T
Pos. 1174: T → A
Pos. 1278: C → G
Pos. 1503: C → A
Pos. 1742: Gap → C
Pos. 1780: T → C
Pos. 1795: A → C
Pos. 2029: T → A
Pos. 2115: T → A
Pos. 2195: T → C
Pos. 2400: Gap → G
Pos. 2663: A → T
Pos. 3299: C → T
Pos. 3321: A → T
Tyrosinase
Pos. 25: T → A
Pos. 166: G → A

Aplastodiscus perviridis group

Cytochrome *b*
Pos. 46: C → T
Pos. 64: T → A
Pos. 161: A → G
Pos. 183: A → T
Pos. 189: C → T
Pos. 201: T → C
Pos. 229: C → T
Pos. 362: T → A
Pos. 399: C → T
12S
Pos. 103: Gap → G
Pos. 132: Gap → C
Pos. 164: T → Gap
Pos. 169: A → G
Pos. 310: T → C
Pos. 368: A → G
Pos. 615: T → A
Pos. 646: T → A
Pos. 650: T → C
Pos. 880: C → T
Pos. 1036: C → T
Pos. 1326: G → A
Pos. 1392: C → T
Pos. 1626: Gap → G
tRNA valine
Pos. 58: T → C
16S
Pos. 136: A → Gap
Pos. 336: C → T
Pos. 589: T → C
Pos. 618: A → G
Pos. 636: T → C
Pos. 656: T → C
Pos. 749: C → T
Pos. 876: G → A
Pos. 968: G → A
Pos. 979: C → T
Pos. 1277: G → A
Pos. 1286: A → G
Pos. 1314: A → G
Pos. 1649: C → T
Pos. 1718: C → T
Pos. 1788: T → C
Pos. 1799: C → T
Pos. 1819: A → T
Pos. 1953: T → C
Pos. 2364: A → Gap
Pos. 2381: T → C
Pos. 2552: T → C
Pos. 2616: A → T
Pos. 2802: C → Gap
Pos. 2821: Gap → T
Pos. 3004: A → Gap
Pos. 3077: T → C
Pos. 3181: G → A
Pos. 3266: C → T
Pos. 3281: A → G
Pos. 3297: A → C
Pos. 3516: T → C
RAG-1
Pos. 311 C → T
Tyrosinase
Pos. 438: C → T

Bokermannohyla

Cytochrome *b*
Pos. 116: C → T
Pos. 361: T → Gap
Pos. 370: Gap → A
Pos. 376: T → C
12S
Pos. 140: C → Gap
Pos. 171: G → Gap
Pos. 181: Gap → T
Pos. 322: C → T
Pos. 729: C → T
Pos. 890: A → C
Pos. 943: A → G
Pos. 1084: T → C
Pos. 1145: T → A
Pos. 1243: A → CT
Pos. 1338: Gap → C
Pos. 1342: A → G
Pos. 1366: C → Gap
Pos. 1369: T → G
Pos. 1568: A → T
Pos. 1599: A → G
Pos. 1630: A → C
tRNA valine
Pos. 78: T → A
Pos. 109: T → C
16S
Pos. 0: G → A
Pos. 166: Gap → A
Pos. 443: C → AT
Pos. 731: C → Gap
Pos. 749: C → T
Pos. 829: C → T
Pos. 860: G → A
Pos. 1041: Gap → C
Pos. 1103: T → Gap
Pos. 1129: G → A
Pos. 1330: C → A
Pos. 1436: A → Gap
Pos. 1757: T → C
Pos. 1783: C → T
Pos. 1865: T → A
Pos. 1985: A → C
Pos. 1998: C → G
Pos. 2041: A → T
Pos. 2059: A → T
Pos. 2570: A → G
Pos. 2618: T → Gap
Pos. 2694: T → C
Pos. 2697: T → C
Pos. 2966: A → T
Pos. 3027: G → A
Pos. 3173: G → Gap
Pos. 3324: T → C
Pos. 3330: A → Gap
Pos. 3425: C → T
28S
Pos. 443: G → Gap
RAG-1
Pos. 251 G → A
Pos. 380 T → C
Rhodopsin
Pos. 78: G → C
Pos. 93: T → A
Pos. 220: G → A
Tyrosinase
Pos. 31: A → G
Pos. 300: A → G
Pos. 315: C → G
Pos. 357: T → C
Pos. 387: T → C
Pos. 403: G → A
Pos. 506: C → G

Bokermannohyla circumdata group

Cytochrome *b*
Pos. 49: A → C
Pos. 109: A → G
Pos. 120: A → G
Pos. 201: A → C
Pos. 330: C → T
Pos. 334: A → T
Pos. 356: T → C
Pos. 367: C → T
Pos. 399: C → T
12S
Pos. 33: G → A

APPENDIX 5
(*Continued*)

Pos. 69: C → T
Pos. 131: T → C
Pos. 227: T → C
Pos. 370: A → T
Pos. 512: T → C
Pos. 547: A → T
Pos. 729: T → A
Pos. 823: A → G
Pos. 869: C → T
Pos. 1024: C → T
Pos. 1144: T → G
Pos. 1272: G → A
Pos. 1348: T → C
Pos. 1408: A → G
Pos. 1427: T → C
Pos. 1645: A → C
16S
Pos. 11: T → C
Pos. 411: C → T
Pos. 498: C → T
Pos. 630: T → A
Pos. 692: A → G
Pos. 726: A → G
Pos. 751: C → A
Pos. 887: T → A
Pos. 1049: C → T
Pos. 1085: T → C
Pos. 1492: T → A
Pos. 1649: T → A
Pos. 1654: T → A
Pos. 1688: T → C
Pos. 1880: A → C
Pos. 2110: C → T
Pos. 2176: C → T
Pos. 2209: Gap → C
Pos. 2229: C → T
Pos. 2611: Gap → A
Pos. 2825: T → A
Pos. 2866: C → T
Pos. 3222: T → C
Pos. 3516: T → C
28S
Pos. 240: Gap → C
Pos. 498: Gap → G

***Bokermannohyla pseudopseudis* group**

Cytochrome *b*
Pos. 76: A → G
Pos. 111: C → T
Pos. 135: G → A
Pos. 140: A → T
Pos. 253: C → T
Pos. 334: A → C
Pos. 347: A → T
Pos. 374: C → T
Pos. 381: C → T
12S
Pos. 83: A → G
Pos. 159: A → T
Pos. 164: T → C
Pos. 297: C → T
Pos. 370: A → G
Pos. 452: T → C
Pos. 615: T → C
Pos. 1048: T → A
Pos. 1181: Gap → A
Pos. 1317: C → A
Pos. 1326: G → A
16S
Pos. 285: Gap → C
Pos. 286: Gap → C
Pos. 691: G → A
Pos. 702: A → G
Pos. 774: T → A
Pos. 960: G → A
Pos. 974: A → T
Pos. 1140: A → T
Pos. 1607: A → G
Pos. 1710: T → G
Pos. 1953: T → A
Pos. 2025: C → T
Pos. 2229: C → A
Pos. 2250: C → T
Pos. 2262: G → A
Pos. 2330: C → T
Pos. 2473: T → A
Pos. 2518: A → G
Pos. 2608: Gap → T
Pos. 2646: G → A
Pos. 2856: T → A
Pos. 3097: C → A
Pos. 3380: T → C
Pos. 3381: T → A
Pos. 3403: C → T
RAG-1
Pos. 365: T → C
Pos. 422: T → C
Pos. 428: A → C

Hyloscirtus

Cytochrome *b*
Pos. 14: A → CT
Pos. 101: C → AG
Pos. 134: C → T
Pos. 302: A → C
Pos. 322: C → A
12S
Pos. 460: T → C
Pos. 462: T → A
Pos. 490: Gap → C
Pos. 565: A → Gap
Pos. 636: A → T
Pos. 817: G → A
Pos. 842: Gap → C
Pos. 1174: C → A
Pos. 1211: T → A
Pos. 1440: C → A
Pos. 1532: Gap → CT
tRNA valine
Pos. 82: C → T
Pos. 89: A → C
Pos. 99: G → A
16S
Pos. 254: T → Gap
Pos. 272: T → AC
Pos. 325: Gap → T
Pos. 427: T → A
Pos. 576: T → C
Pos. 602: A → C
Pos. 854: A → T
Pos. 889: A → G
Pos. 914: C → A
Pos. 949: T → C
Pos. 1062: A → Gap
Pos. 1192: Gap → C
Pos. 1577: A → T
Pos. 1587: T → A
Pos. 1616: C → A
Pos. 1631: T → G
Pos. 1673: AC → Gap
Pos. 1705: C → A
Pos. 1718: C → Gap
Pos. 1985: A → T
Pos. 2258: A → T
Pos. 2544: G → A
Pos. 2756: Gap → T
Pos. 3140: C → A
Pos. 3288: A → T
Pos. 3326: T → C
28S
Pos. 303: Gap → T
Pos. 346: Gap → C
Pos. 391: Gap → T
Pos. 744: Gap → T
RAG-1
Pos. 257 C → T
Pos. 338 C → T
Pos. 425 G → A
Rhodopdsin
Pos. 256: C → T
Tyrosinase
Pos. 3: C → T
Pos. 72: C → T
Pos. 257: C → T

***Hyloscirtus armatus* group**

Cytochrome *b*
Pos. 3: C → T
Pos. 23: T → C
Pos. 67: C → T
Pos. 127: C → T
Pos. 135: G → A
Pos. 167: C → T
Pos. 178: C → T
Pos. 189: C → T
Pos. 248: C → A
Pos. 290: C → A
Pos. 369: T → C
12S
Pos. 22: G → A
Pos. 26: A → G
Pos. 176: A → T
Pos. 194: T → C
Pos. 227: T → C
Pos. 411: T → C
Pos. 414: C → T
Pos. 455: AC → T
Pos. 547: A → T
Pos. 558: C → T
Pos. 793: T → C
Pos. 835: T → C
Pos. 869: C → T
Pos. 1043: C → T
Pos. 1084: T → C
Pos. 1095: C → T
Pos. 1100: G → A
Pos. 1101: C → T
Pos. 1141: C → T
Pos. 1153: T → G
Pos. 1187: T → C
Pos. 1203: T → A
Pos. 1303: A → T
Pos. 1446: A → C
Pos. 1515: A → T
Pos. 1574: Gap → A
Pos. 1575: Gap → C
Pos. 1630: A → T
Pos. 1636: C → A
Pos. 1649: A → C
tRNA valine
Pos. 95: C → T
16S
Pos. 139: Gap → A
Pos. 175: Gap → C
Pos. 220: A → T
Pos. 244: A → T
Pos. 498: C → T
Pos. 543: T → C
Pos. 726: A → T
Pos. 731: C → T
Pos. 767: A → C
Pos. 822: A → T
Pos. 862: C → T
Pos. 996: A → T
Pos. 1104: Gap → A
Pos. 1140: AC → T
Pos. 1175: Gap → A
Pos. 1491: A → T
Pos. 1503: C → A
Pos. 1534: A → C
Pos. 1572: T → C
Pos. 1688: C → A
Pos. 1780: T → C
Pos. 1865: T → A
Pos. 1894: T → A
Pos. 1897: T → C
Pos. 1928: C → A
Pos. 1949: T → A
Pos. 1961: A → G
Pos. 2122: G → A
Pos. 2308: T → A
Pos. 2432: A → G
Pos. 2461: C → T
Pos. 2476: C → T
Pos. 2552: T → C
Pos. 3059: A → T
Pos. 3140: A → T
Pos. 3280: A → C
Pos. 3281: A → T
Pos. 3288: T → C
Pos. 3375: T → A
Pos. 3431: C → T
Pos. 3442: C → T
28S
Pos. 302: A → G
Pos. 1000: G → Gap
Rhodopdsin
Pos. 63: G → A
Pos. 135: C → T
Pos. 270: A → T
Pos. 279: C → A
Tyrosinase
Pos. 47: A → G
Pos. 52: C → T
Pos. 56: A → C
Pos. 109: C → T
Pos. 167: G → T
Pos. 170: A → C
Pos. 188: G → A
Pos. 258: T → A
Pos. 273: C → G
Pos. 279: C → T
Pos. 297: C → T
Pos. 343: G → A
Pos. 344: T → C
Pos. 529: C → T

***Hyloscirtus bogotensis* group**

Cytochrome *b*
Pos. 126: G → A
Pos. 153: T → C
Pos. 168: A → T
Pos. 220: T → C

APPENDIX 5
(*Continued*)

Pos. 232: C → A
Pos. 253: C → T
Pos. 338: T → C
Pos. 376: T → A
12S
Pos. 28: A → G
Pos. 45: T → C
Pos. 68: A → G
Pos. 110: A → Gap
Pos. 152: A → G
Pos. 164: T → C
Pos. 295: A → C
Pos. 447: Gap → C
Pos. 550: T → C
Pos. 619: G → T
Pos. 622: T → A
Pos. 650: T → C
Pos. 767: C → T
Pos. 991: Gap → A
Pos. 1094: A → G
Pos. 1118: C → T
Pos. 1270: A → G
Pos. 1307: T → C
Pos. 1509: G → A
Pos. 1521: G → A
Pos. 1568: A → T
Pos. 1657: G → A
tRNA valine
Pos. 55: A → G
Pos. 80: T → Gap
Pos. 85: G → Gap
Pos. 90: A → Gap
Pos. 98: A → G
16S
Pos. 12: C → T
Pos. 107: A → Gap
Pos. 392: A → C
Pos. 411: C → Gap
Pos. 452: T → Gap
Pos. 665: A → G
Pos. 691: G → A
Pos. 876: G → A
Pos. 891: G → A
Pos. 904: A → T
Pos. 947: C → T
Pos. 952: A → T
Pos. 969: A → G
Pos. 1049: C → Gap
Pos. 1480: T → C
Pos. 1534: A → T
Pos. 1780: T → A
Pos. 1819: A → Gap
Pos. 1948: T → C
Pos. 1998: C → A
Pos. 2041: A → T
Pos. 2125: T → C
Pos. 2457: G → A
Pos. 2533: T → C
Pos. 2663: A → Gap
Pos. 2664: A → Gap
Pos. 2672: C → Gap
Pos. 2719: CT → A
Pos. 2820: A → Gap
Pos. 2856: T → G
Pos. 2966: A → C
Pos. 2990: A → C
Pos. 3039: A → T
Pos. 3048: A → Gap
Pos. 3063: G → A
Pos. 3106: T → C
Pos. 3385: T → C
Pos. 3458: T → C
Pos. 3524: C → T
Pos. 3538: G → A
RAG-1
Pos. 4 C → A
Pos. 5 A → G
Pos. 143 G → A
Pos. 168 G → A
Pos. 169 T → C
Pos. 170 G → A
Pos. 305 C → T
Pos. 311 C → T
Pos. 323 T → C
Rhodopdsin
Pos. 133: C → T
Pos. 135: C → A
Pos. 291: G → A
Pos. 308: T → A
Tyrosinase
Pos. 183: A → G
Pos. 214: C → T
Pos. 220: A → G
Pos. 294: C → T
Pos. 299: A → C
Pos. 315: C → T
Pos. 342: C → T

Hyloscirtus larinopygion group

12S
Pos. 65: C → T
Pos. 454: T → C
Pos. 490: C → T
Pos. 601: T → C
Pos. 908: A → T
Pos. 1113: T → C
Pos. 1116: A → T
Pos. 1174: A → T
Pos. 1216: C → A
Pos. 1321: T → C
Pos. 1407: G → A
Pos. 1409: G → A
Pos. 1426: C → T
Pos. 1429: C → T
Pos. 1678: A → G
tRNA valine
Pos. 12: C → T
16S
Pos. 347: C → T
Pos. 742: T → A
Pos. 819: T → 4
Pos. 911: A → G
Pos. 920: G → A
Pos. 1092: A → T
Pos. 1228: C → 4
Pos. 1265: A → G
Pos. 1325: A → C
Pos. 1510: A → G
Pos. 1561: C → T
Pos. 2103: A → T
Pos. 2395: A → C
Pos. 2450: T → C
Pos. 2768: CT → A
Pos. 3287: T → C

Hypsiboas

Cytochrome *b*
Pos. 376: T → A
12S
Pos. 45: T → C
Pos. 476: C → A
Pos. 650: T → A
Pos. 958: A → G
Pos. 1048: T → A
Pos. 1107: C → T
Pos. 1407: G → A
Pos. 1429: C → T
16S
Pos. 163: Gap → T
Pos. 188: A → T
Pos. 272: T → A
Pos. 876: G → A
Pos. 996: A → G
Pos. 1169: Gap → T
Pos. 1692: Gap → A
Pos. 1894: T → C
Pos. 1978: Gap → A
Pos. 2182: Gap → A
Pos. 2217: T → Gap
Pos. 2812: T → C
Pos. 3086: A → T
Pos. 3166: C → A
Pos. 3239: A → C
Pos. 3249: A → T
28S
Pos. 355: Gap → C
Pos. 358: Gap → C
Pos. 57: C → T
Pos. 373: C → T
Tyrosinase
Pos. 257: C → T
Pos. 288: C → T
Pos. 407: T → A

Hypsiboas albopunctatus group

Cytochrome *b*
Pos. 63: T → C
Pos. 76: A → T
Pos. 109: A → G
Pos. 126: C → A
Pos. 128: T → C
Pos. 153: T → C
Pos. 180: C → A
Pos. 253: C → T
Pos. 271: T → C
Pos. 327: A → T
Pos. 415: C → T
12S
Pos. 131: T → C
Pos. 227: T → C
Pos. 650: A → C
Pos. 1045: T → A
Pos. 1158: Gap → C
Pos. 1159: Gap → C
Pos. 1217: T → C
Pos. 1376: T → C
Pos. 1573: A → T
Pos. 1670: C → T
16S
Pos. 107: A → Gap
Pos. 173: Gap → A
Pos. 308: A → Gap
Pos. 998: C → T
Pos. 1092: A → T
Pos. 1125: A → G
Pos. 1129: G → A
Pos. 1183: A → Gap
Pos. 1300: A → G
Pos. 1419: T → A
Pos. 1737: C → A
Pos. 1757: C → T
Pos. 1810: T → A
Pos. 1840: Gap → T
Pos. 2187: A → T
Pos. 2203: A → T
Pos. 2694: T → C
Pos. 2846: Gap → C
Pos. 3054: T → C
Pos. 3189: G → A
Pos. 3222: T → Gap
Pos. 3516: T → A

Hypsiboas faber group

Cytochrome *b*
Pos. 173: A → T
Pos.
186: A → G
12S
Pos. 131: T → C
16S
Pos. 11: T → C
Pos. 206: A → T
Pos. 347: C → A
Pos. 367: C → A
Pos. 573: A → T
Pos. 663: A → C
Pos. 775: C → T
Pos. 780: C → A
Pos. 821: T → C
Pos. 904: T → A
Pos. 1421: Gap → A
Pos. 1458: A → T
Pos. 1510: A → Gap
Pos. 1673: A → T
Pos. 1874: T → C
Pos. 2381: T → A
Pos. 2602: G → T
Pos. 2663: A → T
Pos. 2820: A → C
Pos. 2977: A → T
Pos. 2995: A → C
Pos. 3081: A → T
Pos. 3351: Gap → A
RAG-1
Pos. 1 C → A
SIA
Pos. 283: G → A

Hypsiboas pellucens group

12S
Pos. 42: T → C
Pos. 183: A → T
Pos. 297: C → T
Pos. 319: A → T
Pos. 320: A → T
Pos. 342: T → C
Pos. 392: T → C
Pos. 455: C → T
Pos. 541: T → C
Pos. 550: T → C
Pos. 641: A → T
Pos. 646: T → A
Pos. 661: G → A
Pos. 673: C → T
Pos. 716: C → Gap
Pos. 731: Gap → A
Pos. 767: T → C
Pos. 841: A → T
Pos. 1023: T → C
Pos. 1122: A → T
Pos. 1187: T → C
Pos. 1203: T → A
Pos. 1214: Gap → A
Pos. 1233: G → A
Pos. 1316: A → G
Pos. 1321: T → C

APPENDIX 5
(*Continued*)

Pos. 1337: T → C
Pos. 1369: T → G
Pos. 1392: C → T
Pos. 1441: A → C
Pos. 1445: C → T
Pos. 1549: A → T
Pos. 1579: C → T
Pos. 1605: A → T
Pos. 1630: A → C
tRNA valine
Pos. 101: A → G
16S
Pos. 12: C → T
Pos. 136: A → T
Pos. 206: A → Gap
Pos. 334: Gap → A
Pos. 498: C → A
Pos. 573: A → T
Pos. 610: A → T
Pos. 691: G → A
Pos. 736: C → A
Pos. 761: T → C
Pos. 790: G → A
Pos. 826: A → G
Pos. 836: A → C
Pos. 839: C → T
Pos. 892: G → A
Pos. 904: T → A
Pos. 911: A → G
Pos. 928: T → G
Pos. 946: C → T
Pos. 980: T → C
Pos. 1013: T → A
Pos. 1062: C → T
Pos. 1173: Gap → C
Pos. 1235: C → A
Pos. 1245: Gap → G
Pos. 1261: T → C
Pos. 1345: T → A
Pos. 1389: A → T
Pos. 1458: A → Gap
Pos. 1468: A → T
Pos. 1480: A → T
Pos. 1510: A → C
Pos. 1532: T → C
Pos. 1607: A → Gap
Pos. 1628: Gap → T
Pos. 1641: Gap → A
Pos. 1727: A → T
Pos. 1813: A → C
Pos. 1847: A → C
Pos. 1932: C → A
Pos. 1953: A → T
Pos. 2029: T → C
Pos. 2030: G → A
Pos. 2035: C → A
Pos. 2077: A → T
Pos. 2086: C → T
Pos. 2091: A → C
Pos. 2094: A → C
Pos. 2109: Gap → A
Pos. 2117: A → Gap
Pos. 2267: T → A
Pos. 2308: C → T
Pos. 2450: T → C
Pos. 2510: T → C
Pos. 2517: G → A
Pos. 2518: A → G
Pos. 2525: A → T
Pos. 2538: C → T
Pos. 2569: T → C
Pos. 2583: A → G
Pos. 2613: T → A
Pos. 2618: T → A
Pos. 2656: A → G
Pos. 2719: C → T
Pos. 2906: T → C
Pos. 2953: A → G
Pos. 2956: A → T
Pos. 3041: G → A
Pos. 3077: T → A
Pos. 3093: T → C
Pos. 3111: A → G
Pos. 3166: A → C
Pos. 3234: T → A
Pos. 3249: T → C
Pos. 3285: G → A
Pos. 3286: C → T
Pos. 3426: A → T
Pos. 3454: T → G
Pos. 3518: Gap → T

Hypsiboas pulchellus group

Cytochrome *b*
Pos. 26: T → A
Pos. 126: C → T
Pos. 145: C → T
Pos. 214: C → T
Pos. 330: C → T
Pos. 347: A → C
12S
Pos. 180: C → T
Pos. 601: T → A
Pos. 650: A → T
Pos. 1317: A → T
Pos. 1423: A → T
Pos. 1645: C → T
tRNA valine
Pos. 4: A → T
Pos. 101: A → G
16S
Pos. 71: A → C
Pos. 130: T → C
Pos. 254: T → A
Pos. 566: A → T
Pos. 602: A → T
Pos. 667: A → C
Pos. 702: A → T
Pos. 732: A → G
Pos. 788: C → T
Pos. 1169: T → A
Pos. 1235: C → A
Pos. 1315: T → A
Pos. 1436: A → T
Pos. 1468: A → C
Pos. 1572: T → A
Pos. 1579: Gap → C
Pos. 1607: A → T
Pos. 1705: T → G
Pos. 1810: T → C
Pos. 1813: A → C
Pos. 1878: C → T
Pos. 1887: C → T
Pos. 1952: T → A
Pos. 2025: C → T
Pos. 2089: A → T
Pos. 2262: G → A
Pos. 2588: C → T
Pos. 2754: Gap → C
Pos. 2825: T → A
Pos. 2856: T → A
Pos. 2866: C → A
Pos. 2985: T → A
Pos. 3239: C → Gap
Rhodopsin
Pos. 10: G → A
Tyrosinase
Pos. 91: C → T
Pos. 154: C → T
Pos. 177: C → T
Pos. 178: C → G
Pos. 182: G → T
Pos. 211: C → G
Pos. 444: G → A

Hypsiboas punctatus group

Cytochrome *b*
Pos. 49: A → C
Pos. 109: A → C
Pos. 192: T → C
Pos. 253: C → T
12S
Pos. 268: T → C
Pos. 1045: T → Gap
Pos. 1317: C → T
16S
Pos. 56: C → Gap
Pos. 272: A → G
Pos. 294: C → T
Pos. 543: T → C
Pos. 920: G → A
Pos. 1103: T → Gap
Pos. 1259: CT → A
Pos. 1654: T → C
Pos. 1878: C → T
Pos. 1887: C → T
Pos. 2308: C → T
Pos. 2719: C → Gap
Pos. 2742: T → Gap
Pos. 2753: A → Gap
Pos. 2768: C → Gap
Pos. 2906: T → A
Pos. 2975: C → Gap
Pos. 2982: C → Gap
Pos. 2995: A → Gap
Pos. 3054: T → A
Pos. 3140: C → T
Pos. 3222: T → Gap
Pos. 3516: T → A

Hypsiboas semilineatus group

Cytochrome *b*
Pos. 1: A → T
Pos. 46: C → T
Pos. 63: T → C
Pos. 76: A → T
Pos. 153: T → C
Pos. 167: C → T
Pos. 180: C → T
Pos. 181: T → A
Pos. 195: A → C
Pos. 232: C → T
Pos. 280: C → T
Pos. 290: C → A
Pos. 347: A → C
Pos. 353: T → C
Pos. 374: C → T
Pos. 381: C → T
12S
Pos. 33: G → A
Pos. 271: T → A
Pos. 332: C → A
Pos. 348: T → A
Pos. 370: A → C
Pos. 414: C → T
Pos. 528: A → C
Pos. 602: A → T
Pos. 619: G → A
Pos. 650: A → T
Pos. 673: C → T
Pos. 677: A → T
Pos. 765: A → G
Pos. 774: A → G
Pos. 797: G → A
Pos. 815: T → C
Pos. 836: T → C
Pos. 875: C → T
Pos. 1001: A → C
Pos. 1215: A → T
Pos. 1330: A → T
Pos. 1336: C → T
Pos. 1372: G → A
Pos. 1378: A → T
Pos. 1392: C → T
Pos. 1413: C → T
Pos. 1439: C → A
Pos. 1670: C → A
tRNA valine
Pos. 94: C → A
Pos. 95: C → T
16S
Pos. 134: Gap → A
Pos. 211: Gap → T
Pos. 294: C → A
Pos. 323: C → A
Pos. 472: A → Gap
Pos. 579: A → T
Pos. 580: A → T
Pos. 606: C → A
Pos. 611: A → G
Pos. 654: T → A
Pos. 679: C → T
Pos. 732: A → G
Pos. 819: T → Gap
Pos. 911: A → G
Pos. 914: C → T
Pos. 1004: T → G
Pos. 1021: T → A
Pos. 1160: C → A
Pos. 1242: T → A
Pos. 1246: T → A
Pos. 1325: A → C
Pos. 1436: A → T
Pos. 1510: A → T
Pos. 1530: C → T
Pos. 1596: A → T
Pos. 1616: C → A
Pos. 1692: A → C
Pos. 1727: A → C
Pos. 1799: C → A
Pos. 1847: A → T
Pos. 1895: A → T
Pos. 1922: C → A
Pos. 1950: T → A
Pos. 1970: A → T
Pos. 2035: C → A
Pos. 2086: C → T
Pos. 2089: A → C
Pos. 2125: T → A
Pos. 2156: C → A
Pos. 2182: A → T
Pos. 2229: C → A
Pos. 2310: A → C
Pos. 2313: T → A
Pos. 2406: T → Gap

APPENDIX 5
(*Continued*)

Pos. 2441: C → A
Pos. 2454: A → T
Pos. 2457: G → A
Pos. 2551: A → C
Pos. 2672: T → Gap
Pos. 2856: T → A
Pos. 2929: C → Gap
Pos. 2953: A → Gap
Pos. 3014: A → G
Pos. 3125: A → T
Pos. 3127: C → T
Pos. 3199: C → T
Pos. 3249: T → Gap
Pos. 3291: A → G
Pos. 3330: A → T
28S
Pos. 355: C → Gap
Pos. 431: G → Gap
Rhodopsin
Pos. 155: T → C
Pos. 270: A → T
Pos. 271: G → C
Pos. 308: T → C
SIA
Pos. 151: C → T
Pos. 241: G → C
Pos. 253: T → C
Pos. 268: A → G
Pos. 313: G → A
Pos. 322: C → T
Tyrosinase
Pos. 70: T → G
Pos. 96: G → A
Pos. 156: C → T
Pos. 174: A → G
Pos. 260: C → A
Pos. 262: T → C
Pos. 299: A → C
Pos. 417: C → G
Pos. 429: C → T
Pos. 475: C → T
Pos. 514: G → A

Myersiohyla

12S
Pos. 39: A → G
Pos. 271: T → C
Pos. 342: T → C
Pos. 356: T → C
Pos. 392: T → C
Pos. 452: T → C
Pos. 547: A → C
Pos. 615: T → A
Pos. 672: C → A
Pos. 835: T → C
Pos. 1043: C → T
Pos. 1645: A → Gap
Pos. 1674: A → C
tRNA valine
Pos. 56: T → C
16S
Pos. 94: C → A
Pos. 272: T → G
Pos. 392: A → T
Pos. 434: A → T
Pos. 517: A → C
Pos. 606: C → T
Pos. 777: A → C
Pos. 848: A → T
Pos. 1043: Gap → C
Pos. 1062: A → C
Pos. 1160: T → A
Pos. 1278: T → C
Pos. 1614: A → C
Pos. 1865: T → C
Pos. 1951: A → T
Pos. 2127: G → A
Pos. 2203: A → T
Pos. 2392: A → C
Pos. 2398: A → C
Pos. 2449: T → A
Pos. 2509: C → T
Pos. 2566: T → C
Pos. 2618: T → A
Pos. 2780: A → Gap
Pos. 2812: T → C
Pos. 2856: T → C
Pos. 2906: T → C
Pos. 2997: C → Gap
Pos. 3041: G → Gap
Pos. 3056: T → C
Pos. 3106: T → C
Pos. 3222: T → C
Pos. 3287: T → C
Pos. 3385: T → C

Dendropsophini + Hylini + Lophiohylini

Cytochrome *b*
Pos. 11: A → C
Pos. 376: T → A
12S
Pos. 1174: C → T
Pos. 1440: C → A
Pos. 1670: T → C
16S
Pos. 107: A → T
Pos. 399: T → C
Pos. 853: T → A
Pos. 854: A → T
Pos. 914: C → A
Pos. 1062: A → T
Pos. 1436: A → T
Pos. 1468: T → A
Pos. 1847: A → G
Pos. 2267: T → A
Pos. 2844: A → T
Pos. 2966: A → T
28S
Pos. 233: G → Gap
RAG-1
Pos. 5 A → G
Pos. 125 A → G
Rhodopsin
Pos. 10: A → G
Pos. 105: G → A
Pos. 316: A → G
Tyrosinase
Pos. 210: G → A
Pos. 407: T → A
Pos. 408: T → A
Pos. 506: C → G

Dendropsophini

Cytochrome *b*
Pos. 137: T → C
Pos. 201: A → T
Pos. 220: T → C
12S
Pos. 451: T → C
Pos. 547: A → C
Pos. 641: A → Gap
Pos. 841: A → C
Pos. 869: C → T
16S
Pos. 162: C → T
Pos. 259: Gap → A
Pos. 1799: A → C
Pos. 2025: C → T
Pos. 2680: A → T
Pos. 2820: A → Gap
Pos. 3173: G → Gap
Pos. 3230: T → A
Pos. 3326: T → C
28S
Pos. 400: T → C
Pos. 419: C → G
Pos. 1014: G → Gap
Rhodopsin
Pos. 256: C → T
Tyrosinase
Pos. 145: T → C
Pos. 303: A → G

Dendropsophus

Cytochrome *b*
Pos. 3: C → A
Pos. 183: A → T
Pos. 253: T → C
Pos. 369: T → AC
Pos. 414: T → C
12S
Pos. 636: G → A
Pos. 869: T → C
Pos. 1008: T → C
Pos. 1267: A → T
Pos. 1402: A → G
Pos. 1407: G → A
Pos. 1429: C → T
16S
Pos. 299: Gap → T
Pos. 392: A → C
Pos. 551: T → Gap
Pos. 573: A → T
Pos. 579: A → T
Pos. 686: G → A
Pos. 761: T → C
Pos. 777: A → C
Pos. 876: A → G
Pos. 877: G → A
Pos. 979: C → T
Pos. 1469: Gap → T
Pos. 1949: A → C
Pos. 2080: A → G
Pos. 2156: A → C
Pos. 2217: T → C
Pos. 2244: T → C
Pos. 2583: A → G
Pos. 2802: T → C
Pos. 3048: T → C
Pos. 3230: A → C

***Dendropsophus leucophyllatus* group**

Cytochrome *b*
Pos. 36: T → C
Pos. 71: C → A
Pos. 116: C → T
Pos. 125: C → T
Pos. 134: C → T
Pos. 153: C → T
Pos. 173: A → T
Pos. 253: C → T
Pos. 405: A → C
12S
Pos. 37: T → C
Pos. 159: C → T
Pos. 678: Gap → C
Pos. 716: A → C
Pos. 729: C → T
Pos. 838: T → A
Pos. 897: A → C
Pos. 943: A → G
Pos. 965: T → A
Pos. 1011: A → T
Pos. 1094: T → C
Pos. 1270: A → G
Pos. 1273: A → G
Pos. 1402: G → A
Pos. 1581: Gap → A
Pos. 1675: A → T
Pos. 1678: T → C
16S
Pos. 1308: T → C
Pos. 1480: T → C
Pos. 1491: T → C
Pos. 1878: C → T
Pos. 1922: C → A
Pos. 2086: C → T
Pos. 2091: A → T
Pos. 2105: A → T
Pos. 2107: C → T
Pos. 2378: Gap → A
Pos. 2618: T → A
Pos. 2652: T → C
Pos. 2780: T → C
Pos. 2859: Gap → G
Pos. 2866: A → T
Pos. 2982: A → C
Pos. 3059: A → T
Pos. 3166: C → T
Pos. 3181: G → A
Pos. 3268: C → T
Pos. 3287: T → C
Pos. 3326: C → A
Pos. 3452: A → G
28S
Pos. 295: Gap → G
Pos. 330: Gap → C
Pos. 413: Gap → G
Pos. 544: T → G
Pos. 569: A → C
Pos. 763: Gap → C
Pos. 764: Gap → C
Pos. 974: Gap → C
Pos. 975: Gap → C
Pos. 1025: Gap → G
Pos. 1032: C → G
RAG-1
Pos. 77 T → C
Pos. 215 G → T
Pos. 245 C → T
Rhodopsin
Pos. 115: T → C
Pos. 262: G → A
Pos. 281: C → T
SIA
Pos. 112: C → T
Pos. 113: C → T
Pos. 175: C → T
Tyrosinase
Pos. 73: G → A
Pos. 120: C → T
Pos. 121: C → T
Pos. 170: A → C
Pos. 174: A → G
Pos. 382: A → C

APPENDIX 5
(*Continued*)

Pos. 507: T → C

Dendropsophus marmoratus group

Cytochrome *b*
Pos. 11: C → A
Pos. 97: A → T
Pos. 103: C → T
Pos. 109: G → A
Pos. 204: C → A
Pos. 220: C → T
Pos. 311: A → C
12S
Pos. 10: A → G
Pos. 28: A → G
Pos. 44: A → G
Pos. 145: C → T
Pos. 173: G → A
Pos. 319: A → T
Pos. 347: T → C
Pos. 370: A → G
Pos. 528: A → C
Pos. 651: C → T
Pos. 672: C → A
Pos. 769: G → A
Pos. 821: C → T
Pos. 1233: G → A
Pos. 1509: A → G
Pos. 1539: T → C
Pos. 1561: A → T
tRNA valine
Pos. 95: C → T
16S
Pos. 188: A → Gap
Pos. 206: C → A
Pos. 259: A → Gap
Pos. 347: A → C
Pos. 443: C → T
Pos. 580: A → G
Pos. 606: C → A
Pos. 625: T → C
Pos. 660: Gap → G
Pos. 667: A → C
Pos. 668: T → C
Pos. 767: A → C
Pos. 818: C → Gap
Pos. 996: A → G
Pos. 1015: T → A
Pos. 1826: C → A
Pos. 1839: T → A
Pos. 1894: T → C
Pos. 1895: A → G
Pos. 2161: A → C
Pos. 2229: T → A
Pos. 2250: C → T
Pos. 2268: C → A
Pos. 2313: T → C
Pos. 2356: Gap → A
Pos. 2381: T → C
Pos. 2551: A → G
Pos. 2652: T → C
Pos. 2663: T → C
Pos. 2704: G → A
Pos. 2812: T → A
Pos. 2875: C → A
Pos. 2889: A → G
Pos. 2966: T → C
Pos. 3046: C → T
Pos. 3054: T → A
Pos. 3056: T → G
Pos. 3118: C → A
Pos. 3130: A → T
Pos. 3326: C → T
Pos. 3425: C → T
Pos. 3455: G → A
Pos. 3485: T → C
Pos. 3491: C → T
Pos. 3549: A → G
RAG-1
Pos. 17 A → G
Pos. 77 T → C
Pos. 230 C → T

Dendropsophus microcephalus group

Cytochrome *b*
Pos. 140: A → C
Pos. 241: A → T
Pos. 277: T → C
Pos. 330: T → C
Pos. 334: A → G
Pos. 381: C → T
12S
Pos. 140: C → T
Pos. 338: T → C
Pos. 427: T → C
Pos. 515: C → Gap
Pos. 553: Gap → C
Pos. 654: T → C
Pos. 875: C → T
16S
Pos. 192: C → A
Pos. 254: T → Gap
Pos. 299: T → A
Pos. 392: C → A
Pos. 443: C → A
Pos. 464: Gap → C
Pos. 573: T → C
Pos. 580: A → C
Pos. 914: A → C
Pos. 1183: A → Gap
Pos. 1402: A → T
Pos. 1727: T → A
Pos. 1737: T → C
Pos. 1839: CT → A
Pos. 1880: CT → A
Pos. 1950: T → A
Pos. 1951: A → T
Pos. 2080: G → A
Pos. 2112: T → C
Pos. 2151: T → C
Pos. 2250: C → T
Pos. 2663: T → A
Pos. 2713: T → Gap
Pos. 2719: T → C
Pos. 2736: A → C
Pos. 2966: T → A
Pos. 3032: T → A
Pos. 3051: Gap → A
Pos. 3054: T → A

Dendropsophus parviceps group

Cytochrome *b*
Pos. 76: A → C
Pos. 105: A → C
Pos. 244: A → T
Pos. 331: C → T
Pos. 420: A → C
12S
Pos. 28: A → G
Pos. 142: C → T
Pos. 174: G → A
Pos. 528: A → C
Pos. 1630: A → C
Pos. 1640: T → A
16S
Pos. 220: C → G
Pos. 427: T → A
Pos. 876: G → A
Pos. 980: C → T
Pos. 1176: Gap → C
Pos. 1281: T → C
Pos. 1423: Gap → A
Pos. 1491: T → Gap
Pos. 1519: T → C
Pos. 1532: A → C
Pos. 2151: T → A
Pos. 2376: C → T
Pos. 2618: T → A
Pos. 3313: T → C
Tyrosinase
Pos. 438: C → T
Pos. 471: C → T

Lysapsus

Cytochrome *b*
Pos. 111: C → A
Pos. 149: A → C
Pos. 180: C → A
Pos. 238: CT → A
Pos. 265: C → A
Pos. 274: C → T
Pos. 334: A → G
Pos. 420: AC → T
12S
Pos. 10: G → A
Pos. 115: A → T
Pos. 148: C → A
Pos. 615: T → C
Pos. 716: A → G
Pos. 733: A → T
Pos. 890: A → T
Pos. 1561: T → C
16S
Pos. 254: T → Gap
Pos. 370: Gap → C
Pos. 580: A → G
Pos. 848: A → T
Pos. 1077: C → A
Pos. 1468: C → T
Pos. 1705: C → Gap
Pos. 1744: Gap → A
Pos. 1824: C → T
Pos. 1826: C → A
Pos. 2192: Gap → C
Pos. 2229: T → C
Pos. 2395: T → C
Pos. 2831: Gap → A
Pos. 2913: T → A
Pos. 2966: T → A
Pos. 2982: T → A
Pos. 3081: A → G
Pos. 3266: C → T
Pos. 3280: A → C
Pos. 3297: T → A
RAG-1
Pos. 34 C → T
Pos. 149 A → C
Pos. 164 G → A
Pos. 221 T → C
Pos. 326 G → A
Pos. 392 T → G
Rhodopsin
Pos. 87: A → G
Pos. 185: C → A
SIA
Pos. 289: C → T
Pos. 331: A → G

Pseudis

Cytochrome *b*
Pos. 119: A → C
Pos. 192: T → C
Pos. 290: C → A
Pos. 369: T → A
Pos. 399: C → T
12S
Pos. 36: T → G
Pos. 227: T → C
Pos. 235: AT → C
Pos. 452: T → C
16S
Pos. 162: T → C
Pos. 236: Gap → A
Pos. 434: T → C
Pos. 517: A → G
Pos. 854: T → C
Pos. 1300: A → G
Pos. 1928: CT → A
Pos. 1953: T → A
Pos. 1955: A → C
Pos. 2091: T → C
Pos. 2127: G → A
Pos. 2179: C → T
Pos. 2240: A → G
Pos. 2697: T → A
Pos. 2768: C → T
RAG-1
Pos. 5 G → A
Pos. 20 G → A
Pos. 169 T → A
Pos. 251 G → A

Scarthyla goinorum

Cytochrome *b*
Pos. 6: C → T
Pos. 10: A → T
Pos. 39: T → C
Pos. 49: C → T
Pos. 52: A → C
Pos. 57: C → A
Pos. 67: C → T
Pos. 68: C → T
Pos. 91: T → C
Pos. 108: T → G
Pos. 145: C → T
Pos. 158: A → T
Pos. 164: C → T
Pos. 189: C → T
Pos. 201: T → A
Pos. 202: G → A
Pos. 204: C → A
Pos. 211: T → C
Pos. 262: A → G
Pos. 271: C → T
Pos. 292: T → C
Pos. 311: A → C
Pos. 319: C → T
Pos. 331: C → T
Pos. 376: A → C
Pos. 415: C → T
12S
Pos. 13: G → A
Pos. 22: G → A
Pos. 24: A → C
Pos. 28: A → G
Pos. 33: A → G
Pos. 61: C → T

APPENDIX 5
(*Continued*)

Pos. 98: T → C
Pos. 117: A → C
Pos. 159: C → A
Pos. 169: A → T
Pos. 183: A → G
Pos. 231: C → T
Pos. 295: A → C
Pos. 320: A → G
Pos. 452: T → G
Pos. 454: T → C
Pos. 550: T → C
Pos. 571: A → T
Pos. 600: A → T
Pos. 646: T → A
Pos. 650: T → C
Pos. 675: A → T
Pos. 716: A → C
Pos. 761: T → A
Pos. 814: C → T
Pos. 838: A → T
Pos. 900: T → G
Pos. 1010: T → C
Pos. 1026: T → C
Pos. 1084: T → C
Pos. 1122: T → C
Pos. 1145: T → C
Pos. 1211: CT → A
Pos. 1266: A → G
Pos. 1270: A → G
Pos. 1332: G → A
Pos. 1342: A → Gap
Pos. 1366: C → A
Pos. 1374: C → T
Pos. 1392: T → C
Pos. 1405: A → G
Pos. 1431: T → C
Pos. 1439: C → T
Pos. 1517: A → T
Pos. 1521: G → A
Pos. 1531: C → T
Pos. 1579: A → T
Pos. 1589: T → A
Pos. 1615: Gap → T
Pos. 1657: G → Gap
Pos. 1659: C → T
Pos. 1762: A → G
tRNA valine
Pos. 22: Gap → T
Pos. 39: C → T
Pos. 82: C → T
Pos. 99: G → A
16S
Pos. 3: A → C
Pos. 56: C → Gap
Pos. 254: T → A
Pos. 301: Gap → C
Pos. 355: C → T
Pos. 383: T → A
Pos. 427: T → C
Pos. 452: T → C
Pos. 483: A → C
Pos. 634: A → T
Pos. 636: T → C
Pos. 667: A → G
Pos. 668: T → C
Pos. 686: G → A
Pos. 689: A → T
Pos. 809: T → C
Pos. 814: T → A
Pos. 844: A → C
Pos. 848: A → C
Pos. 853: A → T
Pos. 854: T → A
Pos. 892: G → A
Pos. 946: C → T
Pos. 952: A → C
Pos. 996: A → G
Pos. 1057: T → Gap
Pos. 1062: T → G
Pos. 1085: T → C
Pos. 1092: T → C
Pos. 1103: T → C
Pos. 1113: A → C
Pos. 1118: A → C
Pos. 1125: T → C
Pos. 1188: Gap → T
Pos. 1189: Gap → T
Pos. 1200: A → T
Pos. 1211: A → T
Pos. 1235: C → A
Pos. 1247: Gap → A
Pos. 1248: Gap → G
Pos. 1249: Gap → A
Pos. 1278: T → C
Pos. 1329: Gap → C
Pos. 1332: A → C
Pos. 1337: T → Gap
Pos. 1424: Gap → C
Pos. 1436: T → G
Pos. 1451: T → G
Pos. 1480: T → Gap
Pos. 1506: Gap → A
Pos. 1532: C → A
Pos. 1585: A → G
Pos. 1587: T → C
Pos. 1607: A → G
Pos. 1614: A → C
Pos. 1649: A → Gap
Pos. 1654: A → T
Pos. 1673: A → T
Pos. 1727: A → T
Pos. 1757: T → Gap
Pos. 1795: T → G
Pos. 1799: C → A
Pos. 1823: T → C
Pos. 1865: T → A
Pos. 1874: T → A
Pos. 1887: T → C
Pos. 1894: T → C
Pos. 1971: C → T
Pos. 1997: G → C
Pos. 1999: Gap → T
Pos. 2019: A → T
Pos. 2057: A → C
Pos. 2058: A → T
Pos. 2059: A → T
Pos. 2069: A → T
Pos. 2070: A → C
Pos. 2086: C → T
Pos. 2089: C → G
Pos. 2112: T → A
Pos. 2250: C → T
Pos. 2288: A → G
Pos. 2308: T → C
Pos. 2310: A → C
Pos. 2315: A → G
Pos. 2364: A → Gap
Pos. 2407: Gap → C
Pos. 2510: T → A
Pos. 2518: A → T
Pos. 2544: G → A
Pos. 2548: T → C
Pos. 2566: T → C
Pos. 2575: G → A
Pos. 2588: C → T
Pos. 2604: G → A
Pos. 2605: G → A
Pos. 2618: T → C
Pos. 2680: T → A
Pos. 2768: C → A
Pos. 2789: C → A
Pos. 2866: A → Gap
Pos. 2889: A → Gap
Pos. 2929: C → Gap
Pos. 2946: G → Gap
Pos. 2956: C → Gap
Pos. 2966: T → Gap
Pos. 3036: T → C
Pos. 3054: T → C
Pos. 3071: A → T
Pos. 3125: A → T
Pos. 3127: T → A
Pos. 3138: A → T
Pos. 3202: Gap → T
Pos. 3260: C → T
Pos. 3285: G → T
Pos. 3287: T → C
Pos. 3290: A → G
Pos. 3292: C → A
Pos. 3318: T → C
Pos. 3357: A → T
Pos. 3375: T → A
Pos. 3380: T → A
Pos. 3429: T → C
Pos. 3451: A → G
Pos. 3487: T → C
Pos. 3491: C → A
RAG-1
Pos. 5 G → T
Pos. 29 G → A
Pos. 137 T → C
Pos. 173 C → T
Pos. 182 A → G
Pos. 200 C → A
Pos. 260 C → T
Pos. 297 T → C
Pos. 368 C → T
Pos. 395 T → C
Rhodopsin
Pos. 54: A → T
Pos. 135: C → G
Pos. 181: A → G
Pos. 244: G → T
Pos. 299: T → A
Pos. 305: C → T
SIA
Pos. 21: A → G
Pos. 169: T → A
Pos. 385: T → C

Scinax

Cytochrome *b*
Pos. 97: A → C
Pos. 192: T → C
12S
Pos. 333: C → A
Pos. 636: G → A
Pos. 745: Gap → C
Pos. 1113: C → T
Pos. 1147: A → G
Pos. 1245: T → A
Pos. 1267: A → T
Pos. 1670: C → A
tRNA valine
Pos. 5: T → C
Pos. 87: G → T
Pos. 107: A → G
16S
Pos. 234: T → C
Pos. 349: Gap → A
Pos. 376: A → C
Pos. 606: C → A
Pos. 611: A → G
Pos. 914: A → T
Pos. 1088: Gap → C
Pos. 1118: A → T
Pos. 1183: A → Gap
Pos. 1219: A → T
Pos. 1324: A → C
Pos. 1332: A → G
Pos. 1389: T → A
Pos. 1472: Gap → T
Pos. 1510: A → T
Pos. 1587: T → A
Pos. 1807: A → C
Pos. 1826: C → T
Pos. 1847: G → T
Pos. 1861: T → C
Pos. 1987: Gap → T
Pos. 2156: A → T
Pos. 2406: T → A
Pos. 2443: Gap → A
Pos. 2660: C → T
Pos. 2829: Gap → A
Pos. 2856: T → C
Pos. 2889: A → G
Pos. 2906: T → C
Pos. 2975: A → C
Pos. 2982: T → C
Pos. 3035: C → T
Pos. 3036: T → G
Pos. 3056: T → C
Pos. 3090: G → A
Pos. 3175: Gap → A
Pos. 3199: A → C
Pos. 3268: C → T
Pos. 3283: A → G
Pos. 3294: T → C
Pos. 3361: Gap → CT
28S
Pos. 219: Gap → A
Pos. 238: G → C
Pos. 322: Gap → A
Pos. 327: T → A
Pos. 394: Gap → T
Pos. 397: Gap → T
Pos. 403: Gap → G
Pos. 542: Gap → A
Pos. 558: G → T
Pos. 569: A → C
Pos. 1144: C → A
Pos. 1145: G → A
RAG-1
Pos. 4 C → G
Pos. 11 A → G
Pos. 116 C → G
Pos. 165 C → A
Pos. 169 T → C
Pos. 170 G → A
Pos. 185 T → C
Pos. 194 G → A
Pos. 410 A → C
Pos. 425 G → A
Rhodopsin

APPENDIX 5
(*Continued*)

Pos. 10: G → A
Pos. 123: T → C
SIA
Pos. 211: C → T
Pos. 218: C → T
Pos. 241: G → C
Pos. 250: C → T
Pos. 280: C → T

***Scinax catharinae* clade**

Cytochrome *b*
Pos. 3: C → A
Pos. 10: A → G
Pos. 53: G → A
Pos. 109: G → C
Pos. 152: T → C
Pos. 199: G → A
Pos. 239: C → T
Pos. 244: A → G
Pos. 288: A → T
Pos. 299: T → C
Pos. 327: C → T
Pos. 353: C → T
Pos. 359: A → T
Pos. 376: A → C
12S
Pos. 227: T → Gap
Pos. 241: T → A
Pos. 297: T → C
Pos. 414: C → T
Pos. 460: T → A
Pos. 659: Gap → C
Pos. 965: T → C
Pos. 1122: T → C
Pos. 1307: T → C
Pos. 1392: T → A
Pos. 1422: G → A
Pos. 1441: C → A
tRNA valine
Pos. 59: C → T
Pos. 69: G → A
16S
Pos. 76: Gap → A
Pos. 254: T → C
Pos. 279: Gap → G
Pos. 367: T → Gap
Pos. 383: T → C
Pos. 736: T → C
Pos. 742: T → C
Pos. 836: A → T
Pos. 1052: Gap → C
Pos. 1078: Gap → A
Pos. 1174: T → Gap
Pos. 1348: Gap → A
Pos. 1534: C → T
Pos. 1544: G → A
Pos. 1718: C → A
Pos. 1737: T → A
Pos. 1842: A → C
Pos. 1883: C → A
Pos. 1948: G → C
Pos. 1985: A → C
Pos. 1997: G → A
Pos. 2027: A → T
Pos. 2054: C → T
Pos. 2086: C → T
Pos. 2110: A → C
Pos. 2112: T → C
Pos. 2205: T → C
Pos. 2208: A → C
Pos. 2266: T → C
Pos. 2310: A → T
Pos. 2376: A → G
Pos. 2422: C → T
Pos. 2584: A → T
Pos. 2600: G → A
Pos. 2616: A → T
Pos. 2768: C → T
Pos. 2789: C → T
Pos. 2802: T → A
Pos. 2866: A → C
Pos. 2913: T → C
Pos. 2946: G → Gap
Pos. 2997: C → T
Pos. 3127: T → A
Pos. 3138: A → G
Pos. 3146: T → A
Pos. 3249: A → G
Pos. 3277: G → A
Pos. 3295: T → C
Pos. 3297: T → A
Pos. 3431: C → T
28S
Pos. 1467: G → Gap
Pos. 1476: Gap → C
Rhodopsin
Pos. 135: C → T
Pos. 145: C → T
Pos. 202: T → C
Pos. 291: G → T
Pos. 292: T → A
SIA
Pos. 72: T → C
Pos. 199: G → A
Pos. 292: G → C
Pos. 382: G → A
Pos. 397: T → A

***Scinax ruber* clade**

Cytochrome *b*
Pos. 241: A → T
12S
Pos. 42: T → C
Pos. 250: A → C
Pos. 600: A → G
Pos. 642: Gap → A
Pos. 650: T → C
Pos. 654: T → C
Pos. 673: C → G
Pos. 729: T → A
Pos. 759: A → C
Pos. 869: T → C
Pos. 958: A → G
Pos. 1135: G → A
Pos. 1144: T → A
Pos. 1153: T → G
Pos. 1509: A → G
tRNA valine
Pos. 95: C → T
16S
Pos. 58: C → T
Pos. 107: T → A
Pos. 427: T → A
Pos. 517: A → T
Pos. 726: A → C
Pos. 1203: T → A
Pos. 1246: T → C
Pos. 1337: T → C
Pos. 1438: Gap → A
Pos. 1529: A → C
Pos. 1530: A → T
Pos. 1614: A → G
Pos. 1795: T → C
Pos. 1874: T → C
Pos. 1951: A → T
Pos. 2029: T → C
Pos. 2030: G → A
Pos. 2163: Gap → T
Pos. 2267: A → T
Pos. 2672: A → T
Pos. 2674: T → C
Pos. 2719: T → C
Pos. 2753: T → C
Pos. 3027: A → C
Pos. 3054: T → C
Pos. 3075: T → A
Pos. 3166: C → T
Pos. 3516: A → T
28S
Pos. 381: Gap → T
Pos. 393: Gap → G
Pos. 395: Gap → C
Pos. 396: Gap → C
Pos. 415: Gap → G
Rhodopsin
Pos. 120: C → T
Pos. 160: C → T
Pos. 244: G → T

Sphaenorhynchus

Cytochrome *b*
Pos. 17: A → T
Pos. 26: T → A
Pos. 36: A → C
Pos. 45: C → T
Pos. 49: C → T
Pos. 68: C → T
Pos. 115: C → T
Pos. 214: C → T
Pos. 244: A → T
Pos. 289: C → T
Pos. 331: C → T
Pos. 356: T → C
Pos. 381: C → T
12S
Pos. 36: A → T
Pos. 68: A → C
Pos. 196: G → A
Pos. 206: A → T
Pos. 251: G → A
Pos. 256: C → T
Pos. 319: A → G
Pos. 343: T → C
Pos. 484: A → T
Pos. 521: T → A
Pos. 672: C → A
Pos. 743: A → T
Pos. 760: C → T
Pos. 765: G → A
Pos. 769: G → A
Pos. 821: C → T
Pos. 965: T → A
Pos. 1052: A → T
Pos. 1113: C → Gap
Pos. 1123: Gap → A
Pos. 1233: G → A
Pos. 1245: T → C
Pos. 1332: G → A
Pos. 1343: CT → Gap
Pos. 1366: C → T
Pos. 1374: C → T
Pos. 1409: G → A
Pos. 1412: C → A
Pos. 1415: Gap → T
Pos. 1426: C → T
Pos. 1496: T → C
Pos. 1539: T → A
Pos. 1651: A → T
Pos. 1761: T → C
tRNA valine
Pos. 39: C → T
Pos. 56: T → C
Pos. 74: A → T
Pos. 75: A → T
16S
Pos. 12: C → T
Pos. 255: Gap → G
Pos. 548: A → T
Pos. 771: T → A
Pos. 780: C → A
Pos. 818: C → A
Pos. 827: T → C
Pos. 829: C → T
Pos. 860: G → A
Pos. 902: T → A
Pos. 950: C → T
Pos. 1010: G → A
Pos. 1019: C → T
Pos. 1204: Gap → A
Pos. 1331: T → C
Pos. 1347: Gap → A
Pos. 1389: T → C
Pos. 1419: T → A
Pos. 1443: T → G
Pos. 1458: A → T
Pos. 1503: C → T
Pos. 1510: A → T
Pos. 1800: Gap → T
Pos. 1826: C → A
Pos. 1839: T → A
Pos. 1883: C → A
Pos. 1948: GT → A
Pos. 2019: A → T
Pos. 2043: A → T
Pos. 2086: C → T
Pos. 2098: G → Gap
Pos. 2108: Gap → T
Pos. 2120: A → T
Pos. 2544: G → A
Pos. 2551: A → T
Pos. 2672: A → T
Pos. 2975: A → T
Pos. 3059: A → C
Pos. 3081: A → G
Pos. 3145: T → A
Pos. 3166: C → A
Pos. 3277: G → A
Pos. 3299: C → T
Pos. 3313: T → A
Pos. 3425: C → T
Pos. 3455: G → A
RAG-1
Pos. 15 C → A
Pos. 44 A → G
Pos. 47 C → T
Pos. 58 A → G
Pos. 64 A → G
Pos. 89 T → C
Pos. 164 G → A
Pos. 194 G → A
Pos. 248 A → C
Pos. 272 C → T
Pos. 275 C → T
Pos. 317 T → C

APPENDIX 5
(*Continued*)

Pos. 332 G → A
Pos. 357 C → T
Pos. 365 T → C
Pos. 371 A → C
Pos. 386 T → A
Pos. 398 A → T
Pos. 410 A → C
Pos. 425 G → A
Rhodopsin
Pos. 45: C → T
Pos. 93: C → T
Pos. 160: C → T
Pos. 220: G → T
Pos. 224: G → T
Pos. 235: C → T
Pos. 272: C → T
Pos. 290: C → T
Pos. 308: T → A
Pos. 314: C → T
Tyrosinase
Pos. 7: T → A
Pos. 10: A → C
Pos. 11: C → T
Pos. 20: T → A
Pos. 72: C → T
Pos. 139: A → G
Pos. 183: A → G
Pos. 197: C → T
Pos. 209: T → C
Pos. 210: A → G
Pos. 211: C → A
Pos. 276: T → C
Pos. 288: C → T
Pos. 291: G → C
Pos. 294: C → T
Pos. 330: T → C
Pos. 333: A → G
Pos. 375: T → C
Pos. 376: T → G
Pos. 393: C → T
Pos. 406: C → A
Pos. 408: A → C
Pos. 423: T → C
Pos. 424: G → A
Pos. 447: A → G
Pos. 472: Gap → T
Pos. 478: G → Gap
Pos. 481: T → C
Pos. 508: T → C
Pos. 513: G → A

Xenohyla

Cytochrome *b*
Pos. 6: C → T
Pos. 10: A → G
Pos. 32: A → G
Pos. 49: C → A
Pos. 52: A → T
Pos. 88: C → T
Pos. 108: A → G
Pos. 137: C → T
Pos. 164: C → T
Pos. 170: A → T
Pos. 199: G → A
Pos. 201: T → C
Pos. 229: C → T
Pos. 262: A → C
Pos. 271: C → T
Pos. 277: T → C
Pos. 290: C → T
Pos. 292: T → C
Pos. 313: A → G
Pos. 322: C → A
Pos. 353: C → T
Pos. 362: T → G
Pos. 402: T → C
Pos. 411: T → C
Pos. 420: A → T
12S
Pos. 13: G → A
Pos. 140: C → T
Pos. 148: C → A
Pos. 159: C → A
Pos. 171: G → T
Pos. 320: A → C
Pos. 379: A → G
Pos. 455: C → T
Pos. 499: Gap → T
Pos. 528: A → G
Pos. 547: C → Gap
Pos. 600: A → G
Pos. 645: Gap → A
Pos. 654: T → Gap
Pos. 683: A → C
Pos. 733: T → G
Pos. 774: A → G
Pos. 815: T → C
Pos. 817: G → A
Pos. 927: A → T
Pos. 1043: C → T
Pos. 1094: A → T
Pos. 1278: G → A
Pos. 1303: A → G
Pos. 1321: T → A
Pos. 1376: A → G
Pos. 1399: A → G
Pos. 1434: T → C
Pos. 1441: C → A
Pos. 1549: AT → C
Pos. 1649: A → T
Pos. 1670: C → T
tRNA valine
Pos. 46: T → G
Pos. 75: A → C
Pos. 76: A → G
Pos. 86: T → C
16S
Pos. 130: C → T
Pos. 191: Gap → T
Pos. 192: C → A
Pos. 259: A → G
Pos. 272: T → C
Pos. 323: C → A
Pos. 336: C → A
Pos. 427: T → A
Pos. 434: A → T
Pos. 472: T → A
Pos. 498: T → C
Pos. 543: T → C
Pos. 654: T → C
Pos. 668: T → A
Pos. 718: T → C
Pos. 742: T → C
Pos. 755: A → C
Pos. 767: A → T
Pos. 775: T → G
Pos. 784: C → A
Pos. 792: A → G
Pos. 821: T → A
Pos. 854: T → C
Pos. 900: T → C
Pos. 908: T → C
Pos. 1025: T → C
Pos. 1160: T → C
Pos. 1174: T → A
Pos. 1183: A → C
Pos. 1246: T → C
Pos. 1259: T → C
Pos. 1272: T → A
Pos. 1274: A → G
Pos. 1309: Gap → C
Pos. 1324: A → G
Pos. 1436: T → G
Pos. 1443: T → C
Pos. 1534: C → A
Pos. 1741: C → T
Pos. 1896: A → C
Pos. 1925: A → T
Pos. 2027: A → T
Pos. 2028: G → C
Pos. 2089: C → T
Pos. 2112: T → C
Pos. 2115: A → T
Pos. 2130: C → T
Pos. 2154: T → A
Pos. 2161: A → T
Pos. 2229: T → G
Pos. 2240: A → G
Pos. 2262: AG → T
Pos. 2616: A → C
Pos. 2618: T → C
Pos. 2664: A → T
Pos. 2694: T → C
Pos. 2801: Gap → T
Pos. 2865: Gap → C
Pos. 2956: A → G
Pos. 3018: T → A
Pos. 3027: T → C
Pos. 3056: T → C
Pos. 3086: T → A
Pos. 3234: T → C
Pos. 3426: A → G
Pos. 3454: T → C
Pos. 3487: T → C

Hylini

Cytochrome *b*
Pos. 29: Gap → C
Pos. 31: A → C
Pos. 33: C → Gap
Pos. 57: C → A
Pos. 90: T → A
Pos. 101: C → T
Pos. 126: G → T
Pos. 127: C → T
Pos. 137: T → A
Pos. 353: C → T
12S
Pos. 117: A → CT
Pos. 140: C → T
Pos. 148: C → T
Pos. 432: T → A
Pos. 455: C → T
Pos. 528: A → T
Pos. 594: A → G
Pos. 595: A → T
Pos. 716: A → T
Pos. 1008: T → C
Pos. 1094: A → T
Pos. 1211: T → C
Pos. 1265: C → T
Pos. 1417: G → T
Pos. 1422: G → A
Pos. 1649: A → T
Pos. 1670: C → A
Pos. 1678: A → C
tRNA valine
Pos. 39: C → A
28S
Pos. 150: A → T
Pos. 153: T → C
Pos. 342: C → G
Pos. 400: T → Gap
Pos. 454: G → C
Pos. 516: G → C
Pos. 563: G → C
Pos. 569: A → T
Pos. 863: G → Gap
Pos. 870: G → Gap
Pos. 876: A → Gap
Pos. 1003: Gap →G
Pos. 1017: Gap →T
Pos. 1080: Gap →G
Pos. 1103: G → C
RAG-1
Pos. 1: C → T
Pos. 101: T → C
Pos. 114: T → A
Pos. 115: C → G
Pos. 143: G → C
Pos. 151: A → C
Pos. 169: T → C
Pos. 178: A → G
Pos. 194: G → A
Pos. 359: A → C
Pos. 374: G → A
Rhodopsin
Pos. 12: A → G
Pos. 220: G → A
Pos. 271: C → G
Pos. 281: T → C
Pos. 287: C → T
SIA
Pos. 280: C → T
Pos. 349: T → A
Tyrosinase
Pos. 6: G → A
Pos. 33: T → A
Pos. 86: A → C
Pos. 160: T → C
Pos. 175: A → 4
Pos. 180: 4 → T
Pos. 394: C → A
Pos. 454: C → G
Pos. 455: T → C

Acris

Cytochrome *b*
Pos. 40: A → G
Pos. 63: C → Gap
Pos. 68: C → T
Pos. 125: T → C
Pos. 137: A → C
Pos. 152: T → C
Pos. 155: A → C
Pos. 201: A → C
Pos. 207: C → T
Pos. 223: A → C
Pos. 302: A → T
Pos. 306: A → C
Pos. 311: A → C
Pos. 362: A → T
Pos. 369: A → T
Pos. 387: T → A

APPENDIX 5
(*Continued*)

Pos. 396: A → C
Pos. 408: C → T
12S
Pos. 142: C → T
Pos. 206: A → C
Pos. 229: Gap → A
Pos. 233: Gap → A
Pos. 332: A → C
Pos. 457: T → A
Pos. 547: A → T
Pos. 670: A → T
Pos. 778: A → C
Pos. 841: A → T
Pos. 864: C → T
Pos. 908: A → C
Pos. 927: A → T
Pos. 965: C → T
Pos. 1245: T → A
Pos. 1307: T → A
Pos. 1332: G → A
Pos. 1423: A → T
Pos. 1568: A → T
Pos. 1649: T → C
Pos. 1674: A → C
tRNA valine
Pos. 6: G → A
Pos. 39: A → T
Pos. 105: C → T
16S
Pos. 172: A → C
Pos. 188: A → C
Pos. 272: G → A
Pos. 443: C → G
Pos. 452: T → C
Pos. 459: T → C
Pos. 498: T → C
Pos. 517: T → C
Pos. 784: C → T
Pos. 848: C → A
Pos. 853: A → G
Pos. 914: A → C
Pos. 950: C → A
Pos. 1077: T → A
Pos. 1235: C → A
Pos. 1265: A → T
Pos. 1325: A → Gap
Pos. 1375: Gap → C
Pos. 1480: T → Gap
Pos. 1673: A → T
Pos. 1699: A → T
Pos. 1807: A → C
Pos. 1819: A → T
Pos. 1870: A → C
Pos. 1949: A → T
Pos. 1965: T → A
Pos. 2030: G → A
Pos. 2072: T → C
Pos. 2080: A → G
Pos. 2122: T → G
Pos. 2179: C → T
Pos. 2203: T → C
Pos. 2233: T → A
Pos. 2244: T → C
Pos. 2250: C → T
Pos. 2253: A → T
Pos. 2381: T → C
Pos. 2422: C → T
Pos. 2577: G → T
Pos. 2676: A → T
Pos. 2787: T → A
Pos. 2889: A → C
Pos. 2982: T → C
Pos. 3140: C → T
Pos. 3280: A → T
RAG-1
Pos. 5 G → A
Pos. 71 G → A
Pos. 125 G → A
Pos. 170 G → A
Pos. 359 C → T
Pos. 422 T → C
Rhodopsin
Pos. 21: C → T
Pos. 54: A → G
Pos. 60: T → C
Pos. 166: C → T
Pos. 211: G → A
SIA
Pos. 160: T → C
Pos. 247: C → G
Pos. 259: A → T
Pos. 268: A → G
Pos. 397: T → A
Tyrosinase
Pos. 9: T → C
Pos. 10: A → C
Pos. 20: T → C
Pos. 25: T → C
Pos. 28: T → C
Pos. 34: T → C
Pos. 43: T → C
Pos. 73: A → G
Pos. 102: A → G
Pos. 127: T → C
Pos. 150: C → T
Pos. 167: G → A
Pos. 168: T → C
Pos. 169: G → C
Pos. 180: T → C
Pos. 195: A → G
Pos. 204: A → C
Pos. 215: G → C
Pos. 231: A → C
Pos. 254: A → G
Pos. 307: A → G
Pos. 312: T → C
Pos. 315: A → G
Pos. 321: C → G
Pos. 330: T → C
Pos. 352: C → T
Pos. 384: A → G
Pos. 387: T → C
Pos. 407: A → G
Pos. 447: A → G
Pos. 453: T → C
Pos. 491: C → A
Pos. 493: T → G
Pos. 496: A → G
Pos. 507: T → C

Anotheca spinosa

Cytochrome *b*
Pos. 10: A → T
Pos. 24: G → A
Pos. 52: A → T
Pos. 53: G → A
Pos. 57: A → C
Pos. 91: T → C
Pos. 155: A → G
Pos. 167: T → C
Pos. 170: A → T
Pos. 173: A → G
Pos. 183: C → T
Pos. 189: C → T
Pos. 212: T → A
Pos. 213: G → A
Pos. 214: C → T
Pos. 217: A → G
Pos. 247: C → T
Pos. 248: C → A
Pos. 249: T → C
Pos. 256: A → T
Pos. 290: C → T
Pos. 299: T → C
Pos. 316: C → T
Pos. 353: T → C
Pos. 359: A → G
Pos. 363: A → G
Pos. 376: A → G
Pos. 408: C → T
Pos. 417: G → C
12S
Pos. 9: T → C
Pos. 22: G → A
Pos. 45: C → T
Pos. 83: G → A
Pos. 88: C → T
Pos. 102: T → C
Pos. 174: A → G
Pos. 271: C → A
Pos. 313: C → T
Pos. 347: T → C
Pos. 383: G → A
Pos. 389: T → C
Pos. 391: A → T
Pos. 414: C → A
Pos. 422: Gap → T
Pos. 423: Gap → T
Pos. 432: A → Gap
Pos. 455: C → T
Pos. 460: T → C
Pos. 480: A → G
Pos. 489: G → Gap
Pos. 512: T → A
Pos. 600: T → G
Pos. 602: A → T
Pos. 608: A → G
Pos. 611: A → G
Pos. 654: T → C
Pos. 661: A → G
Pos. 686: G → A
Pos. 726: A → T
Pos. 788: G → A
Pos. 797: T → C
Pos. 802: C → T
Pos. 900: T → G
Pos. 928: A → G
Pos. 958: A → G
Pos. 963: Gap → T
Pos. 995: T → C
Pos. 1002: C → T
Pos. 1023: T → C
Pos. 1043: C → T
Pos. 1095: C → T
Pos. 1096: G → A
Pos. 1100: G → A
Pos. 1101: T → G
Pos. 1113: T → C
Pos. 1177: C → T
Pos. 1194: T → C
Pos. 1211: T → C
Pos. 1215: A → C
Pos. 1265: T → C
Pos. 1273: A → G
Pos. 1274: T → C
Pos. 1278: G → A
Pos. 1296: C → T
Pos. 1317: C → T
Pos. 1366: C → T
Pos. 1378: G → A
Pos. 1385: G → A
Pos. 1408: A → G
Pos. 1427: T → C
Pos. 1434: T → C
Pos. 1439: C → A
Pos. 1449: G → A
Pos. 1544: Gap → T
Pos. 1585: A → T
Pos. 1645: T → C
Pos. 1649: T → C
Pos. 1651: A → T
Pos. 1664: A → G
Pos. 1670: T → C
Pos. 1674: A → C
Pos. 1693: C → T
Pos. 1699: Gap → T
tRNA valine
Pos. 46: T → C
Pos. 55: A → G
Pos. 99: G → A
16S
Pos. 94: C → T
Pos. 118: C → T
Pos. 130: C → T
Pos. 206: T → C
Pos. 272: G → A
Pos. 536: C → T
Pos. 559: T → C
Pos. 566: T → C
Pos. 610: T → C
Pos. 611: A → G
Pos. 668: T → C
Pos. 699: A → Gap
Pos. 712: A → Gap
Pos. 742: T → A
Pos. 771: T → C
Pos. 818: C → T
Pos. 821: A → T
Pos. 876: A → G
Pos. 952: A → G
Pos. 959: G → A
Pos. 1022: A → C
Pos. 1025: T → C
Pos. 1085: A → Gap
Pos. 1121: Gap → T
Pos. 1140: A → T
Pos. 1183: A → G
Pos. 1223: T → C
Pos. 1246: T → C
Pos. 1278: C → T
Pos. 1292: T → G
Pos. 1510: A → G
Pos. 1529: A → G
Pos. 1548: T → C
Pos. 1600: C → A
Pos. 1607: C → T
Pos. 1635: Gap → C
Pos. 1710: T → A
Pos. 1718: T → C
Pos. 1727: A → C
Pos. 1813: T → C
Pos. 2032: A → Gap
Pos. 2039: G → A
Pos. 2059: A → C

APPENDIX 5
(*Continued*)

Pos. 2071: T → C
Pos. 2130: T → C
Pos. 2138: Gap → C
Pos. 2156: C → T
Pos. 2169: A → G
Pos. 2170: A → G
Pos. 2217: T → C
Pos. 2229: T → C
Pos. 2262: G → A
Pos. 2267: A → G
Pos. 2280: A → T
Pos. 2364: A → Gap
Pos. 2392: A → G
Pos. 2518: A → G
Pos. 2524: T → C
Pos. 2544: A → G
Pos. 2615: A → G
Pos. 2655: A → G
Pos. 2660: C → T
Pos. 2694: T → C
Pos. 2719: T → C
Pos. 2768: T → C
Pos. 2787: T → C
Pos. 2960: T → G
Pos. 3014: T → C
Pos. 3036: T → A
Pos. 3039: A → G
Pos. 3071: A → G
Pos. 3094: T → C
Pos. 3281: A → C
Pos. 3282: T → C
Pos. 3297: C → T
Pos. 3321: A → G
Pos. 3324: T → C
Pos. 3363: Gap → T
Pos. 3380: A → T
Pos. 3419: G → A
Pos. 3458: T → C
Pos. 3462: C → T
RAG-1
Pos. 11 A → G
Pos. 77 T → C
Pos. 89 T → C
Pos. 149 A → C
Pos. 179 A → G
Pos. 185 G → T
Pos. 263 G → A
Pos. 293 G → A
Pos. 395 C → T
Rhodopsin
Pos. 28: A → T
Pos. 57: C → T
Pos. 89: A → T
Pos. 93: C → A
Pos. 114: C → T
SIA
Pos. 21: A → G
Pos. 292: G → C
Tyrosinase
Pos. 0: A → T
Pos. 6: A → T
Pos. 46: G → C
Pos. 97: G → A
Pos. 124: T → C
Pos. 139: A → C
Pos. 164: A → G
Pos. 194: A → G
Pos. 357: C → T
Pos. 418: G → A
Pos. 426: C → A
Pos. 484: T → C
Pos. 526: C → T
Pos. 537: T → G

Bromeliohyla bromeliacia

Cytochrome *b*
Pos. 62: T → C
Pos. 63: C → T
Pos. 76: C → T
Pos. 116: C → T
Pos. 149: A → T
Pos. 161: A → G
Pos. 183: A → T
Pos. 186: A → G
Pos. 241: A → G
Pos. 283: C → T
Pos. 286: C → T
Pos. 331: T → Gap
Pos. 359: A → G
Pos. 369: A → C
Pos. 381: C → T
Pos. 405: CT → A
Pos. 420: A → G
12s
Pos. 28: A → G
Pos. 180: C → T
Pos. 206: A → T
Pos. 310: T → C
Pos. 370: T → C
Pos. 412: T → C
Pos. 421: A → C
Pos. 438: A → T
Pos. 452: T → C
Pos. 454: T → C
Pos. 455: T → C
Pos. 512: T → C
Pos. 541: A → T
Pos. 627: Gap → T
Pos. 631: Gap → G
Pos. 641: A → C
Pos. 736: C → T
Pos. 1002: C → T
Pos. 1094: T → C
Pos. 1136: A → G
Pos. 1187: C → T
Pos. 1233: G → A
Pos. 1374: C → T
Pos. 1407: G → A
Pos. 1429: C → T
Pos. 1455: T → C
Pos. 1469: Gap → T
Pos. 1496: T → C
Pos. 1639: Gap → T
tRNA valine
Pos. 2: A → T
Pos. 55: A → C
Pos. 74: C → G
Pos. 94: C → T
Pos. 98: A → G
16S
Pos. 8: A → G
Pos. 111: Gap → A
Pos. 152: Gap → T
Pos. 162: C → T
Pos. 383: A → G
Pos. 459: T → G
Pos. 589: C → T
Pos. 618: A → G
Pos. 640: A → T
Pos. 648: G → A
Pos. 736: T → C
Pos. 754: A → G
Pos. 763: G → A
Pos. 780: C → T
Pos. 788: C → T
Pos. 890: G → A
Pos. 941: G → A
Pos. 948: C → T
Pos. 979: C → T
Pos. 1085: A → G
Pos. 1187: A → T
Pos. 1211: A → Gap
Pos. 1235: C → Gap
Pos. 1289: A → G
Pos. 1314: A → G
Pos. 1328: A → G
Pos. 1332: G → A
Pos. 1468: A → T
Pos. 1561: C → T
Pos. 1574: A → T
Pos. 1596: A → T
Pos. 1673: A → G
Pos. 1757: CT → A
Pos. 1799: A → T
Pos. 1861: C → T
Pos. 1925: A → T
Pos. 1975: A → C
Pos. 1985: A → T
Pos. 2029: T → C
Pos. 2063: A → G
Pos. 2094: A → G
Pos. 2110: A → G
Pos. 2151: C → T
Pos. 2201: Gap → C
Pos. 2202: Gap → A
Pos. 2233: T → C
Pos. 2312: T → A
Pos. 2423: A → C
Pos. 2450: C → T
Pos. 2620: C → T
Pos. 2655: A → G
Pos. 2697: T → C
Pos. 2753: A → G
Pos. 2856: T → C
Pos. 3010: C → T
Pos. 3143: A → G
Pos. 3199: A → T
Pos. 3291: A → G
Pos. 3303: C → T
Pos. 3310: A → T
Pos. 3320: G → A
Pos. 3324: T → C
Pos. 3326: T → C
Pos. 3425: C → T
Pos. 3455: G → A
Pos. 3458: T → C
28s
Pos. 561: C → A
Pos. 812: C → A
RAG-1
Pos. 179: A → G
Rhodopsin
Pos. 9: C → T
Pos. 95: C → T
Pos. 154: C → T
Pos. 244: G → T
Pos. 268: A → T
Pos. 279: C → A
SIA
Pos. 133: C → A
Pos. 256: A → G
Tyrosinase
Pos. 106: C → T
Pos. 112: C → T
Pos. 127: T → C
Pos. 176: A → G
Pos. 197: T → A
Pos. 254: A → G
Pos. 263: C → T
Pos. 267: C → T
Pos. 269: C → T
Pos. 297: C → T
Pos. 299: A → C
Pos. 300: A → G
Pos. 354: G → C

Charadrahyla

Cytochrome *b*
Pos. 128: A → T
Pos. 274: T → C
Pos. 353: T → C
12S
Pos. 183: A → G
Pos. 328: G → A
Pos. 337: C → T
Pos. 454: T → C
Pos. 571: A → C
Pos. 1002: C → T
Pos. 1010: T → A
Pos. 1061: T → C
Pos. 1113: C → Gap
Pos. 1116: C → T
Pos. 1236: T → C
Pos. 1343: T → C
Pos. 1383: C → A
Pos. 1441: C → A
Pos. 1461: C → T
tRNA valine
Pos. 61: C → T
16S
Pos. 2: T → C
Pos. 130: C → T
Pos. 452: T → C
Pos. 770: Gap → C
Pos. 780: C → Gap
Pos. 1174: T → C
Pos. 1265: A → G
Pos. 1328: A → G
Pos. 1330: C → T
Pos. 1332: G → T
Pos. 1643: T → A
Pos. 1673: A → C
Pos. 1817: A → T
Pos. 1861: C → A
Pos. 1870: A → C
Pos. 2253: A → G
Pos. 2268: C → A
Pos. 2461: C → T
Pos. 2569: T → C
Pos. 2616: A → T
Pos. 2694: T → C
Pos. 2780: A → Gap
Pos. 2802: T → A
Pos. 2913: T → C
Pos. 3010: C → A
Pos. 3111: G → A
Pos. 3118: C → A
Pos. 3130: A → T
Pos. 3154: A → G
Pos. 3389: C → T
Pos. 3425: C → T
SIA
Pos. 175: C → T
Pos. 376: T → C

APPENDIX 5
(*Continued*)

Tyrosinase
Pos. 86: C → A
Pos. 102: A → G
Pos. 172: A → G
Pos. 432: T → C

Duellmanohyla

Cytochrome *b*
Pos. 229: C → T
Pos. 277: T → C
Pos. 292: T → C
Pos. 313: T → C
Pos. 366: T → C
Pos. 376: T → C
Pos. 399: T → C
12S
Pos. 13: A → G
Pos. 22: G → A
Pos. 131: T → Gap
Pos. 272: A → G
Pos. 414: C → T
Pos. 427: C → T
Pos. 726: A → Gap
Pos. 1010: T → A
Pos. 1333: A → C
Pos. 1405: A → G
Pos. 1408: A → G
Pos. 1412: C → T
Pos. 1427: T → C
Pos. 1431: T → C
Pos. 1500: Gap → A
16S
Pos. 172: A → C
Pos. 234: A → Gap
Pos. 272: G → T
Pos. 376: T → C
Pos. 755: T → A
Pos. 949: T → C
Pos. 1160: T → C
Pos. 1699: A → C
Pos. 1826: T → C
Pos. 2164: Gap → T
Pos. 2308: C → T
Pos. 2551: A → G
Pos. 2742: T → A
Pos. 2787: A → Gap
Pos. 3054: A → G
Pos. 3222: T → C
Pos. 3249: T → C
Pos. 3375: T → C
Pos. 3487: T → C
RAG-1
Pos. 35 A → G
Rhodopsin
Pos. 28: A → T
SIA
Pos. 175: C → T
Pos. 241: G → A
Tyrosinase
Pos. 70: T → G
Pos. 517: T → C
Pos. 527: A → G

Ecnomiohyla

Cytochrome *b*
Pos. 49: C → T
Pos. 136: C → T
Pos. 152: T → C
Pos. 176: C → T
Pos. 183: A → T
Pos. 189: C → T
Pos. 229: C → T
Pos. 369: A → T
12S
Pos. 102: T → C
Pos. 164: C → A
Pos. 322: C → T
Pos. 427: C → T
16S
Pos. 1118: A → C
Pos. 1183: T → A
Pos. 1230: Gap → T
Pos. 1235: C → A
Pos. 1491: A → T
Pos. 1585: A → G
Pos. 1741: C → T
Pos. 1870: A → T
Pos. 1925: A → T
Pos. 2069: T → A
Pos. 2089: A → C
Pos. 2190: C → Gap
Pos. 2229: T → C
Pos. 2441: C → T
Pos. 2457: G → A
Pos. 3056: C → A
Pos. 3173: G → A
Pos. 3222: T → Gap
Pos. 3249: T → C
Pos. 3285: G → A
Pos. 3315: A → T
RAG-1
Pos. 242 G → A
Rhodopsin
Pos. 28: A → T
Pos. 281: C → T
Pos. 316: A → G

Exerodonta

Cytochrome *b*
Pos. 71: A → C
Pos. 115: C → T
Pos. 232: C → A
Pos. 247: C → T
Pos. 256: A → T
Pos. 334: A → G
Pos. 411: T → C
12S
Pos. 227: T → C
Pos. 322: C → A
Pos. 370: A → G
Pos. 392: T → C
Pos. 594: G → T
Pos. 673: T → C
Pos. 760: C → A
Pos. 1376: A → G
Pos. 1392: T → A
Pos. 1585: A → G
Pos. 1601: T → A
Pos. 1602: T → A
Pos. 1636: A → T
Pos. 1649: T → C
Pos. 1651: A → G
16S
Pos. 151: Gap → T
Pos. 284: Gap → A
Pos. 434: A → T
Pos. 443: C → T
Pos. 755: A → T
Pos. 758: A → C
Pos. 853: A → T
Pos. 890: G → A
Pos. 948: C → T
Pos. 1153: A → C
Pos. 1160: T → C
Pos. 1351: Gap → A
Pos. 1389: T → A
Pos. 1468: A → T
Pos. 1534: C → T
Pos. 1587: T → C
Pos. 1817: A → T
Pos. 1819: A → T
Pos. 1839: T → C
Pos. 2024: G → A
Pos. 2067: A → T
Pos. 2130: T → A
Pos. 2263: C → T
Pos. 2615: A → C
Pos. 2676: A → T
Pos. 2780: A → C
Pos. 2812: T → A
Pos. 2929: C → T
Pos. 2946: G → Gap
Pos. 3081: A → T
Pos. 3234: A → T
Pos. 3290: A → G
Pos. 3426: G → T
Pos. 3439: T → C
Pos. 3454: C → A
28S
Pos. 544: G → C
RAG-1
Pos. 32 A → G
Pos. 128 T → C
Pos. 155 T → C
Pos. 248 A → G
Pos. 293 G → A
Pos. 413 T → C
Rhodopsin
Pos. 232: C → T
Pos. 259: C → T
Pos. 281: C → T
Pos. 299: T → C
SIA
Pos. 81: C → T
Pos. 106: C → A
Pos. 205: T → C
Pos. 211: C → T
Pos. 331: G → A
Pos. 376: T → C
Tyrosinase
Pos. 4: C → T
Pos. 105: G → C
Pos. 179: A → G
Pos. 257: C → T
Pos. 327: T → C
Pos. 514: G → C

***Exerodonta sumichrasti* group**

Cytochrome *b*
Pos. 24: G → A
Pos. 45: C → T
Pos. 126: T → C
Pos. 153: C → T
Pos. 167: C → T
Pos. 176: C → T
Pos. 189: C → T
Pos. 198: T → C
Pos. 214: C → T
Pos. 217: A → G
Pos. 241: A → G
Pos. 296: C → T
Pos. 331: C → T
Pos. 366: T → C
Pos. 367: C → T
Pos. 380: C → T
Pos. 383: T → C
Pos. 417: A → C
12S
Pos. 24: A → G
Pos. 115: A → T
Pos. 159: A → T
Pos. 231: T → C
Pos. 241: T → C
Pos. 333: C → A
Pos. 452: T → C
Pos. 541: T → C
Pos. 558: A → C
Pos. 594: T → C
Pos. 641: A → G
Pos. 733: A → T
Pos. 778: A → G
Pos. 869: C → T
Pos. 1043: C → T
Pos. 1211: C → T
Pos. 1549: A → T
Pos. 1625: T → C
16S
Pos. 107: C → A
Pos. 234: T → C
Pos. 472: C → A
Pos. 656: T → C
Pos. 708: A → G
Pos. 718: T → C
Pos. 736: T → C
Pos. 758: C → T
Pos. 774: T → G
Pos. 780: C → T
Pos. 834: A → G
Pos. 862: T → C
Pos. 914: A → T
Pos. 1574: A → T
Pos. 1699: A → C
Pos. 1727: A → T
Pos. 1826: T → C
Pos. 2057: T → C
Pos. 2069: T → C
Pos. 2200: T → C
Pos. 2248: A → G
Pos. 2381: T → A
Pos. 2587: T → C
Pos. 2615: C → T
Pos. 2715: Gap → T
Pos. 2982: T → C
Pos. 2995: A → C
Pos. 3010: C → T
Pos. 3087: Gap → C
Pos. 3125: T → C
Pos. 3209: T → C
Pos. 3230: T → A
RAG-1
Pos. 392 T → A
Rhodopsin
Pos. 9: C → T
Pos. 36: G → A
Pos. 133: C → T
Pos. 167: A → C
SIA
Pos. 21: A → G
Pos. 205: C → A
Tyrosinase
Pos. 420: A → G

Hyla

Cytochrome *b*

APPENDIX 5
(*Continued*)

Pos. 11: C → A
Pos. 67: C → T
Pos. 250: T → C
Pos. 417: G → A
12S
Pos. 560: Gap → T
Pos. 778: A → G
Pos. 814: C → T
Pos. 1101: T → C
Pos. 1346: T → C
Pos. 1549: A → Gap
16S
Pos. 543: T → C
Pos. 780: C → A
Pos. 1103: A → T
Pos. 1246: T → A
Pos. 1436: T → A
Pos. 1713: Gap → A
Pos. 1925: T → C
Pos. 2267: A → T
Pos. 2787: T → Gap
Pos. 2812: T → A
Pos. 2858: Gap → C
Rhodopsin
Pos. 316: A → G
Tyrosinase
Pos. 73: G → A
Pos. 484: T → C
Pos. 493: T → C

***Hyla arborea* group**

Cytochrome *b*
Pos. 145: C → T
Pos. 271: C → T
12S
Pos. 13: A → G
Pos. 34: T → C
Pos. 152: T → A
Pos. 169: T → C
Pos. 268: T → C
Pos. 455: C → T
Pos. 880: C → G
Pos. 1039: Gap → T
Pos. 1043: C → A
Pos. 1365: Gap → C
Pos. 1561: A → T
16S
Pos. 664: A → T
Pos. 718: T → C
Pos. 1057: T → C
Pos. 1389: T → A
Pos. 1402: A → C
Pos. 1799: A → C
Pos. 2089: A → C
Pos. 2820: A → C
Pos. 2856: T → A
Pos. 3239: A → Gap
Pos. 3282: T → C
RAG-1
Pos. 4 C → T
Pos. 380 C → T
Pos. 395 C → T
Rhodopsin
Pos. 93: C → A
Pos. 245: G → T
Pos. 262: G → A
Tyrosinase
Pos. 29: C → A
Pos. 31: A → C
Pos. 120: A → T
Pos. 186: C → A
Pos. 245: C → T
Pos. 315: G → A

***Hyla cinerea* group**

Cytochrome *b*
Pos. 53: G → A
Pos. 108: G → A
Pos. 125: T → C
Pos. 149: A → T
Pos. 183: A → T
Pos. 214: C → T
Pos. 286: C → T
Pos. 338: T → C
Pos. 366: T → C
12S
Pos. 597: T → C
Pos. 1105: A → T
Pos. 1113: T → C
Pos. 1422: G → A
Pos. 1589: C → A
16S
Pos. 107: C → A
Pos. 177: Gap → C
Pos. 272: G → A
Pos. 517: T → C
Pos. 521: A → T
Pos. 1603: T → C
Pos. 1699: T → C
Pos. 1874: T → C
Pos. 2058: C → A
Pos. 2156: C → A
Pos. 2161: A → T
Pos. 2280: A → T
RAG-1
Pos. 83 A → G
Pos. 284 A → G
SIA
Pos. 250: C → T
Pos. 20: T → G
Pos. 257: C → T
Pos. 506: G → A

***Hyla eximia* group**

Cytochrome *b*
Pos. 153: T → C
Pos. 167: T → C
Pos. 238: T → C
16S
Pos. 162: T → C
Pos. 566: T → C
Pos. 1376: T → C
Pos. 1842: A → G
Pos. 2107: A → G
Pos. 2620: C → T

***Hyla versicolor* group**

Cytochrome *b*
Pos. 49: C → G
Pos. 103: C → T
Pos. 108: G → A
Pos. 161: A → G
Pos. 214: C → T
Pos. 286: C → T
Pos. 289: C → T
Pos. 313: C → T
Pos. 356: C → T
Pos. 383: A → T
Pos. 417: A → C
12S
Pos. 285: A → T
Pos. 352: G → A
Pos. 560: T → Gap
Pos. 565: T → C
Pos. 571: A → C
Pos. 738: A → T
Pos. 1278: G → A
Pos. 1579: A → Gap
Pos. 1671: Gap → T
16S
Pos. 521: A → T
Pos. 573: A → T
Pos. 822: A → T
Pos. 906: T → C
Pos. 965: C → T
Pos. 1092: A → G
Pos. 1167: A → T
Pos. 1203: T → C
Pos. 1223: C → T
Pos. 1718: C → T
Pos. 1741: C → A
Pos. 1749: T → C
Pos. 1799: A → T
Pos. 1807: A → G
Pos. 1925: C → T
Pos. 2057: C → T
Pos. 2089: A → T
Pos. 2177: C → T
Pos. 2233: T → C
Pos. 2280: A → G
Pos. 2508: T → C
Pos. 2997: C → T
Pos. 3010: C → T
Pos. 3140: C → T
Pos. 3389: C → T
Pos. 3524: C → T
Pos. 3538: G → A
Rhodopsin
Pos. 316: G → A
SIA
Pos. 211: C → T
Tyrosinase
Pos. 120: A → T

Isthmohyla

Cytochrome *b*
Pos. 68: T → C
Pos. 91: T → C
Pos. 167: T → C
Pos. 247: C → T
Pos. 265: C → T
Pos. 376: A → C
12S
Pos. 117: C → T
Pos. 169: T → A
Pos. 348: T → C
Pos. 550: T → A
Pos. 565: T → C
Pos. 726: A → T
Pos. 1002: C → T
tRNA valine
Pos. 4: A → G
16S
Pos. 323: C → T
Pos. 355: T → C
Pos. 559: T → C
Pos. 580: T → C
Pos. 611: A → G
Pos. 1015: T → A
Pos. 1657: Gap → C
Pos. 1727: A → C
Pos. 1865: C → T
Pos. 2043: A → T
Pos. 2107: A → G
Pos. 2112: CT → A
Pos. 2156: C → T
Pos. 2208: AT → C
Pos. 2217: T → C
Pos. 2544: A → G
Pos. 2776: A → Gap
Pos. 2820: A → T
Pos. 2982: T → C
Pos. 3056: C → T
Pos. 3111: G → A
Pos. 3154: A → G
Pos. 3173: T → C
Pos. 3237: T → A
Pos. 3281: A → G
Pos. 3282: T → C
Rhodopsin
Pos. 93: C → T
Pos. 124: C → A

Megastomatohyla mixe

Cytochrome *b*
Pos. 10: C → A
Pos. 46: C → T
Pos. 49: C → A
Pos. 57: A → G
Pos. 101: T → A
Pos. 109: G → A
Pos. 125: T → C
Pos. 137: C → T
Pos. 145: C → T
Pos. 164: C → T
Pos. 168: A → G
Pos. 184: A → C
Pos. 204: C → A
Pos. 214: C → T
Pos. 223: A → C
Pos. 238: T → A
Pos. 241: A → C
Pos. 292: T → C
Pos. 302: A → G
Pos. 327: C → A
Pos. 338: T → C
Pos. 366: T → C
Pos. 383: A → T
Pos. 414: T → A
Pos. 415: C → T
12S
Pos. 34: T → C
Pos. 61: C → T
Pos. 68: A → C
Pos. 69: C → T
Pos. 110: A → Gap
Pos. 183: A → T
Pos. 269: A → T
Pos. 326: A → G
Pos. 339: T → C
Pos. 434: G → A
Pos. 440: A → G
Pos. 451: T → C
Pos. 452: T → A
Pos. 480: A → G
Pos. 521: T → C
Pos. 558: A → Gap
Pos. 579: Gap → G
Pos. 619: G → T
Pos. 646: C → T
Pos. 650: T → G
Pos. 726: A → C
Pos. 736: C → A
Pos. 738: A → C
Pos. 769: G → A

APPENDIX 5
(*Continued*)

Pos. 821: C → T
Pos. 835: T → C
Pos. 869: C → T
Pos. 908: A → C
Pos. 989: A → G
Pos. 1036: C → T
Pos. 1043: C → A
Pos. 1048: T → C
Pos. 1067: C → T
Pos. 1089: T → C
Pos. 1105: A → Gap
Pos. 1122: T → C
Pos. 1128: T → C
Pos. 1144: T → C
Pos. 1244: A → G
Pos. 1245: T → C
Pos. 1278: G → A
Pos. 1327: A → G
Pos. 1366: C → T
Pos. 1392: T → A
Pos. 1405: A → G
Pos. 1408: A → G
Pos. 1412: C → T
Pos. 1418: A → C
Pos. 1427: T → C
Pos. 1431: T → C
Pos. 1439: C → T
Pos. 1455: T → C
Pos. 1537: Gap → T
Pos. 1561: A → C
Pos. 1568: A → G
Pos. 1651: A → T
Pos. 1664: A → T
tRNA valine
Pos. 39: A → G
Pos. 46: T → C
Pos. 59: C → T
Pos. 69: G → A
Pos. 76: AG → T
16S
Pos. 0: G → A
Pos. 107: C → T
Pos. 130: C → A
Pos. 234: A → T
Pos. 294: A → Gap
Pos. 323: C → T
Pos. 376: A → T
Pos. 418: T → C
Pos. 600: Gap → A
Pos. 630: A → T
Pos. 636: T → C
Pos. 665: A → T
Pos. 702: A → G
Pos. 731: T → C
Pos. 784: C → A
Pos. 807: G → A
Pos. 818: C → T
Pos. 839: C → T
Pos. 876: A → G
Pos. 906: T → A
Pos. 908: T → A
Pos. 954: G → A
Pos. 968: G → A
Pos. 1012: T → Gap
Pos. 1092: T → A
Pos. 1153: A → C
Pos. 1167: T → C
Pos. 1228: A → Gap
Pos. 1253: Gap → C
Pos. 1259: T → C
Pos. 1310: C → A
Pos. 1331: A → T
Pos. 1332: G → A
Pos. 1405: T → A
Pos. 1480: C → A
Pos. 1544: A → G
Pos. 1572: T → C
Pos. 1574: A → T
Pos. 1614: A → G
Pos. 1727: A → T
Pos. 1740: Gap → T
Pos. 1768: A → Gap
Pos. 1861: C → T
Pos. 1865: C → A
Pos. 1928: C → T
Pos. 1932: T → C
Pos. 1977: G → C
Pos. 1997: G → A
Pos. 2054: C → A
Pos. 2068: C → T
Pos. 2070: A → C
Pos. 2107: A → C
Pos. 2110: A → T
Pos. 2130: T → A
Pos. 2177: C → T
Pos. 2298: C → T
Pos. 2398: A → C
Pos. 2450: C → T
Pos. 2544: A → G
Pos. 2588: C → T
Pos. 2605: G → A
Pos. 2669: A → G
Pos. 2683: Gap → A
Pos. 2691: C → T
Pos. 2787: T → Gap
Pos. 2812: T → C
Pos. 2906: T → A
Pos. 2946: G → T
Pos. 2990: A → Gap
Pos. 2997: C → Gap
Pos. 3004: A → T
Pos. 3014: T → Gap
Pos. 3036: T → C
Pos. 3127: T → C
Pos. 3143: A → G
Pos. 3145: T → C
Pos. 3236: Gap → T
Pos. 3268: C → T
Pos. 3278: C → T
Pos. 3287: T → C
Pos. 3298: G → A
Pos. 3385: T → C
Pos. 3426: G → A
Pos. 3454: C → T
Pos. 3486: A → G
Pos. 3545: A → G
28s
Pos. 205: A → G
Pos. 569: T → C
Pos. 779: Gap → C
Pos. 780: Gap → C
Pos. 1073: G → A
Pos. 1078: C → A
RAG-1
Pos. 117: A → G
Pos. 137: T → C
Pos. 155: T → C
Pos. 179: A → G
Rhodopsin
Pos. 28: A → T
Pos. 39: A → G
Pos. 135: C → T
Pos. 205: C → T
Pos. 219: C → T
Pos. 256: C → T
SIA
Pos. 6: G → A
Pos. 127: A → G
Pos. 211: C → T
Pos. 235: G → A
Pos. 259: A → G
Pos. 322: C → T
Pos. 373: C → T
Tyrosinase
Pos. 19: T → G
Pos. 26: C → A
Pos. 96: A → G
Pos. 133: AC → G
Pos. 179: A → G
Pos. 191: A → G
Pos. 261: A → G
Pos. 307: A → G
Pos. 308: A → C
Pos. 394: A → G
Pos. 456: G → C
Pos. 484: T → C
Pos. 511: G → A

Plectrohyla

Cytochrome *b*
Pos. 45: C → T
Pos. 189: C → T
Pos. 238: T → A
Pos. 310: A → C
Pos. 402: T → C
12S
Pos. 9: T → C
Pos. 502: Gap → C
Pos. 601: A → G
Pos. 650: T → C
Pos. 1113: C → T
Pos. 1118: C → T
Pos. 1579: A → G
16S
Pos. 188: A → T
Pos. 459: T → A
Pos. 654: T → A
Pos. 906: T → A
Pos. 1085: T → A
Pos. 1103: T → C
Pos. 1741: C → T
Pos. 1826: T → C
Pos. 1948: T → C
Pos. 2039: G → A
Pos. 2154: C → A
Pos. 2229: T → A
Pos. 2267: A → T
Pos. 2820: A → T
Pos. 2985: T → C
Pos. 3326: T → C
28S
Pos. 525: G → Gap
RAG-1
Pos. 362 C → A
Pos. 395 T → C
SIA
Pos. 3: T → C
Pos. 142: C → G
Pos. 148: C → T
Tyrosinase
Pos. 37: C → T
Pos. 58: G → A
Pos. 86: C → A
Pos. 172: A → G
Pos. 300: A → G
Pos. 324: G → A
Pos. 416: A → G
Pos. 475: C → T

***Plectrohyla bistincta* group**

Cytochrome *b*
Pos. 101: T → AG
Pos. 204: A → T
Pos. 319: C → T
Pos. 356: T → C
12S
Pos. 295: A → C
Pos. 427: C → T
Pos. 512: T → A
Pos. 1002: C → T
Pos. 1005: C → A
16S
Pos. 517: T → C
Pos. 1219: A → T
Pos. 1223: C → T
Pos. 1618: Gap → T
Pos. 1649: T → A
Pos. 2190: C → A
RAG-1
Pos. 74 T → C

***Plectrohyla guatemalensis* group**

Cytochrome *b*
Pos. 3: C → T
Pos. 111: C → T
Pos. 131: A → G
Pos. 229: C → T
Pos. 244: A → T
Pos. 271: C → T
Pos. 383: T → C
Pos. 396: A → G
12S
Pos. 180: C → T
Pos. 251: G → A
Pos. 646: C → T
Pos. 751: A → C
Pos. 1270: A → G
Pos. 1307: T → C
Pos. 1321: T → A
Pos. 1521: G → A
Pos. 1659: C → T
tRNA valine
Pos. 110: T → A
16S
Pos. 12: C → T
Pos. 355: C → T
Pos. 498: T → C
Pos. 691: G → A
Pos. 767: A → G
Pos. 839: C → T
Pos. 1092: T → A
Pos. 1458: T → C
Pos. 1718: T → C
Pos. 2057: T → C
Pos. 2240: A → G
Pos. 2854: Gap → C
Pos. 3010: C → T
Pos. 3027: T → C
Pos. 3242: Gap → T
28S
Pos. 891: C → T

Pseudacris

Cytochrome *b*

APPENDIX 5
(*Continued*)

Pos. 36: A → CT
Pos. 39: T → C
Pos. 71: A → C
Pos. 153: C → T
Pos. 189: C → T
Pos. 253: T → C
Pos. 274: T → C
Pos. 319: C → T
Pos. 327: C → A
Pos. 354: A → G
Pos. 383: A → T
12S
Pos. 556: Gap → A
Pos. 838: A → T
Pos. 843: T → C
Pos. 1113: C → T
tRNA valine
Pos. 59: C → T
Pos. 69: G → A
16S
Pos. 664: A → T
Pos. 1085: T → A
Pos. 1211: A → Gap
Pos. 1223: C → Gap
Pos. 1561: C → T
Pos. 1710: T → C
Pos. 2025: C → T
Pos. 2112: T → A
Pos. 2836: Gap → T
Pos. 3035: C → T
Pos. 3208: Gap → T
28S
Pos. 464: G → T
Pos. 525: G → Gap
Pos. 909: C → A
Tyrosinase
Pos. 191: A → G
Pos. 283: G → T
Pos. 324: G → A
Pos. 382: A → C
Pos. 396: A → C

Ptychohyla

Cytochrome *b*
Pos. 111: C → T
12S
Pos. 1113: C → T
Pos. 1422: A → G
16S
Pos. 308: A → G
Pos. 1298: C → T
Pos. 1532: C → T
Pos. 1953: T → A
Pos. 2143: Gap → T
Pos. 2785: T → C
Pos. 3278: C → T
Pos. 3298: G → A

Smilisca

Cytochrome *b*
Pos. 119: CT → A
Pos. 198: T → A
Pos. 274: T → C
Pos. 280: C → T
Pos. 330: C → T
Pos. 383: A → T
Pos. 411: T → C
12S
Pos. 206: A → G
Pos. 231: T → A
Pos. 244: A → T
Pos. 330: C → T
Pos. 336: G → A
Pos. 386: A → T
Pos. 566: Gap → A
Pos. 600: T → A
Pos. 729: T → A
Pos. 880: C → A
Pos. 1101: T → C
Pos. 1316: A → T
Pos. 1330: A → T
Pos. 1614: T → Gap
Pos. 1632: Gap → C
Pos. 1678: T → C
tRNA valine
Pos. 39: A → G
16S
Pos. 443: T → A
Pos. 853: A → G
Pos. 906: T → C
Pos. 1103: A → T
Pos. 1235: A → T
Pos. 1468: A → C
Pos. 1743: Gap → T
Pos. 2117: A → T
Pos. 2267: A → T
Pos. 2820: A → C
Pos. 2849: A → T
Pos. 3127: T → C
SIA
Pos. 232: A → G
Pos. 292: G → A

Tlalocohyla

Cytochrome *b*
Pos. 90: A → T
Pos. 128: A → T
Pos. 158: C → T
Pos. 244: A → T
Pos. 259: C → T
Pos. 322: A → C
Pos. 330: C → T
Pos. 381: C → T
Pos. 387: T → A
12S
Pos. 40: C → T
Pos. 61: C → A
Pos. 131: T → C
Pos. 231: T → A
Pos. 297: T → C
Pos. 348: T → C
Pos. 353: G → A
Pos. 378: G → A
Pos. 437: C → T
Pos. 521: T → G
Pos. 528: A → C
Pos. 582: C → A
Pos. 970: A → C
Pos. 1001: A → C
Pos. 1122: T → A
Pos. 1265: T → C
Pos. 1346: T → A
Pos. 1417: T → C
Pos. 1531: C → Gap
16S
Pos. 188: A → C
Pos. 323: C → A
Pos. 336: C → A
Pos. 399: A → T
Pos. 459: T → A
Pos. 589: C → T
Pos. 634: T → A
Pos. 718: T → C
Pos. 777: A → C
Pos. 853: A → T
Pos. 874: T → C
Pos. 906: T → C
Pos. 982: A → G
Pos. 1024: C → T
Pos. 1183: T → A
Pos. 1275: G → A
Pos. 1376: T → Gap
Pos. 1451: T → C
Pos. 1458: T → A
Pos. 1870: A → T
Pos. 1874: T → A
Pos. 1878: C → A
Pos. 1928: C → A
Pos. 1948: T → A
Pos. 1994: A → T
Pos. 2008: C → T
Pos. 2059: A → T
Pos. 2069: T → A
Pos. 2151: T → C
Pos. 2200: T → A
Pos. 2398: A → T
Pos. 2587: T → C
Pos. 2785: A → C
Pos. 2913: T → C
Pos. 2975: A → T
Pos. 3056: C → A
Pos. 3118: C → T
Pos. 3260: C → T
Pos. 3291: A → G
Pos. 3318: T → C
Pos. 3357: A → T
Pos. 3428: C → T
Pos. 3429: T → C
Pos. 3451: A → G
Rhodopsin
Pos. 185: C → A
Pos. 262: G → A
Pos. 296: T → G
Pos. 300: C → T
SIA
Pos. 3: T → C
Pos. 289: A → C
Pos. 340: A → G
Tyrosinase
Pos. 0: A → C
Pos. 6: A → G
Pos. 26: C → G
Pos. 49: C → T
Pos. 118: T → C
Pos. 155: C → G
Pos. 170: A → C
Pos. 171: G → C
Pos. 177: A → C
Pos. 254: A → G
Pos. 327: T → C
Pos. 453: T → C
Pos. 466: A → C

Triprion

Cytochrome *b*
Pos. 2: C → T
Pos. 23: T → C
Pos. 39: C → T
Pos. 68: T → C
Pos. 79: A → G
Pos. 88: C → T
Pos. 94: C → T
Pos. 126: T → G
Pos. 127: T → C
Pos. 137: C → T
Pos. 140: A → C
Pos. 145: C → T
Pos. 149: A → G
Pos. 153: T → C
Pos. 158: C → T
Pos. 164: C → T
Pos. 176: C → T
Pos. 180: C → T
Pos. 204: C → A
Pos. 241: A → G
Pos. 265: C → T
Pos. 286: C → T
Pos. 311: A → G
Pos. 367: C → T
Pos. 399: C → T
12S
Pos. 13: A → G
Pos. 38: T → C
Pos. 41: T → C
Pos. 70: C → T
Pos. 117: C → A
Pos. 149: Gap → A
Pos. 169: T → A
Pos. 227: T → C
Pos. 326: A → G
Pos. 352: A → G
Pos. 532: Gap → C
Pos. 547: T → C
Pos. 550: T → C
Pos. 565: T → C
Pos. 582: T → G
Pos. 716: A → C
Pos. 733: T → A
Pos. 738: A → G
Pos. 778: A → G
Pos. 814: C → T
Pos. 864: C → Gap
Pos. 869: C → T
Pos. 880: C → T
Pos. 1105: C → T
Pos. 1122: T → C
Pos. 1362: T → C
Pos. 1402: A → T
Pos. 1405: A → G
Pos. 1423: A → C
Pos. 1431: T → C
Pos. 1440: T → A
Pos. 1441: C → T
Pos. 1549: A → C
Pos. 1561: A → T
Pos. 1761: C → T
Pos. 1762: G → A
tRNA valine
Pos. 4: A → G
Pos. 59: C → T
Pos. 69: G → A
Pos. 90: A → G
Pos. 101: A → G
Pos. 108: T → C
16S
Pos. 162: T → G
Pos. 434: A → T
Pos. 517: T → C
Pos. 543: T → C
Pos. 630: A → G
Pos. 656: T → C
Pos. 726: A → T
Pos. 780: C → T
Pos. 839: T → C
Pos. 890: A → G

APPENDIX 5
(*Continued*)

Pos. 914: A → G
Pos. 1103: A → G
Pos. 1174: T → C
Pos. 1259: T → C
Pos. 1436: T → A
Pos. 1443: T → C
Pos. 1480: T → C
Pos. 1650: Gap → C
Pos. 1737: C → T
Pos. 1741: C → A
Pos. 1817: A → G
Pos. 1948: T → C
Pos. 1953: T → C
Pos. 2063: A → G
Pos. 2089: A → T
Pos. 2142: C → A
Pos. 2587: T → C
Pos. 2613: A → G
Pos. 2849: A → G
Pos. 2913: T → C
Pos. 2985: T → C
Pos. 3081: A → T
Pos. 3209: G → A
Pos. 3249: C → T
Pos. 3326: C → T
RAG-1
Pos. 68: A → C
Pos. 107: A → G
Pos. 122: A → G
Pos. 302: C → T
SIA
Pos. 48: C → T
Pos. 106: C → A
Tyrosinase
Pos. 12: C → T
Pos. 22: G → A
Pos. 49: C → T
Pos. 248: G → T
Pos. 268: C → T
Pos. 312: C → T
Pos. 394: A → C
Pos. 401: G → A
Pos. 416: G → A
Pos. 432: C → T
Pos. 450: C → G
Pos. 456: G → C
Pos. 481: G → T
Pos. 493: T → C
Pos. 506: G → A
Pos. 514: G → A

Hylini + Lophiohylini

Cytochrome *b*
Pos. 14: A → T
Pos. 97: A → C
Pos. 310: C → A
12S
Pos. 231: A → T
Pos. 761: T → C
Pos. 890: A → C
Pos. 965: T → C
Pos. 1116: A → C
16S
Pos. 272: T → G
Pos. 383: T → A
Pos. 848: A → C
Pos. 906: A → T
Pos. 1223: Gap → C
Pos. 1796: Gap → A
Pos. 1817: T → A
Pos. 2057: A → CT
Pos. 2151: T → C
Pos. 2618: T → A
Pos. 2787: Gap → T
28S
Pos. 249: C → Gap
Pos. 327: T → Gap
SIA
Pos. 331: A → G
Tyrosinase
Pos. 315: C → A
Pos. 429: T → C
Pos. 481: T → G

Lophiohylini

Cytochrome *b*
Pos. 3: C → A
Pos. 36: A → C
Pos. 265: C → A
Pos. 268: A → C
Pos. 302: A → C
12S
Pos. 24: A → T
Pos. 285: A → C
Pos. 593: T → C
Pos. 672: C → A
Pos. 771: C → T
Pos. 817: G → A
Pos. 908: A → T
Pos. 1589: T → A
tRNA valine
Pos. 6: G → A
Pos. 105: C → T
16S
Pos. 138: Gap → AC
Pos. 573: A → T
Pos. 736: T → A
Pos. 758: A → T
Pos. 814: T → A
Pos. 836: A → C
Pos. 878: C → T
Pos. 978: G → A
Pos. 1160: T → A
Pos. 1174: T → C
Pos. 1419: T → C
Pos. 1470: Gap → C
Pos. 1710: T → C
Pos. 1789: Gap → T
Pos. 1842: A → Gap
Pos. 1880: A → T
Pos. 1953: T → A
Pos. 2041: A → C
Pos. 2091: T → C
Pos. 2110: A → T
Pos. 2156: A → C
Pos. 2525: A → T
Pos. 2694: T → A
Pos. 2889: A → C
Pos. 3004: A → C
Pos. 3297: T → A
28S
Pos. 390: C → T
Pos. 532: Gap → A
Pos. 544: G → C
RAG-1
Pos. 89 T → C
Pos. 233 A → G
Pos. 248 A → C
Pos. 317 T → C
Pos. 341 C → T
Pos. 371 A → T
SIA
Pos. 36: T → C
Pos. 145: A → G
Pos. 148: C → T
Pos. 211: C → T
Pos. 235: G → A
Pos. 373: C → T
Tyrosinase
Pos. 0: AC → T
Pos. 4: C → G
Pos. 212: G → A
Pos. 268: C → T
Pos. 333: A → T
Pos. 372: T → C
Pos. 396: A → G

Aparasphenodon brunoi

Cytochrome *b*
Pos. 42: T → C
Pos. 71: A → G
Pos. 76: C → A
Pos. 97: C → T
Pos. 105: A → G
Pos. 108: G → A
Pos. 152: C → T
Pos. 164: C → T
Pos. 167: C → T
Pos. 183: C → T
Pos. 214: C → T
Pos. 223: A → T
Pos. 235: A → G
Pos. 247: C → T
Pos. 250: C → T
Pos. 296: C → T
Pos. 327: C → T
Pos. 330: C → T
Pos. 331: C → T
Pos. 367: C → T
Pos. 396: A → G
Pos. 399: C → T
Pos. 414: C → T
Pos. 415: C → T
Pos. 420: C → A
12s
Pos. 10: A → G
Pos. 66: G → A
Pos. 68: A → C
Pos. 159: C → G
Pos. 183: A → C
Pos. 194: T → C
Pos. 206: A → T
Pos. 227: C → T
Pos. 452: T → C
Pos. 521: T → C
Pos. 550: C → T
Pos. 594: A → C
Pos. 646: C → T
Pos. 693: G → A
Pos. 864: C → Gap
Pos. 965: C → T
Pos. 970: A → C
Pos. 1043: C → T
Pos. 1270: A → G
Pos. 1392: T → A
Pos. 1402: G → C
Pos. 1599: C → T
Pos. 1636: C → T
Pos. 1670: C → T
16S
Pos. 1085: T → C
Pos. 1310: C → T
Pos. 1325: C → T
Pos. 1468: A → G
Pos. 1470: C → T
Pos. 1718: T → C
Pos. 1737: T → C
Pos. 1795: C → T
Pos. 1874: C → A
Pos. 1878: T → C
Pos. 1928: T → C
Pos. 1998: A → C
Pos. 2027: A → G
Pos. 2028: G → A
Pos. 2029: T → C
Pos. 2063: A → G
Pos. 2072: T → C
Pos. 2130: C → T
Pos. 2151: C → T
Pos. 2203: A → C
Pos. 2240: A → G
Pos. 2253: A → G
Pos. 2395: A → G
Pos. 2566: C → T
Pos. 2568: C → T
Pos. 2844: G → C
Pos. 2856: A → T
Pos. 2866: A → T
Pos. 2982: C → T
Pos. 2990: C → T
Pos. 3014: T → C
Pos. 3032: T → C
Pos. 3127: T → C
Pos. 3189: G → A

Argenteohyla siemersi

Cytochrome *b*
Pos. 3: C → T
Pos. 17: A → G
Pos. 57: A → G
Pos. 63: C → T
Pos. 76: C → T
Pos. 108: G → C
Pos. 109: G → A
Pos. 128: A → G
Pos. 186: A → G
Pos. 223: A → G
Pos. 238: T → A
Pos. 239: C → T
Pos. 292: T → A
Pos. 311: A → G
Pos. 319: C → T
Pos. 334: G → A
Pos. 344: A → G
Pos. 378: T → C
Pos. 396: A → T
Pos. 408: A → T
12S
Pos. 36: A → G
Pos. 133: Gap → A
Pos. 141: Gap → T
Pos. 159: C → A
Pos. 285: C → A
Pos. 492: Gap → T
Pos. 493: Gap → T
Pos. 672: A → C
Pos. 673: C → T
Pos. 880: A → T
Pos. 1010: T → C
Pos. 1084: T → C
Pos. 1309: A → T
Pos. 1346: T → C
Pos. 1392: T → C
Pos. 1413: A → T

APPENDIX 5
(*Continued*)

Pos. 1422: G → A
Pos. 1589: A → C
Pos. 1674: C → T
tRNA valine
Pos. 72: G → A
Pos. 98: G → A
16S
Pos. 0: G → A
Pos. 11: C → T
Pos. 138: A → T
Pos. 172: A → C
Pos. 308: A → G
Pos. 356: T → C
Pos. 452: T → C
Pos. 726: A → C
Pos. 827: T → C
Pos. 831: A → T
Pos. 839: C → T
Pos. 1022: G → A
Pos. 1049: T → C
Pos. 1062: T → C
Pos. 1278: T → C
Pos. 1443: T → C
Pos. 1458: A → G
Pos. 1510: A → G
Pos. 1649: T → C
Pos. 1795: C → A
Pos. 1874: C → T
Pos. 1944: A → G
Pos. 2016: T → C
Pos. 2024: G → A
Pos. 2091: C → T
Pos. 2125: T → C
Pos. 2187: A → G
Pos. 2203: A → T
Pos. 2233: T → C
Pos. 2250: C → A
Pos. 2263: C → T
Pos. 2267: T → C
Pos. 2285: A → G
Pos. 2345: C → T
Pos. 2392: A → T
Pos. 2416: G → A
Pos. 2450: C → T
Pos. 2728: Gap → A
Pos. 2889: C → Gap
Pos. 3039: A → G
Pos. 3059: A → C
Pos. 3116: Gap → G
Pos. 3199: A → G
Pos. 3285: G → A
Pos. 3397: Gap → G
28S
Pos. 262: C → Gap
Pos. 505: G → Gap
Pos. 532: A → T
RAG-1
Pos. 6: T → C
Pos. 128 T → G
Pos. 183 C → G
Pos. 324 G → C
Pos. 380 C → T
SIA
Pos. 205: T → G
Tyrosinase
Pos. 91: C → T
Pos. 284: C → T
Pos. 312: T → C
Pos. 324: G → A
Pos. 339: C → A
Pos. 351: C → T
Pos. 416: A → G

Corythomantis greenengi

Cytochrome *b*
Pos. 10: A → C
Pos. 45: C → T
Pos. 60: A → G
Pos. 67: C → T
Pos. 71: A → C
Pos. 126: G → A
Pos. 127: C → T
Pos. 155: A → G
Pos. 211: C → T
Pos. 268: T → A
Pos. 274: C → T
Pos. 327: C → A
Pos. 381: C → T
Pos. 393: C → T
Pos. 411: T → C
12S
Pos. 18: T → C
Pos. 24: T → C
Pos. 34: T → C
Pos. 152: A → C
Pos. 250: A → T
Pos. 440: A → G
Pos. 452: T → C
Pos. 454: T → C
Pos. 460: T → A
Pos. 576: A → T
Pos. 593: C → T
Pos. 683: A → G
Pos. 729: T → C
Pos. 775: G → A
Pos. 814: C → T
Pos. 864: C → T
Pos. 875: C → A
Pos. 965: C → T
Pos. 1048: T → C
Pos. 1144: T → C
Pos. 1194: A → C
Pos. 1297: T → C
Pos. 1307: T → C
Pos. 1315: A → C
Pos. 1316: A → G
Pos. 1376: A → G
Pos. 1509: A → G
Pos. 1585: A → T
16S
Pos. 3: A → G
Pos. 107: T → A
Pos. 138: A → C
Pos. 220: C → T
Pos. 411: C → A
Pos. 452: T → A
Pos. 543: T → C
Pos. 606: C → A
Pos. 622: Gap → C
Pos. 625: T → C
Pos. 634: T → Gap
Pos. 665: A → C
Pos. 667: A → G
Pos. 668: T → C
Pos. 736: A → T
Pos. 751: C → A
Pos. 758: T → C
Pos. 777: A → T
Pos. 787: T → C
Pos. 844: A → T
Pos. 863: C → T
Pos. 890: G → A
Pos. 997: C → T
Pos. 1025: T → C
Pos. 1049: T → Gap
Pos. 1080: Gap → A
Pos. 1085: T → C
Pos. 1174: C → A
Pos. 1261: G → T
Pos. 1267: Gap → G
Pos. 1451: T → G
Pos. 1530: A → G
Pos. 1614: A → T
Pos. 1620: T → C
Pos. 1654: A → T
Pos. 1705: T → A
Pos. 1741: T → A
Pos. 1817: A → Gap
Pos. 1844: Gap → C
Pos. 1865: T → A
Pos. 1893: G → A
Pos. 1952: T → C
Pos. 2025: C → T
Pos. 2034: A → G
Pos. 2041: CT → G
Pos. 2043: A → T
Pos. 2058: A → C
Pos. 2068: T → C
Pos. 2107: A → T
Pos. 2120: A → T
Pos. 2122: T → C
Pos. 2130: C → T
Pos. 2154: T → C
Pos. 2156: C → T
Pos. 2190: A → G
Pos. 2229: A → T
Pos. 2525: T → A
Pos. 2812: T → A
Pos. 2872: Gap → C
Pos. 3014: T → A
Pos. 3032: T → C
Pos. 3125: A → T
28S
Pos. 563: G → T
Pos. 569: A → T
RAG-1
Pos. 59 G → A
Pos. 110 C → T
Pos. 131 G → A
Pos. 197 T → C
Pos. 201 A → C
Pos. 233 G → A
Pos. 398 A → C
Rhodopsin
Pos. 9: C → T
Pos. 135: C → T
Pos. 219: C → T
SIA
Pos. 27: G → A
Pos. 100: A → T
Pos. 151: C → A
Pos. 241: G → A
Tyrosinase
Pos. 58: G → A
Pos. 144: G → C
Pos. 230: C → T
Pos. 257: C → T
Pos. 270: G → A
Pos. 321: C → T
Pos. 342: C → T
Pos. 360: G → T
Pos. 435: C → T
Pos. 450: C → T
Pos. 475: C → T

Itapotihyla langsdorffii

Cytochrome *b*
Pos. 13: A → C
Pos. 14: T → A
Pos. 17: A → C
Pos. 24: G → A
Pos. 36: C → G
Pos. 63: C → T
Pos. 91: T → C
Pos. 115: C → T
Pos. 158: C → G
Pos. 227: A → T
Pos. 241: A → C
Pos. 244: A → T
Pos. 259: C → T
Pos. 277: T → C
Pos. 296: C → T
Pos. 299: T → C
Pos. 319: C → T
Pos. 327: C → T
Pos. 334: A → C
Pos. 344: A → G
Pos. 363: A → G
Pos. 383: A → T
Pos. 396: A → C
Pos. 420: A → G
12S
Pos. 18: T → C
Pos. 26: A → G
Pos. 33: A → G
Pos. 36: A → T
Pos. 148: C → T
Pos. 169: A → C
Pos. 206: A → G
Pos. 297: T → A
Pos. 452: T → C
Pos. 541: C → A
Pos. 594: A → G
Pos. 615: T → C
Pos. 650: T → C
Pos. 672: A → G
Pos. 683: A → G
Pos. 743: A → T
Pos. 761: C → T
Pos. 880: A → T
Pos. 989: A → G
Pos. 1008: T → C
Pos. 1010: T → A
Pos. 1048: T → A
Pos. 1118: C → A
Pos. 1269: T → C
Pos. 1321: T → C
Pos. 1343: T → C
Pos. 1392: T → C
Pos. 1422: G → A
Pos. 1429: C → A
Pos. 1439: C → T
Pos. 1631: Gap → T
Pos. 1649: A → Gap
Pos. 1761: T → C
16S
Pos. 172: A → C
Pos. 347: C → T
Pos. 355: C → A
Pos. 376: A → T
Pos. 498: T → C
Pos. 548: A → C
Pos. 634: A → C
Pos. 753: A → T

APPENDIX 5
(*Continued*)

Pos. 757: A → G
Pos. 848: C → A
Pos. 863: C → T
Pos. 1004: G → A
Pos. 1077: T → G
Pos. 1211: A → G
Pos. 1228: A → C
Pos. 1246: T → A
Pos. 1259: T → A
Pos. 1278: T → C
Pos. 1419: C → A
Pos. 1443: T → G
Pos. 1468: A → G
Pos. 1727: A → Gap
Pos. 1823: T → C
Pos. 1932: T → A
Pos. 1949: A → G
Pos. 2043: A → C
Pos. 2059: A → C
Pos. 2089: C → T
Pos. 2110: T → C
Pos. 2112: T → A
Pos. 2115: A → T
Pos. 2130: C → T
Pos. 2156: C → T
Pos. 2176: C → T
Pos. 2525: T → C
Pos. 2669: A → T
Pos. 2844: T → A
Pos. 2901: T → C
Pos. 2956: A → G
Pos. 2997: C → G
Pos. 3010: T → A
Pos. 3014: T → A
Pos. 3018: T → C
Pos. 3032: T → C
Pos. 3239: A → G
Pos. 3287: T → A
28S
Pos. 312: C → T
Pos. 1482: G → C
Pos. 1483: T → G
RAG-1
Pos. 4 C → T
Pos. 44 A → G
Pos. 71 G → A
Pos. 173 C → T
Pos. 311 C → T
Pos. 357 C → T
Rhodopsin
Pos. 316: G → A
Tyrosinase
Pos. 104: G → A
Pos. 148: C → T
Pos. 203: G → A
Pos. 270: G → A
Pos. 297: C → T
Pos. 399: A → T
Pos. 444: G → A
Pos. 459: C → T
Pos. 471: C → T

Nyctimantis rugiceps

Cytochrome *b*
Pos. 10: A → C
Pos. 39: C → T
Pos. 45: C → T
Pos. 53: G → A
Pos. 57: A → T
Pos. 62: G → A
Pos. 91: T → C
Pos. 101: T → A
Pos. 140: A → G
Pos. 145: T → G
Pos. 150: T → C
Pos. 161: A → G
Pos. 170: A → C
Pos. 189: C → T
Pos. 201: T → C
Pos. 213: G → C
Pos. 217: T → A
Pos. 232: A → C
Pos. 238: T → G
Pos. 262: A → C
Pos. 268: T → A
Pos. 274: C → T
Pos. 290: C → T
Pos. 299: T → C
Pos. 316: C → T
Pos. 347: A → G
Pos. 365: T → C
Pos. 366: T → C
Pos. 376: T → C
Pos. 383: A → G
Pos. 390: A → G
Pos. 394: A → G
Pos. 408: A → G
16S
Pos. 996: A → G
Pos. 1103: T → C
Pos. 1153: C → T
Pos. 1228: A → G
Pos. 1242: T → C
Pos. 1246: T → G
Pos. 1443: T → Gap
Pos. 1503: A → G
Pos. 1574: A → T
Pos. 1602: T → C
Pos. 1607: T → G
Pos. 1654: A → Gap
Pos. 1727: A → T
Pos. 1766: Gap → C
Pos. 1826: C → T
Pos. 1894: T → C
Pos. 1925: C → T
Pos. 1960: A → G
Pos. 2030: G → A
Pos. 2034: A → G
Pos. 2091: C → A
Pos. 2094: A → G
Pos. 2115: A → G
Pos. 2117: T → C
Pos. 2200: A → G
Pos. 2229: A → G
Pos. 2233: T → G
Pos. 2265: T → C
Pos. 2279: T → A
Pos. 2288: A → G
Pos. 2315: A → G
Pos. 2461: C → T
Pos. 2508: T → C
Pos. 2518: A → C
Pos. 2525: T → C
Pos. 2544: G → A
Pos. 2564: T → C
Pos. 2570: A → T
Pos. 2616: A → G
Pos. 2643: A → G
Pos. 2694: A → G
Pos. 2737: Gap → T
Pos. 2889: C → A
Pos. 2937: A → T
Pos. 2966: C → T
Pos. 2975: A → G
Pos. 2997: C → T
Pos. 3081: A → T
Pos. 3106: T → A
Pos. 3138: A → G
Pos. 3230: C → T
Pos. 3239: A → T
Pos. 3272: Gap → T
Pos. 3285: G → T
Pos. 3326: C → T
Pos. 3406: T → C
Pos. 3425: C → T
Pos. 3486: A → G

Osteocephalus

12S
Pos. 46: A → T
Pos. 386: A → T
Pos. 521: T → C
Pos. 646: T → C
Pos. 673: T → Gap
Pos. 675: A → C
Pos. 1327: A → G
Pos. 1579: G → T
tRNA valine
Pos. 98: G → A
16S
Pos. 367: T → A
Pos. 498: T → A
Pos. 576: A → T
Pos. 616: A → G
Pos. 1015: T → A
Pos. 1741: T → C
Pos. 1813: T → A
Pos. 1839: C → A
Pos. 1847: A → T
Pos. 1948: C → A
Pos. 2019: A → T
Pos. 2041: C → A
Pos. 2058: A → T
Pos. 2059: A → C
Pos. 2080: A → C
Pos. 2117: T → C
Pos. 2244: T → A
Pos. 2308: T → C
Pos. 2450: C → T
Pos. 2508: T → C
Pos. 2509: C → T
Pos. 2538: C → T
Pos. 2780: A → T
Pos. 3018: T → A
RAG-1
Pos. 127 T → C

Osteopilus

Cytochrome *b*
Pos. 127: C → T
Pos. 128: A → CT
Pos. 201: A → C
Pos. 299: T → C
12S
Pos. 36: A → G
Pos. 110: A → C
Pos. 131: T → A
Pos. 368: A → G
Pos. 592: C → T
Pos. 781: A → C
Pos. 864: C → T
Pos. 1245: C → T
Pos. 1683: C → A
16S
Pos. 580: A → C
Pos. 625: T → G
Pos. 780: C → A
Pos. 839: C → A
Pos. 853: A → T
Pos. 1353: A → T
Pos. 1470: C → A
Pos. 1607: T → C
Pos. 1789: T → A
Pos. 1823: T → C
Pos. 2089: C → A
Pos. 2233: T → C
Pos. 2820: A → T
Pos. 3054: T → C
Pos. 3516: A → C
RAG-1
Pos. 58 A → G
Pos. 230 C → T
Pos. 266 C → T
Pos. 404 T → C
Pos. 425 G → A
Tyrosinase
Pos. 43: T → C
Pos. 127: T → C
Pos. 157: C → T
Pos. 218: G → A
Pos. 294: C → T
Pos. 357: T → C
Pos. 381: C → T
Pos. 396: G → A
Pos. 444: G → T
Pos. 526: C → T

Phyllodytes

Cytochrome *b*
Pos. 10: A → C
Pos. 33: C → T
Pos. 46: C → T
Pos. 48: Gap → A
Pos. 53: G → Gap
Pos. 68: C → A
Pos. 71: A → C
Pos. 79: A → C
Pos. 111: C → T
Pos. 136: C → T
Pos. 183: A → T
Pos. 199: G → A
Pos. 201: A → T
Pos. 214: C → T
Pos. 223: A → T
Pos. 241: A → T
Pos. 244: A → C
Pos. 246: A → G
Pos. 290: C → T
Pos. 331: CT → A
Pos. 402: T → C
Pos. 403: G → A
Pos. 414: T → A
12S
Pos. 22: G → A
Pos. 34: T → C
Pos. 45: T → C
Pos. 46: A → T
Pos. 61: C → A
Pos. 251: G → A
Pos. 278: C → T
Pos. 281: A → C
Pos. 293: G → A
Pos. 313: C → T
Pos. 322: C → A
Pos. 348: T → C

APPENDIX 5
(*Continued*)

Pos. 427: C → A
Pos. 455: C → Gap
Pos. 480: A → G
Pos. 521: T → C
Pos. 547: A → Gap
Pos. 601: A → C
Pos. 619: G → A
Pos. 621: A → G
Pos. 670: A → G
Pos. 816: A → T
Pos. 864: C → T
Pos. 1061: T → A
Pos. 1128: T → C
Pos. 1135: G → A
Pos. 1177: C → T
Pos. 1187: C → T
Pos. 1233: G → A
Pos. 1316: A → G
Pos. 1383: C → A
Pos. 1405: A → G
Pos. 1431: T → C
Pos. 1509: A → G
Pos. 1602: T → A
Pos. 1640: T → C
Pos. 1664: A → C
Pos. 1692: G → A
tRNA valine
Pos. 56: T → C
Pos. 61: C → T
Pos. 76: A → G
Pos. 77: A → T
Pos. 94: C → T
16S
Pos. 2: T → C
Pos. 12: C → A
Pos. 130: C → A
Pos. 367: AT → C
Pos. 383: A → C
Pos. 452: T → C
Pos. 483: A → T
Pos. 536: C → T
Pos. 579: A → G
Pos. 592: T → C
Pos. 623: Gap → C
Pos. 625: T → C
Pos. 658: A → Gap
Pos. 668: T → Gap
Pos. 691: G → A
Pos. 780: C → T
Pos. 784: C → T
Pos. 941: G → C
Pos. 960: G → A
Pos. 968: G → A
Pos. 969: A → G
Pos. 1009: G → A
Pos. 1085: T → A
Pos. 1140: A → T
Pos. 1223: C → A
Pos. 1259: T → C
Pos. 1289: A → G
Pos. 1480: T → C
Pos. 1585: A → G
Pos. 1592: G → C
Pos. 1603: T → C
Pos. 1673: A → C
Pos. 1699: A → C
Pos. 1839: T → C
Pos. 1925: A → T
Pos. 1928: C → G
Pos. 2030: G → A
Pos. 2058: A → C
Pos. 2139: Gap → C
Pos. 2268: C → A
Pos. 2284: G → A
Pos. 2312: T → A
Pos. 2319: T → C
Pos. 2441: C → Gap
Pos. 2450: C → T
Pos. 2457: G → A
Pos. 2477: C → T
Pos. 2484: T → C
Pos. 2496: G → A
Pos. 2503: C → A
Pos. 2518: A → G
Pos. 2551: A → G
Pos. 2568: C → T
Pos. 2652: T → C
Pos. 2711: C → T
Pos. 2800: Gap → C
Pos. 2856: T → A
Pos. 2982: T → A
Pos. 3039: A → T
Pos. 3041: G → A
Pos. 3127: T → C
Pos. 3166: C → Gap
Pos. 3173: G → A
Pos. 3189: G → A
Pos. 3267: Gap → T
Pos. 3277: G → A
Pos. 3299: C → T
Pos. 3439: T → C
Pos. 3447: G → A
Pos. 3449: C → A
Pos. 3458: T → C
28S
Pos. 260: Gap → C
Pos. 261: Gap → C
Pos. 283: Gap → T
Pos. 318: Gap → A
Pos. 440: Gap → G
Pos. 441: Gap → G
Pos. 484: C → G
Pos. 738: Gap → G
Pos. 741: Gap → C
Pos. 925: Gap → G
Pos. 1048: Gap → G
Rhodopsin
Pos. 10: G → A
Pos. 279: C → A
Pos. 296: T → C
Pos. 311: C → T
SIA
Pos. 106: C → T
Pos. 250: C → T
Tyrosinase
Pos. 22: G → A
Pos. 43: T → C
Pos. 52: C → T
Pos. 73: A → G
Pos. 103: G → A
Pos. 127: T → C
Pos. 157: C → A
Pos. 177: C → T
Pos. 209: T → C
Pos. 215: G → A
Pos. 233: C → A
Pos. 256: G → A
Pos. 282: A → C
Pos. 285: C → T
Pos. 343: G → A
Pos. 345: G → T
Pos. 490: G → A
Pos. 507: T → G
Pos. 529: C → T
Pos. 537: T → G

Tepuihyla edelcae

12S
Pos. 26: A → G
Pos. 231: T → A
Pos. 251: G → A
Pos. 449: Gap → C
Pos. 451: T → C
Pos. 452: T → C
Pos. 454: T → C
Pos. 528: A → T
Pos. 594: A → G
Pos. 696: A → G
Pos. 875: C → A
Pos. 970: A → C
Pos. 989: A → G
Pos. 999: T → C
Pos. 1010: T → C
Pos. 1144: T → C
Pos. 1211: T → C
Pos. 1309: C → G
Pos. 1441: T → C
Pos. 1602: T → A
Pos. 1640: T → C
Pos. 1683: C → T
16S
Pos. 56: C → Gap
Pos. 162: C → T
Pos. 220: T → A
Pos. 336: C → A
Pos. 376: A → T
Pos. 383: C → G
Pos. 411: C → T
Pos. 589: T → C
Pos. 630: A → G
Pos. 668: T → A
Pos. 671: A → G
Pos. 718: T → C
Pos. 736: A → G
Pos. 742: T → A
Pos. 754: A → G
Pos. 755: A → G
Pos. 758: T → C
Pos. 814: A → T
Pos. 890: G → A
Pos. 996: A → G
Pos. 1012: T → C
Pos. 1018: T → C
Pos. 1057: C → T
Pos. 1082: Gap → C
Pos. 1160: A → C
Pos. 1174: C → T
Pos. 1328: A → G
Pos. 1419: C → T
Pos. 1436: T → C
Pos. 1470: C → T
Pos. 1534: T → C
Pos. 1699: A → T
Pos. 1705: T → G
Pos. 1727: A → T
Pos. 1783: C → T
Pos. 1796: A → T
Pos. 1799: A → T
Pos. 1823: T → A
Pos. 1880: T → C
Pos. 1883: C → T
Pos. 1894: T → C
Pos. 2039: G → A
Pos. 2063: A → G
Pos. 2067: A → G
Pos. 2154: T → C
Pos. 2177: C → T
Pos. 2217: T → C
Pos. 2395: A → T
Pos. 2533: T → C
Pos. 2564: T → C
Pos. 2566: T → C
Pos. 2616: A → G
Pos. 2676: A → G
Pos. 3010: T → A
Pos. 3027: T → C
Pos. 3056: T → C
Pos. 3077: T → C
Pos. 3111: G → A
Pos. 3138: A → G
Pos. 3140: C → T
Pos. 3166: C → T
Pos. 3222: C → T
Pos. 3234: T → A
Pos. 3287: T → C
Pos. 3295: T → C
Pos. 3298: G → A
Pos. 3439: T → C
RAG-1
Pos. 419: C → T

Trachycephalus

Cytochrome *b*
Pos. 36: C → A
Pos. 173: A → C
Pos. 201: A → C
Pos. 247: C → T
12S
Pos. 169: A → T
Pos. 838: A → T
Pos. 880: A → C
Pos. 1636: C → Gap
Pos. 1674: C → T
16S
Pos. 130: C → A
Pos. 188: AT → C
Pos. 718: T → A
Pos. 836: C → A
Pos. 1259: T → C
Pos. 1443: T → C
Pos. 1470: C → A
Pos. 1534: T → C
Pos. 2229: A → C
Pos. 2525: T → C
Pos. 2753: A → C
Pos. 2827: Gap → T
Pos. 3287: T → C
RAG-1
Pos. 6 T → C
Pos. 125 G → A
Pos. 242 G → A
Rhodopsin
Pos. 96: T → C
Pos. 154: C → A
Pos. 160: C → T
Pos. 209: C → T
Pos. 220: G → A
Tyrosinase
Pos. 70: T → A
Pos. 251: C → T
Pos. 351: C → T
Pos. 456: G → A
Pos. 490: G → A
Pos. 497: C → A

APPENDIX 5
(*Continued*)

Pos. 511: G → A

Phyllomedusinae

Cytochrome *b*
Pos. 11: A → C
Pos. 53: G → A
Pos. 71: A → T
Pos. 78: C → Gap
Pos. 88: C → T
Pos. 126: G → A
Pos. 134: C → T
Pos. 136: C → T
Pos. 204: C → T
12S
Pos. 13: G → A
Pos. 22: G → A
Pos. 83: A → G
Pos. 235: A → T
Pos. 278: C → T
Pos. 281: A → T
Pos. 293: G → A
Pos. 313: C → A
Pos. 389: T → A
Pos. 528: A → T
Pos. 602: A → C
Pos. 641: AT → G
Pos. 658: A → G
Pos. 672: C → A
Pos. 771: C → T
Pos. 775: G → A
Pos. 814: C → T
Pos. 817: G → A
Pos. 838: A → T
Pos. 900: T → A
Pos. 965: T → C
Pos. 1166: Gap → C
Pos. 1321: T → C
Pos. 1392: T → C
Pos. 1439: C → T
Pos. 1568: A → T
tRNA valine
Pos. 57: C → T
Pos. 76: A → C
16S
Pos. 403: Gap → A
Pos. 427: T → C
Pos. 579: A → G
Pos. 616: A → C
Pos. 626: Gap → C
Pos. 664: A → T
Pos. 758: A → T
Pos. 807: G → A
Pos. 861: A → C
Pos. 890: A → G
Pos. 904: A → T
Pos. 948: T → C
Pos. 1167: A → T
Pos. 1758: Gap → A
Pos. 1799: A → T
Pos. 1819: A → T
Pos. 1948: T → C
Pos. 2045: A → C
Pos. 2069: A → T
Pos. 2070: A → C
Pos. 2127: G → A
Pos. 2154: T → A
Pos. 2161: A → T
Pos. 2179: C → T
Pos. 2203: A → T
Pos. 2396: Gap → C
Pos. 2669: A → T
Pos. 2768: C → T
Pos. 2906: T → C
Pos. 2953: A → G
Pos. 3041: G → A
Pos. 3097: A → C
Pos. 3126: A → T
Pos. 3145: T → A
Pos. 3222: T → C
Pos. 3234: A → Gap
Pos. 3285: G → A
Pos. 3292: C → T
Pos. 3429: T → C
Pos. 3451: A → G
28S
Pos. 223: Gap → G
Pos. 232: Gap → G
Pos. 327: T → G
Pos. 505: G → T
Pos. 558: G → T
Pos. 564: Gap → A
Pos. 825: Gap → C
Pos. 876: A → C
Pos. 934: Gap → T
Rhodopsin
Pos. 10: A → G
Pos. 16: A → T
Pos. 18: G → T
Pos. 93: C → T
Pos. 105: G → A
Pos. 145: C → T

Agalychnis

12S
Pos. 73: T → C
Pos. 159: C → T
Pos. 164: T → C
Pos. 277: A → T
Pos. 550: T → A
Pos. 558: T → C
Pos. 599: T → C
Pos. 864: C → T
Pos. 1144: T → C
Pos. 1321: C → T
Pos. 1539: C → T
tRNA valine
Pos. 39: T → C
16S
Pos. 220: T → A
Pos. 479: Gap → A
Pos. 536: C → T
Pos. 904: T → C
Pos. 2151: T → C
Pos. 2312: T → A
Pos. 3097: C → T
Pos. 3111: G → A
Pos. 3290: A → T

Cruziohyla calcarifer

Cytochrome *b*
Pos. 10: A → C
Pos. 13: A → C
Pos. 33: C → T
Pos. 64: C → T
Pos. 105: A → C
Pos. 108: A → C
Pos. 115: C → T
Pos. 116: C → T
Pos. 137: T → A
Pos. 144: C → T
Pos. 152: T → C
Pos. 158: C → G
Pos. 183: C → A
Pos. 202: G → A
Pos. 214: C → T
Pos. 265: C → T
Pos. 271: C → T
Pos. 290: C → T
Pos. 306: A → G
Pos. 313: A → G
Pos. 327: C → T
Pos. 334: A → C
Pos. 347: A → C
Pos. 362: A → C
Pos. 411: T → C
Pos. 415: C → T
12S
Pos. 61: C → T
Pos. 73: T → C
Pos. 88: C → T
Pos. 98: T → Gap
Pos. 142: C → T
Pos. 152: A → C
Pos. 173: G → A
Pos. 206: A → T
Pos. 231: A → Gap
Pos. 280: C → T
Pos. 291: G → A
Pos. 319: A → T
Pos. 359: A → T
Pos. 370: A → T
Pos. 391: C → T
Pos. 512: T → C
Pos. 521: T → C
Pos. 550: T → A
Pos. 599: T → C
Pos. 613: C → T
Pos. 646: T → C
Pos. 673: C → T
Pos. 692: T → C
Pos. 729: T → A
Pos. 776: G → A
Pos. 812: C → T
Pos. 862: Gap → T
Pos. 869: C → A
Pos. 875: C → G
Pos. 908: A → C
Pos. 1002: C → T
Pos. 1061: T → C
Pos. 1116: A → T
Pos. 1144: T → C
Pos. 1194: A → C
Pos. 1307: T → A
Pos. 1408: A → C
Pos. 1600: Gap → C
Pos. 1670: T → C
tRNA valine
Pos. 3: A → T
Pos. 11: G → A
Pos. 54: C → T
16S
Pos. 3: A → Gap
Pos. 4: A → C
Pos. 14: Gap → C
Pos. 51: Gap → C
Pos. 107: A → C
Pos. 118: A → C
Pos. 172: A → C
Pos. 294: A → G
Pos. 347: C → T
Pos. 355: C → T
Pos. 443: T → A
Pos. 452: T → C
Pos. 539: Gap → A
Pos. 544: Gap → C
Pos. 573: A → Gap
Pos. 586: Gap → C
Pos. 592: T → C
Pos. 634: A → G
Pos. 665: T → G
Pos. 668: T → A
Pos. 692: A → T
Pos. 718: T → C
Pos. 763: G → A
Pos. 767: A → T
Pos. 784: C → T
Pos. 788: C → T
Pos. 798: T → C
Pos. 827: T → C
Pos. 920: G → A

APPENDIX 5
(*Continued*)

Pos. 972: T → A
Pos. 1008: A → C
Pos. 1049: T → A
Pos. 1153: A → T
Pos. 1174: T → A
Pos. 1235: C → T
Pos. 1242: C → T
Pos. 1468: T → A
Pos. 1480: T → C
Pos. 1491: A → C
Pos. 1572: T → C
Pos. 1631: T → C
Pos. 1783: C → T
Pos. 1817: T → C
Pos. 1823: T → C
Pos. 1826: T → A
Pos. 1887: T → C
Pos. 1925: A → G
Pos. 2016: T → C
Pos. 2018: T → A
Pos. 2039: G → A
Pos. 2064: C → T
Pos. 2208: A → C
Pos. 2217: T → A
Pos. 2250: C → T
Pos. 2379: Gap → T
Pos. 2391: Gap → C
Pos. 2406: T → C
Pos. 2450: C → T
Pos. 2517: G → A
Pos. 2566: T → C
Pos. 2581: C → T
Pos. 2605: G → A
Pos. 2616: A → T
Pos. 2652: T → C
Pos. 2664: A → T
Pos. 2671: Gap → C
Pos. 2711: C → T
Pos. 2741: Gap → C
Pos. 2856: T → A
Pos. 2913: T → C
Pos. 2985: T → C
Pos. 3010: T → A
Pos. 3032: T → A
Pos. 3048: A → T
Pos. 3071: A → T
Pos. 3083: T → C
Pos. 3088: A → G
Pos. 3195: Gap → T
Pos. 3199: A → C
Pos. 3303: C → T
Pos. 3310: A → T
Pos. 3316: A → T
Pos. 3320: G → A
Pos. 3357: A → T
Pos. 3431: C → T
Pos. 3432: A → G
Pos. 3458: T → C
Pos. 3499: C → T
Pos. 3516: A → G
28S
Pos. 207: Gap → G
Pos. 208: C → T
Pos. 238: G → Gap
Pos. 306: T → G
Pos. 373: C → T
Pos. 390: C → T
Pos. 509: G → Gap
Pos. 511: C → T
Pos. 516: G → A
Pos. 653: C → T
Rhodopsin
Pos. 6: T → C
Pos. 9: C → T
Pos. 314: C → T

Hylomantis

Cytochrome *b*
Pos. 33: C → T
Pos. 98: C → T
Pos. 126: A → G
Pos. 170: T → C
Pos. 204: T → C
Pos. 250: T → A
Pos. 274: C → T
Pos. 316: T → C
Pos. 402: T → C
12S
Pos. 83: G → A
Pos. 251: G → A
Pos. 528: T → A
Pos. 875: C → T
Pos. 1549: A → C
tRNA valine
Pos. 98: A → G
16S
Pos. 50: Gap → C
Pos. 252: Gap → T
Pos. 347: C → T
Pos. 399: T → Gap
Pos. 452: T → C
Pos. 459: T → C
Pos. 625: T → C
Pos. 774: T → A
Pos. 1160: T → A
Pos. 1242: C → T
Pos. 1278: T → C
Pos. 1334: A → T
Pos. 1737: T → C
Pos. 1783: C → T
Pos. 2112: T → Gap
Pos. 2605: G → A
Pos. 2616: A → T
Pos. 2866: A → Gap
Pos. 2875: A → Gap
Pos. 2906: C → Gap
Pos. 2946: A → C
Pos. 3277: G → A
Pos. 3375: T → C
Rhodopsin
Pos. 305: C → T

Pachymedusa dacnicolor

12S
Pos. 28: A → G
Pos. 33: A → G
Pos. 49: C → T
Pos. 117: A → T
Pos. 307: G → A
Pos. 370: A → G
Pos. 381: C → T
Pos. 386: A → T
Pos. 414: C → T
Pos. 427: A → G
Pos. 434: G → A
Pos. 451: T → C
Pos. 480: A → G
Pos. 519: Gap → G
Pos. 601: C → T
Pos. 646: T → C
Pos. 658: G → A
Pos. 672: A → C
Pos. 733: T → A
Pos. 736: A → T
Pos. 750: C → T
Pos. 780: C → T
Pos. 835: T → C
Pos. 908: A → C
Pos. 1105: A → T
Pos. 1128: T → C
Pos. 1153: T → G
Pos. 1166: C → T
Pos. 1187: C → T
Pos. 1233: G → A
Pos. 1307: T → C
Pos. 1317: A → G
Pos. 1426: T → C
Pos. 1429: C → A
Pos. 1439: T → C
Pos. 1509: A → G
Pos. 1622: Gap → G
Pos. 1630: A → T
Pos. 1761: T → C
tRNA valine
Pos. 6: G → A
Pos. 34: Gap → T
Pos. 55: A → C
Pos. 84: T → C
Pos. 95: C → T
Pos. 105: C → T
16S
Pos. 94: A → Gap
Pos. 130: A → G
Pos. 272: T → A
Pos. 323: C → T
Pos. 493: Gap → G
Pos. 513: Gap → A
Pos. 580: A → G
Pos. 654: T → A
Pos. 663: T → A
Pos. 667: A → T
Pos. 772: Gap → A
Pos. 777: C → Gap
Pos. 807: A → G
Pos. 818: C → T
Pos. 872: C → T
Pos. 959: A → G
Pos. 983: G → A
Pos. 1034: G → Gap
Pos. 1049: T → A
Pos. 1167: T → A
Pos. 1208: Gap → A
Pos. 1268: C → T
Pos. 1281: T → C
Pos. 1370: Gap → T
Pos. 1371: Gap → T
Pos. 1468: T → C
Pos. 1491: A → T
Pos. 1699: T → A
Pos. 1855: A → T
Pos. 2007: A → T
Pos. 2033: A → T
Pos. 2041: A → T
Pos. 2049: G → A
Pos. 2054: T → C
Pos. 2060: C → T
Pos. 2070: C → A
Pos. 2105: A → G
Pos. 2107: C → T
Pos. 2552: T → C
Pos. 2606: A → G
Pos. 2717: Gap → T
Pos. 2797: Gap → C
Pos. 2844: A → T
Pos. 2913: T → G
Pos. 3071: A → T
Pos. 3083: T → C
Pos. 3121: A → T
Pos. 3181: G → A
Pos. 3189: G → T
Pos. 3199: A → T
Pos. 3249: G → Gap
Pos. 3260: C → Gap
Pos. 3266: C → T
Pos. 3268: C → T
Pos. 3291: A → T

APPENDIX 5
(*Continued*)

Pos. 3439: T → C
Pos. 3504: C → T
Pos. 3507: C → T
SIA
Pos. 93: C → T
Pos. 220: G → A

Phasmahyla

Cytochrome *b*
Pos. 10: A → C
Pos. 36: A → T
Pos. 99: T → C
Pos. 137: T → A
Pos. 173: A → T
Pos. 207: C → T
Pos. 248: C → T
Pos. 250: T → A
Pos. 280: C → T
Pos. 356: C → T
Pos. 362: A → T
Pos. 380: C → T
12S
Pos. 61: C → T
Pos. 69: C → T
Pos. 142: C → T
Pos. 173: G → A
Pos. 281: T → A
Pos. 319: A → T
Pos. 432: T → A
Pos. 518: Gap → C
Pos. 547: A → T
Pos. 600: T → C
Pos. 835: T → C
Pos. 861: Gap → C
Pos. 908: A → C
Pos. 989: A → T
Pos. 1036: C → T
Pos. 1048: T → A
Pos. 1058: Gap → T
Pos. 1164: Gap → T
Pos. 1233: G → A
Pos. 1454: G → A
Pos. 1549: A → T
Pos. 1645: T → C
tRNA valine
Pos. 59: C → T
Pos. 69: G → A
Pos. 82: C → T
16S
Pos. 162: C → T
Pos. 343: Gap → T
Pos. 355: C → T
Pos. 580: A → C
Pos. 668: T → A
Pos. 718: T → A
Pos. 751: C → T
Pos. 761: T → C
Pos. 780: C → T
Pos. 822: A → T
Pos. 861: C → A
Pos. 1085: T → A
Pos. 1324: A → T
Pos. 1510: A → T
Pos. 1534: A → Gap
Pos. 1606: Gap → A
Pos. 1699: T → Gap
Pos. 1705: T → A
Pos. 1787: C → T
Pos. 1874: T → C
Pos. 1878: C → T
Pos. 1932: T → C
Pos. 1951: A → T
Pos. 1964: C → T
Pos. 2018: T → A
Pos. 2026: A → C
Pos. 2028: G → A
Pos. 2030: G → T
Pos. 2057: A → T
Pos. 2059: A → T
Pos. 2112: T → A
Pos. 2345: C → T
Pos. 2381: T → A
Pos. 2398: C → T
Pos. 2416: G → A
Pos. 2422: C → T
Pos. 2552: T → C
Pos. 2566: T → C
Pos. 2581: C → T
Pos. 2583: A → G
Pos. 2586: C → T
Pos. 2674: C → T
Pos. 2711: C → T
Pos. 2975: A → T
Pos. 3036: T → A
Pos. 3059: A → C
Pos. 3111: G → A
Pos. 3140: C → T
Pos. 3199: A → G
Pos. 3230: T → C
Pos. 3323: A → T
Pos. 3375: T → Gap
Pos. 3484: G → A
Pos. 3491: C → A
Pos. 3551: C → T

Phyllomedusa

12S
Pos. 65: C → A
Pos. 251: G → A
Pos. 313: A → T
Pos. 327: A → T
Pos. 391: C → T
Pos. 434: G → A
Pos. 530: Gap → C
Pos. 864: C → A
Pos. 1066: C → T
Pos. 1130: Gap → C
Pos. 1177: T → Gap
Pos. 1585: T → A
Pos. 1614: A → T
tRNA valine
Pos. 98: A → G
16S
Pos. 348: Gap → A
Pos. 427: C → T
Pos. 483: T → C
Pos. 573: A → T
Pos. 610: T → C
Pos. 634: A → T
Pos. 1025: T → C
Pos. 1077: T → A
Pos. 1153: A → C
Pos. 1274: A → G
Pos. 1737: T → C
Pos. 1819: T → A
Pos. 1897: T → C
Pos. 2045: C → T
Pos. 2094: A → Gap
Pos. 2107: C → A
Pos. 2203: T → C
Pos. 2217: T → C
Pos. 2233: T → A
Pos. 2285: A → G
Pos. 2567: T → C
Pos. 2664: A → T
Pos. 3143: G → A
RAG-1
Pos. 68 A → G
Rhodopsin
Pos. 133: C → T
Pos. 305: C → T
Pos. 314: C → T
SIA
Pos. 148: C → T
Tyrosinase
Pos. 2: T → C
Pos. 444: C → T

Pelodryadinae

Cytochrome *b*
Pos. 62: G → T
Pos. 164: C → T
12S
Pos. 61: C → A
Pos. 169: A → Gap
Pos. 194: T → C
Pos. 432: T → A
Pos. 619: G → A
Pos. 621: A → G
Pos. 661: A → G
Pos. 880: A → C
Pos. 1174: C → T
Pos. 1303: A → T
Pos. 1317: A → T
Pos. 1670: T → A
tRNA valine
Pos. 98: A → G
16S
Pos. 265: Gap → A
Pos. 459: T → A
Pos. 643: Gap → A
Pos. 821: T → A
Pos. 902: T → A
Pos. 914: C → A
Pos. 959: A → G
Pos. 1077: T → A
Pos. 1085: T → A
Pos. 1235: C → A
Pos. 1324: A → C
Pos. 1447: Gap → C
Pos. 1725: Gap → T
Pos. 1896: A → C
Pos. 1900: C → T
Pos. 1945: G → A
Pos. 2112: T → A
Pos. 2200: T → A
Pos. 2224: A → T
Pos. 2267: T → A
Pos. 2268: C → A
Pos. 2381: T → A
Pos. 2676: A → T
Pos. 2719: T → C
Pos. 2860: Gap → A
Pos. 3086: T → A
Pos. 3181: G → A
Pos. 3260: C → T
Pos. 3274: A → T
Pos. 3280: A → T
Pos. 3297: T → A
RAG-1
Pos. 8 A → G
Pos. 89 T → C
Pos. 134 C → T
Pos. 350 C → T
Pos. 410 C → T
Rhodopsin
Pos. 99: G → A
Pos. 270: A → T
Tyrosinase
Pos. 273: C → G
Pos. 282: A → C
Pos. 449: C → G
Pos. 455: T → C
Pos. 456: G → A

Note added in proof

While this paper was in press, two relevant contributions were published, each one describing a new species of *Hyla*. Köhler et al. (2005) described *Hyla coffea*, and tentatively assigned it to the *Hyla microcephala* group. For these reasons, we include this species in the resurrected genus *Dendropsophus*, as ***Dendropsophus coffea*** (Köhler, Jungfer, and Reichle, 2005) **new comb.** We follow the authors in tentatively assigning it to the *Dendropsophus microcephalus* group, increasing the number of species currently included in this group to 31. Carvalho e Silva and Carvalho e Silva (2005) described as *Hyla eugenioi* the species that we included in this paper as *Hyla* sp. 1 (aff. *H. ehrhardti*). Therefore, we include this species in *Aplastodiscus*, as ***Aplastodiscus eugenioi*** (Carvalho e Silva and Carvalho e Silva, 2005) **new comb.** Following our results, and the authors' assigning the species to the former *Hyla albofrenata* complex of the *H. albomarginata* group, we consider it a member of the *Aplastodiscus albofrenatus* group, increasing to seven the number of species of the group. Carvalho e Silva and Carvalho e Silva (2005) also noticed that the species of the former *Hyla albofrenata* complex of the *H. albomarginata* group (now the *Aplastodiscus albofrenatus* group) have a red-orange iris, while species of the former *H. albosignata* complex (now the *Aplastodiscus albosignatus* group) have a characteristic ring (red externally, gray internally).

References

Carvalho e Silva, A.M.P.T., and S.P. Carvalho e Silva. 2005. New species of the *Hyla albofrenata* group, from the states of Rio de Janeiro and São Paulo, Brazil (Anura, Hylidae). Journal of Herpetology 38: 73–81.

Köhler, J., K.H. Jungfer, and S. Reichle. 2005. Another new species of small *Hyla* (Anura, Hylidae) from amazonian sub-andean forest of western Bolivia. Journal of Herpetology 39: 43–50.

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