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THE AMPHIBIAN TREE OF LIFE

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ABSTRACT

The evidentiary basis of the currently accepted classification of living amphibians is discussed and shown not to warrant the degree of authority conferred on it by use and tradition. A new taxonomy of living amphibians is proposed to correct the deficiencies of the old one. This new taxonomy is based on the largest phylogenetic analysis of living Amphibia so far accomplished. We combined the comparative anatomical character evidence of Haas (2003) with DNA sequences from the mitochondrial transcription unit H1 (12S and 16S ribosomal RNA and $tRNA^{Valine}$ genes, ≈ 2,400 bp of mitochondrial sequences) and the nuclear genes histone H3, rhodopsin, tyrosinase, and seven in absentia, and the large ribosomal subunit 28S (≈ 2,300 bp of nuclear sequences; ca. 1.8 million base pairs; $\bar{x}$ = 3.7 kb/terminal). The dataset includes 532 terminals sampled from 522 species representative of the global diversity of amphibians as well as seven of the closest living relatives of amphibians for outgroup comparisons.

The primary purpose of our taxon sampling strategy was to provide strong tests of the monophyly of all ''family-group'' taxa. All currently recognized nominal families and subfamilies were sampled, with the exception of Protohynobiinae (Hynobiidae). Many of the currently recognized genera were also sampled. Although we discuss the monophyly of genera, and provide remedies for nonmonophyly where possible, we also make recommendations for future research.

A parsimony analysis was performed under Direct Optimization, which simultaneously optimizes nucleotide homology (alignment) and tree costs, using the same set of assumptions throughout the analysis. Multiple search algorithms were run in the program POY over a period of seven months of computing time on the AMNH Parallel Computing Cluster.

Results demonstrate that the following major taxonomic groups, as currently recognized, are nonmonophyletic: Ichthyophiidae (paraphyletic with respect to Uraeotyphlidae), Caeciliidae (paraphyletic with respect to Typhlonectidae and Scolecomorphidae), Salamandroidea (paraphyletic with respect to Sirenidae), Leiopelmatanura (paraphyletic with respect to Ascaphidae), Discoglossanura (paraphyletic with respect to Bombinatoridae), Mesobatrachia (paraphyletic with respect to Neobatrachia), Pipanura (paraphyletic with respect to Bombinatoridae and Discoglossidae/Alytidae), Hyloidea (in the sense of containing Heleophrynidae; paraphyletic with respect to Ranoidea), Leptodactylidae (polyphyletic, with Batrachophrynidae forming the sister taxon of Myobatrachidae + Limnodynastidae, and broadly paraphyletic with respect to Hemiphractinae, Rhinodermatidae, Hylidae, Allophrynidae, Centrolenidae, Brachycephalidae, Dendrobatidae, and Bufonidae), Microhylidae (polyphyletic, with Brevicipitinae being the sister taxon of Hemisotidae), Microhylinae (poly/paraphyletic with respect to the remaining non-brevicipitine microhylids), Hyperoliidae (para/polyphyletic, with Leptopelinae forming the sister taxon of Arthroleptidae + Astylosternidae), Astylosternidae (paraphyletic with respect to Arthroleptinae), Ranidae (paraphyletic with respect to Rhacophoridae and Mantellidae). In addition, many subsidiary taxa are demonstrated to be nonmonophyletic, such as (1) *Eleutherodactylus* with respect to *Brachycephalus*; (2) *Rana* (sensu Dubois, 1992), which is polyphyletic, with various elements falling far from each other on the tree; and (3) *Bufo*, with respect to several nominal bufonid genera.

A new taxonomy of living amphibians is proposed, and the evidence for this is presented to promote further investigation and data acquisition bearing on the evolutionary history of amphibians. The taxonomy provided is consistent with the International Code of Zoological Nomenclature (ICZN, 1999).

Salient features of the new taxonomy are (1) the three major groups of living amphibians, caecilians/Gymnophiona, salamanders/Caudata, and frogs/Anura, form a monophyletic group, to which we restrict the name Amphibia; (2) Gymnophiona forms the sister taxon of Batrachia (salamanders + frogs) and is composed of two groups, Rhinatrematidae and Stegokrotaphia; (3) Stegokrotaphia is composed of two families, Ichthyophiidae (including Uraeotyphlidae) and Caeciliidae (including Scolecomorphidae and Typhlonectidae, which are regarded as subfamilies); (4) Batrachia is a highly corroborated monophyletic group, composed of two taxa, Caudata (salamanders) and Anura (frogs); (5) Caudata is composed of two taxa, Cryptobranchoidei (Cryptobranchidae and Hynobiidae) and Diadectosalamandroidei **new taxon** (all other salamanders); (6) Diadectosalamandroidei is composed of two taxa, Hydatinosalamandroidei

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new taxon (composed of Perennibranchia and Treptobranchia **new taxon**) and Plethosalamandroidei **new taxon**; (7) Perennibranchia is composed of Proteidae and Sirenidae; (8) Treptobranchia **new taxon** is composed of two taxa, Ambystomatidae (including Dicamptodontidae) and Salamandridae; (9) Plethosalamandroidei **new taxon** is composed of Rhyacotritonidae and Xenosalamandroidei **new taxon**; (10) Xenosalamandroidei is composed of Plethodontidae and Amphiumidae; (11) Anura is monophyletic and composed of two clades, Leiopelmatidae (including Ascaphidae) and Lalagobatrachia **new taxon** (all other frogs); (12) Lalagobatrachia is composed of two clades, Xenoanura (Pipidae and Rhinophrynidae) and Sokolanura **new taxon** (all other lalagobatrachians); (13) Bombinatoridae and Alytidae (former Discoglossidae) are each others' closest relatives and in a clade called Costata, which, excluding Leiopelmatidae and Xenoanura, forms the sister taxon of all other frogs, Acosmanura; (14) Acosmanura is composed of two clades, Anomocoela (= Pelobatoidea of other authors) and Neobatrachia; (15) Anomocoela contains Pelobatoidea (Pelobatidae and Megophryidae) and Pelodytoidea (Pelodytidae and Scaphiopodidae), and forms the sister taxon of Neobatrachia, together forming Acosmanura; (16) Neobatrachia is composed of two clades, Heleophrynidae, and all other neobatrachians, Phthanobatrachia **new taxon**; (17) Phthanobatrachia is composed of two major units, Hyloides and Ranoides; (18) Hyloides comprises Sooglossidae (including Nasikabatrachidae) and Notogaeanura **new taxon** (the remaining hyloids); (19) Notogaeanura contains two taxa, Australobatrachia **new taxon** and Nobleobatrachia **new taxon**; (20) Australobatrachia is a clade composed of Batrachophrynidae and its sister taxon, Myobatrachoidea (Myobatrachidae and Limnodynastidae), which forms the sister taxon of all other hyloids, excluding sooglossids; (21) Nobleobatrachia **new taxon,** is dominated at its base by frogs of a treefrog morphotype, several with intercalary phalangeal cartilages—*Hemiphractus* (Hemiphractidae) forms the sister taxon of the remaining members of this group, here termed Meridianura **new taxon**; (22) Meridianura comprises Brachycephalidae (former Eleutherodactylinae + *Brachycephalus*) and Cladophrynia **new taxon**; (23) Cladophrynia is composed of two groups, Cryptobatrachidae (composed of *Cryptobatrachus* and *Stefania*, previously a fragment of the polyphyletic Hemiphractinae) and Tinctanura **new taxon**; (24) Tinctanura is composed of Amphignathodontidae (*Gastrotheca* and *Flectonotus*, another fragment of the polyphyletic Hemiphractinae) and Athesphatanura **new taxon**; (25) Athesphatanura is composed of Hylidae (Hylinae, Pelodryadinae, and Phyllomedusinae, and excluding former Hemiphractinae, whose inclusion would have rendered this taxon polyphyletic) and Leptodactyliformes **new taxon**; (26) Leptodactyliformes is composed of Diphyabatrachia **new taxon** (composed of Centrolenidae [including *Allophryne*] and Leptodactylidae, sensu stricto, including *Leptodactylus* and relatives) and Chthonobatrachia **new taxon**; (27) Chthonobatrachia is composed of a reformulated Ceratophryidae (which excludes such genera as *Odontophrynus* and *Proceratophrys* and includes other taxa, such as *Telmatobius*) and Hesticobatrachia **new taxon**; (28) Hesticobatrachia is composed of a reformulated Cycloramphidae (which includes *Rhinoderma*) and Agastorophrynia **new taxon**; (29) Agastorophrynia is composed of Bufonidae (which is partially revised) and Dendrobatoidea (Dendrobatidae and Thoropidae); (30) Ranoides **new taxon** forms the sister taxon of Hyloides and is composed of two major monophyletic components, Allodapanura **new taxon** (microhylids, hyperoliids, and allies) and Natatanura **new taxon** (ranids and allies); (31) Allodapanura is composed of Microhylidae (which is partially revised) and Afrobatrachia **new taxon**; (32) Afrobatrachia is composed of Xenosyneunitanura **new taxon** (the ''strange-bedfellows'' Brevicipitidae [formerly in Microhylidae] and Hemisotidae) and a more normal-looking group of frogs, Laurentobatrachia **new taxon** (Hyperoliidae and Arthroleptidae, which includes Leptopelinae and former Astylosternidae); (33) Natatanura **new taxon** is composed of two taxa, the African Ptychadenidae and the worldwide Victoranura **new taxon**; (34) Victoranura is composed of Ceratobatrachidae and Telmatobatrachia **new taxon**; (35) Telmatobatrachia is composed of Micrixalidae and a worldwide group of ranoids, Ametrobatrachia **new taxon**; (36) Ametrobatrachia is composed of Africanura **new taxon** and Saukrobatrachia **new taxon**; (37) Africanura is composed of two taxa: Phrynobatrachidae (*Phrynobatrachus*, including *Dimorphognathus* and *Phrynodon* as synonyms) and Pyxicephaloidea; (38) Pyxicephaloidea is composed of Petropedetidae (*Conraua*, *Indirana*, *Arthroleptides*, and *Petropedetes*), and Pyxicephalidae (including a number of African genera, e.g. *Amietia* [including *Afrana*], *Arthroleptella*, *Pyxicephalus*, *Strongylopus*, and *Tomopterna*); and (39) Saukrobatrachia **new taxon** is the sister taxon of Africanura and is composed of Dicro-

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glossidae and Aglaioanura **new taxon,** which is, in turn, composed of Rhacophoroidea (Mantellidae and Rhacophoridae) and Ranoidea (Nyctibatrachidae and Ranidae, sensu stricto).

Many generic revisions are made either to render a monophyletic taxonomy or to render a taxonomy that illuminates the problems in our understanding of phylogeny, so that future work will be made easier. These revisions are: (1) placement of *Ixalotriton* and *Lineatriton* (Caudata: Plethodontidae: Bolitoglossinae) into the synonymy of *Pseudoeurycea*, to render a monophyletic *Pseudoeurycea*; (2) placement of *Haideotriton* (Caudata: Plethodontidae: Spelerpinae) into the synonymy of *Eurycea*, to render a monophyletic *Eurycea*; (3) placement of *Nesomantis* (Anura: Sooglossidae) into the synonymy of *Sooglossus*, to assure a monophyletic *Sooglossus*; (4) placement of *Cyclorana* and *Nyctimystes* (Anura: Hylidae: Pelodryadinae) into *Litoria*, but retaining *Cyclorana* as a subgenus, to provide a monophyletic *Litoria*; (5) partition of ''*Limnodynastes*'' (Anura: Limnodynastidae) into *Limnodynastes* and *Opisthodon* to render monophyletic genera; (6) placement of *Adenomera*, *Lithodytes*, and *Vanzolinius* (Anura: Leptodactylidae) into *Leptodactylus*, to render a monophyletic *Leptodactylus*; (7) partition of ''*Eleutherodactylus*'' (Anura: Brachycephalidae) into *Craugastor*, ''*Eleutherodactylus*'', ''*Euhyas*'', ''*Pelorius*'', and *Syrrhophus* to outline the taxonomic issues relevant to the paraphyly of this nominal taxon to other nominal genera; (8) partition of ''*Bufo*'' (Anura: Bufonidae) into a number of new or revived genera (i.e., *Amietophrynus* **new genus,** *Anaxyrus*, *Chaunus*, *Cranopsis*, *Duttaphrynus* **new genus,** *Epidalea*, *Ingerophrynus* **new genus,** *Nannophryne*, *Peltophryne*, *Phrynoidis*, *Poyntonophrynus* **new genus**; *Pseudepidalea* **new genus,** *Rhaebo*, *Rhinella*, *Vandijkophrynus* **new genus**); (9) placement of the monotypic *Spinophrynoides* (Anura: Bufonidae) into the synonymy of (formerly monotypic) *Altiphrynoides* to make for a more informative taxonomy; (10) placement of the *Bufo taitanus* group and *Stephopaedes* (as a subgenus) into the synonymy of *Mertensophryne* (Anura: Bufonidae); (11) placement of *Xenobatrachus* (Anura: Microhylidae: Asterophryinae) into the synonymy of *Xenorhina* to render a monophyletic *Xenorhina*; (12) transfer of a number of species from *Plethodontohyla* to *Rhombophryne* (Microhylidae: Cophylinae) to render a monophyletic *Plethodontohyla*; (13) placement of *Schoutedenella* (Anura: Arthroleptidae) into the synonymy of *Arthroleptis*; (14) transfer of *Dimorphognathus* and *Phrynodon* (Anura: Phrynobatrachidae) into the synonymy of *Phrynobatrachus* to render a monophyletic *Phrynobatrachus*; (15) placement of *Afrana* into the synonymy of *Amietia* (Anura: Pyxicephalidae) to render a monophyletic taxon; (16) placement of *Chaparana* and *Paa* into the synonymy of *Nanorana* (Anura: Dicroglossidae) to render a monophyletic genus; (17) recognition as genera of *Ombrana* and *Annandia* (Anura: Dicroglossidae: Dicroglossinae) pending placement of them phylogenetically; (18) return of *Phrynoglossus* into the synonymy of *Occidozyga* to resolve the paraphyly of *Phrynoglossus* (Anura: Dicroglossidae: Occidozyginae); (19) recognition of *Feihyla* **new genus** for *Philautus palpebralis* to resolve the polyphyly of ''*Chirixalus*''; (20) synonymy of ''*Chirixalus*'' with *Chiromantis* to resolve the paraphyly of ''*Chirixalus*''; (21) recognition of the genus *Babina*, composed of the former subgenera of *Rana*, *Babina* and *Nidirana* (Anura: Ranidae); (22) recognition of the genera *Clinotarsus*, *Humerana*, *Nasirana*, *Pelophylax*, *Pterorana*, *Pulchrana*, and *Sanguirana*, formerly considered subgenera of *Rana* (Anura: Ranidae), with no special relationship to *Rana* (sensu stricto); (23) consideration of *Glandirana* (Anura: Ranidae), formerly a subgenus of *Rana*, as a genus, with *Rugosa* as a synonym; (24) recognition of *Hydrophylax* (Anura: Ranidae) as a genus, with *Amnirana* and most species of former *Chalcorana* included in this taxon as synonyms; (25) recognition of *Hylarana* (Anura: Ranidae) as a genus and its content redefined; (26) redelimitation of *Huia* to include as synonyms *Eburana* and *Odorrana* (both former subgenera of *Rana*); (27) recognition of *Lithobates* (Anura: Ranidae) for all species of North American ''*Rana*'' not placed in *Rana* sensu stricto (*Aquarana*, *Pantherana*, *Sierrana*, *Trypheropsis*, and *Zweifelia* considered synonyms of *Lithobates*); (28) redelimitation of the genus *Rana* as monophyletic by inclusion as synonyms *Amerana*, *Aurorana*, *Pseudoamolops*, and *Pseudorana*, and exclusion of all other former subgenera; (29) redelimitation of the genus *Sylvirana* (Anura: Ranidae), formerly a subgenus of *Rana*, with *Papurana* and *Tylerana* included as synonyms.

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INTRODUCTION

Amphibians (caecilians, frogs, and salamanders) are a conspicuous component of the world's vertebrate fauna. They currently include 5948 recognized species with representatives found in virtually all terrestrial and freshwater habitats, in all but the coldest and driest regions or the most remote oceanic islands. The number of recognized species of amphibians has grown enormously in recent years, about a 48.2% increase since 1985 (Frost, 1985, 2004, unpubl. data). This growth reflects the increasing ease of collecting in remote locations and a significant growth of active scientific communities in a few megadiverse countries. Unfortunately, the rapid increase in knowledge of amphibian species diversity is coincident with a massive and global decline in amphibian populations (Alford and Richards, 1999; Houlahan et al., 2000; Young et al., 2001; S.N. Stuart et al., 2004) due to a diversity of factors, including habitat loss and fragmentation (Green, 2005; Halliday, 2005) but also possibly due to global environmental changes (Donnelly and Crump, 1998; Blaustein and Kiesecker, 2002; Heyer, 2003; Licht, 2003) and such proximate causes as emerging infectious diseases (Collins and Storfer, 2003).

Understanding of amphibian evolutionary history has not kept pace with knowledge of amphibian species diversity. For all but a few groups, there is only a rudimentary evolutionary framework upon which to cast the theories of cause, predict which lineages are most likely to go extinct, or even comprehend the amount of genetic diversity being lost (Lips et al., 2005). Indeed, it is arguable whether our general understanding of frog phylogenetics has progressed substantially beyond the seminal works of the late 1960s to early 1980s (Inger, 1967; Kluge and Farris, 1969; J.D. Lynch, 1971, 1973; Farris et al., 1982a). The major advances in frog taxonomy in the 1980s and 1990s were dominated by nomenclatural and largely literature-based phenotypic sorting (e.g., Dubois, 1980, 1981, 1984b; Laurent, 1986; Dubois, 1987 ''1986'', 1992) that provided other workers with digestible ''chunks'' to discuss and evaluate phylogenetically. This has begun to change in the 2000s with the infusion of significant amounts of molecular evidence into the discussion of large-scale amphibian diversification. But, although recent molecular studies have been very illuminating (e.g., Biju and Bossuyt, 2003; Darst and Cannatella, 2004; Faivovich et al., 2005; Roelants and Bossuyt, 2005; San Mauro et al., 2005), so far they have not provided the general roadmap for future research that a larger and more detailed study could provide.

Among the three major taxonomic components of amphibian diversity, caecilians appear to have been the focus of the most significant study of large-scale evolutionary history (Gower et al., 2002; Gower and Wilkinson, 2002; M. Wilkinson et al., 2002; M. Wilkinson et al., 2003; San Mauro et al., 2004; M.H. Wake et al., 2005), although this may be an artifact of the relatively small size of the group (173 species currently recognized) and the few, mostly coordinated, workers. Salamanders are the best-known group at the species level, but salamander phylogenetic work has largely focused on the generic and infrageneric levels of investigation (e.g., Zhao, 1994; Titus and Larson, 1996; Highton, 1997, 1998, 1999; García-París and Wake, 2000; Highton and Peabody, 2000; Jockusch et al., 2001; Parra-Olea and Wake, 2001; Jockusch and Wake, 2002; Parra-Olea et al., 2002; Steinfartz et al., 2002; Parra-Olea et al., 2004; Sites et al., 2004), although there have been several important efforts at an overall synthesis of morphological and molecular evidence (Larson and Dimmick, 1993; Larson et al., 2003; Wiens et al., 2005).

Research on frog phylogenetics has also focused primarily on generic and infrageneric studies (e.g., Graybeal, 1997; Cannatella et al., 1998; Mendelson et al., 2000; Sheil et al., 2001; Channing et al., 2002a; Dawood et al., 2002; Faivovich, 2002; Glaw and Vences, 2002; Pramuk, 2002; Cunningham and Cherry, 2004; Drewes and Wilkinson, 2004; B.J. Evans et al., 2004; Pauly et al., 2004; Crawford and Smith, 2005; Matsui et al., 2005), and broader discussions of frog phylogenetics have been predominantly narrative rather than quantitative (e.g., Cannatella and Hillis, 1993; Ford and Cannatella, 1993; Cannatella and Hillis, 2004). Illumi-

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nating large-scale studies have appeared recently (Biju and Bossuyt, 2003; Haas, 2003; Darst and Cannatella, 2004; Roelants and Bossuyt, 2005; Van der Meijden et al., 2005; Faivovich et al., 2005). Nevertheless, a study of a broad sampling of amphibians, based on a large number of terminals, has not been attempted to date.

A serious impediment in amphibian biology, and systematics generally, with respect to advancing historically consistent taxonomies, is the social conservatism resulting in the willingness of many taxonomists to embrace, if only tacitly, paraphyletic groupings, even when the evidence exists to correct them. The reason for this is obvious. Recognizing paraphyletic groups is a way of describing trees in a linear way for the purpose of telling *great* stories and providing favored characters a starring role. Because we think that storytelling reflects a very deep element of human communication, many systematists, as normal storytelling humans, are unwilling to discard paraphyly. Unfortunately, the *great* stories of science, those popular with the general public and some funding agencies, almost never evidence careful analysis of data and precise reasoning or language. And, for much of its history, systematics focused on *great* narrative stories about ''adaptive radiations'' and ''primitive'', ''transitional'', and ''advanced'' groups rather than the details of phylogeny. These *stories* were almost always about favored characters (e.g., pectoral girdle anatomy, reproductive modes) within a sequence of paraphyletic groupings to the detriment of a full and detailed understanding of evolutionary history.

When one deconstructs the existing taxonomy of frogs, for example, one is struck by the number of groups delimited by very small suites of characters and the special pleading for particular characters that underlies so much of the taxonomic reasoning. Factoring in the systematic philosophy at the time many of these groups were named, both the origin of the problems and the illogic of perpetuating the status quo become apparent.

Our goal in this study is to provide remedies for the problems noted above, by way of performing a large phylogenetic analysis across all living amphibians and providing a taxonomy consistent with phylogeny that will serve as a general road map for further research. That such a diverse group of biologists (see list of authors) would be willing to set aside their legitimate philosophical differences to produce this work demonstrates the seriousness of the need. We hope that by providing considerable new data and new hypotheses of relationship that we will engender efforts to test our phylogenetic hypotheses and generate new ones. Regardless, the days are over of construing broad conclusions from small analyses of small numbers of taxa using small amounts of molecular or morphological data. We also think that the time is past for authoritarian classifications, rich in special pleading and weak on evidence (e.g., Dubois, 1992; Delorme et al., 2005; Dubois, 2005). In short, we hope that this publication will help change the nature of the conversation among scientists regarding amphibian systematics, moving it away from the sociologically conservative to the scientifically conservative. As noted by Cannatella and Hillis (2004: 444), the need for ''scaling up'' the rate of data collection is certainly evident (e.g., compare the evidentiary content of Cannatella and Hillis, 1993, with Cannatella and Hillis, 2004).

Nevertheless, even if we are successful in providing a roadmap for future work, this will not assure the health of amphibian systematics. Clearly, the task of understanding the evolution and ecological, morphological, and taxonomic diversity of amphibians is massive, yet funding remains insufficient to maintain a healthy amphibian systematics commmunity. Further, the institutional, interinstitutional, national and international infrastructure needed to promote the systematics research program needs to be greatly enhanced with respect to state-of-the-art collection facilities, digital libraries of all relevant systematic literature, interoperable collection databases, and associated GIS and mapping-related capacity, supercomputers and the improved analytical software to drive them, remotely accessible visualization instrumentation and specimen images, and enhanced data-aquisition technology, including massive through-put DNA sequencing, in addition to already-identified personnel, training, and financial needs related to exploring life

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on this planet and maintaining large research collections (Q.D. Wheeler et al., 2004; Page et al., 2005). There has been the salutary development of additional support in the training of systematists (e.g., Rodman and Cody, 2003) and important successes in increasing systematics capacity in a few megadiverse countries (e.g., Brazil; see de Carvalho et al., 2005), but it is also clear that increased research support is needed to assure another generation of evolutionary biologists capable of the detailed anatomical work to document how organisms have changed and diversified through time. But, especially in this time of increasing optimization of university hiring and retention policies on the ability of faculty to garner extramural funding, additional funding is needed to make sure that jobs exist for the systematists that are being trained.

About the collaboration: This collaboration was undertaken with the knowledge that everyone involved would have to compromise on deeply held convictions regarding the nature of evidence, methods of analysis, and what constitutes a reasonable assumption, as well as the nature of taxonomic nomenclature. Nevertheless, all data are provided either through GenBank or from http://research.amnh.org/herpetology/downloads.html, and we expect several of the coauthors to deal in greater detail with the problems and taxonomic hypotheses noted in this paper, on the basis of even greater amounts of data with various taxonomic units within Amphibia and from their own points of view. We are unanimous in thinking that the capacity for systematic work needs to be expanded, and given existing university hiring and retention practices, this expansion can only take place through enhanced funding.

MATERIALS AND METHODS

Conventions and Abbreviations

Commands used in computer programs are italicized. Tissues are referenced in appendix 1 with the permanent collection number for the voucher specimen or, if that is unavailable, the tissue-collection number or field-voucher number. (See appendix 1 for acronyms.)

General Analytical Approach: Theoretical Considerations

Choice of Phylogenetic Method: All phylogenetic methods minimize the number of character transformations required to explain the observed variation. Unweighted (equally weighted) parsimony analysis minimizes hypothesized transformations globally, whereas the assumptions (expressed as differential probabilities or costs) about the evolutionary process or perceived importance of different classes of transformations employed in statistical (maximum-likelihood, Bayesian analysis) and weighted parsimony methods minimize certain classes of transformations at the expense of others. Operational considerations aside (e.g., tree-space searching capabilities), disagreements between the results of unweighted parsimony analysis and the other methods are due to the increased patristic distance required to accommodate the additional assumptions. For this study, we chose to analyze the data under the minimal assumptions of unweighted parsimony. Given the size and complexity of our dataset, an important advantage of parsimony algorithms (whether weighted or unweighted) is that thorough analysis could be achieved in reasonable times given currently available hardware and software.

Nucleotide Homology and the Treatment of Insertions/Deletions (Indels): The method of inferring nucleotide homology (i.e., alignment) and insertions/deletions (indels) and the treatment of indels in evaluating phylogenetic hypotheses are critically important in empirical studies. A given dataset aligned according to different criteria or under different indel treatments may strongly support contradictory solutions (e.g., W.C. Wheeler, 1995; Morrison and Ellis, 1997). Many workers infer indels as part of their procedure to discover nucleotide homology but then either treat the inferred indels as nucleotides of unknown identity by converting gaps into missing data or eliminate gap-containing column vectors altogether, because they are believed to be unreliable or because the method of phylogenetic analysis does not allow them (Swofford et al., 1996). Others argue that indels provide evidence of phylogeny but believe, we think incorrectly, that

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sequence alignment and tree evaluation are logically independent and must be performed separately (e.g., Simmons and Ochoterena, 2000; Simmons, 2004).

We treat indels as evidentially equivalent to any other kind of inferred transformation and as a deductively inferred component of the explanation of DNA sequence diversity observed among the sampled terminals. Furthermore, because nucleotides lack the structural and/or developmental complexity necessary to test their homology separately, hypotheses of nucleotide homology can be evaluated only in reference to a topology (Grant and Kluge, 2004; see also Frost et al., 2001). In recognition of these considerations, we assessed nucleotide homology dynamically by optimizing observed sequences directly onto competing topologies (Sankoff, 1975; Sankoff et al., 1976), thereby heuristically evaluating competing hypotheses by simultaneous searching of tree space. This is achieved using Direct Optimization (W.C. Wheeler, 1994, 1996, 1998, 1999; Phillips et al., 2000; W.C. Wheeler, 2000, 2001, 2002, 2003a, 2003b, 2003c) as implemented in the computer program POY (W.C. Wheeler et al., 1996–2003).

Determination of nucleotide homology is treated as an optimization problem in which the optimal scheme of nucleotide homologies for a given topology is that which requires the fewest transformations overall—that is, that which minimizes patristic distance, thus providing the most parsimonious explanation of the observed diversity. Determining the optimal alignment for a given topology is NP-complete[1] (Wang and Jiang, 1994). For even a minuscule number of sequences, the number of possible alignments is staggeringly large (Slowinski, 1998), making exact solutions impossible for any contemporary dataset, and heuristic algorithms are required to render this problem tractable.

Phylogenetic analysis under Direct Optimization, therefore, addresses two nested NP-complete problems. POY searches simultaneously for the optimal homology/topology combination, and search strategies must take into consideration the extent of the heuristic shortcuts applied at both levels. The details of our analyses are discussed below under Heuristic Homology Assessment and Heuristic Tree Searching, with the general approach being to increase the rigor at both levels as the overall search progresses. In any heuristic analysis, a balance is sought whereby the algorithmic shortcuts speed up analysis enough to permit a sufficiently large and diverse sample of trees and alignments to discover the global optimum during final refinement, but not so severe that the sampling is so sparse or misdirected that the global optimum is not within reach during final refinement. Ideally, indicators of search adequacy (e.g., multiple independent minimum-length hits, stable consensus; see Goloboff, 1999; Goloboff and Farris, 2001; Goloboff et al., 2003) should be employed to judge the adequacy of analysis, as is now reasonable in parsimony analysis of large prealigned datasets (e.g., as performed by the software package TNT; Goloboff et al., 2003). However, current hardware and software limitations make those indicators unreachable in reasonable amounts of time for our dataset analyzed under Direct Optimization. The adequacy of our analysis may only be judged intuitively in light of the computational effort and strategic use of multiple algorithms designed for large datasets.

Taxon Sampling

The 532 terminals (reflecting 7 outgroup species, 522 ingroup species [with three redundancies]) included in our analysis are given in appendix 1. Because this study is predominantly molecular, outgroup sampling was restricted to the closest living relatives of living amphibians and did not include fossil taxa. These included two mammals, two turtles, one crocodylian, one squamate, and a coelacanth as the root. Our study was not designed to identify the sister taxon of tetrapods, and our use of a coelacanth instead of a lungfish was due to expediency and not a decided preference for any particular hypothesis of tetrapod relationship.

The remaining 525 terminals were sampled from the three orders of living amphib-

[1] The notion of NP-completeness extends from formal complexity theory. But, we can regard NP-complete problems as those problems for which there is no practical way to determine or verify an exact solution.

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ians. Our general criteria were (1) availability of tissues and/or sequences on GenBank, and (2) representation of taxonomic diversity. Although taxonomic rank *per se* is meaningless, our taxon sampling was guided to a large degree by generic diversity. Experience suggested that this ''genus-level'' sampling would thoroughly sample the diversity of living amphibians. The median number of species per genus for living taxa is only three, something that we think has to do with human perception of similarity and difference, not evolutionary processes. Some genera (e.g., *Eleutherodactylus*, ca. 605 species) are so large and/or diverse that directed subsampling of species groups was required to evaluate likely paraphyly (e.g., with respect to *Phrynopus*).

Summarizing, our sample constituted about 8.8% of all species of Recent amphibians currently recognized, with approximately the same proportion of species diversity sampled from each order. Of the ca. 467 Recent amphibian genera[2], 326 (69.8%) are represented in our sample. We targeted 17 species of caecilians, representing 16 genera of all 6 family groups. Among salamanders we sampled 51 species from 42 genera of all 10 families. The bulk of our ingroup sample focused on frogs, with 437 terminals targeted. The remaining 457 terminals represent 454 anuran species from ca. 269 genera and 32 anuran families. A more extensive discussion of the terminals and the rationale behind their choice is presented under ''Review of Current Taxonomy''.

Character Sampling

Morphology: The 152 transformation series of morphology were incorporated directly from Haas (2003). Of his original 156 transformations, the gap-weighted morphometric transformations 12 (relative larval dermis thickness), 83 (cornua trabeculae proportions), 116 (ratio of anterior ceratohyal processes), and 117 (relative depth of anterior ceratohyla emargination) were excluded from our analysis because POY is unable to address noninteger transformations. We did include Haas' transformation 102 (presence/absence of larval ribs) which he excluded from analysis because of difficulty in scoring absences; its inclusion did not alter his final topology and provided us the opportunity to incorporate known occurence of larval ribs in our final hypothesis.

Of the 81 frog and 4 salamander species in Haas' (2003) study, our study overlaps in 41 anurans and 2 caudates. We did not combine into one virtual taxon morphology from one species and DNA sequences from another, even if putatively closely related. Although that would have allowed us to incorporate more (and potentially all) morphological data, and in some cases it probably would not have affected our results detrimentally, because of our general skepticism regarding the current understanding of amphibian relationships we were unwilling to assume the monophyly of any group prior to the analysis.

DNA Sequences: In light of the differing levels of diversity included in this study, we sought to sample loci of differing degrees of variability (i.e., rates). From the mitochondrial genome, we targeted the mitochondrial H-strand transcription unit 1 (H1), which includes the 12S ribosomal, $tRNA^{Valine}$, and 16S ribosomal sequences, yielding approximately 2,400 base pairs (bp) generated in 5–7 overlapping fragments. We also targeted the nuclear protein coding genes histone H3 (328 bp), rhodopsin (316 bp), tyrosinase (532 bp), seven in absentia (397 bp), and the nuclear 28S ribosomal gene (ca. 700 bp), giving a total of approximately 2,300 bp of nuclear DNA. Primers used in PCR amplification and cycle-sequencing reactions (and respective citations) are given in table 1. When possible, terminals for which we were unable to generate all fragments were augmented with sequences from GenBank (see appendices 1, 2) under the assumption that the tissues were actually conspecific. The amount of sequence/terminal varied (fig. 1) with a range from 490 bp (*Limnonectes limborgi*) to 4,790 (*Eleutherodactylus pluviacanorus*), and the mean being 3,554 bp (see appendix 1).

[2] The estimate of the number of amphibian genera, for purposes of these comparisons, rests on our perception of common usage. Because we arbitrarily treated many nominal subgenera (e.g., *Clinotarsus*, *Hydrophylax*, *Lithobates*) as genera, our *working* number of genera, for purposes of this manuscript, is considerably larger.

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TABLE 1
Primers Used for Various Loci in This Study and Their Published Sources

Gene	Primer name	Direction	Primer sequence (5′ to 3′)	Source
12S	MVZ59	Forward	ATAGCACTGAAAAYGCTDAGATG	Graybeal, 1997
	MVZ50	Reverse	TYTCGGTGTAAGYGARAKGCTT	Graybeal, 1997
	12S A-L	Forward	AAACTGGGATTAGATACCCCACTAT	Goebel et al., 1999
	12S F-H	Reverse	CTTGGCTCGTAGTTCCCTGGCG	Goebel et al., 1999
	12S L1	Forward	AAAAGCTTCAAACTGGGATTAGATACCCCACTAT	Feller and Hedges, 1998
	L13	Forward	TTAGAAGAGGCAAGTCGTAACATGGTA	Feller and Hedges, 1998
$tRNA^{Val}$	$tRNA^{Val}$-H	Reverse	GGTGTAAGCGARAGGCTTTKGTTAAG	Goebel et al., 1999
16S	AR	Forward	CGCCTGTTTATCAAAAACAT	Palumbi et al., 1991
	BR	Reverse	CCGGTCTGAACTCAGATCACGT	Palumbi et al., 1991
	Wilkinson2	Reverse	GACCTGGATTACTCCGGTCTGA	J.A. Wilkinson et al., 1996
	Titus I	Reverse	GGTGGCTGCTTTTAGGCC	Titus and Larson, 1996
	L2A	Forward	CCAAACGAGCCTAGTGATAGCTGGTT	Hedges, 1994
	H10	Reverse	TGATTACGCTACCTTTGCACGGT	Hedges, 1994
Rhodopsin exon 1	Rhod1A	Forward	ACCATGAACGGAACAGAAGGYCC	Bossuyt and Milinkovitch, 2000
	Rhod1C	Reverse	CCAAGGGTAGCGAAGAARCCTTC	Bossuyt and Milinkovitch, 2000
	Rhod1D	Reverse	GTAGCGGAAGAARCCTTCAAMGTA	Bossuyt and Milinkovitch, 2000
Tyrosinase exon 1	TyrC	Forward	GGCAGAGGAWCRTGCCAAGATGT	Bossuyt and Milinkovitch, 2000
	TyrG	Reverse	TGCTGGCRTCTCTCCARTCCCA	Bossuyt and Milinkovitch, 2000
Histone H3	H3F	Forward	ATGGCTCGTACCAAGCAGACVGC	Colgan et al., 1999
	H3R	Reverse	ATATCCTTRGGCATRATRGTGAC	Colgan et al., 1999
28S	28SV	Forward	AAGGTAGCCAAATGCCTCATC	Hillis and Dixon, 1991
	28SJJ	Reverse	AGTAGGGTAAAACTAACCT	Hillis and Dixon, 1991
Seven in absentia[a]	SIA1 (T3)	Forward	TCGAGTGCCCCGTGTGYTTYGAYTA	Bonacum et al., 2001
	SIA2 (T7)	Reverse	GAAGTGGAAGCCGAAGCAGSWYTGCATCAT	Bonacum et al., 2001

[a] Primers SIA1 and SIA2 were used with the universal T3 and T7 primers following Bonacum et al. (2001).

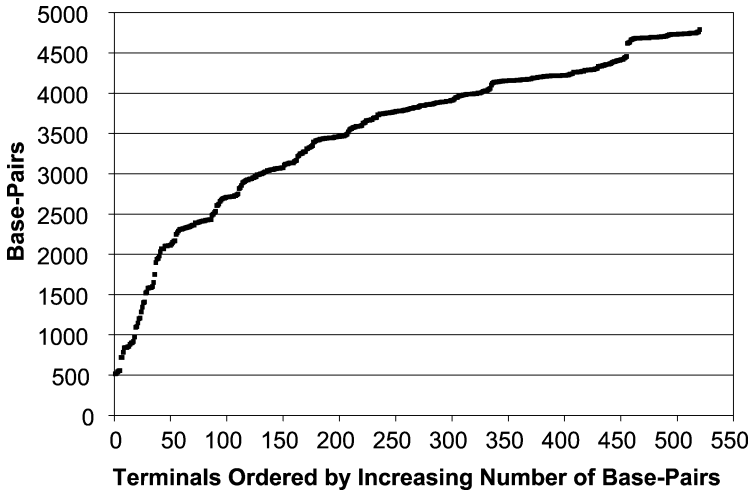

Fig. 1. Number of DNA base-pairs per terminal. For specific terminal data see appendix 1.

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Laboratory Protocols

Whole cellular DNA was extracted from frozen and ethanol-preserved tissues (liver or muscle) using either phenol-chloroform extraction methods or the Qiagen DNeasy kit following manufacturer's guidelines. PCR amplification was carried out in 25 μl reactions using Amersham Biosciences puRe Taq Ready-To-Go Beads. The standard PCR program consisted of an initial denaturing step of 3 minutes at 94°C, 35–40 cycles of 1 minute at 94°C, 1 minute at 45–62°C, and 1–1.5 minutes at 72°C, followed by a final extension step of 6 minutes at 72°C. PCR-amplified products were cleaned using the ARRAYIT kit (TeleChem International) on a Beckman Coulter Biomek 2000 robot. Cycle-sequencing using BigDye Terminators v. 3.0 (Applied Biosystems) were run in 8 μl reactions, and this was followed by isopropanol-ethanol precipitation and sequencing on either an ABI 3700 or ABI 3730XL automated DNA sequencer. Sequences were edited in Sequencher (Gene Codes).

Given the magnitude and complexity of this project (over 8,500 sequences were generated), the potential for errors to accumulate from a variety of sources (e.g., mislabeled vials, contamination, mispipetting, incorrect naming of files) was a serious concern. We took several measures to avoid errors. Tissues, stock solutions (including DNA extracts), and diluted working solutions were stored separately. Extractions were done at different times in batches of no more than 30 samples. Filtered tips were used to manipulate stock DNA extracts. Multichannel pipettes were used whenever possible, and all PCR cleaning was done using a Beckman Coulter Biomek 2000 robot. We extracted 100 tissues twice independently and sequenced at least one locus of each to confirm sequence identity, and we distributed multiple specimens of 10 species among different batches and generated all sequences for each to confirm species identifications and sequence identities and detect errors.

Sequence Preanalysis: Heuristic Error Checking

Numerous steps were taken to detect errors in DNA sequences. As is standard practice, we generated sequences in forward and reverse directions. The ca. 2400 bp of H1 were generated in 5–7 overlapping fragments, which allowed further sequence confirmation. We also compared the sequences generated for multiple extractions of the same tissues, as well as multiple specimens of the same species. Using Sequencher (Gene Codes) we selected all edited sequences for a given locus and used the ''assemble interactively'' option to establish the threshold at which a given sequence would align with any other sequence, which allowed identical and nearly identical sequences to be isolated for inspection. We compared questionable sequences with those of confirmed identity and sequences in GenBank.

The sequences that passed these tests were then aligned using ClustalX (Thompson et al., 1997). The resulting alignments and neighbor-joining trees for each partition were examined to detect aberrant sequences and formatting errors (e.g., reverse-complements). Finally, preliminary phylogenetic analyses were performed, and the resulting topologies were used to identify terminals that required further scrutiny. Extreme variance from expected position suggested the possibility of error and caused us to perform experiments to confirm sequence identities. We clarify that no sequence was eliminated solely because it did not fit our prior notions of relationships. Rather, the topologies were used heuristically to single out terminals/sequences for reexamination.

Once sequence identities were confirmed, sequences derived from the independent DNA extractions were merged. With a few exceptions noted later, those from conspecific specimens were merged into chimeras (with polymorphisms coded as ambiguities) to reduce the number of terminals in the analysis, but all sequences are deposited separately in GenBank (appendix 1).

Molecular Sequence Formatting

To allow integration of incomplete sequence fragments (particularly those obtained from GenBank; see Taxon Sampling Strategy and Character Sampling Strategy, above), accelerate cladogram diagnosis, and reduce memory requirements under Iterative Pass

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TABLE 2
Summary of DNA Sequence Data

Sequence	Number of fragments	Number of terminals for which a gene sequence was available
Mitochondrial ribosomal cluster	25	532
28S	5	343
Histone H3	2	378
Rhodopsin	2	375
Seven in absentia (SIA)	4	302
Tyrosinase	3	202

Optimization, we broke complete sequences into contiguous fragments. (This also improves the performance of POY's implementation of the parsimony ratchet; see Heuristic Tree Searching, below.) We did so sparingly, however, as these breaks constrain homology assessment by prohibiting nucleotide comparisons across fragments, that is, it is assumed that no nucleotides from fragment X are homologous with any nucleotides from fragment Y. As the number of breaks increases, so too does the risk of overly constraining the analysis and failing to discover the globally optimal solution(s).

We, therefore, inserted as few breaks as were necessary to maximize the amount of sequence data included, minimize the insertion of terminal N's, and attain maximum-length fragments of about 500 bases (table 2). Breaks were placed exclusively in highly conserved regions (many of which correspond to commonly used PCR primers), as recovery of such highly invariable regions is largely alignment-method independent and the inserted breaks do not prevent discovery of global optima. These highly conserved regions were identified via preliminary ClustalX (Thompson et al., 1997) alignments under default parameters. Except for their usefulness in placing fragments derived from different PCR primers and detecting errors (see Sequence Preanalysis, above), these preliminary alignments were used solely for the purpose of identifying conserved regions; they did not otherwise inform or constrain our phylogenetic analysis. Once appropriate conserved regions were identified, fragments were separated by inserting ampersands (&). Thus, the multiple fragments of the mtDNA cluster remain in the same file and order. The resulting POY-formatted files can be obtained from http://research.amnh.org/herpetology/downloads.html or from the authors.

Analytical Strategy

We analyzed all data simultaneously using the program POY (W.C. Wheeler et al., 1996–2003) v. 3.0.11a (released May 20, 2003) run on the AMNH Parallel Computing Cluster. We visualized results using Winclada (Nixon, 1999–2002) and performed additional searches of implied alignments by spawning NONA (Goloboff, 1993–1999) from Winclada (see below).

Heuristic Homology Assessment: Numerous algorithms of varying degrees of exhaustiveness have been proposed to optimize unaligned data on a given topology. Our search strategy employed three Direct Optimization algorithms. In order of increasing exhaustiveness and execution time, these were Fixed States Optimization (W.C. Wheeler, 1999), Optimization Alignment (W.C. Wheeler, 1996), and Iterative Pass Optimization (W.C. Wheeler, 2003a). As an indication of the magnitude of the problem of analyzing this 532-terminal dataset, execution time for a single random-addition sequence Wagner build (RAS), without swapping, on a 1.7 GHz Pentium 4 Dell Inspiron 2650 running WindowsXP was 2.69 hours under Fixed States and 3.26 hours under Optimization Alignment.

Although Fixed States Optimization was proposed as a novel means of conceptualizing DNA-sequence homology (W.C. Wheeler, 1999), we employed it here simply as a heuristic shortcut. Because Fixed States is so much faster than the Optimization Alignment algorithm, it allowed us to sample more thoroughly the universe of trees. (The speed-up for multiple replicates is actually much greater than noted earlier for a random-addition sequence Wagner build, as generating the initial state set is the slowest step in Fixed States analysis.) The trees obtained in Fixed States analyses were then used as starting points for further analysis under Optimization Alignment. The potential exists for the

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globally optimal tree (or trees that would lead to the global optimum when swapped under a more exhaustive optimization algorithm) to be rejected from the pool of candidates under the heuristic. To minimize this risk, we also generated a smaller pool of candidate trees under Optimization Alignment. The resulting 10 optimal and near-optimal candidate trees were then submitted to final evaluation and refinement under Iterative Pass optimization using *iterativelowmem* to reduce memory requirements. (For details on tree-searching algorithms see Heuristic Tree Searching, below.)

We did not employ *exact* during most searches, although we did use that command in the final stages of analysis. To verify lengths reported in POY, we output the implied alignment (W.C. Wheeler, 2003b) and binary version of the optimal topology in Hennig86 format with *phastwincladfile* and opened the resulting file in Winclada (Nixon, 1999–2002), following the procedure of Frost et al. (2001). Because each topology may imply a different optimal alignment, when multiple optimal topologies were obtained we examined them separately by inputting each as a separate file using *topofile*. Examination of the implied alignments, whether formatted as Hennig files or as standard alignments (*impliedalignment*), grants another opportunity to detect errors in formatting or sequencing (e.g., reverse complements; see Sequence Preanalysis, above).

HEURISTIC TREE SEARCHING: Efficient search strategies for large datasets are to a certain degree dataset-dependent (Goloboff, 1999), and, as discussed above, common indicators of sufficiency are unrealistic given current technological limitations. Therefore, rather than apply a simple, predefined search strategy (e.g., 100 random-addition sequence Wagner builds + TBR branch swapping), we employed a variety of tree-searching algorithms in our analysis, spending more computing time on those that proved most fruitful. Tree fusing (Goloboff, 1999) and TBR swapping were performed at various points throughout the analysis, and optimal trees from different searches were pooled for final tree fusing and TBR swapping, all of which was refined by submitting optimal topologies to swapping and ratcheting (see below) under Iterative Pass Optimization (W.C. Wheeler, 2003a).

See table 3 for a summary of general searching techniques. Initial runs used the *approxbuild* heuristic to speed up building of starting trees, but the resulting trees required much more subsequent refinement, nullifying the initial speed-up. Remaining analyses were therefore run without *approxbuild*. We conducted searches without *slop* or *checkslop*, both of which increase the pool of trees examined by swapping suboptimal trees found during the search. Although these steps can be highly effective, initial trials showed they were too time-consuming for the dataset (especially under Iterative Pass, where they would also be most relevant).

A variant of Goloboff's (1999) tree drifting was also used to escape local optima. Although it is based loosely on Goloboff's algorithm, the implementation in POY differs significantly in the way it accepts candidate trees during the search (see Goloboff, 1999, for his accept/reject calculation). In POY, the probability of accepting a candidate tree that is equal to or worse than the current optimum (better trees are always accepted) is given by $1/(n + c - b)$, where c is the length of the candidate topology, b is the length of the current optimum (best), and n is a user-specified factor that decreases the probability of accepting a suboptimal tree, effectively allowing the user to control the ease with which the search will drift away from the current optimum (we used the default of 2).

The parsimony ratchet (Nixon, 1999) was proposed for analysis of fixed matrices. Given that there are no prespecified column vectors to be reweighted under dynamic homology, the original approach had to be modified. In the current version of POY, the ratchet is programmed to reweight randomly selected DNA fragments. Our data were divided into 41 fragments (see table 2), so *ratchetpercent 15* randomly reweighted 7 fragments, regardless of their length or relative position. In our analyses we reweighted 15–35% of the fragments and applied weights of 2–8×.

As a complementary approach, we also performed quick searches (few random-addition sequence Wagner builds + SPR) under indel, transversion, and transition costs of 3:

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TABLE 3
Summary of Tree-Searching Methods Combined in Overall Search Strategy
See the text for more detailed explanations and references. Different runs combined multiple procedures, and all runs included SPR and/or TBR refinement.

Searching method	Description of procedure
RAS	Random addition sequence Wagner builds
Constrained RAS	As above, but constrained to agree with an input group inclusion matrix derived from the consensus of topologies within 100–150 steps of present optimum
Subset RAS	Separate analysis of subsets of 10–20 taxa; resulting arrangements used to define starting trees for further analysis of complete data set
Tree drifting	Tree drifting as programmed in POY, using TBR swapping; control factor = 2 (default)
Ratcheting (fragment)	Ratcheting as programmed in POY, with 15–35% of DNA fragments selected randomly and weighted 2–8 times, saving 1 minimum-length tree per replicate
Ratcheting (indel, tv, ts)	Ratcheting approximated by applying relative indel-transversion-transition weights of 311, 131, and 113, saving all minimum length trees
Constrained ratcheting (fragment)	As above, but beginning with the current optimum input as a starting tree and constrained to agree with an input group inclusion matrix derived from the consensus of topologies within 100–150 steps of present optimum
Tree fusing	Standard tree fusing followed by TBR branch swapping, with the maximum number of fusing pairs left unconstrained
Manual rearrangement	Manual movement of branches of current optimum
Ratcheting (original) of final implied alignment	Parsimony ratchet of fixed matrix, as implemented in Winclada

1:1, 1:3:1, and 1:1:3 and included the resulting topologies in the pool of trees submitted to tree-fusing and refinement under equal weights, following the general procedure of d'Haese (2003). Reweighting in this method is not done stochastically and therefore differs from both Nixon's (1999) original and POY's implementation of the ratchet. However, because it weights sets of transformations drawn from throughout the entire dataset, it is likely to capture different patterns in the data and may be a closer approximation to the original ratchet than POY's implementation. Both approaches attempt to escape local optima.

We also performed constrained searches by using Winclada to calculate the strict consensus of trees within an arbitrary number of steps of the present optimal, saving the topology as a treefile, constructing the group-inclusion matrix (Farris, 1973) in the program Jack2Hen (W.C.Wheeler, unpublished; available at http://research.amnh.org/sci-comp/projects/poy.php), and then employing *constraint* in the subsequent searches. To calculate the consensus we included trees within 100–150 steps of the current optimum, the goal being to collapse enough branches for swapping to be effective, but only enough branches to make for significant speed-ups of RAS + swapping, while still allowing discovery of optimal arrangements within the polytomous groups (see Goloboff, 1999: 420). This is effectively a manual approximation of Goloboff's (1999) consensus-based sectorial search procedure, the main difference being that we collapsed branches based only on tree length and not relative fit difference (Goloboff, 1999; Goloboff and Farris, 2001).

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Using constraint files generated in the same way, we also input the current optimum as a starting point for ratcheting. This strategy avoids spending time on RAS builds of the unconstrained parts of the tree (which tend to be highly suboptimal) and seeks to escape local optima in the same way as unconstrained ratcheting, discussed earlier. However, there is a tradeoff in that the arrangements may be less diverse (and therefore unable to find global optima) but are likely to be, on average, closer to the optimum score than those examined through RAS.

As a further manual approximation of sectorial searches, we analyzed subsets of taxa separately by defining reduced datasets with *terminals* files that listed only the targeted terminals. More rigorous searches (at least 100 RAS + TBR for each of the reduced datasets) of these reduced datasets were then performed, and the results were used to specify starting topologies for additional searching of the complete dataset.

As a final attempt to discover more parsimonious solutions in POY, we also rearranged branches of current optima manually. As a general search strategy this would obviously be highly problematic, if for no other reason than that it would bias results. However, we performed this step primarily to ensure that the ''received wisdom'' was evaluated explicitly in our analysis. Our procedure was to open the current optimum in Winclada, target taxa whose placement was strongly incongruent with current taxonomy, and move them to their expected positions (or place them in polytomies, depending on the precision of the expectations). The resulting topology was saved as a treefile that was read into POY as a starting topology for diagnosis and refinement (e.g., swapping, tree-fusing). In this way we were sure that the more heterodox aspects of our results were not due simply to failing to evaluate the orthodox alternatives in our searches.

We analyzed the final implied alignment obtained in the final searches under Iterative Pass Optimization (i.e., the optimal solution found through all searching in POY) by carrying out 10 independent ratchet runs of 200 iterations each, using the default reweightings (Nixon, 1999). This ensured that heuristic shortcuts employed in POY to speed up optimization did not prevent discovery of global optima. It also ensures that users of other programs will be able to duplicate our results given our alignment.

PARALLEL COMPUTING: All POY runs were parallelized across 95 or 64 processors of the AMNH 256-processor Pentium 4 Xeon 2.8 GHz Parallel Computing Cluster. Initial analyses divided replicates among 5 sets of 19 processors using *controllers,* that is, 5 replicates were run simultaneously, each parallelized across 19 processors. Although that strategy may lead to a more efficient parallel implementation of POY (Janies and Wheeler, 2001), a shortcoming is that *catchslaveoutput,* which saves all intermediate results to the standard error file, is disabled when *controllers* is in use. Consequently, crashes (e.g., due to HVAC failures and overheating) or maintenance reboots result in the irrecoverable loss of days or weeks of analysis. To avoid this problem in subsequent runs, we parallelized each replicate across all processors and ran replicates serially, which allowed recovery from interrupted runs by inputting the intermediate results as starting points.

SUPPORT MEASURES: We calculated support using the implied alignment of the optimal hypothesis. That is, the values reported reflect the degree of support by the hypothesized transformation series and not by the data per se. It is preferable to evaluate support based on the unaligned data, as that provides a more direct assessment of evidential ambiguity. (That is, it is possible for a clade to appear strongly supported given a particular alignment, but for support to dissolve when an alternative alignment is considered, meaning that the support by the data themselves is ambiguous.) We based support measures on the implied alignment because (1) it is much less time-consuming than support calculation under dynamic homology, and we preferred to concentrate computational resources on searches for the optimal solution; and (2) these values are directly comparable to those reported in the majority of phylogenetic studies, which derive support values from a single, fixed alignment.

To estimate Bremer values (Bremer, 1994), we output the implied alignment and optimal

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trees in Hennig86 format using *phastwincladfile*, converted it to NEXUS format in Winclada, and then generated a NEXUS inverse-constraints batch file in PRAP (K. Müller, 2004), which was analyzed in PAUP* 4.0 (Swofford, 2002). Given time constraints, tree searches for the Bremer analysis were superficial, consisting of only 2 RAS + TBR per group. Jackknife frequencies were calculated from 1000 replicates of 1 RAS per replicate without TBR swapping; jackknife analysis was performed by spawning NONA from Winclada.

REVIEW OF CURRENT TAXONOMY, THE QUESTIONS, AND TAXON SAMPLING

In this section we review the existing taxonomy of living amphibians and explain which species we sampled and what the justifications were for this sampling[3]. We also examine the evidentiary basis of the current taxonomy in an attempt to evaluate which parts provide a scientific template on which to interpret evolutionary patterns and trends, and which parts form an arbitrary and misleading structure that are merely anointed by time and familiarity or, worse, by authority. The canonical issue is obviously monophyly, so the question becomes: Does our taxonomy reflect evolutionary (i.e., monophyletic) groups? And, regardless of that answer, what is the evidentiary basis of the claims that have been made about amphibian relationships? Can we sample taxa in such a way as to test those claims? In this section we have, where practical, provided specific evidence from the published record as it bears on these questions. The reader should bear in mind that much of the current taxonomy rests on subjective notions of overall similarity and the relative importance of certain characters to specific Linnaean ranks. Even where knowledge claims derive from phylogenetic analysis, the evidence can be highly contingent on a specific phylogenetic context. We have not attempted to provide comparable characters among the taxa because such a description has yet to be accomplished in a detailed way (but see J.D. Lynch, 1973, and Laurent, 1986, for general attempts) and is outside the scope of this study. A general study would obviously change both the delimitation of the characters and the levels of generality.

[3] We do not address literature that appeared after 1 August 2005 (although we do address electronically available ''in-press'' articles that had not yet appeared in hard-copy form by that date). This decision will have excluded some important literature, but the date is well after the submission date of the manuscript (29 May 2005) and a practical end-point was needed.

COMPARABILITY OF SYSTEMATIC STUDIES

Throughout the review of current taxonomy that follows, we make only passing reference to the various analytical techniques used by various authors. There are two reasons for this. Not only is a deep review of techniques of phylogenetic inference beyond the scope of this paper, but it probably would be impossible for us to put together a quorum of authors to support any view beyond that it is monophyletic taxa that we are attempting to apprehend.

Our main concerns regard the repeatability of systematic analyses and that readers understand that many, if not most, of the analyses cited in this section are not rigorously comparable. In morphological studies it is common practice to report on individual transformation series and the logic behind treating these transformations as additive or nonadditive or whether these transformations can be polarized individually or not. This makes these analyses repeatable because workers can duplicate data as well as analytical conditions.

DNA sequence studies, however, have tended not to provide the information necessary for independent workers to repeat analyses, regardless of the accessibility of the original sequence data. In most cases, authors align their sequences manually (which is necessarily idiosyncratic and nonrepeatable, even if one uses models of secondary structure to help). In cases where alignment is done under algorithmic control, it is common to not cite the indel, transversion, and transition costs that went into the alignment, rendering these alignments unrepeatable. Also, many authors ''correct'' alignments by eye without explaining what this means or what these corrections were, further removing alignment from the sphere of repeatabil-

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ity. (This ''correction'' almost always means that the trees become longer.)

Of concern, at least for the AMNH authors, is that the assumptions of alignment may not be consistent with the assumptions of analysis. For instance, an author may have aligned sequences using one transversion: transition cost ratio but subsequently analyzed those data under an evolutionary model that makes entirely different assumptions about these relative costs. If the alignment method is not adequately specified, as is common in published works (e.g., Pauly et al., 2004), one is at a loss to know what component of the ultimate tree structure is due to the assumptions of alignment or to the assumptions of analysis. To illuminate the underlying incomparability of many molecular studies, we have provided in the relevant figure legends, and where this information can be gleaned from the publication, the alignment costs and whether the sequence was excluded for being ''unalignable'' (generally meaning that the authors did not like the number of gaps required to align the sequences), the amount of sequence and from what genes, and the kind of analysis (parsimony, Bayesian, or maximum-likelihood), and, if some general model of nucleotide evolution was assumed, what that model was. Because we are alarmed by the lack of explicitness in the literature regarding underlying assumptions, we urge editors to require that these pieces of information to be included in any works that pass over their desks. Having provided this preface to our review of current taxonomy as a caveat for readers, we now embark on a peregrination through the evidentiary basis of current amphibian taxonomy.

Amphibia

For the purposes of this paper, we are concerned with amphibians not as the fictional ''transitional'' group from fishes to amniotes, but as the taxon enclosing the extant crown clades Gymnophiona (caecilians), Caudata (salamanders), and Anura (frogs), together forming Lissamphibia of Gadow (1901) and most recent authors (e.g., Milner, 1988, 1993, 1994; Ruta et al., 2003; Schoch and Milner, 2004) or Amphibia in the restricted sense of being the smallest taxon enclosing the living crown groups (cf. de Blainville, 1816; Gray, 1825; de Queiroz and Gauthier, 1992; Cannatella and Hillis, 1993, 2004). We concur with authors who restrict application of the name Amphibia to the living crown groups, so for this study we use the terms ''Amphibia'' and ''Lissamphibia'' interchangeably.

Testing lissamphibian monophyly and the relationships among the three crown groups of amphibians was and continues to be daunting because morphologically the groups are mutually very divergent and temporally distant from each other and from nonamphibian relatives. Furthermore, testing lissamphibian monophyly may be outside the ability of this study to address inasmuch as the major controversy has to do with the phylogenetic structure of various fossil groups. Most authors regard Lissamphibia as a taxon imbedded in Temnospondyli (e.g., Estes, 1965; Trueb and Cloutier, 1991; Lombard and Sumida, 1992) whereas others regard frogs to be temnospondyls and salamanders and caecilians to be lepospondyls (Carroll and Currie, 1975; Carroll et al., 1999; Carroll, 2000a; J.S. Anderson, 2001). Laurin (1998a, 1998b, 1998c) regarded Lissamphibia to be completely within Lepospondyli, but more recent work (e.g., Ruta et al., 2003) returned a monophyletic Lissamphibia to the temnospondyls. (See Lebedkina, 2004, and Schoch and Milner, 2004, for extensive reviews of the alternative views of phylogeny of modern amphibian groups.) Because none of these paleontological studies adequately addressed living diversity, we hope that future work will integrate data presented here with fossil taxa as part of the resolution of the problem.

Regardless of the consideration of fossil taxa, the choice of Recent outgroups for analysis is clearly based on knowledge of the relationships of major tetrapod groups. A coelacanth (*Latimeria*) represents a near-relative of tetrapods, and among tetrapods, several amniotes (Mammalia: *Didelphis* and *Gazella*; Testudines: *Pelomedusa* and *Chelydra*; Diapsida: *Iguana* and *Alligator*) represent the nearest living relatives of amphibians. Although our choice of outgroups is made specifically to root the ingroup tree, our choice of terminals will allow weak tests of the var-

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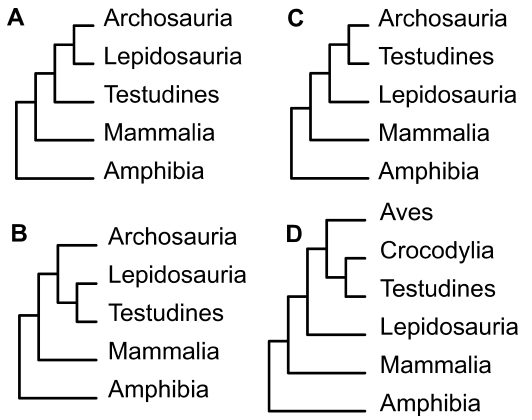

Fig. 2. Four phylogenetic hypotheses of tetrapod relationships. **A,** Gauthier et al. (1988a, 1988b); **B,** Rieppel and de Braga (1996); **C,** Zardoya and Meyer (1998); **D,** Hedges and Poling (1999).

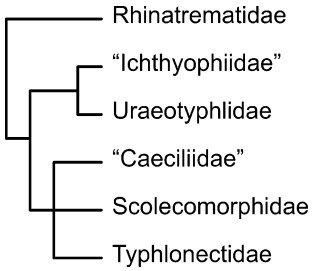

Fig. 3. Currently accepted view of relationships among caecilian families based on Nussbaum and Wilkinson (1989), Hedges and Maxson (1993), M. Wilkinson and Nussbaum (1996), Gower et al. (2002), and M. Wilkinson et al. (2002). Quotation marks denote nonmonophyletic taxa.

ious hypotheses of amniote relationships. The alternative relationships suggested by various authors is large, and an extensive discussion of these alternatives is outside the scope of this paper. Nevertheless, we show four topologies in figure 2. The most popular tree of amniote groups among paleontologists is shown in figure 2A and reflects the preferred topology of Gauthier et al. (1988a, 1988b), although some authors suggested, also on the basis of morphological evidence, that turtles are the sister taxon of lepidosaurs, with archosaurs and mammals successively more distantly related (Rieppel and de Braga, 1996; fig. 2B). This position, however, was disputed by M. Wilkinson et al. (1997). Also relevant to our study, some recent DNA sequence studies have found turtles to form the sister taxon of archosaurs (Zardoya and Meyer, 1998; Iwabe et al., 2005; fig. 2C), and others found turtles to be the sister taxon of archosaurs to the exclusion of lepidosaurs, with mammals outside this group (Hedges and Poling, 1999; Mannen and Li, 1999; fig. 2D). Our data will provide a weak test of these alternatives.

Assuming lissamphibian monophyly, the relationships among the three major groups of living lissamphibians remain controversial. On the basis of a parsimony analysis of morphological data, Laurin (1998a, 1998b, 1998c) suggested that salamanders are paraphyletic with respect to caecilians (although Laurin himself considered this conclusion implausible). Previously published molecular data placed salamanders as the sister taxon of either caecilians (Larson, 1991; Feller and Hedges, 1998) or frogs (Iordansky, 1996; Zardoya and Meyer, 2000, 2001; San Mauro et al., 2004; Roelants and Bossuyt, 2005; San Mauro et al., 2005). The latter arrangement is most favored by morphologists (e.g., Trueb and Cloutier, 1991). Additional tests using morphological data of the relative placement of the living lissamphibians will require evaluation of fossils, such as Albanerpetontidae (McGowan and Evans, 1995; Milner, 2000; Gardner, 2001, 2002) and the putative Mesozoic and Tertiary caecilians, salamanders, and frogs (Estes, 1981; Jenkins and Walsh, 1993; Shubin and Jenkins, 1995; Sanchíz, 1998; Carroll, 2000a; Gao and Shubin, 2001, 2003).

Gymnophiona

Caecilians (6 families, 33 genera, 173 species) are found almost worldwide in tropical terrestrial, semiaquatic, and aquatic habitats. A reasonably well-corroborated cladogram exists for at least the major groups of caecilians (Nussbaum and Wilkinson, 1989; Hedges and Maxson, 1993; M. Wilkinson and Nussbaum, 1996, 1999; Gower et al., 2002; M. Wilkinson et al., 2002; fig. 3). Taxon sampling has not been dense and taxonomic assignments are almost certain to change with the addition of new taxa and ev-

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idence. Nevertheless, it appears that most caecilian taxa are monophyletic, with the exception of ''Ichthyophiidae'' with respect to Uraeotyphlidae (Gower et al., 2002) and ''Caeciliidae'', which includes most of the diversity (93 species; 54% of all caecilians) and which is paraphyletic with respect to Typhlonectidae (M.H. Wake, 1977; M. Wilkinson, 1991) and possibly with respect to Scolecomorphidae (M.H. Wake, 1993; M. Wilkinson et al., 2003).

The following taxa were sampled:

RHINATREMATIDAE (2 GENERA, 9 SPECIES): A South American group, Rhinatrematidae is hypothesized to be the sister taxon of remaining caecilians and is clearly composed of the most generally plesiomorphic living caecilians (Nussbaum, 1977, 1979; Duellman and Trueb, 1986; San Mauro et al., 2004). They retain a tail (a plesiomorphy) but share the putatively derived characters of high numbers of secondary annuli, having an os basale, and lacking the fourth ceratobranchial. We sampled one species each of the two nominal genera (*Rhinatrema bivittatum* and *Epicrionops* sp.) to optimize characters for the family appropriately and to test the monophyly of this group.

ICHTHYOPHIIDAE (2 GENERA, 39 SPECIES) AND URAEOTYPHLIDAE (1 GENUS, 5 SPECIES): Tropical Asian Ichthyophiidae was hypothesized to form the sister taxon of Uraeotyphlidae (M. Wilkinson and Nussbaum, 1996; San Mauro et al., 2004), or to include Uraeotyphlidae (cf. Gower et al., 2002), or, currently less corroborated, to be the sister taxon of Uraeotyphlidae plus stegokrotaphic caecilians (i.e., ''Caeciliidae'' + Scolecomorphidae + Typhlonectidae; Nussbaum, 1979; Duellman and Trueb, 1986). The morphological diagnosis of Ichthyophiidae is contingent on whether *Uraeotyphlus* is within or outside of Ichthyophiidae, but the presence of angulate annuli anteriorly in ichthyophiids remains an apomorphy among these phylogenetic hypotheses. We have sampled one striped *Ichthyophis* (*Ichthyophis* sp.) that is not suspected to be close to *Uraeotyphlus* and one unstriped *Ichthyophis* (*I.* cf. *peninsularis*), which we suspect (M. Wilkinson and D.J. Gower, unpubl. data) to be phylogenetically close to *Uraeotyphlus*. Monophyly of the endemic and monotypic Indian group Uraeotyphlidae is supported by the morphological character of the tentacle being positioned below the naris. Our sole sample of this taxon is *Uraeotyphlus narayani*.

SCOLECOMORPHIDAE (2 GENERA, 6 SPECIES): The East African Scolecomorphidae was suggested to form the sister taxon of ''Caeciliidae'' + Typhlonectidae (Nussbaum, 1979), but because this suggestion was based on one of the early phylogenetic studies of caecilians, the sampling over which this generalization was made was small. Subsequent studies from mtDNA (M. Wilkinson et al., 2003) and morphology (M.H. Wake, 1993; M. Wilkinson, 1997) suggested that Scolecomorphidae, like Typhlonectidae, is imbedded within ''Caeciliidae''. The monophyly of Scolecomorphidae is well-corroborated by morphology (Nussbaum, 1979; M. Wilkinson, 1997). Nevertheless, we sampled members of each of the two nominal genera (*Crotaphatrema tchabalmbaboensis* and *Scolecomorphus vittatus*), both as a test of scolecomorphid monophyly and to help optimize molecular characters for the family to the appropriate branch[4].

TYPHLONECTIDAE (5 GENERA, 14 SPECIES): The South American Typhlonectidae is a morphologically well-corroborated taxon of secondarily aquatic caecilians (M.H. Wake, 1977; Nussbaum, 1979; M. Wilkinson, 1991), clearly derived out of ''Caeciliidae''. Although there are several nominal genera of typhlonectids, because of the highly apomorphic nature and highly corroborated monophyly of the taxon we sampled only *Typhlonectes natans*.

''CAECILIIDAE'' (21 GENERA, 100 SPECIES):

[4] A minor but controversial issue is exposed here among the coauthors. Throughout the text, ''phylogenetic tree'' and ''cladogram'' are used interchangeably, although there is good reason to consider the latter to be the operational basis of the former (Platnick, 1977). A related issue is that we prefer the nomenclature of transformation series containing characters (e.g., Wiley, 1981; Grant and Kluge, 2004), rather than the more operational terminology of characters containing character states. Character transformations happen through time along lineages (i.e., along branches in the tree, therby rendering the notion of branch length). We use the term ''branch'' rather than the more operational ''node'' (a term from computer science, not biology). In other words, we attempt to use evolutionary terms rather than the operational equivalents that have enjoyed considerable usage. Frost bears responsibility for this decision.

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This nominal taxon can be diagnosed only in the sense of being coextensive with the ''higher'' caecilians (Stegokrotaphia of Cannatella and Hillis, 1993) in lacking a tail, having a stegokrotaphic skull, and not being either a scolecomorphid or typhlonectid. We chose taxa from within the pantropical ''Caeciliidae'' that on the basis of previously published results (M.H. Wake, 1993; M. Wilkinson et al., 2003) we predicted would illuminate the paraphyly of ''Caeciliidae'' with respect to the presumptively derivative groups Typhlonectidae and Scolecomorphidae. We sampled: *Boulengerula uluguruensis* (Africa), *Caecilia tentaculata* (South America), *Dermophis oaxacae* (Mexico), *Gegeneophis ramaswanii* (India), *Geotrypetes seraphini* (Africa), *Herpele squalostoma* (Africa), *Hypogeophis rostratus* (Seychelles), *Schistometopum gregorii* (Africa), and *Siphonops hardyi* (South America).

CAUDATA

Salamanders (10 families, 62 genera, 548 species) are largely Holarctic and Neotropical and are the best known amphibian group, even though their phylogeny is notoriously problematic because of the confounding effects of paedomorphy on interpreting their morphology by (Larson et al., 2003; Wiens et al., 2005). Apparently independent paedomorphic lineages include Cryptobranchidae, Proteidae, and Sirenidae, as well as various lineages within Ambystomatidae and Salamandridae. Larson et al. (2003) provided an extensive discussion of salamander systematics, offering detailed discussion of the existing issues, although much of the supporting evidence was not disclosed. Until recently, Larson and Dimmick (1993) provided the received wisdom on salamander relationships based on a combined analysis of morphology (29 transformation series) and molecules (177 informative sites from rRNA sequences; fig. 4). The branch associated with internal fertilization in their tree (all salamanders excluding Sirenidae, Cryptobranchidae, and Hynobiidae) is corroborated primarily by a number of morphological characters that are functionally related to the secretion of a spermatophore (Sever, 1990; Sever et al., 1990; Sever, 1991a, 1991b, 1992, 1994).

Gao and Shubin (2001) provided a parsimony analysis of DNA sequences and morphology (including relevant fossils) suggesting that Sirenidae is not the sister taxon of the remaining salamander families, but the sister taxon of Proteidae (fig. 5). Otherwise, their results were largely congruent with those of Larson and Dimmick (1993). The exemplars used for their family-group tree were not provided nor were the distribution of morphological characters sufficiently detailed to allow us to include their data. Further, Larson et al. (2003), on the basis of molecular data alone (the data themselves not presented or adequately described beyond noting that they are from nuclear rRNA and mtDNA sequences), suggested the tree shown in figure 6. Larson et al. (2003) also noted that phylogenetic analysis of most morphological characters, other than those associated with spermatophore production, do not support the monophyly of their Salamandroidea (sensu Duellman and Trueb, 1986; all salamander families other than Sirenidae, Hynobiidae, and Cryptobranchidae). Although we address salamander phylogeny through the application of a large amount of molecular data, we did not address the morphological data set presented by Larson and Dimmick (1993) and Gao and Shubin (2001, 2003) because of the lack of correspondence between our exemplars and theirs and because this would have required reconciliation of these data with the frog morphology data we did include, an undertaking that is outside the scope of this study.

Most recently, Wiens et al. (2005) provided an analysis that included additional characters of morphology and the addition of data from RAG-1 DNA sequences (fig. 7). These authors presented results from different analytical approaches (e.g., maximum-likelihood, Bayesian, parsimony). We illustrate only the parsimony analysis of morphology + molecules, which most closely approximates our own assumption set. A paper by San Mauro et al. (2005) provided substantially similar results using the RAG-1 gene also used by Wiens et al. (2005).

SIRENIDAE (2 GENERA, 4 SPECIES): Sirenidae is a North American, pervasively paedomorphic taxon, whose members are obligately aquatic and possess large external gills and

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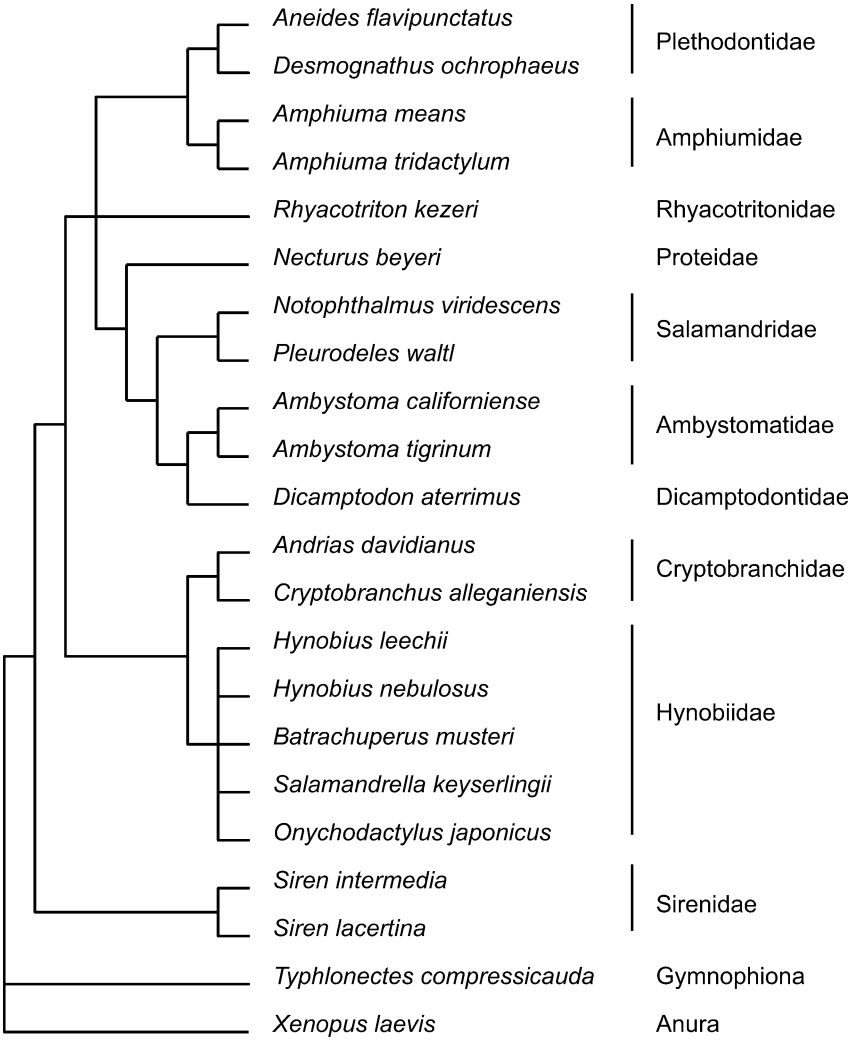

Fig. 4. Relationships of salamanders suggested by Larson and Dimmick (1993). Families are noted on right. *Typhlonectes* and *Xenopus* were employed as outgroups. Consensus of 40 equally-parsimonious trees (length = 460, ci = 0.59). Data are 32 morphological and 177 molecular (nu rDNA) character transformations (from Larson, 1991). The method of DNA alignment was not specified. Gaps were excluded as evidence.

lack pelvic girdles and hind limbs as well as eyelids. Only two genera (*Siren* and *Pseudobranchus*) are recognized. Sirenidae has been considered the sister taxon of the remaining salamanders by most authors because of its lack of internal fertilization (this is assumed on the basis of its lacking spermatophore-producing glands and not on any observation regarding its reproductive behavior) and its primitive jaw closure mechanism (Larson and Dimmick, 1993). Other morphological similarities (such as external gills and reduced maxillae) shared with other obligate paedomorphs have been more-or-less universally considered by authors to be convergent. Nevertheless, Gao and Shubin (2001), on the basis of an analysis of living and fossil taxa, concluded that sirenids are the sister taxon of proteids (fig. 5). Wiens et al. (2005) suggested, on the basis of a parsimony analysis of DNA sequences and morphology, that sirenids are the sister taxon of

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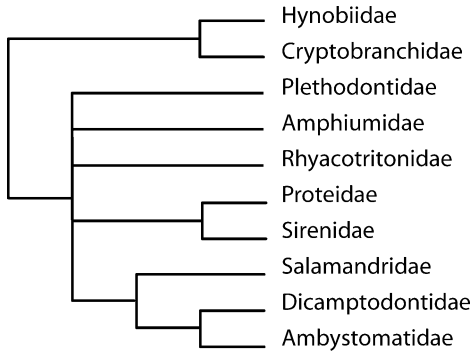

Fig. 5. Tree of salamander families from Gao and Shubin (2001; fossil terminals pruned) based on a parsimony analysis of nu rRNA sequence data from Larson and Dimmick (1993) and 60 morphological transformation series (length = 402; ci = 0.549; ri = 0.537). The sequence alignment method was not disclosed. Indels (i.e., gaps) were treated as evidence.

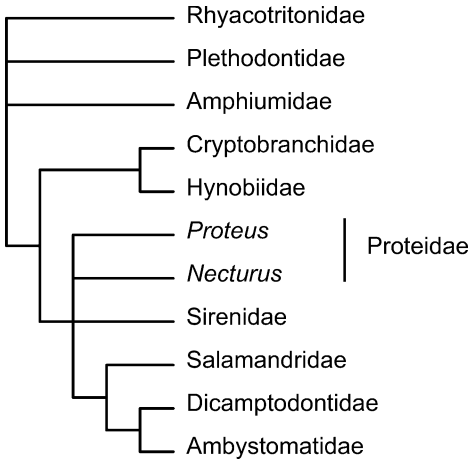

Fig. 6. Relationships of salamander families suggested by Larson et al. (2003) on the basis of undisclosed nu rRNA and mtDNA sequence data.

all other salamanders (fig. 7), although their Bayesian analysis placed Sirenidae as the sister taxon of Salamandroidea, with Cryptobranchoidea outside the inclusive group. We selected representatives of each nominal genus: *Siren lacertina*, *S. intermedia*, and *Pseudobranchus striatus*.

HYNOBIIDAE (7 GENERA, 46 SPECIES): The Asian Hynobiidae and Asian and North American Cryptobranchidae are usually considered each others' closest relatives because they share the putatively plesiomorphic condition of external fertilization and have the m. pubotibialis and m. puboischiotibialis fused to each other (Noble, 1931; Larson et al., 2003; Wiens et al., 2005). Hynobiids have aquatic larvae and transformed adults, and they retain angular bones in the lower jaw (presumed plesiomorphies). Morphological evidence in support of monophyly of this group are septomaxilla absent (also absent in plethodontids and ambystomatids), first hypobranchial and first ceratobranchial fused (also in *Amphiuma*), second ceratobranchial in two elements, and palatal dentition replaced from the posterior of the vomer (also in ambystomatids; Larson and Dimmick, 1993). Our selection of hynobiid taxa was restricted to *Ranodon sibiricus* and *Batrachuperus pinchoni*. Larson et al. (2003) suggested that *Onychodactylus*, especially, and several genera that we could not obtain (e.g., *Hynobius*), are not bounded phylogenetically by these taxa, so our analysis will not provide a rigorous test of hynobiid monophyly.

CRYPTOBRANCHIDAE (2 GENERA, 3 SPECIES): Cryptobranchids are a Holarctic group represented by only three species in two genera, *Cryptobranchus* (eastern North America) and *Andrias* (eastern temperate Asia). We included all three species, *Cryptobranchus alleganiensis*, *Andrias davidianus*, and *A. japonicus*, to test the monophyly of *Andrias* and optimize ''family'' evidence to the appropriate branch. The monophyly of Cryptobranchidae is not seriously in doubt as these giant, obligately paedomorphic salamanders are highly apomorphic in many ways, such as in lacking gills or functional lungs, and instead respiring across the extensive skin surface. Like Hynobiidae and Sirenidae (presumably), cryptobranchids lack internal fertilization.

PROTEIDAE (2 GENERA, 6 SPECIES): Proteidae is another obligate paedomorphic perennibranch clade considered to be monophyletic because of its loss of the maxillae (also very reduced in sirenids, apparently independently) and the basilaris complex of inner ear (also lost in sirenids, plethodontids, and some salamandrids), and because it has other characters associated with paedomorphy, such as lacking a m. rectus abdominis (Noble, 1931). Unlike sirenids, cryptobranchids,

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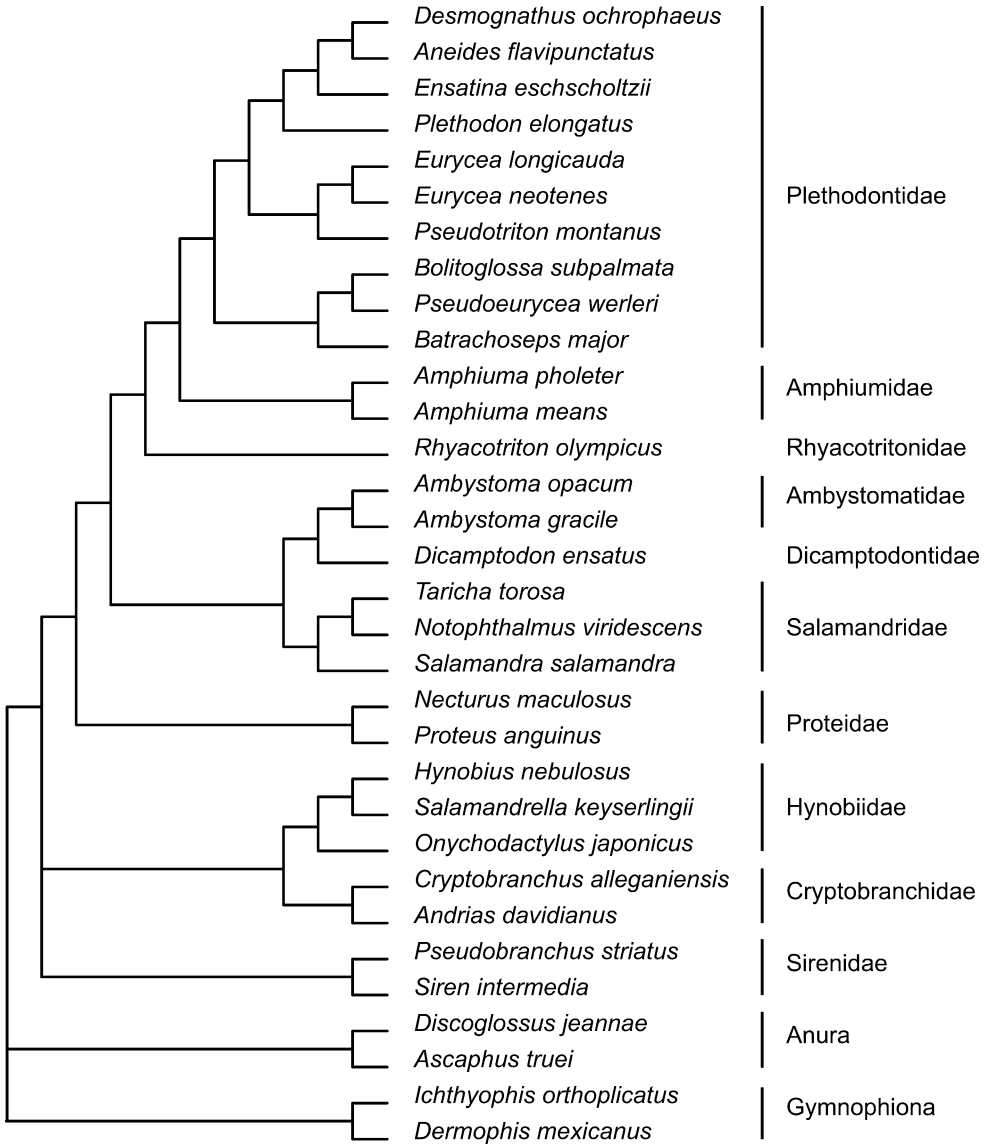

Fig. 7. Relationships of salamanders suggested by Wiens et al. (2005). Families are noted on right. Results reflect a parsimony analysis of 326 character transformations of morphology (221 parsimony-informative), and DNA sequences from nu rRNA (212 bp from Larson, 1991; 147 parsimony-informative) and RAG-1 (1,530 bp; 624 parsimony-informative). Sequence alignment was made using Sequencher (Gene Codes Corp.). Morphological characters identified as paedomorphic were treated as unknown for adult morphology and in some cases hypothetical terminals were related-species chimaeras of composite molecular and morphological data. Molecular transformations were weighted equally in analysis. Inferred insertion-deletion events were coded as binary characters separate from the nucleotide sequence characters and indel-required gaps within sequences were coded as missing. The tree was rooted on Gymnophiona + Anura.

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and hynobiids, but like other salamander families, proteids employ internal fertilization through use of a spermatophore (Noble, 1931). In our analysis, we included two species of *Necturus* (of North America), *N.* cf. *beyeri* and *N. maculosus*, but were unsuccessful in amplifying DNA of the only other genus, *Proteus* (which is found only in the western Balkans). Nevertheless, Trontelj and Goricki (2003) did study *Proteus* and provided molecular evidence consistent with the monophyly of Proteidae, and Wiens et al. (2005), also reporting on both *Necturus* and *Proteus*, subsequently provided strong evidence in favor of its monophyly.

RHYACOTRITONIDAE (1 GENUS, 4 SPECIES): Western North American *Rhyacotriton* was originally placed in its own subfamily within Ambystomatidae (Tihen, 1958) but was shown to be distantly related to ambystomatines by Edwards (1976), Sever (1992), and Larson and Dimmick (1993), who considered it to be a family distinct from Ambystomatidae. Wiens et al. (2005) considered, on the basis of their parsimony analysis, that Rhyacotritonidae is the sister taxon of Amphiumidae + Plethodontidae. Good and Wake (1992) provided the most recent revision. Rhyacotritonidae retains a reduced ypsiloid cartilage and has at least one apomorphy associated with the glandular structure of the cloaca (Sever, 1992). Inasmuch as the four species are seemingly very closely related and morphologically very similar, we sampled only *Rhyacotriton cascadae*, although this leaves the taxon's monophyly untested.

AMPHIUMIDAE (1 GENUS, 3 SPECIES): The amphiumas of eastern North America have reduced limbs and are obligate aquatic paedomorphs. They have internal fertilization and a suite of morphological features that are associated with spermatophore formation and internal fertilization. Some authors have associated Amphiumidae with Plethodontidae (sharing fused maxillae and reproductive behavior patterns; e.g., Salthe, 1967; Larson and Dimmick, 1993) and recent molecular studies place them here as well (Wiens et al., 2005). The three species are very similar and share many apomorphies, so we restricted our sampling to *Amphiuma tridactylum*.

PLETHODONTIDAE (4 SUBFAMILIES, 27 GENERA, 374 SPECIES): Plethodontidae includes the large majority of salamander species, with most being in North America, Central America, and South America, with *Speleomantes* found in Mediterranean Europe and *Karsenia* found in the Korean Peninsula (Min et al., 2005). The monophyly of the group is not seriously questioned, as its members share a number of morphological synapomorphies such as nasolabial grooves in transformed adults and the absence of lungs (found in other groups as well; Larson and Dimmick, 1993). Starting in 2004, and while this project was in progress, understanding of the evolution of Plethodontidae moved into a dynamic state of flux with the publication of a series of important studies addressing substantial amounts of DNA sequence data and morphology (Chippindale et al., 2004; Mueller et al., 2004; Macey, 2005; Wiens et al., 2005). Before 2004, plethodontid phylogeny appeared to be reasonably well understood (D.B. Wake, 1966; D.B. Wake and Lynch, 1976; J.F. Lynch and Wake, 1978; D.B. Wake et al., 1978; Maxson et al., 1979; Larson et al., 1981; Maxson and Wake, 1981; Hanken and Wake, 1982; J.F. Lynch et al., 1983; D.B. Wake and Elias, 1983; Lombard and Wake, 1986; D.B. Wake, 1993; Jackman et al., 1997; García-París and Wake, 2000; Parra-Olea et al., 2004) with the group putatively composed of two monophyletic subfamilies (fig. 8), Desmognathinae and Plethodontinae, although the morphological evidence for any suprageneric group other than Desmognathinae and Bolitoglossini (a tribe in Plethodontinae as then defined) was equivocal.

Desmognathines (2 genera, 20 species; *Desmognathus* + *Phaeognathus*) as traditionally understood share nine morphological characters suggested to be synapomorphies (Schwenk and Wake, 1993; Larson et al., 2003), although at least some of them may be manifestations of a single transformation having to do with the unique method of jaw closure: (1) heavily ossified and strongly articulated skull and mandible; (2) dorsoventrally flattened, wedge-like head; (3) modified anterior trunk vertebrae; (4) enlarged dorsal spinal muscles; (5) hindlimbs larger than forelimbs; (6) stalked occipital condyles; (7) enlarged quadratopectoralis mus-

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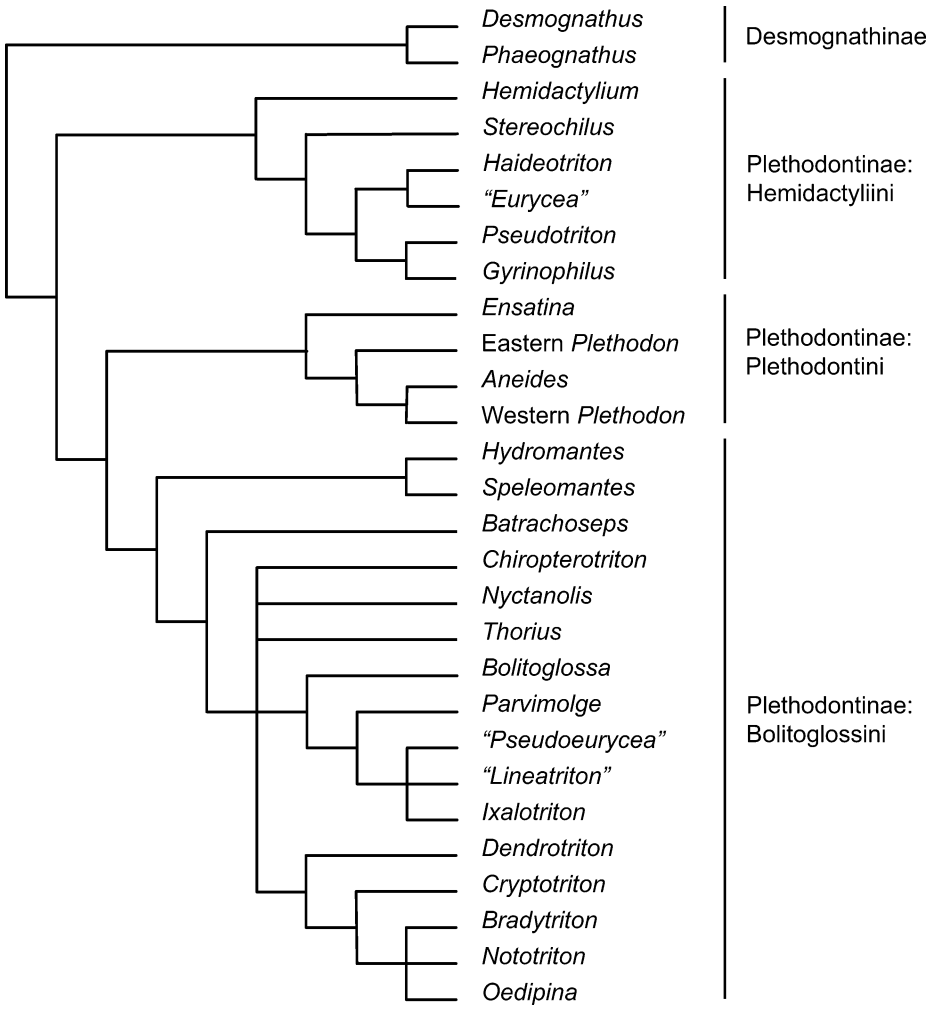

Fig. 8. Composite tree of hypothesized relationships among Plethodontidae as inferred from 1966–2004 literature; subfamilies and tribes noted on the right (D.B. Wake, 1966; D.B. Wake and Lynch, 1976; J.F. Lynch and Wake, 1978; D.B. Wake et al., 1978; Maxson et al., 1979; Larson et al., 1981; Maxson and Wake, 1981; Hanken and Wake, 1982; J.F. Lynch et al., 1983; D.B. Wake and Elias, 1983; Lombard and Wake, 1986; D.B. Wake, 1993; Jackman et al., 1997; García-París and Wake, 2000; and Parra-Olea et al., 2004). Quotation marks denote nonmonophyletic taxa.

cles; (8) modified atlas; and (9) presence of atlantomandibular ligaments. Most species have a biphasic life history, but at least some species have either nonfeedling larvae or direct development (Tilley and Bernardo, 1993). Plethodontinae in the pre-2004 sense (fig. 8) did not have strong morphological evidence in support of its monophyly, although Lombard and Wake (1986) suggested that possessing three embryonic or larval epibranchials is synapomorphic. Within Plethodontinae were included three nominal tribes: Hemidactyliini, Plethodontini, and Bolitoglossini.

Hemidactyliini (5 genera, 33 species) was the only putative plethodontine group with free-living larvae and transformation into adults (although this is shared with most desmognathines). Lombard and Wake (1986) suggested that *Hemidactylium* is the sister taxon of *Stereochilus* + (*Eurycea*, *Gyrinophilus*, and *Pseudotriton*) but provided only

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a single morphological character (parietal with a distinct ventrolateral shelf) in support of the monophyly of this group.

Plethodontini (3 genera, 62 species), as traditionally understood, was a heterogeneous assemblage composed of *Plethodon*, *Aneides*, and the more distant *Ensatina* (1 nominal species, but likely containing many species under any meaningful definition of that term; see Highton, 1998). Lombard and Wake (1986) suggested two morphological characters in support of the monophyly of this group (radii expanded and fused to basibranchial, and presence of a posterior maxillary facial lobe).

As traditionally viewed (before 2004), Bolitoglossini (15 genera, 222 species) represented a highly-speciose group in the New World tropics and west-coastal North America, with isolated representation in Mediterranean Europe. The group was characterized by having a projectile tongue, although this also appears in other plethodontids.

Lombard and Wake (1986) proposed a (nonparsimonious) scenario in which they suggested 10 synapomorphies of Bolitoglossini, all associated with the structure and function of the tongue. They regarded the supergenus *Hydromantes* (*Hydromantes* + *Speleomantes*) to be the sister taxon of the supergenus *Bolitoglossa* + supergenus *Batrachoseps* (containing solely *Batrachoseps*) based on two synapomorphies. Elias and Wake (1983) discussed phylogeny within Bolitoglossini and suggested the topology *Hydromantes* [including *Speleomantes*] + (*Batrachoseps* (*Nyctanolis* + other bolitoglossine genera)). Synapomorphies given by Elias and Wake (1983) for Bolitoglossini are (1) urohyal lost; (2) radii fused to the basibranchial; (3) long epibranchials relative to the ceratobranchials; (4) second ceratobranchial modified for force transmission; (5) presence of a cylindrical muscle complex around the tongue; (6) juvenile otic capsule configuration. The synapomophry for *Batrachoseps* + *Nyctanolis* + other bolitoglossine genera was reduction in number of caudosacral vertebrae to two. For the supergenus *Bolitoglossa* (*Nyctanolis* + other genera of bolitoglossines, excluding *Batrachoseps* and supergenus *Hydromantes*), they suggested that having the tail base with complex of breakage specializations was synapomorphic and for the supergenus *Bolitoglossa* excluding *Nyctanolis* they suggested that fused maxillae was a synapomorphy.

As noted above, in 2004–2005 three studies appeared that transformed our understanding of plethodontid relationships (Mueller et al., 2004; Chippindale et al., 2004; Macey, 2005). Although there are three relevant analyses, there are only two data sets. Mueller et al. (2004; fig. 9) presented a Bayesian analysis of complete mtDNA genomes; this data set was reanalyzed by parsimony and extensively discussed by Macey (2005; fig. 10). Another data set and analysis of combined morphology and DNA sequence evidence was provided by Chippindale et al. (2004; fig. 11).

All three studies suggested strongly not only that Plethodontinae (as traditionally understood) is paraphyletic with respect to Desmognathinae, but that the traditional view of plethodontid relationships was largely mistaken, presumably due in part to the special pleading for particular characters that underpinned the older system of subfamilies and tribes. Mueller et al. (2004) found that all three of the traditionally recognized plethodontine tribes, Bolitoglossini, Hemidactyliini, and Plethodontini, are polyphyletic. Chippindale et al. (2004) found Hemidactyliini and Plethodontini to be polyphyletic, with Bolitoglossini insufficiently sampled to test its monophyly rigorously. Macey (2005; fig. 10) also rejected the monophyly of Bolitoglossini and Hemidactyliini, in his reanalysis of the data of Mueller et al. (2004). Mueller et al. (2004; fig. 9) placed *Hemidactylium* as the sister taxon of *Batrachoseps* (a bolitoglossine) and the remaining hemidactyliines as the sister of a group of bolitoglossines (excluding *Hydromantes* and *Speleomantes*). Chippindale et al. (2004; fig. 11) considered *Hemidactylium* to be the sister taxon of all other bolitoglossines and hemidactyliines, and the remaining hemidactyliines to form the sister taxon of *Hemidactylium* + bolitoglossines (*Hydromantes* and *Speleomantes* not analyzed).

Chippindale et al (2004; fig. 11) provided a new taxonomy, recognizing a newly formulated Plethodontinae (including Plethodontini and Desmognathinae of the older tax-

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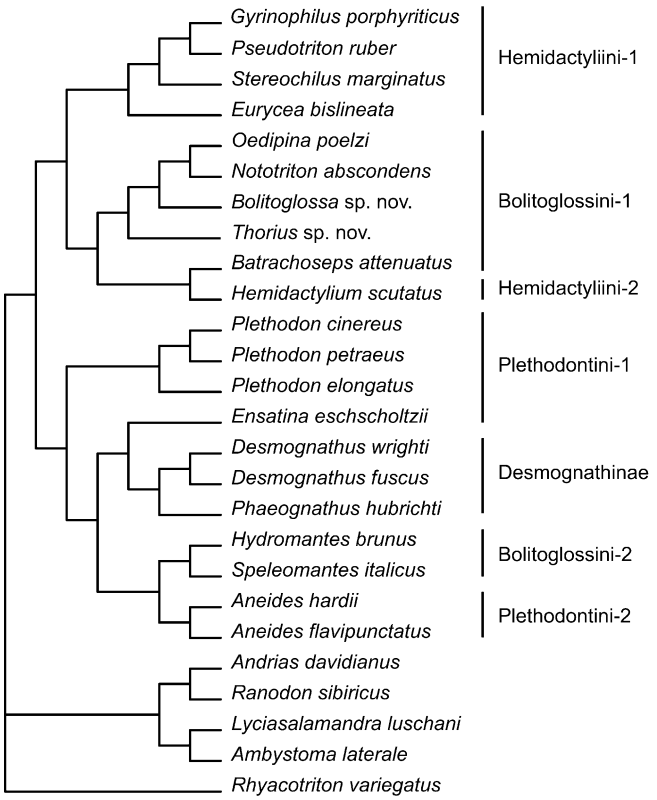

Fig. 9. Tree of Plethodontidae by Mueller et al. (2004), with the traditional taxonomic assignments (Desmognathinae + tribes of Plethodontinae; Wake, 1966) placed on the right, with taxonomic fragments numbered for clarity. The generic taxonomy was updated to reflect name changes of former *Salamandra luschani* to *Lyciasalamandera* (Veith and Steinfartz, 2004) and *Hydromantes italicus* to *Speleomantes*. The results reflect a Bayesian analysis of entire mt DNA genomes (number of informative sites not stated, but analyzed fragments totalled 14,040 bp), with control region and ambiguously alignable region excluded. Sequences were aligned with default costs of GCG v. 10.3 (Accelrys, San Diego; cost of 8 for gap creation and extension cost of 2) and subsequently adjusted manually. It was not stated whether gaps were treated as evidence or as missing data.

onomy). The sister taxon of Plethodontinae was not named in their taxonomy, the component parts being named Hemidactyliinae (for *Hemidactylium* alone), Spelerpinae (for the remainder of the old Hemidactyliini), and Bolitoglossinae (identical in content to the old Bolitoglossini, these authors not having studied *Hydromantes* sensu lato). Mueller et al. (2004), followed by Macey (2005), showed that *Hydromantes* (in the sense of including *Speleomantes*) is not imbedded in Bolitoglossini, as previously supposed, but is imbedded in Plethodontinae. Macey (2005) arrived at the same taxonomy as Chippindale et al. (2004), although Macey (2005) placed *Hemidactylium* (Hemidactyliinae) as the sister taxon of the remaining plethodontids.

Clearly, the analyses of mtDNA-sequence data by Mueller et al. (2004) and Macey (2005) and of nuDNA, mtDNA, and morphology by Chippindale et al. (2004) [5] are

[5] The Bayesian analysis of plethodontid relationships presented by Min et al. (2005) was based on a subset of the data provided by Chippindale et al. (2004) and Wiens et al. (2005), with the addition of sequences of *Karsenia koreana* and *Hydromantes brunus*. Because that analysis rests on a smaller amount of data than the earlier studies and was performed solely to place the newly-discovered *Karsenia* (as the sister taxon of *Aneides* + desmognathines), we restrict our comments about this paper to the placement of *Karsenia*.

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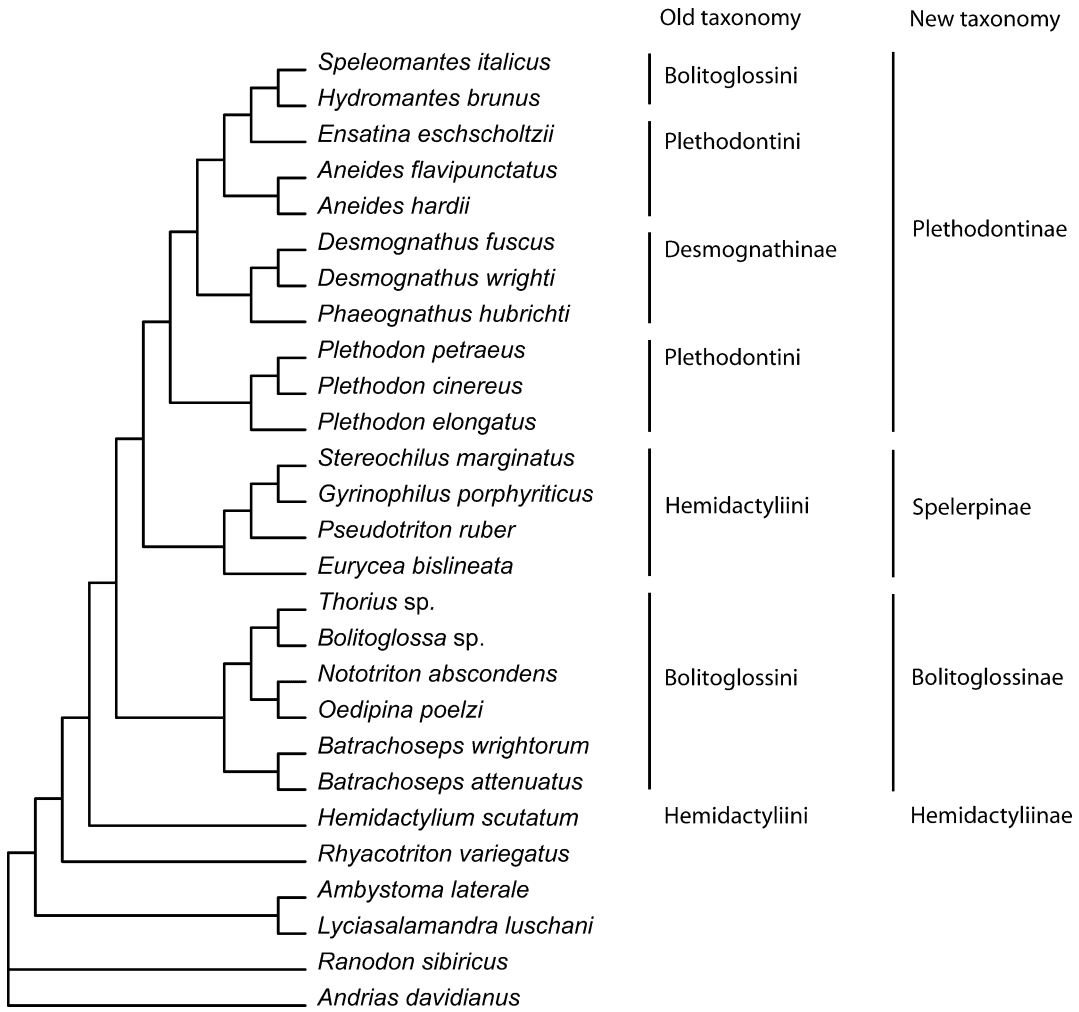

Fig. 10. Parsimony tree of Plethodontidae by Macey (2005), a reanalysis of entire mt DNA genome sequence data provided by Mueller et al. (2004). On right are the traditional taxonomy and Macey's revised subfamilial taxonomy, which is substantially identical to that suggested by Chippindale et al. (2004; fig. 11). The generic taxonomy is updated to reflect name changes of former *Salamandra luschani* (Veith and Steinfartz, 2004) and *Hydromantes italicus*.

strongly discordant with previous (and more limited) morphological and molecular results. Because of the timing of the appearance of these papers, our selection of taxa was chosen to address the older, more traditional view but may provide a weak test of the new view of plethodontid phylogeny and taxonomy.

We included in our analysis *Hemidactylium scutatum* (Hemidactyliinae) as well as the more ''typical'' hemidactyliines (Spelerpinae of Chippindale et al., 2004, and Macey, 2005): *Eurycea wilderae* and *Gyrinophilus porphyriticus*.

Of the new Plethodontinae (composed of former Desmognathinae, Plethodontini, and supergenus *Hydromantes* of Bolitoglossini) we sampled broadly. We included one species of western *Plethodon*, *P. dunni*, and one species of eastern *Plethodon*, *P. jordani*. We also included *Aneides hardii* and *Ensatina eschscholtzii*. Mueller et al. (2004), based on

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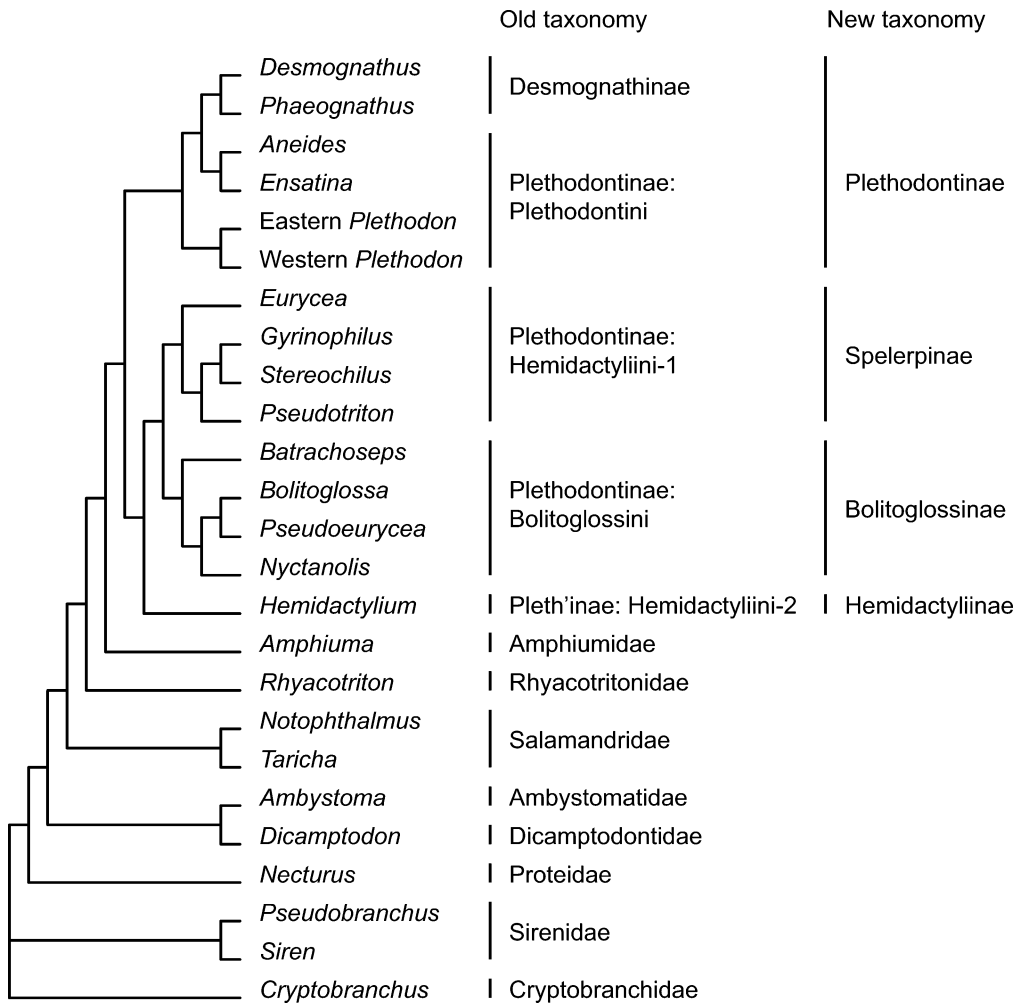

Fig. 11. Tree of Plethodontidae suggested by Chippindale et al. (2004) based on parsimony analysis of 104 transformation series of morphology and 1,493 informative sites of nu DNA (RAG-1) and mt DNA (cytochrome *c* and ND4a). On the right (left to right) are the old taxonomy of plethodontids and the taxonomy recommended by Chippindale et al. (2004). Sequences were aligned manually with only single-codon indels; gaps were considered missing data in the analysis.

analysis of mtDNA, rejected the monophyly of Plethodontini, placing *Ensatina* as the sister taxon of desmognathines. (In a parsimony analysis of the same data, Macey, 2005, placed *Ensatina* as the sister taxon of *Hydromantes*.) The monophyly of *Plethodon*, in particular, is controversial, with some authors (e.g., Larson et al., 1981; Mahoney, 2001) finding the western species to be closer to *Aneides* to the exclusion of eastern species, and others (e.g., Chippindale et al., 2004; Mueller et al., 2004; Macey, 2005) finding *Plethodon* and *Aneides* to be rather distantly related. We bracketed the diversity (Titus and Larson, 1996) of desmognathines (the pre-2004 Desmognathinae) by sampling *Phaeognathus hubrichti*, *Desmognathus quadramaculatus*, and *D. wrighti*. Of the supergenus *Hydromantes*, formerly in Bolitoglossini, we sampled *Hydromantes platycephalus* and *Speleomantes italicus*.

Of Bolitoglossinae we sampled 11 of the 14 nominal genera: supergenus *Batrachoseps* (*B. attenuatus* and *B. wrightorum*), and su-

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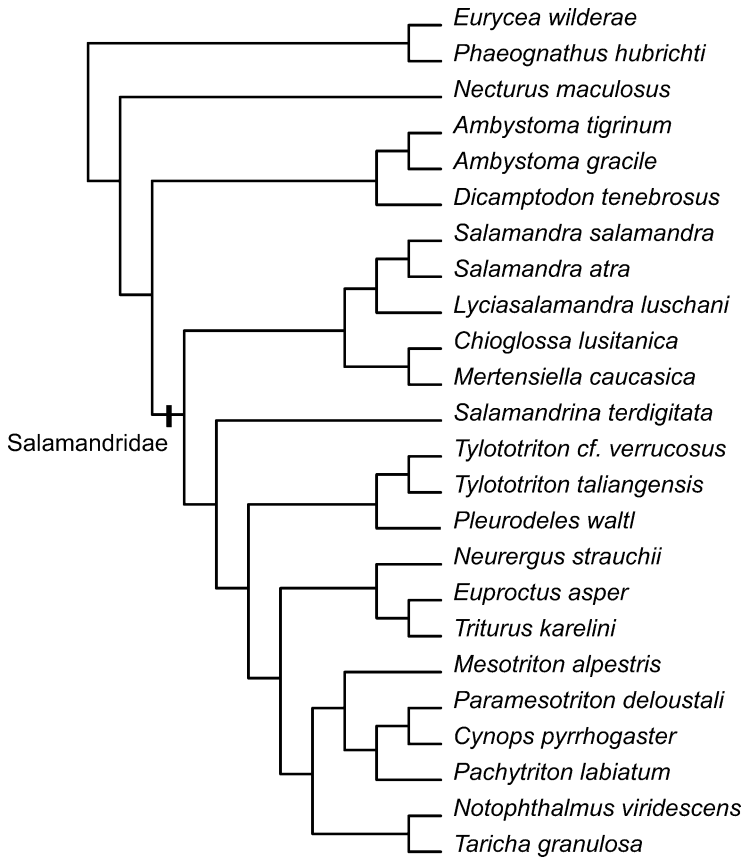

Fig. 12. Salamandrid relationships suggested by Titus and Larson (1995) based on a parsimony analysis of 44 morphological character transformations and 431 informative sites of ca. 1.8 kb of the 12S and 16S mt rRNA and $tRNA^{Val}$ fragments of mtDNA. Sequence alignment was done using MALIGN (W.C. Wheeler and Gladstein, 1992) with equal weighting of transversions and transitions and a gap penalty cost of 6. Sequence data and morphology in parsimony analysis had equal costs and gaps were treated as evidence. The tree was rooted on *Eurycea* + *Phaeognathus*; tree length = 2,081. Generic names are updated to reflect the naming of *Lyciasalamandra* (Veith and Steinfartz, 2004) and the partition of *Triturus* into *Mesotriton*, *Lissotriton* (not studied by Titus and Larson, 1995), *and Triturus* (García-París et al., 2004b).

pergenus *Bolitoglossa* (*Bolitoglossa rufescens*, *Cryptotriton alvarezdeltoroi*, *Dendrotriton rabbi*, *Ixalotriton niger*, *Lineatriton lineolus*, *Nototriton abscondens*, *Oedipina uniformis*, *Parvimolge townsendi*, *Pseudoeurycea conanti*, and *Thorius* sp.).

SALAMANDRIDAE (18 GENERA, 73 SPECIES): Salamandridae is found more-or-less throughout the Holarctic, with the bulk of its phylogenetic and species diversity in temperate Eurasia. Salamandrids are characterized by strongly keratinized skin in adults (except for the strongly aquatic *Pachytriton*), in addition to two cranial characters (presence of a frontosquamosal arch and fusion of the premaxillaries [reversed in *Pleurodeles* + *Tylototriton*, and *Chioglossa*]).

Titus and Larson (1995) provided a phylogenetic tree on the basis of a study of mt rRNA and morphology data (fig. 12). Scholz (1995; fig. 13) obtained similar results on the basis of morphology and courtship behavior. Zacj and Arntzen (1999) also reported on phylogenetics of *Triturus*, showing (as did Titus and Larson, 1995) that it is composed of two groups: (1) *Triturus vulgaris* + *Tri-*

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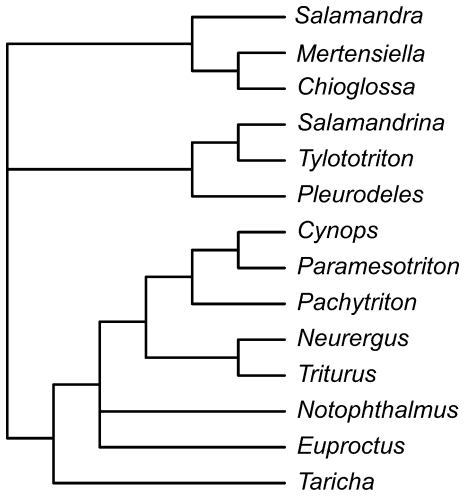

Fig. 13. Consensus of salamandrid relationships suggested by Scholz (1995) based on a parsimony analysis of 27 character transformations of morphology and behavior. *Triturus* in Scholz's sense included what is now *Lissotriton*, *Mesotriton*, and *Triturus* (García-París et al., 2004b).

turus marmoratus species groups; (2) and *Triturus cristatus* group, but not addressing its polyphyly. Steinfartz et al. (2002) reported on salamandrid phylogeny and substantiated the polyphyly of *Triturus* and of *Mertensiella*. Subsequently (and appearing after this analysis was completed), García-París et al. (2004b) partitioned the polyphyletic ''*Triturus*'' into three genera (*Triturus*, *Lissotriton*, and *Mesotriton*), based on the suggestions that (1) *Triturus*, sensu stricto (*Triturus cristatus* + *T. marmoratus* species groups) is most closely related to *Euproctus*; (2) *Mesotriton* (*Triturus alpestris*) is the sister taxon of a group composed of *Cynops*, *Paramesotriton*, and *Pachytriton*); and (3) *Lissotriton* (*Triturus vulgaris* species group) is of uncertain relationship to the other components, but does not form a monophyletic group with either *Mesotriton* or *Triturus*. García-París et al. (2004a: 602) also suggested that ongoing molecular work (evidence undisclosed), will show *Euproctus* to be paraphyletic and that *Triturus vittatus* will not be included within *Triturus*, the oldest available name for this taxon being *Ommatotriton* Gray, 1850.

We could not address these final issues, these appearing well after the manuscript was written, but we chose taxa that should allow the basic structure of salamandrid phylogeny to be elucidated. To bracket this suggested topology with appropriate taxonomic samples we chose *Euproctus asper*, *Neurergus crocatus*, *Notophthalmus viridescens*, *Pachytriton brevipes*, *Paramesotriton* sp., *Pleurodeles waltl*, *Salamandra salamandra*, *Taricha* sp., *Triturus cristatus*, and *Tylototriton shanjing*.

DICAMPTODONTIDAE (1 GENUS, 4 SPECIES): The North American *Dicamptodon* is related to Ambystomatidae (Larson and Dimmick, 1993; fig. 4) and, like them, some populations are neotenic (Nussbaum, 1976). Like other salamandroid salamanders they have internal fertilization and a suite of morphological features associated with forming and collecting spermatophores. *Dicamptodon* differs from Ambystomatidae in glandular features of the cloaca and in attaining a large size, but is considered by most workers as the sister taxon of Ambystomatidae (e.g., Larson et al., 2003—fig. 6; Wiens et al., 2005—fig. 7). We sampled both *Dicamptodon aterrimus* and *D. tenebrosus*.

AMBYSTOMATIDAE (1 GENUS, 31 SPECIES): North American Ambystomatidae is a morphologically compact family having internal fertilization via a spermatophore and the suite of morphological characters that support this attribute. Some populations exhibit neotenic aquatic adults.

The last summary of phylogeny within the group based on explicit evidence was presented by Shaffer et al. (1991; see also Larson et al., 2003), who provided a cladogram based on 32 morphological transformation series and 26 allozymic transformation series. The basal dichotomy in this tree is between *Ambystoma gracile* + *A. maculatum* + *A. talpoideum* on one hand, and all other species of *Ambystoma*, on the other. We were unable to obtain any of these three species, but we did sample *Ambystoma cingulatum*, *A. mexicanum* and *A. tigrinum*. *Ambystoma mexicanum* and *A. tigrinum* are very closely related, and *A. cingulatum* is distantly related to them. This is a weaker test of monophyly than we would have liked because it does not include *A. gracile*, *A. maculatum*, or *A. talpoideum*. Further, Larson et al. (2003) suggested that, in addition to *A. gracile*, *A. ma-*

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culatum, and *A. talpoideum*, *A. jeffersonianum*, *A. laterale*, *A. macrodactylum*, and *A. opacum* were likely to be outside of the taxa bracketed by our species, although the evidence for this was not presented.

ANURA

Frogs (32 families, ca. 372 genera, 5227 species) constitute the vast majority (88%) of living species of amphibians and the bulk of their genetic, physiological, ecological, and morphological diversity. Despite numerous studies that point towards its deficiencies (e.g. Kluge and Farris, 1969; Lynch, 1973; Sokol, 1975, 1977; Duellman and Trueb, 1986; Ruvinsky and Maxson, 1996; Maglia, 1998; Emerson et al., 2000; Maglia et al., 2001; Scheltinga et al., 2002; Haas, 2003; Roelants and Bossuyt, 2005; San Mauro et al., 2005; Van der Meijden et al., 2005), the current classification continues in many of its parts to reflect sociological conservatism and the traditional preoccupation with groupings by subjective impressions of overall similarity; special pleading for characters considered to be of transcendent importance; and notions of ''primitive'', ''transitional'', and ''advanced'' groups instead of evolutionary propinquity. Understanding of frog relationships remains largely a tapestry of conflicting opinion, isolated lines of evidence, unsubstantiated assertion, and unresolved paraphyly and polyphyly. Indeed, the current taxonomy of frogs is based on a relatively small sampling of species and in many cases the putative morphological characteristics of major clades within Anura are overly-generalized, overly-interpreted, and reified through generations of literature reviews (e.g., Ford and Cannatella, 1993), of which this review is presumably guilty as well. This general lack of detailed understanding of anuran relationships has been exacerbated by the explosive discovery of new species in the past 20 years.

Currently, the most widely cited review of frog phylogeny is Ford and Cannatella (1993; fig. 14), which provided a narrative discussion of the evidence for a novel view of frog phylogeny without providing all of the underlying data from which this discussion was largely derived. The result was that the extent of character conflict within their data set was never adequately exposed. More recently, Haas (2003; fig. 15) provided a discussion of frog evolution, based primarily on new larval characters. Haas did, however, exclude several of the adult characters included by Ford and Cannatella (1993) as insufficiently characterized or assayed. More recently, important discussions of phylogeny have been made in the context of DNA sequence studies (Roelants and Bossuyt, 2005—fig. 16; San Mauro et al., 2005—fig. 17) that will be cited throughout our review.

The monophyly of frogs (Anura) relative to other living amphibians has not been generally questioned[6] (although the universality of this taxon with respect to some fossil antecedent taxa has (e.g., Griffiths, 1963; Roĉek, 1989, 1990), and the number of morphological characters corroborating this monophyly is large—e.g., (1) reduction of vertebrae to 9 or fewer; (2) atlas with a single centrum; (3) hindlimbs significantly longer than forelimbs, including elongation of ankle bones; (4) fusions of radius and ulna and tibia and fibula; (5) fusion of caudal vertebral segments into a urostyle; (6) fusion of hyobranchial elements into a hyoid plate; (7) presence of keratinous jaw sheaths and keratodonts on larval mouthparts; (8) a single median spiracle in the larva, a characteristic of the Type III tadpole (consideration of this as a synapomorphy being highly contingent on the preferred overall cladogram); (9) skin with large subcutaneous lymph spaces; and (10) two m. protractor lentis attached to lens, based on very narrow taxon sampling (Saint-Aubain, 1981; Ford and Cannatella, 1993).

Haas (2003) suggested (fig. 15) an additional 20 synapomorphies from larval morphology: (1) paired venae caudalis lateralis short; (2) operculum fused to abdominal wall; (3) m. geniohyoideus origin from ceratobranchials I–II; (4) m. interhyoideus posterior absent; (5) larval jaw depressors originate from palatoquadrate; (6) ramus maxillaris (cranial nerve V_2) medial to the m. le-

[6] Roček and Vesely (1989) suggested a diphyletic origin of Anura based on a hypothesized nonhomology between the rostral plate of pipoid larvae and the cornua trabeculae of other anuran larvae. The developmental homology of these structures was later established (Olsson and Hanken, 1996; de Sá and Swart, 1999).

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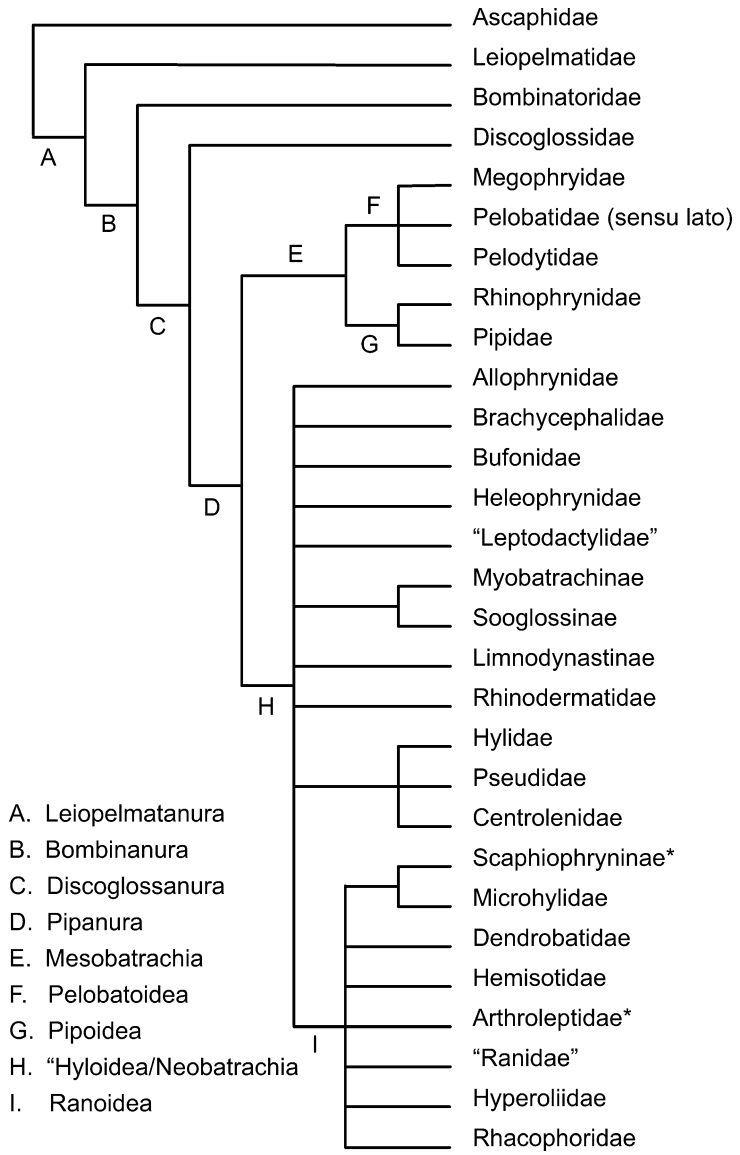

Fig. 14. Narrative tree of relevant anuran taxa by Ford and Cannatella (1993). A branch subtending Hylidae + Pseudidae in the original figure is collapsed per errata distributed with reprint. An asterisk was used by these authors to denote a metataxon, and quotation marks to denote nonmonophyly.

vator manidbulae longus; (7) ramus mandibularis (cranial nerve V_3) anterior (dorsal) to the m. levator mandibulae longus; (8) ramus mandibularis (cranial nerve V_3) anterior (dorsal) to the externus group; (9) cartilago labialis superior (suprarostral cartilage) present; (10) two perilymphatic foramina; (11) hypobrachial skeletal parts as planum hypobranchiale; (12) processus urobranchialis short, not reaching beyond the hypobranchial plates; (13) commisura proximalis I present; (14) commisura proximalis II present; (15) commisura proximalis III present; (16) ceratohyal with diarthrotic articulation present, medial part broad; (17) cleft between hyal arch and branchial arch I closed; (18)

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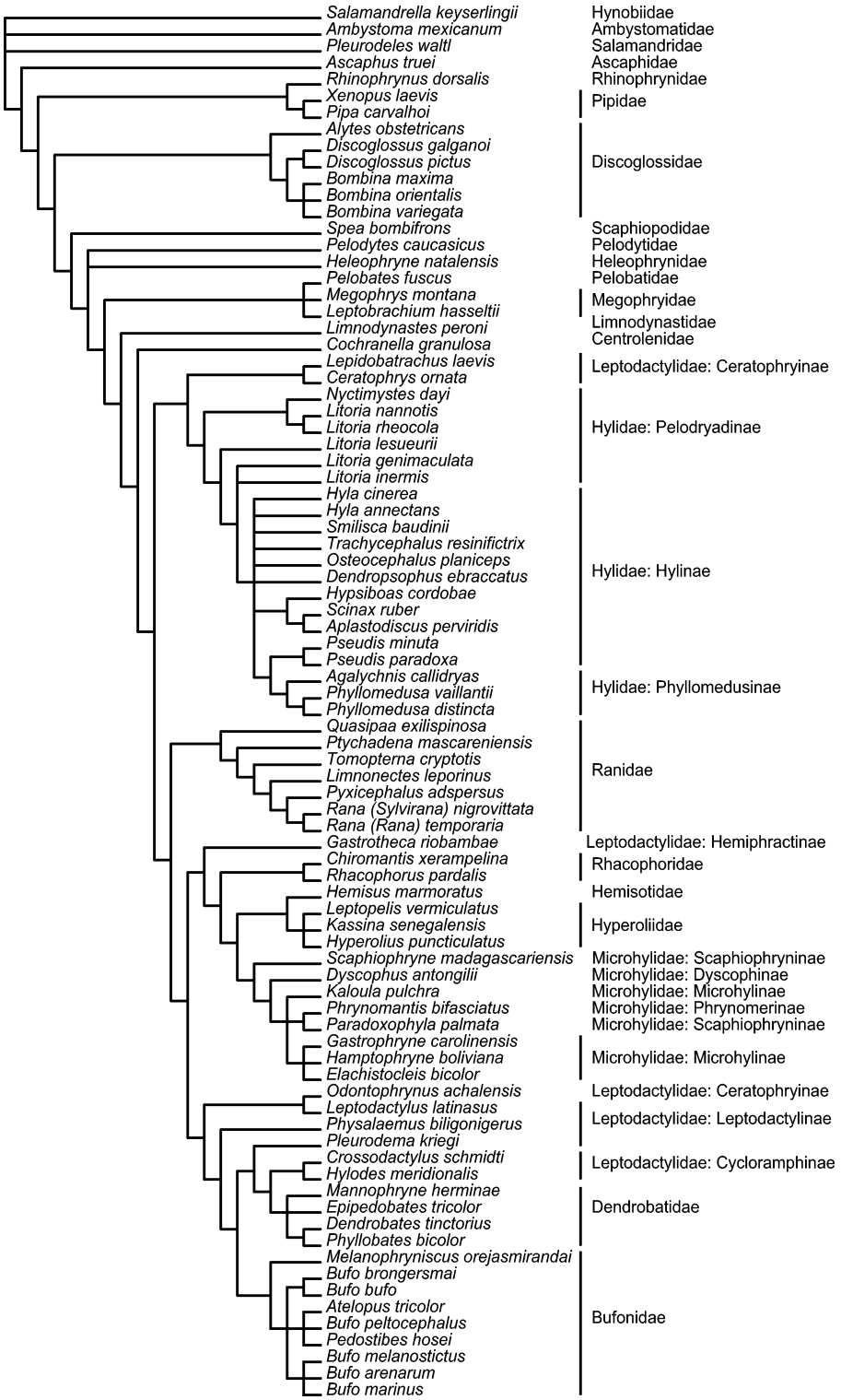

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ligamentum cornuquadratum present; (19) ventral valvular velum present; (20) branchial food traps present. Haas also suggested that the following were synapomorphies not mentioned as such by Ford and Cannatella (1993): (1) amplexus inguinal; (2) vertical pupil shape; (3) clavicle overlapping scapula anteriorly; and (4) cricoid cartilage as a closed ring.

''Primitive'' Frogs

We first address the groups that are sometimes referred to collectively as Archaeobatrachia (Duellman, 1975) and traditionally are considered ''primitive'', even though the component taxa have their own apomorphies and the preponderance of evidence suggests strongly that they do not form a monophyletic group (Roelants and Bossuyt, 2005; San Mauro et al., 2005).

Ascaphidae (1 genus, 2 species): Ford and Cannatella (1993) considered North American *Ascaphus* (Ascaphidae) to be the sister taxon of all other frogs (fig. 14), although on the basis of allozyme study by Green et al. (1989) and, more recently, Roelants et al. (2005; fig. 16) and San Mauro et al. (2005; fig. 17), on the basis of evidence from DNA sequences, suggested that Ascaphidae + Leiopelmatidae forms a monophyletic group. Báez and Basso (1996) presented a phylogenetic analysis designed to explore the relationships of the fossil anurans *Vieraella* and *Notobatrachus* with the extant taxa *Ascaphus*, *Leiopelma*, *Bombina*, *Alytes*, and *Discoglossus*. Despite their restricted taxon sampling, their results also support the monophyly of *Ascaphus* + *Leiopelma*, although the authors considered their evidence weak for reasons of difficulty in evaluating characters.

Green and Cannatella (1993) did not find a monophyletic *Ascaphus* + *Leiopelma*. *Ascaphus* and *Leiopelma* share the presence of a m. caudalipuboischiotibialis and nine presacral vertebrae (Ford and Cannatella, 1993), both considered plesiomorphic within Anura[7]. *Ascaphus* has an intromittant organ (apomorphic) in males and a highly modified torrent-dwelling tadpole. The vertebrae are amphicoelous and ectochordal (Nicholls, 1916; Laurent, 1986), presumably plesiomorphic at this level of generality. Our sampled species for this taxon is *Ascaphus truei*, one of the two closely-related species.

Leiopelmatidae (1 genus, 4 species): Isolated in New Zealand, Leiopelmatidae, like Ascaphidae, is a generally very plesiomorphic group of frogs. Nevertheless, it possesses apomorphies, such as ventral inscription ribs, found nowhere else among frogs (Noble, 1931; Laurent, 1986; Ford and Cannatella, 1993). Unlike *Ascaphus*, *Leiopelma* does not have feeding larvae (Archey, 1922; Altig and McDiarmid, 1999; Bell and Wassersug, 2003). As in Ascaphidae, the vertebrae are amphicoelous and ectochordal with a persistent notochord (Noble, 1924; Ritland, 1955) and both vocal sacs and vocalization are absent (Noble and Putnam, 1931).

Ford and Cannatella (1993) suggested that Leiopelmatidae is the nearest relative of all other frogs (excluding Ascaphidae) and listed five synapomorphies in support of this grouping (their Leiopelmatanura): (1) elongate arms on the sternum; (2) loss of the ascending process of the palatoquadrate; (3) sphenethmoid ossifying in the anterior position; (4) exit of the root of the facial nerve from the braincase through the facial foramen, anterior to the auditory capsule, rather than via the anterior acoustic foramen into the auditory capsule; (5) palatoquadrate ar-

[7] Ritland (1955) suggested the possibility that the m. caudalipuboischiotibialis is not homologous with the tail-wagging muscles of salamanders but instead, an accessory coccygeal head of the m. semimembranosus. In that case, the character would be judged to be a synapomorphy of *Ascaphus* + *Leiopelma*, rather than a symplesiomorphy shared by those taxa.

←

Fig. 15. Anuran relationships suggested by Haas (2003). Consensus of 144 equally parsimonious trees discovered by parsimony analysis of 151 character-transformation series (excluding his morphometric characters 12, 83, 116, and 117, as well as 102) of larval and adult morphology and reproductive mode (ci = 0.31; ri 0.77). Taxonomy is updated to reflect subsequent publications.

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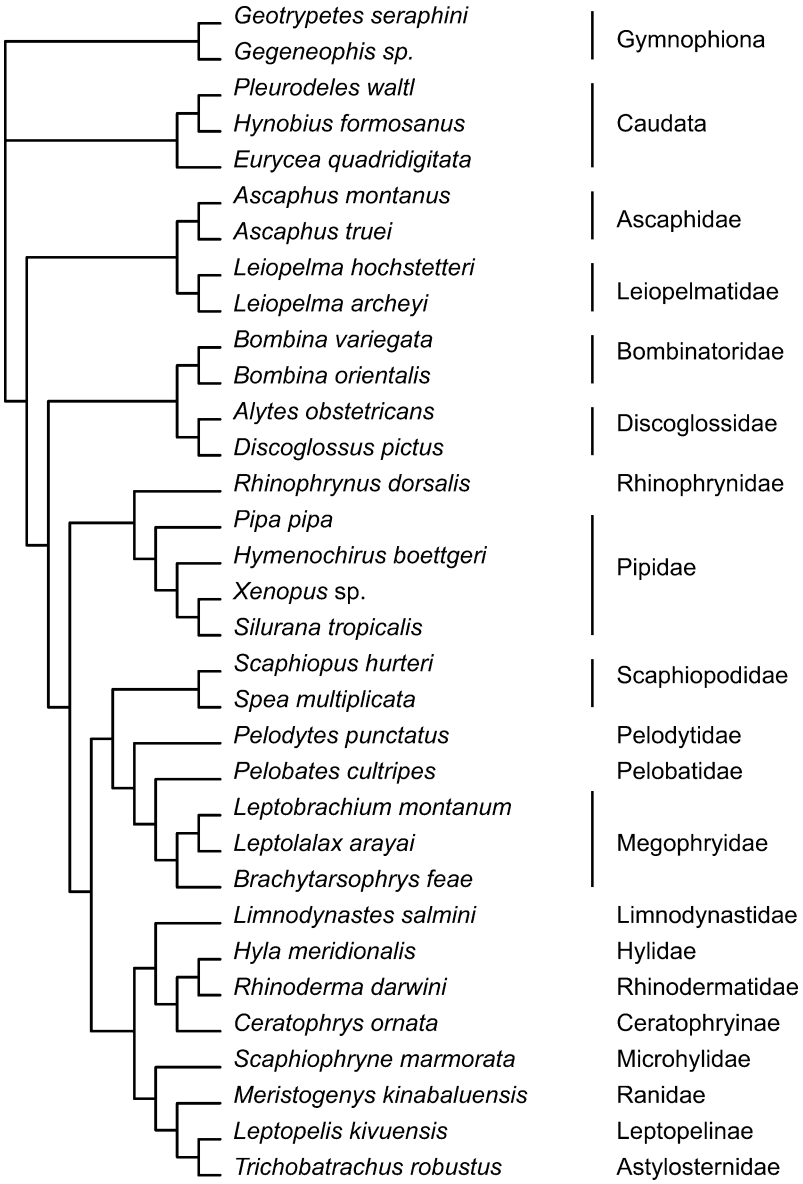

Fig. 16. Tree of amphibians provided by Roelants and Bossuyt (2005). This tree reflects a maximum-likelihood analysis of 3,963 aligned positions (2,022 variable and 1,788 parsimony-informative) of three protein-coding nuDNA genes (ca. 555 bp of RAG-1, ca. 675 bp of CXCR-4, ca. 1280 bp of NCX-1) and ca. 1940 bp of the mitochondrial genome (part of 16S and $tRNA^{Met}$, and all of $tRNA^{Leu}$, $tRNA^{Ile}$, ND-1, and $tRNA^{Gln}$). Alignment was done initially using ClustalX (Thompson et al., 1997; presumably applying default cost functions) followed by a probabilistic method implemented in the program ProAlign (Löytynoja and Milinkovitch, 2003) and, in the case of 16S and tRNA seqments, subsequently modified manually, guided by models of secondary structure for *Xenopus*. Gaps were treated as missing data and ambiguously aligned sequences were excluded. The model of evolution assumed was GTR + Γ + I.

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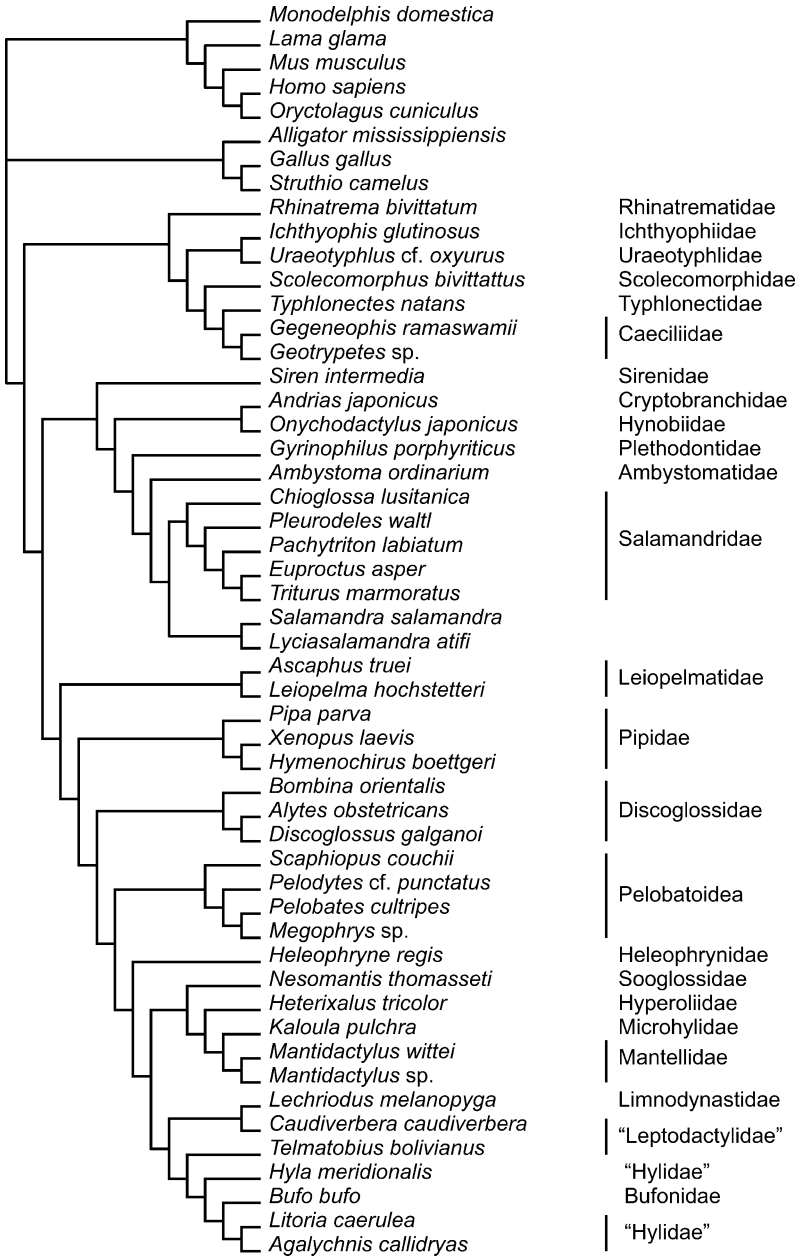

Fig. 17. Tree of amphibians provided by San Mauro et al. (2005). This tree reflects a maximum-likelihood analysis of 1,368 bp of the nuclear protein-coding gene RAG-1, assuming the GTR + Γ + I substitution model (as suggested by ModelTest v. 3.6; Posada and Crandall, 1998). Sequence alignment was made manually with only one gap excluded from analysis.

ticulates with the braincase via a pseudobasal process rather than a basal process.

Characters 4 (facial nerve exit) and 5 (palatoquadrate articulation) are polarized with respect to salamanders; the other three characters were likely polarized on the assumption that *Ascaphus* is plesiomorphic and the sister taxon of remaining frogs, thereby pre-

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supposing the results, although this was not stated. With respect to character 1 (the triradiate sternum), the parsimony cost of this transformation on the overall tree is identical if Ascaphidae and Leiopelmatidae are sister taxa and Bombinatoridae and Discoglossidae are sister taxa. The remaining characters, 2 and 3, were not discussed with respect to outgroups or reversals in the remainder of Ford and Cannatella's tree, implying that they are unreversed and unique.

With *Ascaphus*, *Leiopelma* shares the apomorphy of columella not present (N.G. Stephenson, 1951). Haas (2003) did not include *Leiopelma* in his analysis of exotrophic larval morphology because of their endotrophy. We included in our analysis *Leiopelma archeyi* and *L. hochstetteri*, which bracket the phylogenetic diversity of Leiopelmatidae (E.M. Stephenson et al., 1974), although it is not sufficient to test hypotheses of the evolution of direct development (exoviviparity in this case; Thibaudeau and Altig, 1999) within *Leiopelma*.

DISCOGLOSSIDAE[8] (2 GENERA, 12 SPECIES) AND BOMBINATORIDAE (2 GENERA, 10 SPECIES): Ford and Cannatella (1993; fig. 14) suggested that *Bombina* + *Barbourula* forms the sister taxon of all other frogs, exclusive of Leiopelmatidae and Ascaphidae, although recent molecular evidence (Roelants and Bossuyt, 2005; fig. 16) placed Bombinatoridae and Discoglossidae in the familiar position of sister taxa.

Ford and Cannatella's (1993) arrangement (fig. 14; i.e., paraphyly of Bombinatoridae + Discoglossidae) required a partition of the traditionally recognized Discoglossidae (sensu lato) to place *Bombina* and *Barbourula* in their own family, Bombinatoridae. In their system, Bombinatoridae + its sister taxon (all frogs excluding Leiopelmatidae and Ascaphidae) was named Bombianura. Bombianura is corroborated by four synapomorphies: (1) fusion of the halves of the sphenethmoid; (2) reduction to eight presacral vertebrae; (3) loss of the m. epipubicus (regained in *Xenopus*); and (4) loss of the m. caudalipuboischiotibialis. In addition, Abourachid and Green (1999) noted that although *Leiopelma* and *Ascaphus* do hop, they swim with alternating sweeps of the hind legs (the presumably plesiomorphic condition), unlike those in Bombianura, which swim with coordinated thrusts of the hind limbs, a likely synapomorphy.

Bombinatoridae was considered (Ford and Cannatella, 1993) to have as synapomorphies (1) expanded flange of the quadratojugal, and (2) presence of endochondral ossifications in the hyoid plate (both unreversed). We sampled four species of *Bombina*: *B. bombina*, *B. microdeladigitora*, *B. orientalis*, and *B. variegata*. The genus may be monophyletic, but no rigorous phylogenetic study has been performed so far, and paraphyly of *Bombina* with respect to *Barbourula* remains an open question. We could not obtain tissues of *Barbourula* so its phylogenetic position will remain questionable. *Bombina* has aquatic feeding tadpoles, but larvae of *Barbourula* are unknown and are suspected to be endotrophic (Altig and McDiarmid, 1999). Discoglossidae (sensu stricto) also has free-living aquatic tadpoles (Boulenger, 1892 "1891"; Altig and McDiarmid, 1999).

Ford and Cannatella (1993; fig. 14) also posited a taxon, Discoglossanura, composed of Discoglossidae (sensu stricto) and the remaining frogs (exclusive of Ascaphidae, Leiopelmatidae, and Bombinatoridae) which they suggested to be monophyletic on the basis of two synapomorphies: (1) bicondylar sacrococcygeal articulation; and (2) episternum present. Monophyly of Discoglossidae (sensu stricto) was supported by their possession of (1) V-shaped parahyoid bones (also in *Pelodytes*) and (2) a narrow epipubic cartilage plate.

Haas (2003; fig. 15) presented a cladogram that is both deeply at variance with the relationships suggested by Ford and Cannatella (1993) and, at least with respect to this part of their cladogram, consistent with the molecular evidence presented by Roelants and Bossuyt (2005; fig. 16). Haas (2003) presented six morphological synapomorphies of Discoglossidae + Bombinatoridae (as Discoglossidae, sensu lato) and rejected Discoglossidae (sensu Ford and Cannatella) as paraphyletic, placing *Alytes* as the sister taxon

[8] Sanchíz (1998) and Dubois (2005) noted that the name with priority for this taxon is Alytidae. However, to reflect the relevant literature we retain the name Discoglossidae in this section.

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of the remaining members of Discoglossidae + Bombinatoridae. Synapomorphies of Haas' Discoglossidae are: (1) origin of m. intermandibularis restricted to the medial face of the cartilago meckelii; (2) larval m. levator mandibulae externus present as two bundles (profundus and superficialis); (3) posterior processes of pars alaris double; (4) cartilaginous roofing of the cavum cranii present only as taenia traversalis; (5) vertebral centra formation epichordal; and (6) processus urobranchialis absent. Synapomorphies suggested by Haas (2003; fig. 15) for Discoglossidae, excluding *Alytes* are (1) epidermal melanocytes forming an orthogonal pattern; (2) advertisement call inspiratory; and (3) pupil an inverted drop-shape (triangular). Of Discoglossidae (sensu stricto), we sampled one species of *Alytes* (*A. obstetricans*) and two species of *Discoglossus* (*D. galganoi* and *D. pictus*). Discoglossidae and Bombinatoridae show opisthocoelous and epichordal vertebrae according to Mookerjee (1931), Griffiths (1963), and Haas (2003). Kluge and Farris (1969: 23) suggested that vertebral development in *Discoglossus pictus* is perichordal, although Haas (2003) reported it as epichordal.

Roelants and Bossuyt (2005; fig. 16) and, with denser taxon sampling, San Mauro et al. (2005; fig. 17) provided substantial amounts of DNA evidence suggesting strongly that Bombinatoridae + Discoglossidae forms a monophyletic group, thereby rejecting Discoglossanura, Leiopelmatanura, and Bombianura of Ford and Cannatella (1993).

''Transitional'' Frogs

The following few groups traditionally have been considered ''transitional'' from the primitive to advanced frogs, even though one component taxon in particular, Pipidae, is highly apomorphic in several ways. The monophyly of this collection of families was supported by some authors (e.g., Ford and Cannatella, 1993; García-París et al., 2003), but recent morphological (e.g., Haas, 2003; Pugener et al., 2003) and DNA sequence evidence (Roelants and Bossuyt, 2005; San Mauro et al., 2005) does not support its monophyly.

Ford and Cannatella (1993; fig. 14) suggested this group, Mesobatrachia, to be monophyletic and composed of Pipoidea (Pipidae + Rhinophrynidae) and Pelobatoidea (Pelobatidae [including Scaphiopodidae] + Megophryidae + Pelodytidae). They provided four synapomorphies for their Mesobatrachia: (1) closure of the frontoparietal fontanelle by juxtaposition of the frontoparietal bones (not in *Pelodytes* or *Spea*); (2) partial closure of the hyoglossal sinus by the ceratohyals; (3) absence of the taenia tecti medialis; and (4) absence of the taenia tecti transversum.

Pugener et al. (2003) rejected Mesobatrachia and suggested three synapomorphies for a clade composed of all frogs excluding pipoids. (This statement is based on Pugener et al.'s, 2003, figure 12; they provided no comprehensive list of synapomorphies.)

Haas (2003; fig. 15), in contrast, suggested a number of characters that placed Pipoidea as the sister taxon of all frogs except Ascaphidae (although he did not study *Leiopelma*). This is consistent with the molecular studies of San Mauro et al. (2005; fig. 17). Haas' characters also placed Pelobatoidea (as represented by his exemplars) as a paraphyletic series of *Spea*, (*Pelodytes*, *Heleophryne*), and *Pelobates* + *Megophrys* + *Leptobrachium*, ''between'' Discoglossidae (sensu lato) and *Limnodynastes* on a pectinate tree. This is inconsistent with the results of Roelants and Bossuyt (2005). Larval characters suggested by Haas (2003) to support the group of all frogs exclusive of Ascaphidae and Pipoidea are (1) m. mandibulolabialis present; (2) upper jaw cartilages powered by jaw muscles; (3) larval m. levator mandibulae externus main portion inserts in upper jaw cartilages; (4) insertion of the larval m. levator mandibulae internus in relation to jaw articulation lateral; (5) m. levator mandibulae longus superficialis and profundus in two bundles; (6) processus anterolateralis of crista parotica present; (7) processus muscularis present; (8) distal end of cartilago meckeli with stout dorsal and ventral processes forming a shallow articular fossa; and (9) ligamentum mandibulosuprarostrale present.

García-París et al. (2004b; fig. 18) presented mtDNA sequence evidence for the monophyly of Mesobatrachia although their

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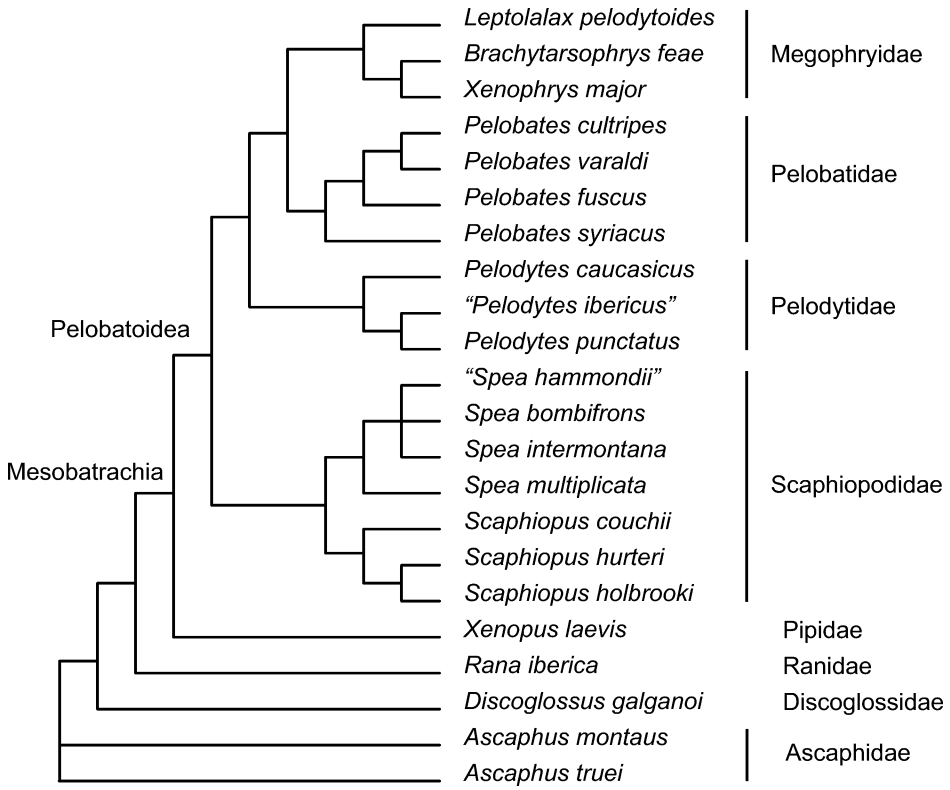

Fig. 18. Tree of Pelobatoidea and outgroups of García-París et al. (2003) based on 1,000 bp of two mitochondrial genes: cytochrome *c* and 16S rRNA. The sequences were aligned using Clustal X (Thompson et al., 1997) using default costs then manually modified based on published secondary-structure models of the 16S gene. Gaps were treated as missing data and data were analyzed under the assumption of the GTR + Γ substitution model, as suggested by ModelTest 3.06 (Posada and Crandall, 1998). The tree was rooted on *Ascaphus montanus* + *A. truei*. Quotation marks denote nonmonophyly.

outgroup sampling (which was limited to *Ascaphus truei*, *A. montanus*, *Discoglossus galganoi*, and *Rana iberica*) provided only a minimal test of this proposition. Even more recently, on the basis of more DNA sequence evidence and better sampling, Roelants and Bossuyt (2005; fig. 16) and San Mauro et al. (2005; fig. 17) found ''Mesobatrachia'' to have its elements in a paraphyletic series with respect to Neobatrachia. Roelants and Bossuyt (2005) found (Ascaphidae + Leiopelmatidae) + (Discoglossoidea + (Pipoidea + (Pelobatoidea + Neobatrachia))) and San Mauro et al. (2005) found Ascaphidae + Leiopelmatidae as the sister taxon of Pipoidea + (Discoglossoidea + (Pelobatidae + Neobatrachia)). In other words, their substantial difference is in Discoglossoidea (= Bombinatoridae + Discoglossidae) and Pipoidea changing places, with San Mauro et al.'s (2005) placement of Pipoidea agreeing with that of Haas (2003).

PIPOIDEA: Pipoidea (Pipidae + Rhinophrynidae) is clearly well corroborated as monophyletic but not clearly resolved with respect to its rather dense fossil record. Ford and Cannatella (1993; fig. 14) considered Pipoidea to be supported by five morphological synapomorphies: (1) lack of mentomeckelian bones; (2) absence of lateral alae of the parasphenoid; (3) fusion of the frontoparietals into an azygous element; (4) greatly enlarged otic capsule; and (5) tadpole with paired spiracles and lacking keratinized jaw sheaths and keratodonts (Type I tadpole). Haas (2003) added a substantial number of larval characters: (1) eye position lateral; (2) opercular canal and spiracles paired; (3) insertion

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of m. levator arcuum branchialium reaching medially and extending on proximal parts of ceratobranchial IV; (4) m. constrictor branchialis I absent; (5) m. levator mandibulae internus shifted anteriorly; (6) m. levator mandibulae longus originates exclusively from arcus subocularis; (7) posterolateral projections of the crista parotica with expansive flat chondrifications; (8) arcus subocularis with a distinct processus lateralis posterior projecting laterally from the posterior palatoquadrate; (9) articulation of cartilago labialis superior with cornu trabeculae fused into rostral plate; and (10) forelimb erupts out of limb pouch, outside of peribranchial space. In addition, recent DNA sequence data (Roelants and Bossuyt, 2005; fig. 16) strongly support a monophyletic group of Rhinophrynidae + Pipidae.

RHINOPHRYNIDAE (1 GENUS, 1 SPECIES): Tropical North American and Central American *Rhinophrynus dorsalis* is a burrowing frog with a number of apomorphies with respect to its nearest living relative, Pipidae: (1) division of the distal condyle of the femur into lateral and medial condyles; (2) modification of the prehallux and distal phalanx of the first digit into a spade for digging; (3) tibiale and fibulare short and stocky, with distal ends fused; and (4) an elongate atlantal neural arch. In addition to the previous characters provided by Ford and Cannatella (1993; fig. 14), Haas (2003; fig. 15) provided (1) larval m. geniohyoideus absent; (2) larval m. levator mandibulae externus present in two bundles (profundus and superficialis); (3) ramus mandibularis (cranial nerve V_3) posterior (ventral) to m. levator mandibulae externus group; (4) endolymphatic spaces extend into more than half of the vertebral canal (presacral vertebrae 4 or beyond); (5) branchial food traps divided crescentrically; (6) cricoid ring with dorsal gap; and (7) urobranchial process very long. Available DNA sequence data (e.g., Roelants and Bossuyt, 2005) also suggest strongly that *Rhinophrynus* is the sister taxon of Pipidae. We sampled the single species in this taxon, *Rhinophrynus dorsalis*. Báez and Trueb (1997) noted that *Rhinophrynus* also has amphicoelous ectochordal vertebrae, as in Ascaphidae and Leiopelmatidae, which may be a synapomorphy of Rhinophrynidae at this level of generality.

PIPIDAE (5 GENERA, 30 SPECIES): South American and African Pipidae is a highly apomorphic group of bizarre, highly aquatic species. Ford and Cannatella (1993) provided 11 characters in support of its monophyly: (1) lack of a quadratojugal; (2) presence of an epipubic cartilage; (3) unpaired epipubic muscle; (4) free ribs in larvae; (5) fused articulation between the coccyx and the sacrum; (6) short, stocky scapula; (7) elongate septomaxillary bones; (8) ossified pubis; (9) a single median palatal opening of the eustachian tube; (10) lateral line organs in the adults; and (11) loss of tongue. Báez and Trueb (1997) added to this list (fossil taxa pruned by us for purposes of this discussion): (1) the possession of an optic foramen with a complete bony margin formed by the sphenethmoid; (2) anterior ramus of the pterygoid arises near the anteromedial corner of the otic capsule; (3) parasphenoid fused at least partially with the overlying braincase; (4) vomer without an anterior process if the bone is present; (5) mandible bears a broad-based, bladelike coronoid process along its posteromedial margin; (6) sternal end of the coracoid not widely expanded; (7) anterior ramus of pterygoid dorsal with respect to the maxilla; and (8) premaxillary alary processes expanded dorsolaterally. Haas (2003) provided 11 additional larval characters: (1) origin of the m. subarcualis rectus II–IV placed far laterally; (2) anterior insertion of m. subarcualis rectus II–IV on ceratohyal III; (3) commissurae craniobranchiales present; (4) arcus subocularis round in cross section; (5) one perilymphatic foramen; (6) vertebral centra formation epichordal; (7) processus urobranchialis absent; and (8) ventral valvular velum absent, as well as these additional characters of the adult: (9) advertisement call without airflow; (10) pupil shape round; and (11) pectoral girdle pseudofirmisternal.

On the basis of morphology, Cannatella and Trueb (1988; fig. 19A) considered the generic relationships to be *Xenopus* + (*Silurana* + ((*Hymenochirus* + *Pseudhymenochirus*) + *Pipa*)). Subsequently, de Sá and Hillis (1990; fig. 19B), on the basis of a combined analysis of morphology and mtDNA, proposed the arrangement *Hymenochirus*

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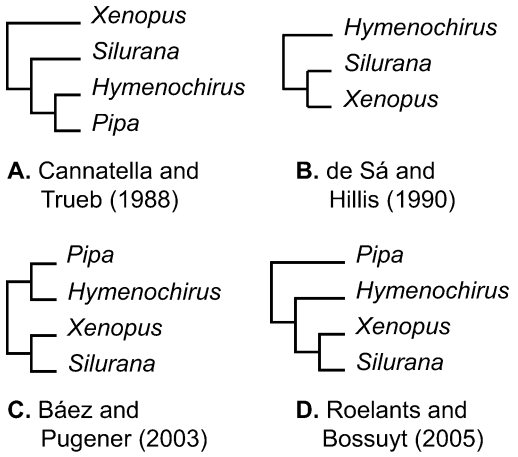

Fig. 19. Trees of intergeneric relationships within Pipidae: **A,** Analysis of Cannatella and Trueb (1988) based on 94 character transformations of morphology and 7 ingroup taxa (4 species of *Pipa* collapsed and *Pseudhymenochirus* considered a synonym of *Hymenochirus* in our figure for clarity of discussion). Monophyly of Pipidae was assumed as well as the sister-taxon relationship of Rhinophrynidae, with pelobatoids accepted as the second taxonomic outgroup (no tree statistics provided). **B,** Analysis of de Sá and Hillis (1990) based on 1.486kb of sequence from nuclear 18S and 28S rDNA and the morphological data from Cannatella and Trueb (1988). Sequences were aligned manually and analyzed under equally weighted parsimony; gaps were not treated as evidence. The tree was rooted on *Spea* (tree length counting only informative characters = 81, ci = 0.74). **C,** Parsimony tree of Báez and Pugener (2003) based on 49 characters of adult morphology, outgroups and fossils pruned for graphic purposes (the effect of this pruning on the number of characters being relevant is not known). The tree was rooted on *Rhinophrynus*, *Discoglossus*, and *Ascaphus*. (The length of original tree = 93, ci = 0.677.) **D,** Relevant section of tree from Roelants and Bossuyt (2005). See figure 16 for information on alignment and analysis.

(*Xenopus* + *Silurana*), and this was further corroborated by Báez and Trueb (1997) and Báez and Pugener (2003; who found [*Hymenochirus* + *Pipa*] + [*Xenopus* + *Silurana*]; fig. 19C), and suggested the following synapomorphies for Dactylethrinae (*Xenopus* + *Silurana*; fossil taxa pruned for this discussion): (1) scapula extremely reduced; (2) margins of olfactory foramina cartilaginous; (3) articular surfaces of the vertebral pre- and postzygopophyses bear sulci and ridges, with the prezygopophyses covering the lateral margin of the postzygopophysis; and (4) anterior process of the pterygoid laminae. They also suggested the following synapomorphies for Pipinae (*Pipa* + *Hymenochirus*) (fossil taxa pruned for purposes of this discussion): (1) wedge-shaped skull; (2) vertebrae with parasagittal spinous processes; (3) anterior position of the posterior margin of the parasphenoid; (4) possession of short coracoids broadly expanded at their sternal ends. In addition, they noted other characters of more ambiguous placement that optimize on this stem in this topology. Recent DNA sequence data (Roelants and Bossuyt, 2005; figs. 16, 19D), however, suggest a topology of *Pipa* + (*Hymenochirus* + (*Xenopus* + *Silurana*)).

We sampled three species of Dactylethrinae (Africa): *Silurana tropicalis*, *Xenopus laevis*, and *X. gilli*. From Pipinae (South America and Africa) we sampled *Hymenochirus boettgeri*, *Pipa pipa*, and *P. carvalhoi*. According to the cladogram provided by Trueb and Cannatella (1986), inclusion of either *Pipa parva* or *P. myersi* would have bracketed the phylogenetic diversity of *Pipa* somewhat better, although our sampling was adequate to test pipine (weakly), dactylethrine, and pipid monophyly, and the placement of Pipidae among other frogs.

PELOBATOIDEA: Pelobatoidea (Megophryidae, Pelobatidae, Pelodytidae, and Scaphiopodidae) has also been the source of considerable controversy. Haas (2003; fig. 15) did not recover the group as monophyletic (see the earlier discussion under Mesobatrachia), although Ford and Cannatella (1993) suggested that synapomorphies include the presence of a palatine process of the maxilla and ossification of the sternum into a bony style. Gao and Wang (2001) found Pelobatoidea to be more closely related to Discoglossidae on the basis of a limited analysis of fossil taxa. But, García-París et al. (2003; fig. 18) suggested that Pelobatoidea is the sister taxon of Pipoidea on the basis of a maximum-likelihood analysis of mtDNA evidence, although their outgroup structure was insufficient to provide a strong test of this proposition. (This position was effectively rejected by recent molecular evidence [Roelants and Bos-

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suyt, 2005; San Mauro et al., 2005; figs. 16, 17].)

Maglia (1998) also provided an analysis of Pelobatoidea, but because she constrained the monophyly of this group we are not sure how to interpret the distribution of her morphological evidence. Pugener et al. (2003) provided a cladogram based on morphology in which Pelobatoidea was recovered as monophyletic (and imbedded within Neobatrachia), but the underlying data were not provided. Roelants and Bossuyt (2005; fig. 16) suggested on the basis of DNA evidence that Pelobatoidea is the sister taxon of Neobatrachia, a result that is consistent with the older view of Savage (1973; cf. Noble, 1931). Dubois (2005) most recently treated all pelobatoids as a single family composed of four subfamilies, but this was merely a change in Linnaean rank without a concomitant change in understanding phylogenetic history.

PELOBATIDAE (1 GENUS, 4 SPECIES) AND SCAPHIOPODIDAE (2 GENERA, 7 SPECIES): Ford and Cannatella (1993; fig. 14) diagnosed Pelobatidae (including Scaphiopodidae in their sense) on the basis of (1) fusion of the joint between the sacrum and urostyle; (2) exostosed frontoparietals; and (3) presence of a metatarsal spade supported by a well-ossified prehallux. As noted earlier, Haas (2003; fig. 15) did not recover Pelobatidae (sensu lato) as monophyletic, instead placing *Spea* phylogenetically far from Pelobatidae, more distant than *Heleophryne*. More recently, García-París et al. (2003; fig. 18) provided molecular data suggesting that Pelobatidae and Scaphiopodidae are not each other's closest relatives. These results were augmented by the DNA sequence studies of Roelants and Bossuyt (2005) and San Mauro et al. (2005), both of which supported Scaphiopodidae as the sister taxon of Pelodytidae + (Pelobatidae + Megophryidae) (figs. 16, 17). All species have typical exotrophic aquatic larvae (Altig and McDiarmid, 1999). We sampled *Spea hammondii*, *Scaphiopus couchii*, and *S. holbrooki* from Scaphiopodidae, and *Pelobates fuscus* and *P. cultripes* from Pelobatidae.

PELODYTIDAE (1 GENUS, 3 SPECIES): Ford and Cannatella (1993; fig. 14) diagnosed Pelodytidae as having a fused astragalus and calcaneum (also found in some Centrolenidae; Sanchíz and de la Riva, 1993) and placed them in their Pelobatoidea as did García-París et al. (2003; fig. 18). Haas (2003), however, recovered *Pelodytes* in a polytomy with *Heleophryne*, Neobatrachia and *Megophrys* + *Pelobates* + *Leptobrachium*. We sampled *Pelodytes punctatus* as our exemplar of Pelodytidae. Larvae in pelodytids are also typical free-living exotrophs (Altig and McDiarmid, 1999).

MEGOPHRYIDAE (11 GENERA, 129 SPECIES): Ford and Cannatella (1993; fig. 14) diagnosed Megophryidae as having (1) a complete or nearly complete absence of ceratohyals in adults; (2) intervertebral cartilages with an ossified center; and (3) paddle-shaped tongue. Haas (2003; fig. 15) recovered a group consisting of the megophryids (*Leptobrachium* and *Megophrys* being his exemplars) and *Pelobates* but did not resolve the megophryids sensu stricto. Evidence for this megophryid + *Pelobates* clade is: (1) distal anterior labial ridge and keratodont-bearing row very short and median; (2) vena caudalis dorsalis present; (3) anterior insertion of the m. subarcualis rectus II–IV on ceratobranchial III; (4) m. mandibulolabialis superior present; (5) adrostral cartilage very large and elongate; and (6) cricoid ring with a dorsal gap.

Dubois (1980) and Dubois and Ohler (1998) suggested that megophryids form two subfamilies based on whether the larvae have funnel-shaped oral discs (Megophryinae), an apomorphy, or nonmodified oral discs (Leptobrachiinae), a plesiomorphy. Megophryinae includes *Atympanophrys*, *Brachytarsophrys*, *Megophrys*, *Ophryophryne*, and *Xenophrys*. Their Leptobrachiinae includes *Leptobrachella*, *Leptolalax*, *Leptobrachium*, *Oreolalax*, *Scutiger*, and *Vibrissaphora*. Delorme and Dubois (2001) presented a consensus tree (fig. 20) based on 54 transformation series of morphology (not including *Vibrissaphora*). This tree suggests that Megophryinae (*Megophrys montana* being their exemplar) is deeply imbedded within a paraphyletic Leptobrachiinae (the remaining megophryid exemplars being of this nominal subfamily); that *Scutiger* is composed of a paraphyletic subgenus *Scutiger* and a monophyletic subgenus *Aelurophryne*), and that

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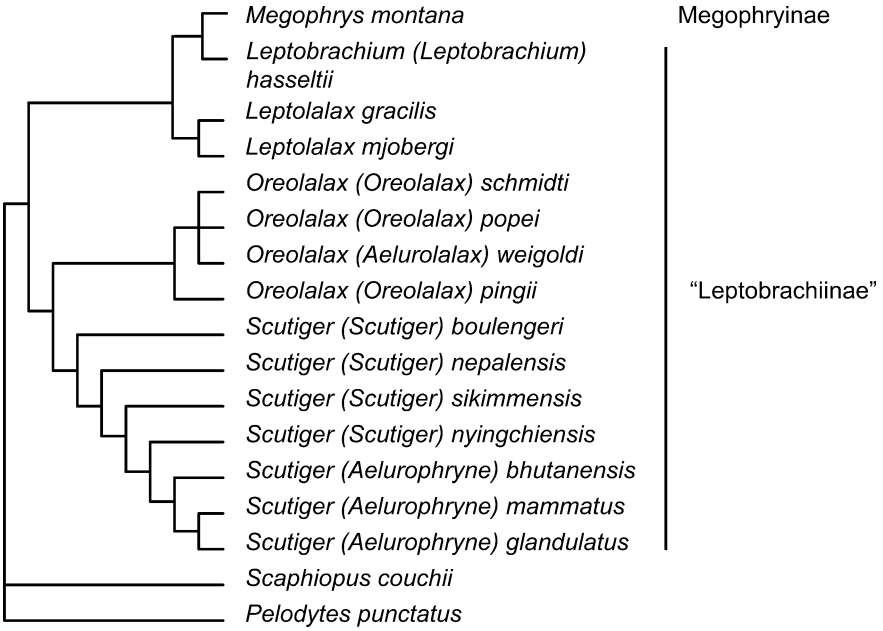

Fig. 20. Consensus of 12 equally parsimonious trees of selected members of Megophryidae of Delorme and Dubois (2001), rooted on *Scaphiopus* and *Pelodytes*. Underlying data were 54 transformation of morphology, rooted on *Pelodytes* and *Scaphiopus* (ci = 0.581; ri = 0.713). Although the tree and a list of the underlying character transformation were provided, no association was made between the character transformations and taxa or particular branches on the tree, rendering the analysis practically unrepeatable. Nominal subfamilies are noted on the right.

Oreolalax is composed of a paraphyletic subgenus *Oreolalax* and a monotypic subgenus *Aelurolalax*.

Within megophryines, Xie and Wang (2000) noted conflict between isozyme and karyological data regarding the monophyly of *Brachytarsophrys*, and also noted that *Atympanophrys* is only dubiously diagnosable from *Megophrys* or *Xenophrys*. They also suggested that *Xenophrys* may not be diagnosable from *Megophrys*.

Lathrop (1997) suggested that, among nominal leptobrachiines, *Leptolalax* has no identified apomorphies. Xie and Wang (2000) noted that *Oreolalax* is diagnosable from *Scutiger* on the basis of unique maxillary teeth and that *Vibrissaphora* has apomorphies (e.g., keratinized spines along the lips of adults), although the effect of recognizing *Oreolalax* and *Vibrissaphora* on the monophyly of *Scutiger* has not been evaluated. Similarly, the monophyly of *Leptobrachium* is undocumented.

The species sampled for DNA sequences were *Brachytarsophrys feae*, *Leptobrachium chapaense*, *L. hasselti*, *Leptolalax bourreti*, *Megophrys nasuta*, *Ophryophryne hansi*, *O. microstoma*, *Xenophrys major* (formerly *X. lateralis*). We were unable to obtain samples of *Atympanophrys*, *Leptobrachella*, *Oreolalax*, *Scutiger*, and *Vibrissaphora*, so, although we are confident that our sampling will allow phylogenetic generalizations to be made regarding the family, most of the problems within the group (e.g., the questionable monophyly of *Leptobrachium*, *Leptolalax*, *Megophrys*, *Scutiger*, and *Xenophrys*) will remain unanswered.

"Advanced" Frogs—Neobatrachia

Neobatrachia[9] includes about 96% of extant frogs and is a poorly understood array of apparently likely paraphyletic groups with apomorphic satellites. So, at this juncture in our discussion the quantity of evidence sug-

[9] There is controversy regarding the appropriate name of this taxon. It is addressed in appendix 6.

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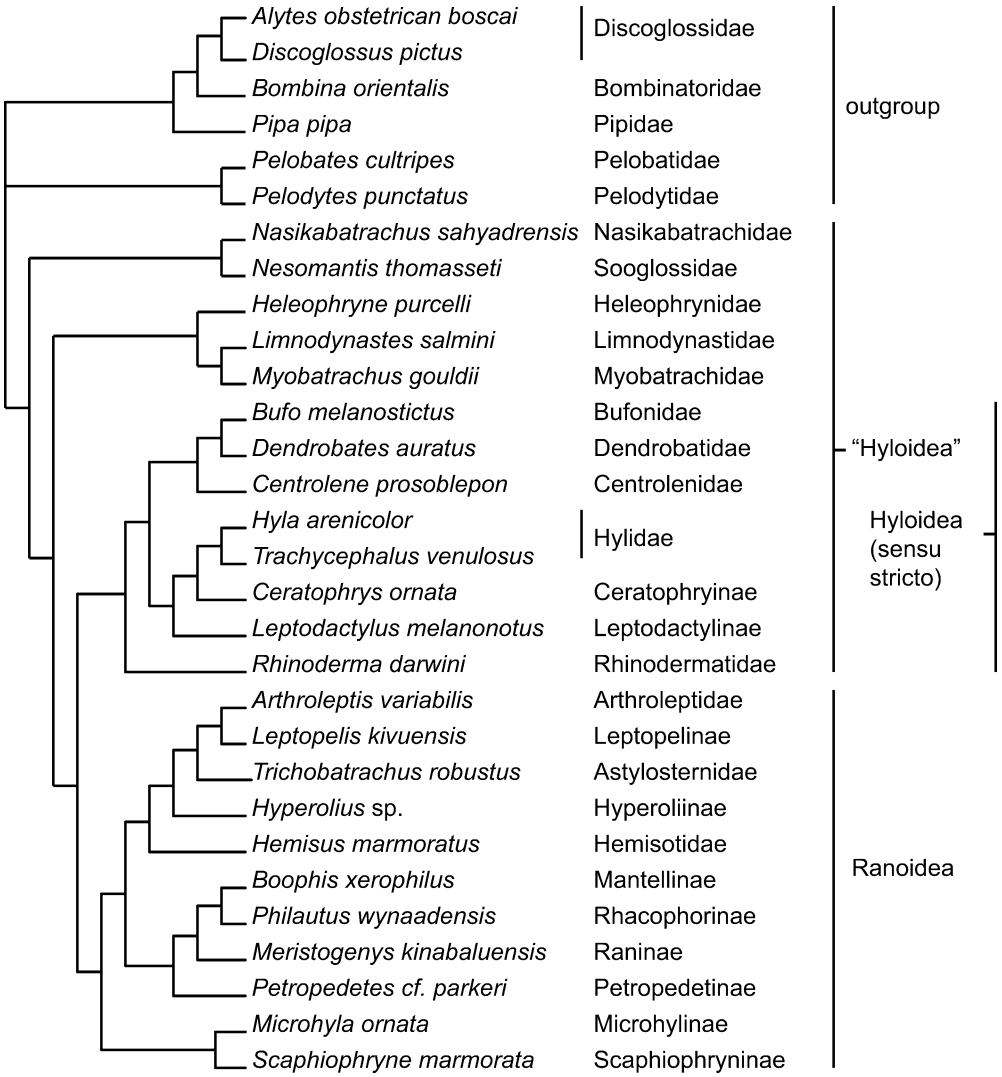

Fig. 21. Bayesian tree of anuran exemplars of Biju and Bossuyt (2003), with particular reference to Neobatrachia. Underlying data are two mtDNA fragments, covering part of 12S rRNA, complete t-RNA^{Val}, and part of 16S rRNA. In addition, one fragment of the nuclear genome: exon 1 of rhodopsin, single exon of RAG-1, and exon 2 of CXCR-4, for a total of 2,325 bp of sequence. Alignment was made using Clustal X (Thompson et al., 1997), alignment costs not disclosed, with ambiguous sections excluded and gaps excluded as evidence. Model of nucleotide substitution assumed for analysis was GTR + Γ+ I.

gested by authors to support major groups, and the quality of published taxonomic reasoning drops significantly to the realm of grouping by overall similarity and special pleading for particularly favored characters. Like the larger-scale Archeobatrachia (primitive frogs), Mesobatrachia (transitional frogs), and Neobatrachia (advanced frogs) of prephylogenetic systematics, Neobatrachia also has within it its own nominally ''primitive'' groups aggregated on plesiomorphy (e.g., Leptodactylidae), as well as its own nominally ''transitional'' and ''advanced'' groups (e.g., Ranidae and Rhacophoridae, Arthroleptidae and Hyperoliidae). Further, the unwillingness of the systematics com-

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munity to change taxonomies in the face of evidence is best illustrated here. For example, Brachycephalidae was shown to be imbedded within the leptodactylid taxon Eleutherodactylinae, but the synonymy was not made by Darst and Canntella (2004), and Leptopelinae was shown to be more closely related to Astylosternidae than to hyperoliine hyperoliids by Vences et al. (2003c), but was retained by those authors in an explicitly paraphyletic Hyperoliidae.

Ford and Cannatella (1993; fig. 14) suggested five characters in support of the monophyly of Neobatrachia: (1) (neo)palatine bone present; (2) fusion of the third distal carpal to other carpals; (3) complete separation of the m. sartorius from the m. semitendinosus; (4) presence of an accessory head of the m. adductor longus; and (5) absence of the parahyoid bone. In addition, Haas (2003; fig. 15) presented the following larval characters (but see Heleophrynidae): (1) upper lip papillation with broad diastema; (2) cartilage of the cavum cranii forms tectum parietale; (3) secretory ridges present; and (4) pupil horizontally elliptical. The character of central importance historically to the recognition of this taxon is the (neo)palatine bone, a character not without its own controversy.

''HYLOIDEA'': The worldwide Hyloidea, for which no morphological synapomorphy has been suggested, was long aggregated on the basis of its being ''primitive'' with respect to the ''more advanced'' Ranoidea, although molecular evidence under certain analytical methods and assumptions supports its monophyly (Ruvinsky and Maxson, 1996; Feller and Hedges, 1998). Hyloidea is defined by the plesiomorphic (at least within Neobatrachia) possession of arciferal pectoral girdles (coracoids not fused) and simple procoelous vertebrae, although descriptions of both characters have been highly reified through repetition and idealization. More recently, Biju and Bossuyt (2001: fig. 21) suggested on the basis of a DNA sequence analysis that Hyloidea, as traditionally viewed, is paraphyletic with respect to Ranoidea, but within ''Hyloidea'' is a monophyletic group largely coextensive with ''Hyloidea'', but excluding Heleophrynidae, Limnodynastidae, Myobatrachidae, Nasikabatrachidae, Sooglossidae, and, presumably Rheobatrachidae as well. Darst and Cannatella (2004; fig. 22) redelimited Hyloidea as the descendants of the most recent common ancestor of Eleutherodactylini, Bufonidae, Centrolenidae, Hylinae, Phyllomedusinae, Pelodryadinae, and Ceratophryinae, thereby excluding Heleophrynidae, Limnodynastidae, Myobatrachidae, Rheobatrachidae, and Sooglossidae (and by implication, presumably Nasikabatrachidae) from Hyloidea[10]. For this discussion, we retain the older, more familiar definition of Hyloidea as all neobatrachians excluding the ranoids.

HELEOPHRYNIDAE (1 GENUS, 6 SPECIES): South African *Heleophryne* was considered by Ford and Cannatella (1993; fig. 14) to be a member of Neobatrachia and Hyloidea. The synapomorphy of Heleophrynidae suggested by these authors includes only absence of keratinous jaw sheaths in exotrophic free-living larvae. Haas (2003; fig. 15), in contrast, placed Heleophrynidae outside Neobatrachia in a pectinate relationship among ''pelobatoids'' or as the sister taxon

[10] Because Darst and Cannatella (2004) used *Limnodynastes* and *Heleophryne* as outgroups to root the remainder of the tree, it was not possible for them to have obtained a tree in which traditional Hyloidea is monophyletic so their statement (p. 46) that ''the placement of some basal neobatrachian clades (Heleophrynidae, Myobatrachidae, and Sooglossidae) remains uncertain'' is actually an assumption of their phylogenetic analysis. Uncited by Darst and Cannatella (2004), Biju and Bossuyt (2003) differentiated between ''Hyloidea'' sensu lato (the traditional view of Hyloidea) and Hyloidea sensu stricto, which they considered to be monophyletic and which, like the concept of Darst and Cannatella (2004), excluded Myobatrachidae, Limnodynastidae, Heleophrynidae, Sooglossidae, and Nasikabatrachidae. Another issue is that Ford and Cannatella (1993) and Cannatella and Hillis (2004) defined the name Hylidae to apply cladographically to the hypothetical ancestor of Hemiphractinae, Hylinae, Pseudinae (now part of Hylinae), and Pelodryadinae, and all of its descendants. However, Darst and Cannatella (2004) implied that their Hylidae was redefined to exclude Hemiphractinae. This redefinition would be necessary to keep content and diagnosis as stable as possible with respect to the traditional use of the term ''Hylidae'', because without this kind of redefinition in a system that aspires to precision, the pretense of precision is lost. For example, the cladographic definition of Hylidae by Ford and Cannatella (1993) and Cannatella and Hillis (2004) applied to the cladogram of Darst and Cannatella (2004) would require that the following be included within Hylidae: Brachycephalidae, Leptodactylidae, Bufonidae, Centrolenidae, Dendrobatidae, and, likely, Rhinodermatidae.

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of *Pelobates*, *Leptobrachium*, and *Megophrys*. *Heleophryne* is included at this level in Haas' analysis by having (1) m. tympanopharyngeus present; (2) m. interhyoideus posterior present; (3) m. diaphragmatopraecordialis present; (4) m. constrictor branchialis I present; and (5) interbranchial septum IV musculature with the lateral fibers of the m. subarcualis rectus II–IV invading the septum, and lacking the characters listed by Haas for Neobatrachia. In addition, the vertical pupil and ectochordal vertebrae tie heleophrynids to myobatrachines, and non-neobatrachians. Recent DNA sequence evidence (San Mauro et al., 2005; fig. 17) strongly supports Heleophrynidae as the sister taxon of all other neobatrachians (although Biju and Bossuyt, 2003, also on the basis of molecular evidence as well had suggested that Heleophrynidae is the sister taxon of Limnodynastidae + Myobatrachidae).

We sampled *Heleophryne purcelli* and *H. regis*. These species are likely close relatives (Boycott, 1982) so broader sampling (to have included *H. rosei*, whose isolation on Table Mountain near Cape Town suggests a likely distant relationship to the other species) would have been preferable.

SOOGLOSSIDAE (2 GENERA, 4 SPECIES) AND NASIKABATRACHIDAE (1 GENUS, 2 SPECIES): Sooglossidae is a putative Gondwanan relict (Savage, 1973) on the Seychelles, possibly related to myobatrachids as evidenced by sharing with that taxon the plesiomorphy of ectochordal vertebrae (J.D. Lynch, 1973), although Bogart and Tandy (1981) suggested a relationship with the arthroleptines (a ranoid group). In fact, the group is plesiomorphic in many characters, being arciferal (although having a bony sternum; see Kaplan, 2004, for discussion of the various meanings of ''arcifery'') and all statements as to its relationships, based on morphology, have been highly conjectural. Biju and Bossuyt (2003; fig. 21) suggested on the basis of DNA sequence evidence that Sooglossidae is the sister taxon of the recently discovered *Nasikabatrachus*, found in the Western Ghats of South India. *Nasikabatrachus* has so far had little of its morphology documented. They also found Sooglossidae + Nasikabatrachidae to form the sister taxon of all other neobatrachians.

We sampled one species each of the nominal sooglossid genera (*Nesomantis thomasseti* and *Sooglossus sechellensis*). Of Nasikabatrachidae we sampled *Nasikabatrachus sahyadrensis* as well as sequences attributed by Dutta et al. (2004) only to an unnamed species of Nasikabatachidae, also from the Western Ghats. Although Dutta et al. did not name their species as new, they explicitly treated it as distinct from *N. sahyadrensis* (Dutta et al., 2004: 214), and we therefore follow their usage. (Our statement that Nasikabatrachidae contains two species rests on this assertion, although any clear diagnosis of the second has yet to be cogently provided.) All species of Sooglossidae that are known are endotrophic according to Thibaudeau and Altig (1999). *Sooglossus sechellensis* has free tadpoles that are carried on the back of the mother. The tadpoles are likely endotrophic, but this is not definitely known (R.A. Nussbaum, personal obs.). Dutta et al. (2004) reported exotrophic tadpoles occurring in fast-flowing streams for their unnamed species of Nasikabatrachidae.

LIMNODYNASTIDAE (8 GENERA, 50 SPECIES), MYOBATRACHIDAE (11 GENERA, 71 SPECIES), AND RHEOBATRACHIDAE (1 GENUS, 2 SPECIES): Different authors consider this taxonomic cluster to be one family (Myobatrachidae, sensu lato) with two or three subfamilies (Heyer and Liem, 1976); to be two families, Limnodynastidae and Myobatrachidae (Zug et al., 2001; Davies, 2003a, 2003b); or to be three families, Limnodynastidae, Myobatrachidae, and Rheobatrachidae (Laurent, 1986). Because Rheobatrachidae (*Rheobatrachus*; Laurent, 1986) was only tentatively associated with Myobatrachidae by Ford and Cannatella (1993), we retain its familial status for clarity of discussion.

Limnodynastidae, Myobatrachidae, and Rheobatrachidae are primarily united on the basis of their geographic propinquity on Australia and New Guinea (Tyler, 1979; Ford and Cannatella, 1993). And, only one line of evidence, that of spermatozoal morphology, has ever suggested that these taxa taken together are monophyletic (Kwon and Lee, 1995). Heyer and Liem (1976) provided a character analysis that assumed familial and generic monophyly, but this was criticized methodologically (Farris et al., 1982a).

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Rheobatrachinae (*Rheobatrachus*) is of uncertain position, although Farris et al. (1982a) in their reanalysis of Heyer and Liem's (1976) data, considered it to be part of Limnodynastinae. Ford and Cannatella (1993) subsequently argued that Rheobatrachinae is more closely related to Myobatrachidae than to Limnodynastidae, although this suggestion, like the first, rests on highly contingent phylogenetic evidence. Moreover, Myobatrachidae may be related to Sooglossidae (J.D. Lynch, 1973) and Limnodynastinae to Heleophrynidae (J.D. Lynch, 1973; Ruvinsky and Maxson, 1996), although these views are largely conjectural inasmuch as the character evidence of J.D. Lynch (1973) was presented in scenario form.

Ford and Cannatella (1993) suggested, on the basis of discussion of characters presented by Heyer and Liem (1976), that Myobatrachidae (Myobatrachinae in their sense and presumably including *Rheobatrachus*) has four morphological synapomorphies: (1) presence of notochordal (ectochordal) vertebrae with intervertebral discs; (2) m. petrohyoideus anterior inserting on the ventral face of the hyoid; and, possibly, (3) reduction of the vomers and concomitant reduction of vomerine teeth (J.D. Lynch, 1971).

Ford and Cannatella (1993) suggested several synapomorphies of Myobatrachidae and Sooglossidae to the exclusion of Limnodynastidae: (1) incomplete cricoid cartilage ring; (2) semitendinosus tendon inserting dorsal to the m. gracilis (in myobatrachines excluding *Taudactylus* and *Rheobatrachus*, which have a ventral trajectory of the tendon; (3) horizontal pupil (except in *Uperoleia*; (also vertical in *Rheobatrachus*; limnodynastines primitively have a vertical pupil according to Heyer and Liem, 1976, although several have horizontal ones); (4) broad alary process (Griffiths, 1959a), which they found in Myobatrachidae and *Rheobatrachus* (as well as in *Adenomera*, *Physalaemus* [in the sense of including *Engystomops* and *Eupemphix*], and *Pseudopaludicola*); and (5) divided sphenethmoid.

Ford and Cannatella (1993) reported at least one synapomorphy for Limnodynastidae: a connection between the m. intermandibularis and m. submentalis (also found in Leptodactylinae and Eleutherodactylinae according to Burton, 1998b). *Rheobatrachus* was diagnosed by having gastric brooding of larvae—an unusual reproductive mode, to say the least. It is tragic that the two species are likely now extinct (Couper, 1992).

Read et al. (2001) provided a phylogenetic study of myobatrachine frogs (fig. 23) based on mtDNA sequence data that assumed monophyly of the group and used only *Limnodynastes* to root the myobatrachine tree. The evolutionary propinquity of *Limnodynastes* (Limnodynastidae) and *Myobatrachus* (Myobatrachidae) was supported on the basis of DNA sequence evidence by Biju and Bossuyt (2003).

We were able to sample at least one species for most of the genera of the three nominal families. For Limnodynastidae we sampled at least one species for all nominal genera: *Adelotus brevis*, *Heleioporus australiacus*, *Lechriodus fletcheri*, *Limnodynastes depressus*, *L. dumerilii*, *L. lignarius*, *L. ornatus*, *L. peronii*, *L. salmini*, *Mixophyes carbinensis*, *Neobatrachus sudelli*, *N. pictus*, *Notaden melanoscaphus*, *Philoria sphagnicola*. Recent authors (e.g., Cogger et al., 1983) have considered *Kyarranus* to be a synonym of *Philoria*, and we follow this. J.D. Lynch (1971) provided morphological

←

Fig. 22. Parsimony tree of Darst and Cannatella (2004) of hyloid frogs and outgroups based on analysis of 12S and 16S fragments of mitochondrial rRNA gene sequences. Sequence alignment was performed using Clustal X (Thompson et al., 1997) under a number of different cost regimes (not disclosed) and then compared with secondary structures and manually manipulated to minimize the number of informative sites under a parsimony criterion. Unalignable regions were excluded and gaps were treated as missing. The number of informative sites was not stated. The tree was rooted on *Limnodynastes* + *Heleophryne*. We updated the taxonomy of the terminals and higher taxonomy to correspond with changes made after the paper was published. Use of *Euhyas* (instead of *Eleutherodactylus*) is our modification to illuminate discussion.

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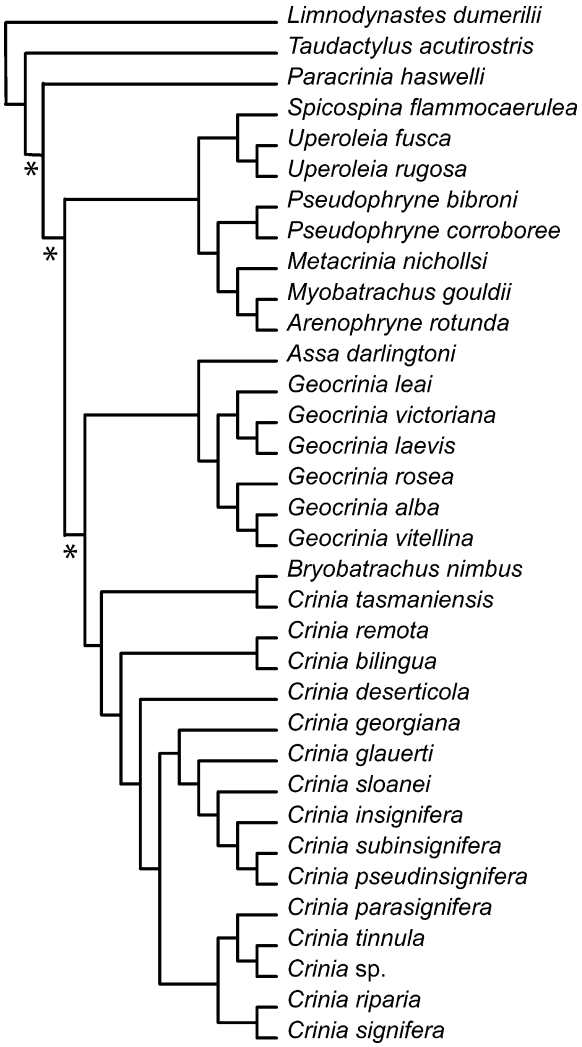

Fig. 23. Parsimony tree of *Crinia*, *Geocrinia*, and allied myobatrachids, of Read et al. (2001). Data were of mtDNA: approximately 621 bp (266 variable) from the 12S rRNA region and 677 bp (383 variable) of ND2. Sequence alignment of 12S and ND2 were done under ClustalX (Thompson et al., 1997) with gap opening and extension costs set at 50, and transversion: transition cost ratio set at 2. Ambiguously alignable regions were excluded. In analysis, transversion:transition costs were set at 2. It was not stated whether gaps were treated as evidence but we infer that gaps were treated as missing data. Branches marked with an asterisk were collapsed in the original publication because of low bootstrap support.

characters that are evidence of monophyly of *Kyarranus* + *Philoria* (e.g., presence of stubby fingers and concealed tympana as well as direct development—Littlejohn, 1963; De Bavay, 1993; Thibaudeau and Altig, 1999).

For Rheobatrachidae, we obtained *Rheobatrachus silus*. And, for Myobatrachidae, we obtained at least single representatives of all nominal genera: *Arenophryne rotunda*, *Assa darlingtoni*, *Crinia nimbus*, *C. signifera*, *Geocrinia victoriana*, *Metacrinia nichollsi*, *Myobatrachus gouldii*, *Paracrinia haswelli*, *Pseudophryne bibroni*, *P. coriacea*, *Spicospina flammocaerulea*, *Taudactylus acutirostris*, and *Uperoleia laevigata*. With exceptions, this taxon selection will not allow us to comment on generic monophyly, but it will identify major monophyletic groups and questions that will guide future research. All rheobatrachids and most myobatrachids have endotrophic larvae and various degrees of direct development (Thibaudeau and Altig, 1999).

''LEPTODACTYLIDAE'' (57 GENERA, 1243 SPECIES): ''Leptodactylidae'' holds the same position in the Americas as Myobatrachidae (sensu lato, as containing Limnodynastidae and Rheobatrachidae) does in Australia—a likely nonmonophyletic hodgepodge ''primitive'' holochordal or rarely stegochordal, arciferal, and procoelous neobatrachian group united by geography and not synapomorphy. ''Leptodactylidae'' is currently divided into five subfamilies, some of which are not clearly monophyletic (or consistently diagnosable) and some of which may be polyphyletic (Ruvinsky and Maxson, 1996; Haas, 2003; Darst and Cannatella, 2004; Faivovich et al., 2005; San Mauro et al., 2005; figs. 17, 22, 24).

J.D. Lynch (1971, 1973) considered leptodactylids to be divided into four subfamilies, on the basis of both synapomorphy and symplesiomorphy: (1) Ceratophryinae (for *Ceratophrys* and *Lepidobatrachus*); (2) Elosiinae (= Hylodinae of other authors; for *Crossodactylus*, *Hylodes*, and *Megaelosia*); (3) Leptodactylinae (for *Barycholos*, *Edalorhina*, *Hydrolaetare*, *Leptodactylus* [including *Adenomera*], *Limnomedusa*, *Lithodytes*, *Paratelmatobius*, *Physalaemus* [including *Engystomops* and *Eupemphix*], *Pleurodema*, and *Pseudopaludicola*); and (4) Telmatobi-

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inae, aggregated on the basis of plesiomorphy. Within his Telmatobiinae Lynch defined five tribes, each aggregated on a variable basis of synapomorphy and symplesiomorphy: Telmatobiini (*Batrachophrynus*, *Caudiverbera*, *Telmatobius*, and *Telmatobufo*); Alsodini (*Batrachyla*, *Eupsophus* [including *Alsodes*], *Hylorina*, and *Thoropa*); Odontophrynini (*Macrogenioglottus*, *Odontophrynus*, and *Proceratophrys*); Grypiscini (*Crossodactylodes*, *Cycloramphus*, and *Zachaenus*); and Eleutherodactylini (*Eleutherodactylus*, *Euparkerella*, *Holoaden*, and *Ischnocnema*, as well as several other genera subsequently placed in the synonymy of *Eleutherodactylus*), with *Scythrophrys* being left incertae sedis. Subsequently, Heyer (1975) provided a preliminary clustering (based on the nonphylogenetic monothetic subset method of Sharrock and Felsenstein, 1975) of the nominal genera within the family that assumed monophyly of both the family and the constituent genera (see Farris et al., 1982a, for criticism of the approach) in which Heyer identified, but did not recognize formally, five units that were recognized subsequently (Laurent, 1986) as Ceratophryinae, Eleutherodactylinae, Cycloramphinae, Leptodactylinae, and Telmatobiinae. J.D. Lynch (1978b) revised the genera of Telmatobiinae, where he recognized three tribes: Telmatobiini (*Alsodes*, *Atelognathus*, *Batrachophrynus*, *Eupsophus*, *Hylorina*, *Insuetophrynus*, *Limnomedusa*, *Somuncuria*, and *Telmatobius*), Calyptocephalellini (*Caudiverbera* and *Telmatobufo*), and Batrachylini (*Batrachyla* and *Thoropa*). The justification for this arrangement was partially based on character argumentation, although plausibility of results was based on subjective notions of overall similarity and relative character importance. A cursory glance at figure 24 (Faivovich et al., 2005) shows that several of these groups are nonmonophyletic.

Burton (1998a) suggested on the basis of hand muscles (although his character polarity was not well supported) that the leptodactylid tribe Calyptocephalellini is more closely related to the South African Heleophrynidae than to other South American leptodactylids. San Mauro et al. (2005; fig. 17) suggested on the basis of DNA sequence data that *Caudiverbera* (Calyptocephalellini) is more closely related to at least some component of Limnodynastidae (*Lechriodus*) than to other South American ''leptodactylids''. Another leptodactylid satellite is Brachycephalidae, a small monophyletic taxon, likely the sister taxon of *Euparkerella* (Leptodactylidae: Eleutherodactylinae) based on digit reduction (Izecksohn, 1988; Giaretta and Sawaya, 1998). Similarly, Rhinodermatidae (*Rhinoderma*) is a small group that is likely also a telmatobiine leptodactylid (Barrio and Rinaldi de Chieri, 1971; Lavilla and Cei, 2001), differing from them in having partial or complete larval development within the male vocal sac and, except for *Eupsophus*, in having endotrophic larvae (Formas et al., 1975; Altig and McDiarmid, 1999).

Laurent (1986) provided the subfamilial taxonomy we employ for discussion (his arrangement being the formalization of the groupings tentatively recommended by Heyer, 1975). He recognized Ceratophryinae (in the larger sense of including J.D. Lynch's Odontophrynini, transferred from Telmatobiinae), Telmatobiinae (including calyptocephallelines and excluding J.D. Lynch's Eleutherodactylini), Cycloramphinae (as Grypiscinae, including Grypscini and Elosiinae of J.D. Lynch), Eleutherodactylinae, and Leptodactylinae.

''CERATOPHRYINAE'' (6 GENERA, 41 SPECIES): Reig (1972) and Estes and Reig (1973) suggested that the leptodactylid subfamily Ceratophryinae was ''ancestral'', in some sense, to Bufonidae, although others rejected this (e.g., J.D. Lynch, 1971, 1973). Laurent (1986), following Heyer (1975), transferred *Macrogenioglottus*, *Odontophrynus*, and *Proceratophrys* (J.D. Lynch's tribe Odontophrynini) into this nominal subfamily, with *Ceratophrys*, *Chacophrys*, and *Lepidobatrachus* being placed in Ceratophryini. Haas (2003; fig. 15) presented morphological evidence that Ceratophryini and Odontophrynini are not each other's closest relatives (following J.D. Lynch, 1971), with *Odontophrynus* most closely related to *Leptodactylus*, and the clade Ceratophryini (*Lepidobatrachus* + *Ceratophrys*) most closely related to hylids, exluding hemiphractines. Duellman (2003) treated the two groups as subfamilies, Odontophryninae and Ceratophryinae, presumably following the results of Haas

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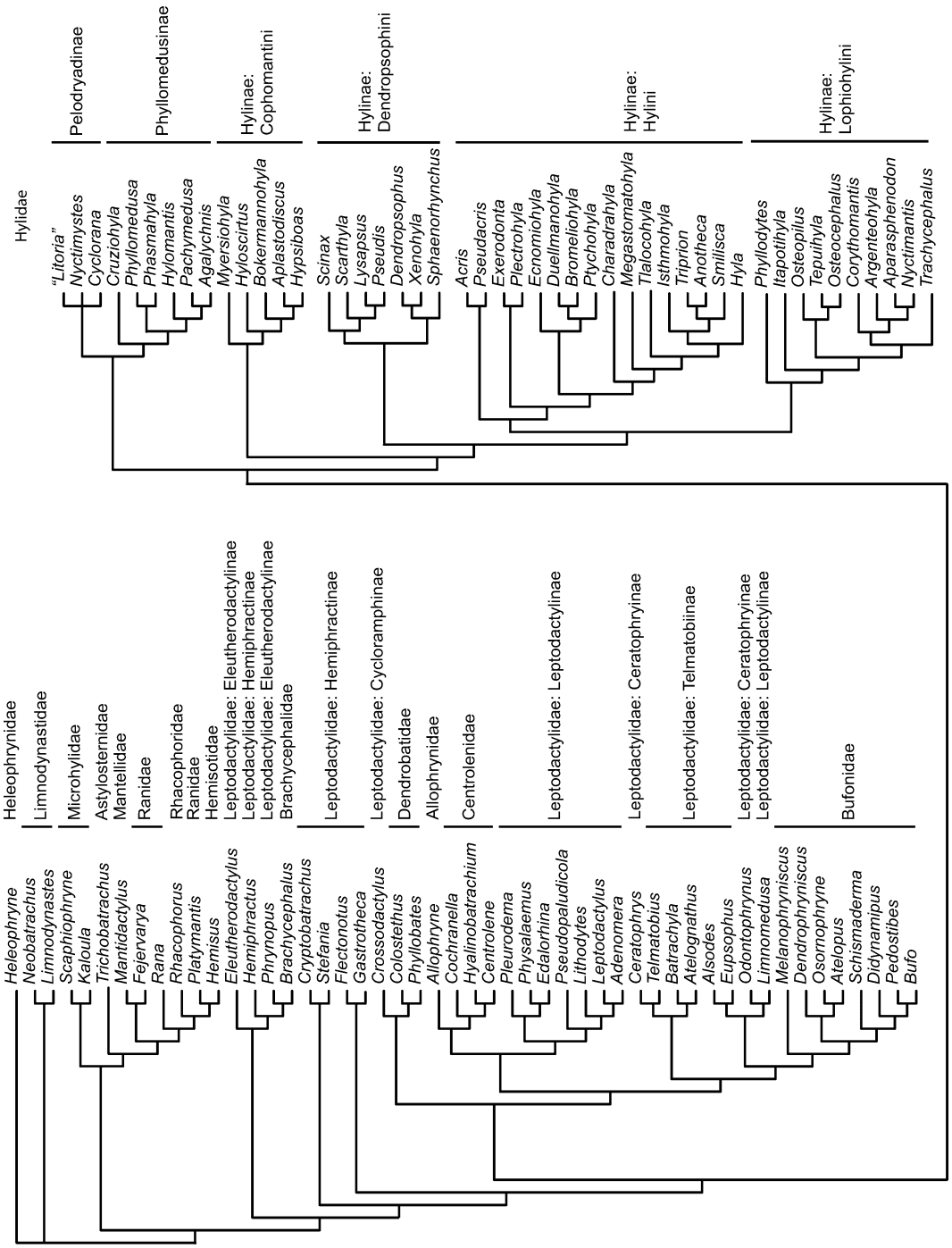

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(2003), and this was followed by Dubois (2005). Faivovich et al. (2005; fig. 24) also found Ceratophryinae to be polyphyletic. We sampled exemplars from all nominal ceratophryid genera except *Macrogenioglottus*, which is similar to *Odontophrynus* (J.D. Lynch, 1971) and karyologically similar to *Proceratophrys* (Silva et al., 2003; *Odontophrynus* not examined in that study) that we doubt that this will be an important problem. Ceratophryini does have synapomorphies, for example: (1) transverse processes of anterior presacral vertebrae widely expanded; (2) cranial bones dermosed; and (3) teeth fanglike, nonpedicellate (J.D. Lynch, 1971, 1982b), although nominal Odontophrynini does not have unambiguously synapomorphies, and the group is united on overall similarity. All ceratophryids have free-living exotrophic larvae (Altig and McDiarmid, 1999). We sampled three species of Ceratophryini (*Ceratophrys cranwelli*, *Chacophrys pierotti*, and *Lepidobatrachus laevis*) and three species of Odontophrynini (*Odontophrynus achalensis*, *O. americanus*, and *Proceratophrys avelinoi*). Our sampling of *Proceratophrys* should have been denser, but this proved a practical impossibility.

"CYCLORAMPHINAE" (10 GENERA, 79 SPECIES): Haas (2003) suggested that this group may be closely related to Dendrobatidae, in part supporting the earlier position of Noble (1926) and J.D. Lynch (1973) that the hylodine part of this nominal subfamily (*Crossodactylus*, *Hylodes*, and *Megaelosia*) is paraphyletic with respect to Dendrobatidae. Faivovich et al. (2005; fig. 24) recovered *Crossodactylus* (their exemplar of this group) as the sister taxon of Dendrobatidae. Laurent (1986) recognized this subfamily, thus unifying J.D. Lynch's (1971, 1973) Grypiscini and Elosiinae (= Hylodinae), although the evidentiary basis for uniting these was based on Heyer's (1975) results based on monothetic subsets, not parsimony. (Note that J.D. Lynch, 1971, had considered his Grypiscini to be close to Eleutherodactylini on the basis of overall similarity.) Grypiscines and hylodines differ in (1) the shape of the transverse processes of the posterior presacral vertebrae, being short in hylodines and not short in grypiscines; (2) the shape of the facial lobe of the maxillae (deep in grypiscines, shallow in hylodines); (3) the shape of the nasals (large and in median contact in grypiscines, small and widely separated in hylodines); and (4) whether the nasal contacts the frontoparietal (contact in grypiscines, no contact in hylodines). We were unable to obtain samples of *Crossodactylodes*, *Rupirana*, or *Zachaenus*, but we did obtain at least one species of every other nominal genus in the group: *Crossodactylus schmidti*, *Cycloramphus boraceiensis*, *Hylodes phyllodes*, *Megaelosia goeldii*, *Paratelmatobius* sp., *Scythrophrys sawayae*, and *Thoropa miliaris*. Denser sampling of this particular taxon would have been preferable, but what we obtained will test cycloramphine monophyly and its putative relationship to Dendrobatidae and will provide an explicit hypothesis of its internal phylogenetic structure as the basis of future studies.

Duellman (2003) did not accept Laurent's (1986) unification of J.D. Lynch's Hylodinae and Grypiscini and recognized Hylodinae (*Crossodactylus*, *Hylodes*, and *Megaelosia*) as a different subfamily from Cycloramphinae. Duellman distinguished Hylodinae and Cycloramphinae by T-shaped terminal phalanges in Hylodinae and knoblike terminal phalanges in Cycloramphinae; and glandular pads on the dorsal surface of the digits, absent in Hylodinae and present in Cycloramphinae. However, neither the particulars of distribution of these characters in the taxa nor the levels of universality of their application as evidence was discussed. Duellman (2003) also suggested that Hylodinae and Cycloramphinae differ in chromosome numbers, with 13 pairs in Cycloramphinae and 3 pairs in Hylodinae. However, Kuramoto

←

Fig. 24. Tree of Hylidae and outgroups from Faivovich et al. (2005), based on 5.5kb sequence from four mitochondrial genes (12S, 16S, $tRNA^{Val}$, cytochrome *c*) and five nuclear genes (rhodopsin, tyrosinase, RAG-1, seven in absentia, 28S) and analyzed by Direct Optimization in POY under equal cost functions. Gaps were treated as evidence.

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(1990) noted that hylodines in Duellman's sense have 11–13 pairs of chromosomes, and cycloramphines in Duellman's sense also have 11–13 pairs, so Duellman's statement is taken to be an error.

ELEUTHERODACTYLINAE (13 GENERA, 782 SPECIES): The only suggested synapomorphy of this taxon is direct terrestrial development of large eggs deposited in small clutches (J.D. Lynch, 1971). The universality of direct development in this group is based on extrapolation from the few species for which direct development has been observed; the occurrence of large, unpigmented eggs, and because free-living larvae are unknown (see cautionary remarks in Thibaudeau and Altig, 1999). Inasmuch as this taxon contains the largest vertebrate genus, *Eleutherodactylus* (ca. 600 species) of which the vast majority are not represented by genetic samples, this taxon will remain inadequately sampled for some time. There has never been any comprehensive phylogenetic study of the relationships within the group and the likelihood of many (or even most) of the non-*Eleutherodactylus* genera being components of *Eleutherodactylus* is high. Indeed, Ardila-Robayo (1979) suggested strongly that for the taxon currently referred to as *Eleutherodactylus* (sensu lato) to be rendered monophyletic it would need to include *Barycholos*, *Geobatrachus*, *Ischnocnema*, and *Phrynopus* (and likely *Adelophryne*, *Phyllonastes*, *Phyzelaphryne*, *Holoaden* and *Euparkerella*, and Brachycephalidae [Izecksohn, 1971; Giaretta and Sawaya, 1998; Darst and Cannatella, 2004; Faivovich et al., 2005][11]). Regardless, many of the nominal eleutherodactyline genera represent rare and extremely difficult animals to obtain (e.g., *Atopophrynus*, *Dischidodactylus*), so our sampling of this particular taxon is clearly inadequate to address most systematic problems. We could not obtain samples of *Adelophryne*, *Atopophrynus*, *Dischidodactylus*, *Euparkerella* (even though it was suggested to be closely related to Brachycephalidae), *Geobatrachus*, *Holoaden*, *Phyllonastes*, or *Phyzelaphryne*. We hope that work in the near future can rectify this with the recognition of major monophyletic groups from within *Eleutherodactylus*. What we could sample of the non-*Eleutherodactylus* eleutherodactyline taxa were *Barycholos ternetzi*, *Ischnocnema quixensis*, and two species of *Phrynopus*. Of *Eleutherodactylus* (sensu lato) we sampled two species of the North American subgenus *Syrrhophus* (*Eleutherodactylus marnocki* of the *E. marnocki* group of J.D. Lynch and Duellman, 1997, and *E. nitidus* of the *E. nitidus* group of J.D. Lynch and Duellman, 1997); one species of the Antillean subgenus *Euhyas* (*Eleutherodactylus planirostris* of the *E. ricordii* group of J.D. Lynch and Duellman, 1997); two species of the South American subgenus *Eleutherodactylus* (*E. binotatus* and *E. juipoca*, both of the *E. binotatus* group of J.D. Lynch, 1978a; see also J.D. Lynch and Duellman, 1997); and six species of the Middle American subgenus *Craugastor*[12] (*E. bufoniformis* of the *E. bufoniformis* group of J.D. Lynch, 2000, *E. alfredi* of the *E. alfredi* group of J.D. Lynch, 2000, *E. augusti* of the *E. augusti* group of J.D. Lynch, 2000, *E. pluvicanorus* of the *E. fraudator* group of Köhler, 2000, *E. punctariolus* and *E.* cf. *ranoides*[13] of the *E. rugulosus* group of J.D. Lynch, 2000) and *E. rhodopis* of the *E. rhodopis* group of J.D. Lynch, 2000). (For expediency, all of these are noted in "Results" in combination with their subgeneric names; e.g., *Eleutherodactylus* (*Syrrhophus*) *marnockii* is treated as *Syrrhophus marnockii*.) As noted earlier, we expect that *Eleutherodactylus* will be found to be paraphyletic with respect to a number of other eleutherodactyline taxa (e.g., *Barycholos*, *Phrynopus*, and *Ischnocnema*) and hope that this selection will allow some illumination of this.

[11] Dubois (2005) noted that if Brachycephalidae is a synonym of Eleutherodactylinae, as suggested by the results of Darst and Cannatella (2004), the appropriate name for this taxon, within Leptodactylidae, would be Brachycephalinae.

[12] *Craugastor* was recently considered to be a genus by Crawford and Smith (2005) and we follow that arrangement, although we refer to *Craugastor* in this section and elsewhere as part of *Eleutherodactylus* (sensu lato) for consistency with the immediately relevant literature.

[13] We report this species as *Craugastor* cf. *ranoides*, because we discovered late in this project that the voucher specimen was lost. However, the identification in the associated field notes was "*Eleutherodactylus rugulosus*" and the only member of the *rugulosus* group (and of *Craugastor*) otherwise in that collection and from that region is *Craugastor ranoides*.

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Nevertheless, we are aware that this tiny fraction of the species diversity of *Eleutherodactylus* is insufficient to fully resolve the phylogeny of this massive taxon and that the value of the results will be in highlighting outstanding problems and providing a basis for future, more densely sampled studies.

LEPTODACTYLINAE (12 GENERA, 159 SPECIES): Monophyly of this group is supported by the possession of foam nests (except in *Limnomedusa* [Langone, 1994] and *Pseudopaludicola* [Barrio, 1954], and in some species of *Pleurodema* [Duellman and Veloso M., 1977]) and the presence of a bony sternum (rather than the cartilaginous sternum of other leptodactylids; J.D. Lynch, 1971). However, Haas (2003; fig. 15) sampled three species of Leptodactylinae (*Physalaemus biligonigerus*, *Leptodactylus latinasus*, and *Pleurodema kriegi*) for mostly larval morphology and found the group to be para- or polyphyletic with respect to *Odontophrynus*, and with *Physalaemus*[14] and *Pleurodema* forming, respectively, more exclusive outgroups of Haas' hylodines and dendrobatids. In Darst and Cannnatella's (2004) phylogenetic analysis of mtDNA (fig. 22), their leptodactyline exemplars are monophyletic in the maximum-likelihood analysis of mtDNA, but polyphyletic in the parsimony analysis. In Faivovich et al.'s (2005; fig. 24) parsimony analysis of multiple mtDNA and nuDNA loci, exemplars of most genera of Leptodactylinae obtained as monophyletic, with the exception of *Limnomedusa*. Therefore, the monophyly of Leptodactylinae is an open question. We could not obtain samples of *Hydrolaetare* (or the recently resurrected *Eupemphix* and *Engystomops*), but we sampled at least one species of each of the other nominal leptodactyline genera: *Adenomera hylaedactyla*, *Edalorhina perezi*, *Leptodactylus fuscus*, *L. ocellatus*, *Limnomedusa macroglossa*, *Lithodytes lineatus*, *Physalaemus gracilis*, *Pleurodema brachyops*, *Pseudopaludicola falcipes*, and *Vanzolinius discodactylus*). Our sampling of *Leptodactylus* is not dense enough to evaluate well the likely paraphyly of this taxon with respect to others, such as *Adenomera* (Heyer, 1998), being restricted to only two of the five nominal species groups. Leptodactylines vary from having endotrophic larvae, facultatively endotrophic larvae (*Adenomera*) to having exotrophic, free-living larvae (*Edalorhina*, *Engystomops*, *Eupemphix*, *Leptodactylus*, *Lithodytes*, *Physalaemus*, *Pleurodema*, *Pseudopaludicola*, *Vanzolinius*; Altig and McDiarmid, 1999).

''TELMATOBIINAE'' (11 GENERA, 98 SPECIES): Telmatobiinae is a similarity grouping of mostly austral South American frogs. As currently employed, contents of this subfamily stem from Laurent's (1986) formalization of Heyer's (1975) informal grouping. Telmatobiines are currently arranged in three tribes (J.D. Lynch, 1971, 1978b; Burton, 1998a): Telmatobiini (*Alsodes*, *Atelognathus*, *Eupsophus*, *Hylorina*, *Insuetophrynus*, *Somuncuria*, and *Telmatobius*); Batrachylini (*Batrachyla* and *Thoropa*); and Calyptocephalellini (*Batrachophrynus*, *Caudiverbera*, and *Telmatobufo*). All telmatobiines have aquatic, exotrophic larvae except *Eupsophus*, which has endotrophic larvae (Altig and McDiarmid, 1999), and *Thoropa*, which is semiterrestrial (Bokermann, 1965; Wassersug and Heyer, 1983; Haddad and Prado, 2005).

Batrachylini (in J.D. Lynch's sense of including *Thoropa*) is diagnosed by having terrestrial eggs and aquatic to semiterrestrial larvae and T-shaped terminal phalanges. Laurent (1986) did not (apparently) accept J.D. Lynch's (1978b) transferral of *Thoropa* into Batrachylini, and retained *Thoropa* in Cycloramphinae following Heyer (1975).

Calyptocephalellini was most recently discussed and diagnosed by Burton (1998a) on the basis of hand musculature, but the character argumentation was essentially that of overall similarity, not synapomorphy. Formas and Espinoza (1975) provided karyological evidence for the monophyly of Calyptocephallelini (although they did not address *Batrachophrynus*). Cei (1970) suggested on the basis of immunology that Calyptocephalellini is phylogenetically distant from leptodactylids, being closer to Heleophrynidae than to any South American leptodactylid group. J.D. Lynch (1978b) suggested the

[14] Nascimento et al. (2005) recently partitioned *Physalaemus* into *Physalaemus*, *Eupemphix*, and *Engystomops* on the basis of phenetic comparisons. Unfortunately, the historical reality of these taxa will remain arguable until a phylogenetic analysis is performed on this group.

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following to be synapomorphies of Calyptocephalellini (composed of solely *Caudiverbera* and *Telmatobufo*): (1) occipital artery enclosed in a bony canal; and (2) very broad pterygoid process of the premaxilla. In addition, (1) a very long cultriform process of the parasphenoid; and (2) presence of a medial process on the pars palatina of the premaxilla are osteological characters suggested by J.D. Lynch possibly to unite *Batrachophrynus* with *Caudiverbera* and *Telmatobufo*.

We sampled representatives of two of the genera of Calyptocephallelini (*Caudiverbera caudiverbera* and *Telmatobufo venustus*). We could not sample *Batrachophrynus*, which was considered a calyptocephalelline by Burton (1998a), and in some of the cladograms presented by J.D. Lynch (1978b) *Batrachyophrynus* was considered to form the sister taxon of his Calyptocephalellini, so its absence from our analysis is unfortunate.

''Telmatobiini'' of J.D. Lynch (1978b) is explicitly paraphyletic with respect to Batrachylini and as such has no diagnosis other than that of the inclusive clade ''Telmatobiini'' + Batrachylini: (1) presence of an outer metatarsal tubercle (dubiously synapomorphic), and (2) reduction of imbrication on the neural arches of the vertebrae. Among species of ''Telmatobiini'' we sampled *Alsodes gargola*, *Atelognathus patagonicus*, *Eupsophus calcaratus*, *Hylorina sylvatica*, *Telmatobius jahuira*, *T.* cf. *simonsi*, and *T.* sp. Of Batrachylini, we sampled *Batrachyla leptopus*. On this basis we provide a weak test of telmatobiine relationships with regard to Batrachylini. We were unable to sample any member of *Insuetophrynus* or *Somuncuria*.

''HEMIPHRACTINAE'' (5 GENERA, 84 SPECIES): Mendelson et al. (2000) provided a cladogram of Hemiphractinae but assumed its monophyly and its hylid affinities, as had all authors since Duellman and Gray (1983) and Duellman and Hoogmoed (1984). Haas (2003) suggested (fig. 15), on the basis of morphological data, that his examplar of Hemiphractinae, *Gastrotheca*, was far from other hylids and imbedded within a heterogeneous group of leptodactylids and ranoids. Darst and Cannatella (2004), who examined one exemplar species each of *Gastrotheca* and *Cryptobatrachus*, suggested on the basis of mtDNA evidence that Hemiphractinae is polyphyletic, with *Cryptobatrachus* closest to direct-developing eleutherodactylines, and *Gastrotheca* imbedded in another group of leptodactylids. Similarly, in the analysis by Faivovich et al. (2005; fig. 24) of multiple mtDNA and nuDNA loci, hemiphractines do not appear as monophyletic. They recovered one clade composed of *Gastrotheca* and *Flectonotus*, one clade composed of *Stefania* and *Cryptobatrachus*, and they found *Hemiphractus* to form a clade with the few included exemplars of Eleutherodactylinae and Brachycephalidae. Further, inasmuch as the sole noncontingent synapomorphy of nominal Hemiphractinae, bell-shaped larval gills, has not been surveyed widely in direct-developing leptodactylids, we consider the morphological evidence for the monophyly of the hemiphractines to be questionable.

Faivovich et al. (2005; fig. 24) transferred ''Hemiphractinae'' out of a reformulated Hylidae and into ''Leptodactylidae'' on the bases that continued inclusion in Hylidae would render Hylidae polyphyletic; its nominal inclusion in ''Leptodactylidae'' did no violence to a taxon already united solely by plesiomorphy and geography; and placing it incertae sedis within Hyloidea was to suggest its possible placement outside of the ''leptodactylid'' region of the overall tree, which it is not. ''Hemiphractinae'' is a grouping of South American frogs united by (1) brooding of eggs on the female's back, generally within a dorsal depression or well-developed pouch; (2) possession in the developing larvae of bell-shaped gills (Noble, 1927); and (3) presence of a broad m. abductor brevis plantae hallucis (Burton, 2004). Larvae may be exotrophic and endotrophic among species of *Gastrotheca* and *Flectonotus*, and endotrophic alone in *Cryptobatrachus*, *Hemiphractus*, and *Stefania*. Based on Faivovich et al.'s (2005) topology (fig. 24), claw-shaped terminal phalanges and presence of intercalary cartilages between the ultimate and penultimate phalanges must be considered either convergent with those found in Hylidae or plesiomorphically retained in hylids (and lost in intervening lineages), while the proximal head of metacarpal II not between prepollex and distal prepollex, and the

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larval spiracle sinistral and ventrolateral (Duellman, 2001) are convergent with those in the Phyllomedusinae. Our sampling of *Gastrotheca* is not dense enough to allow for the detection of the paraphyly suggested by Mendelson et al. (2000). Our sampling precludes evaluation of paraphyly of any of the nominal genera. Nevertheless, we did sample at least one species per genus, which allows us to test the monophyly of the hemiphractines based on more extensive outgroup sampling. Our sampled taxa are *Cryptobatrachus* sp., *Flectonotus* sp., *Gastrotheca fissipes*, *G.* cf. *marsupiata*, *Hemiphractus helioi*, and *Stefania evansi*.

BRACHYCEPHALIDAE (1 GENUS, 8 SPECIES): This tiny group of diminutive south- to southeastern Brazilian species are united by (1) the absence through fusion of a distinguishable sternum; (2) digital reduction (possibly homologous with that in *Euparkerella* and *Phyllonastes* in Eleutherodactylinae); and (3) complete ossification of the epicoracoid cartilages with coracoids and clavicles (Ford and Cannatella, 1993; Kaplan, 2002). Brachycephalidae was suggested to be imbedded within Eleutherodacylinae (Izecksohn, 1971; Giaretta and Sawaya, 1998), which also shows direct development. Further, Darst and Cannatella (2004; fig. 22) provided molecular data to link this taxon to Eleutherodactylinae, but continued its recognition despite the demonstrable paraphyly that its recognition requires. Although there are several named and unnamed species in the genus, the monophyly of the group is not in question (Kaplan, 2002), and we sampled the type species, *Brachycephalus ephippium*, for this study.

RHINODERMATIDAE (1 GENUS, 2 SPECIES): As noted earlier, the Chilean Rhinodermatidae is a likely satellite of a paraphyletic ''Leptodactylidae''; it is like them in having procoelous and holochordal vertebrae. J.D. Lynch (1973) conjectured that Rhinodermatidae is the sister taxon of Bufonidae, whereas Lavilla and Cei (2001) suggested that *Rhinoderma* is within the poorly-defined ''Telmatobiinae'' (''Leptodactylidae''). The only notable synapomorphy of Rhinodermatidae is the rearing of tadpoles within the vocal sacs of the male, although Manzano and Lavilla (1995) also discussed myological characters that are possible synapomorphies. Two species are currently recognized, *Rhinoderma darwinii* and *R. rufum*. We sampled *R. darwinii*.

DENDROBATIDAE (CA. 11 GENERA, 241 SPECIES): The monophyly of Dendrobatidae has been upheld consistently (e.g., Myers and Ford, 1986; Ford, 1993; Haas, 1995; Clough and Summers, 2000; Vences et al., 2000b), but different datasets place Dendrobatidae at various extremes within the neobatrachian clade. It is either nested deeply within hyloids and arguably related to cycloramphine leptodactylids (Noble, 1926, 1931; J.D. Lynch, 1971, 1973; Burton, 1998a; Haas, 2003; Faivovich et al., 2005); the sister group of *Telmatobius* (Vences et al., 2003b); or closely related to Hylinae (Darst and Cannatella, 2004). Alternatively, they have been suggested to be deeply imbedded within ranoids, usually considered close to arthroleptids or petropedetids (Griffiths, 1959b, 1963; Duellman and Trueb, 1986; Ford, 1993; Ford and Cannatella, 1993; Grant et al., 1997). Rigorous evaluation of the support for these contradictory hypotheses is required.

Ford and Cannatella (1993; fig. 14) provided the following as synapomorphies of Dendrobatidae: (1) retroarticular process present on the mandible; (2) conformation of the superficial slip of the m. depressor mandibulae; and (3) cephalic amplexus. They mentioned other features suggested by other authors but that were suspect for one reason or another. Haas (2003; fig. 15) considered the following to be synapomorphies that nest Dendrobatidae within hylodine leptodactylids: (1) guiding behavior observed during courtship; and (2) T- or Y-shaped terminal phalanges. Like most other frogs, most dendrobatids have aquatic free-living tadpoles (with some endotrophy in *Colostethus*), although the parental-care behavior of carrying tadpoles to water on the back of one of the parents appears to be synapomorphic (Altig and McDiarmid, 1999), although among New World anurans it also occurs in *Cycloramphus stejnegeri* (Heyer and Crombie, 1979).

Taxon sampling was designed to provide the maximal ''spread'' of phylogenetic variation with a minimum number of species: *Allobates femoralis*, *Ameerega boulengeri*, *Co-*

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lostethus undulatus, *Dendrobates auratus*, *Mannophryne trinitatis*, *Minyobates claudiae*, *Phobobates silverstonei*, and *Phyllobates lugubris*. We did not sample any representative of *Aromobates*, *Cryptophyllobates*, *Nephelobates*, nor did we sample either of two generally-not-recognized genera *Oophaga* or *Ranitomeya*. On the basis of ongoing work by T. Grant, we think that all of these are imbedded within our sampled genera and their absence does not hamper our ability to test dendrobatid monophyly and place the family in the larger phylogenetic scheme.

ALLOPHRYNIDAE (1 GENUS, 1 SPECIES): South American *Allophryne* has been (1) very provisionally associated with Hylidae (J.D. Lynch and Freeman, 1966); (2) asserted to be in Bufonidae on the basis of morphology (Laurent, 1980 ''1979''; Dubois, 1983; Laurent, 1986), the evidence for this latter position not actually presented until much later by Fabrezi and Langone (2000); (3) imbedded within Centrolenidae, on the basis of morphology (Noble, 1931); or (4) placed as the sister taxon of Centrolenidae on the basis of mtDNA sequence studies (Austin et al., 2002; Faivovich et al., 2005). Cognoscenti of frogs will marvel at the vastness separating these various hypotheses. Ford and Cannatella (1993) noted that *Allophryne* lacks the interacalary cartilages of hylids and centrolenids and suggested that placement in any taxon other than Neobatrachia is misleading. Haas (2003; fig. 15) did not examine *Allophryne*. We sampled the single species, *Allophryne ruthveni*. Larvae are unknown (Altig and McDiarmid, 1999).

CENTROLENIDAE (3 GENERA, 139 SPECIES): Centrolenidae has long been thought to be close to, or the sister taxon of, Hylidae (J.D. Lynch, 1973; Ford and Cannatella, 1993; Duellman, 2001) because of the occurrence of interacalary cartilages between the ultimate and penultimate phalanges. On the basis of mostly-larval morphology, Haas (2003) recovered (weakly) Centrolenidae as the sister taxon of all Neobatrachia except for *Limnodynastes* (Limnodynastidae), because it lacked all characters that Haas' analysis suggested were synapomorphies of Neobatrachia. The analysis of Faivovich et al. (2005; fig. 24) of multiple mtDNA and nuDNA loci recovered an *Allophryne* + Centrolenidae clade nested within a grade of ''Leptodactylidae''. Clearly, the diversity of opinions on the placement of Centrolenidae is great. For our analysis we selected species of the three nominal genera: *Centrolene geckoideum*, *C. prosoblepon*, *Cochranella bejaranoi*, and *Hyalinobatrachium fleischmanni*. Larvae of centrolenids are aquatic or burrowing exotrophs (Altig and McDiarmid, 1999).

HYLIDAE (48 GENERA, 806 SPECIES): Hylidae, as traditionally recognized, was recently shown to be polyphyletic (Ruvinsky and Maxson, 1996; Haas, 2003; Darst and Cannatella, 2004; Faivovich et al., 2005). As an interim measure to resolve this problem Faivovich et al. (2005) transferred ''Hemiphractinae'' into ''Leptodactylidae'', thereby restricting Hylidae to the Holarctic and Neotropical Hylinae, tropical American Phyllomedusinae, and Australo-Papuan Pelodryadinae (and thereby formalizing the implication of Darst and Cannatella, 2004).

Our notions of hylid relationships extend from the recent revision by Faivovich et al. (2005; fig. 24), who provided a phylogenetic analysis of multiple mtDNA and nuDNA loci. Their study addressed 220 hylid exemplar terminals as well as 48 outgroup taxa. For our study, we considered including all terminals from the Faivovich et al. (2005) study, which would have allowed a more rigorous test, but the increased computational burden was judged too great for the expected payoff of increased precision within Hylinae. Our sampling strategy aimed to be sufficiently dense to test the position of hylids among other frogs and the monophyly of the major clades without unduly exacerbating computational problems.

HYLINAE (38 GENERA, 586 SPECIES): Our sampling structure of Hylinae was guided by the results of Faivovich et al. (2005). Beyond their genetic evidence, monophyly of this subfamily is corrobated by at least one morphological synapomorphy: tendo superficialis digiti V (manus) with an additional tendon that arises ventrally from the m. palmaris longus (Da Silva *In* Duellman, 2001). All hylines for which it is known have free-living exotrophic larvae (Altig and McDiarmid, 1999). Faivovich et al. (2005) recognized

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four monophyletic tribes within Hylinae: Cophomantini (*Aplastodiscus*, *Bokermannohyla*, *Hyloscirtus*, *Hypsiboas*, and *Myersiohyla*); Hylini (*Acris*, *Anotheca*, *Bromeliohyla*, *Charadrahyla*, *Duellmanohyla*, *Ecnomiohyla*, *Exerodonta*, *Hyla*, *Isthmohyla*, *Megastomatohyla*, *Pseudacris*, *Plectrohyla*, *Ptychohyla*, *Smilisca* [including former *Pternohyla*], *Tlalocohyla*, and *Triprion*); Dendropsophini (*Dendropsophus*, *Lysapsus*, *Pseudis*, *Scarthyla*, *Scinax*, *Sphaenorhynchus*, and *Xenohyla*); and Lophiohylini (*Aparasphenodon*, *Argenteohyla*, *Corythomantis*, *Itapotihyla*, *Nyctimantis*, *Osteocephalus*, *Osteopilus*, *Phyllodytes*, *Tepuihyla*, and *Trachycephalus*).

In this study we included representatives of these four tribes: Cophomantini (*Aplastodiscus perviridis*, *Hyloscirtus armatus*, *H. palmeri*, *Hypsiboas albomarginatus*, *H. boans*, *H. cinerascens* (formerly *Hypsiboas granosus*; see Barrio-Amorós, 2004: 13), *H. multifasciatus*); Dendropsophini (*Dendropsophus marmoratus*, *D. minutus*, *D. nanus*, *D. parviceps*, *Lysapsus laevis*, *Pseudis paradoxa*, *Scarthyla goinorum*, *Scinax garbei*, *S. ruber*, *Sphaenorhynchus lacteus*); Hylini (*Acris crepitans*, *Anotheca spinosa*, *Charadrahyla nephila*, *Duellmanohyla rufioculis*, *Ecnomiohyla miliaria*, *Exerodonta chimalapa*, *Hyla arbrorea*, *H. cinerea*, *Isthmohyla rivularis*, *Pseudacris crucifer*, *P. ocularis*, *Ptychohyla leonhardschultzei*, *Smilisca phaeota*, *Tlalocohyla picta*, and *Triprion petasatus*); and Lophiohylini (*Argenteohyla siemersi*, *Osteocephalus taurinus*, *Osteopilus septentrionalis*, *Phyllodytes luteolus*, *Trachycephalus jordani*, and *T. venulosus*).

PELODRYADINAE (3 GENERA, 168 SPECIES): Knowledge of phylogenetic relationships among Australo-Papuan hylids is poorly understood, beyond the pervasive paraphyly of nominal ''*Litoria*'' with respect to the other two genera, *Nyctimystes* and *Cyclorana* (Tyler and Davies, 1978; King et al., 1979; Tyler, 1979; Maxson et al., 1985; Hutchinson and Maxson, 1987; Haas and Richards, 1998; Haas, 2003; Faivovich et al., 2005). Faivovich (2005) noted one morphological synapomorphy of Phyllomedusinae + Pelodryadinae, the presence of a tendon of the m. flexor ossis metatarsi II arising only from distal tarsi 2–3. Evidence for the monophyly of Pelodryadinae remains unsettled. Haas (2003), on the basis of six exemplars, recovered the subfamily as paraphyletic with respect to hylines and phyllomedusines. Tyler (1971c) noted the presence of supplementary elements of the m. intermandibularis in both Pelodryadinae (apical) and Phyllomedusinae (posterolateral). These characters were interpreted by Duellman (2001) as nonhomologous and therefore independent apomorphies of their respective groups. If these conditions are homologues as suggested by Faivovich et al. (2005) on the basis of their preferred cladogram, the polarity between the two characters is ambiguous because either the pelodryadine or the phyllomedusinae condition might be ancestral for Phyllomedusinae + Pelodryadinae. Because our study aims to provide a general phylogenetic structure for amphibians, not to resolve all systematic problems, and in light of ongoing research by S. Donnellan, we have not sampled ''*Litoria*'' densely enough to provide a detailed resolution of relationships within Pelodryadinae. Nevertheless, we sampled densely enough to provide additional evidence regarding the paraphyly of ''*Litoria*'' with respect to *Cyclorana* or *Nyctimystes*. Species sampled in this group are *Cyclorana australis*, ''*Litoria*'' *aurea*, ''*L.*'' *freycineti*, ''*L.*'' *genimaculata*, ''*L.*'' *inermis*, ''*L.*'' *lesueurii*, ''*L.*'' *meiriana*, ''*L.*'' *nannotis*, *Nyctimystes dayi*, and *N. pulcher*. All pelodryadines appear to have free-living exotrophic larvae (Tyler, 1985; Altig and McDiarmid, 1999).

PHYLLOMEDUSINAE (7 GENERA, 52 SPECIES): There is abundant morphological and molecular evidence for the monophyly and phylogenetic structure of this subfamily of bizarre frogs. Synapomorphies of the group include: (1) vertical pupil; (2) ventrolateral position of the spiracle; (3) arcus subocularis of larval chondrocranium with distinct lateral processes; (4) ultralow suspensorium; (5) secondary fenestrae parietales; and (6) absence of a passage between the ceratohyal and the ceratobranchial I (Haas, 2003). Faivovich et al. (2005) discussed several other characters likely to be synapomorphies of Phyllomedusinae. Faivovich et al. (2005) demonstrated on the basis of molecular data that *Cruziohyla* is the sister taxon of the remaining genera, which are further divided in two

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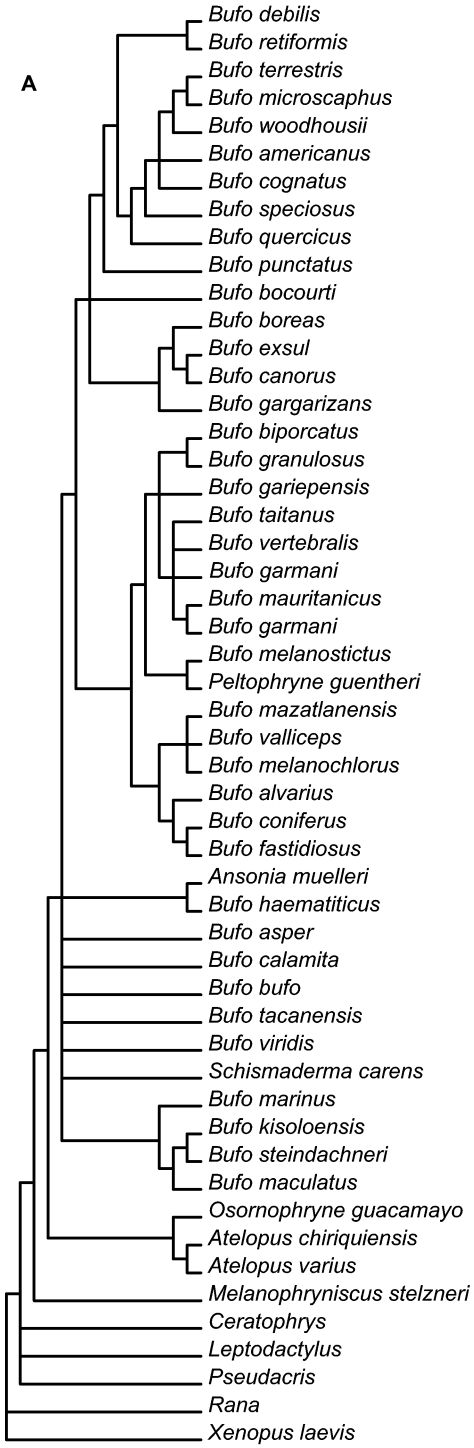

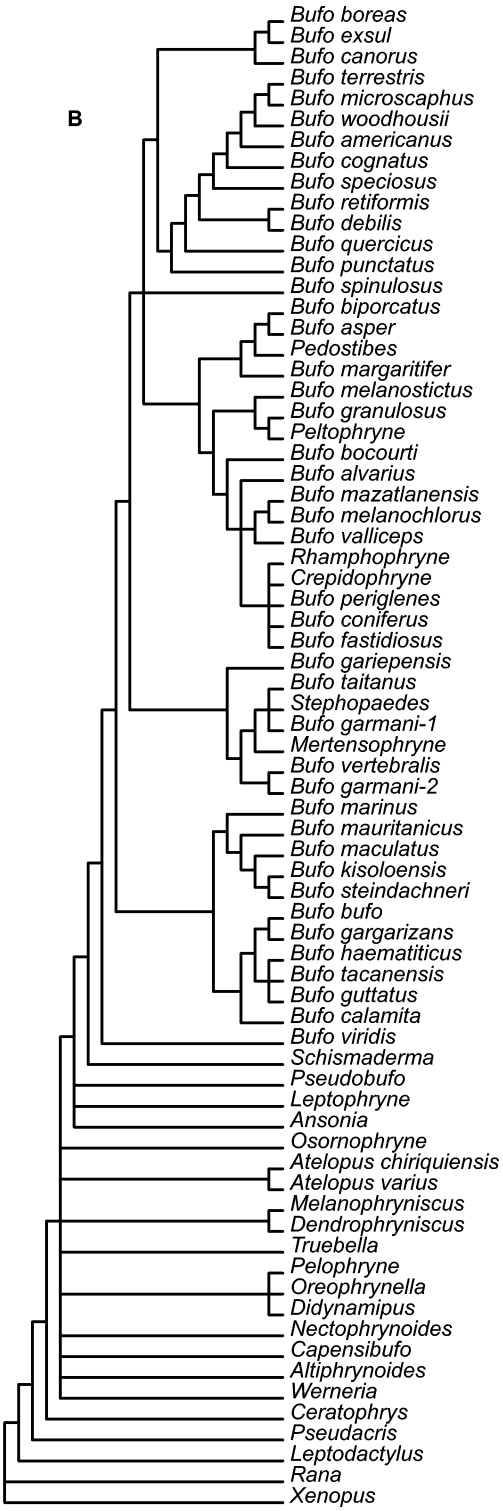

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clades, one containing *Phasmahyla* and *Phyllomedusa*, and the other containing the remaining genera (*Agalychnis*, *Hylomantis*, *Pachymedusa*, and *Phrynomedusa*). Our taxon sampling reflects this understanding: *Agalychnis callidryas*, *Cruziohyla calcarifer*, *Phasmahyla guttata*, and *Phyllomedusa vaillanti*.

BUFONIDAE (35 GENERA, 485 SPECIES): Bufonidae is a worldwide hyloid clade of noncontroversial monophyly, although the 35 genera for the most part are weakly diagnosed (e.g., *Andinophryne*, *Bufo*, *Crepidophryne*, *Pelophryne*, and *Rhamphophryne*). Ford and Canntella (1993) suggested the following synapomorphies for Bufonidae: (1) presence of a Bidder's organ (although absent in *Melanophryniscus* [Echeverria, 1998] and *Truebella* [Graybeal and Cannatella, 1995]); (2) unique pattern of insertion of the m. hyoglossus; (3) absence of the m. constrictor posterior (Trewevas, 1933); (4) teeth absent (also in some basal telmatobiines, *Allophryne*, some dendrobatids, and some rhacophorids); (5) origin of the m. depressor mandibulae solely from the squamosal and associated angle or orientation of the squamosal (Griffiths, 1954; also in several other anurans—see Manzano et al., 2003); (6) presence of an ''otic element'', an independent ossification in the temporal region that fuses to the otic ramus of the squamosal (Griffiths, 1954; also known in two genera of Ceratophryini, *Ceratophrys* and *Chacophrys*, but unknown in *Lepidobatrachus*—Wild, 1997, 1999). Ford and Cannatella (1993) considered characters 2–6 to be insufficiently surveyed but likely synapomorphic. Da Silva and Mendelson (1999) also noted the possibility that the possession of inguinal fat bodies and having a xiphisternum free from the underlying m. rectus abdominis are synapomorphies of Bufonidae, or some subtaxon of that group.

Dubois (1983, 1987 ''1985'') recognized five nominal subfamilies, not predicated on any phylogenetic hypothesis or, seemingly, any concern for monophyly (Graybeal and Cannatella, 1995; Graybeal, 1997).

Graybeal and Cannatella (1995) provided a discussion of the monophyly of most of the genera within Bufonidae that is extremely useful. They noted that many bufonid genera are monotypic and therefore not eligible for tests of monophyly: *Altiphrynoides* Dubois, 1987 ''1986''; *Atelophryniscus* McCranie, Wilson, and Williams, 1989; *Bufoides* Pillai and Yazdani, 1973; *Crepidophryne* Cope, 1889; *Didynamipus* Andersson, 1903, *Frostius* Cannatella, 1986; *Laurentophryne* Tihen, 1960; *Mertensophryne* Tihen, 1960; *Metaphryniscus* Señaris, Ayarzagüena, and Gorzula, 1994; *Pseudobufo* Tschudi, 1838; *Schismaderma* Smith, 1849; and *Spinophrynoides* Dubois, 1987 ''1986''.

Graybeal and Cannatella (1995) noted that many genera lack evidence of monophyly: *Adenomus* Cope, 1861 ''1860''; *Andinophryne* Hoogmoed, 1985; *Bufo* Laurenti, 1768; *Nectophrynoides* Noble, 1926; *Pedostibes* Günther, 1876 ''1875''; *Pelophryne* Barbour, 1938; *Peltophryne* Fitzinger, 1843; *Rhamphophryne* Trueb, 1971; *Stephopaedes* Channing, 1979 ''1978''; and *Wolterstorffina* Mertens, 1939. Graybeal and Cannatella (1995) noted the following genera to show evidence of monophyly: *Ansonia* Stoliczka, 1870; *Atelopus* Duméril and Bibron, 1841;

←

Fig. 25. **A,** Consensus tree of Bufonidae from Graybeal (1997). The tree reflects a parsimony analysis of DNA sequence data. Sequences used were primarily of mtDNA gene regions 12S and 16S (total of 1672 bp, aligned, for 50 species), with the addition of the protein coding mtDNA gene cytochrome *b* (390 bp for 19 species) and the nuDNA protein-coding gene *c-mos* (280 bp for 7 species). The protein-coding genes were aligned manually according to the amino-acid sequence, while the rDNA sequences were performed manually with reference to assumed secondary structure, with gaps excluded as evidence. Length of the component trees is 3,862 steps, ci = 0.305, ri = 0.392. Cunningham and Cherry (2004: 681) noted that her 16S DNA sequences of *Bufo garmani* (U52746) are *Bufo gutturalis*; her *Bufo vertebralis* (U52730) sequences are of *B. maculatus*, and her *B. maculatus* sequences are likely not of *B. maculatus*, but of another species, unidentified by them. **B,** Consensus tree of Bufonidae from Graybeal (1997) based on DNA sequence data (from A) and morphological data (undisclosed).

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Capensibufo Grandison, 1980; *Dendrophryniscus* Jiménez de la Espada, 1871 ''1870''; *Leptophryne* Fitzinger, 1843; *Melanophryniscus* Gallardo, 1961; *Nectophryne* Buchholz and Peters, 1875; *Nimbaphrynoides* Dubois, 1987 ''1986''; *Oreophrynella* Boulenger, 1895; *Osornophryne* Ruiz-Carranza and Hernández-Camacho, 1976; *Truebella* Graybeal and Cannatella, 1995; and *Werneria* Poche, 1903.

Graybeal (1997) provided the latest estimate of phylogeny within the entire Bufonidae. Unfortunately, although the morphological results were presented, the morphological data matrix and morphological transformation series were not, though they presumably are available in her unpublished dissertation (Graybeal, 1995). Her DNA sequence data and analytical methods are available, however. There have been serious reservations published about the quality of Graybeal's 16S sequence data (Harris, 2001; Cunningham and Cherry, 2004)[15] and the paper was largely a narrative largely focused on comparing parsimony, maximum-likelihood, and neighbor-joining techniques. For our discussion we present two of her trees that rest on analytical assumptions similar to our own: (1) a strict consensus of 82 equally parsimonious trees based on the unweighted molecular data alone (fig. 25A); and (2) her combined morphology + molecular tree (fig. 25B). Her molecular results suggest that, of the exemplars treated in that particular tree (fig. 25A), *Melanophryniscus* is the sister taxon of all other bufonids, and *Atelopus* + *Osornophryne* form the sister taxon of the remaining bufonids, excluding *Melanophryniscus*. (This would suggest that presence of a Bidder's organ is not a synapomorphy of Bufonidae, but of a smaller component of that taxon.) She also suggested that *Peltophryne* (the *Bufo peltocephalus* group) is far from other New World bufonids, that *Bufo gargarizans* is far from her other exemplar of the *B. bufo* group (*B. bufo*), and that the two members of the *B. viridis* group (sensu Inger, 1973), *B. calamita* and *B. viridis*, are isolated phylogenetically from each other. Nevertheless, resolution was not strongly corroborated. The combined morphology + molecular analysis provides less resolution at the base of the tree and placed *Bufo viridis* and *B. calamita* far apart, but it did resolve the *Bufo bufo* group as monophyletic (*B. bufo* and *B. gargarizans* being her exemplars). Beyond that, her results do not offer a great deal of resolution. Although Graybeal (1997; fig. 25) and, more recently Pauly et al. (2004; see ''Taxonomy of Living Amphibians'') provided estimates of bufonid phylogeny and started to delineate the paraphyly of ''*Bufo*'' within Bufonidae, taxonomy within ''*Bufo*'' remains largely parsed among similarity-based species groups (Blair, 1972b; Cei, 1972; Inger, 1972; R.F. Martin, 1972). These species groups have enjoyed considerable popularity and longevity of use, but, with exceptions, it is not clear whether their recognition continues to be helpful in promoting scientific progress, inasmuch as no attempt so far has been made to formulate these groups in phylogenetic terms.

Grandison (1981) provided a phylogenetic data set for African bufonids that she assumed were closely related to *Didynamipus*. Her data were reanalyzed and her tree was corrected by Graybeal and Cannatella (1995), and this tree is presented herein (fig. 26). On the basis of Grandison's (1981) evidence, Dubois (1987 ''1985'') partitioned former *Nectophrynoides* into four nominal genera: *Spinophrynoides* (with aquatic larvae), *Altiphrynoides* (with terrestrial larvae), *Nectophrynoides* (ovoviviparous), and *Nimbaphrynoides* (viviparous). Graybeal and Cannatella's (1995; fig. 26) reanalysis suggests, at least on the basis of Grandison's (1981) evidence, that ''*Nectophrynoides*'' (sensu stricto) remains paraphyletic. *Nectophryne* and *Wolterstorffina* also appear paraphyletic in this tree, although Graybeal and Cannatella (1995) suggested additional characters in support of the monophyly of *Nec-*

[15] Harris (2001) was unable to duplicate Graybeal's 16S sequences of *Bufo melanostictus* and *B. calamita*, although her sequences still are most similar to other GenBank sequences of these species. Cunningham and Cherry (2004) were unable to duplicate most of her 16S sequences for the taxa that Cunningham and Cherry (2004) studied; they suggested widespread sequencing errors in Graybeal's study. Whether the inclusion of better-quality sequences would change her results is unknown. Nevertheless, the problems with the DNA sequences and the nondisclosure of the morphological evidence require that her results not be accepted at face value.

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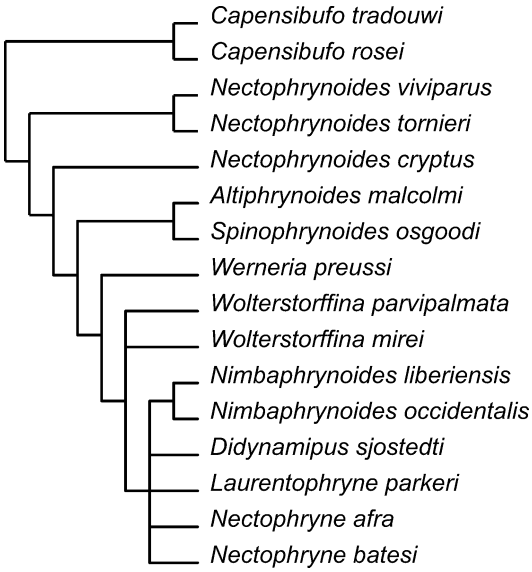

Fig. 26. Tree from Graybeal and Cannatella's (1995) parsimony reanalysis of Grandison's (1981) 24 transformation series of morphology for African bufonids suggested by Grandison (1981) to be related to *Didynamipus* (length = 79, ci = 0.45, ri = 0.68), rooted on a hypothetical ancestor. The taxonomy is updated to include generic changes made by Dubois (1987 ''1985'') subsequent to Grandison's study.

tophryne. This topology may be deeply flawed, however, because Graybeal's (1997) tree of morphology and molecules (fig. 25) show that among the exemplars shared with the study of Grandison (1981), *Altiphrynoides*, *Didynamipus*, *Nectophrynoides*, and *Werneria* are not necessarily particularly closely related. *Didynamipus*, in particular, is more closely related to Asian *Pelophryne* and South American *Oreophrynella* than to the others in the group addressed by Grandison (1981).

Cunningham and Cherry (2004) provided a DNA sequence study of putatively monophyletic African 20-chromosome *Bufo* (fig. 27). They suggested that the 20-chromosome toads form a monophyletic group with a reversal to 22-chromosomes in the *Bufo pardalis* group (their exemplars being *B. pardalis* and *B. pantherinus*). They also suggested that *Stephopaedes* and *Bufo lindneri* (a member of the *B. taitanus* group, long associated with *Mertensophryne* and *Stephopaedes*) form a monophyletic group, that on the basis of larval morphology also includes *Mertensophryne*. The sister taxon of this *Mertensophryne* group they suggested is the *Bufo angusticeps* group, with more distant relatives being the *Bufo vertebralis* group and *Capensibufo*.

Because of this lack of a corroborated global phylogeny of Bufonidae[16], we attempted to sample as widely as possible. The nominal bufonid taxa we, unfortunately, were unable to sample are *Adenomus*, *Altiphrynoides*, *Andinophryne*, *Atelophryniscus*, several of the species groups of nominal *Bufo*, *Bufoides*, *Churamiti*, *Crepidophryne*, *Frostius*, *Laurentophryne*, *Leptophryne*, *Mertensophryne*, *Metaphryniscus*, *Nimbaphrynoides*, *Oreophrynella*, *Parapelophryne*, *Pseudobufo*, and *Truebella*. Several of these (e.g., *Andinophryne*, *Bufoides*, and *Pseudobufo*) are likely imbedded within sampled genera.

At least some of the bufonids are descriptively firmisternal, such as *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, *Oreophrynella*, and *Osornophryne*. Others (*Leptophryne*) approach this condition (Laurent, 1986; but see Kaplan, 2004, for discussion of the various meanings of ''firmisterny''). Some bufonids exhibit various kinds of endotrophy: *Altiphrynoides* (nidicolous; M.H. Wake, 1980), *Didynamipus* (direct development; Grandison, 1981), *Laurentophryne* (direct development; Grandison, 1981), *Nectophryne* (nidicolous; Scheel, 1970), *Nectophrynoides* (oviductal-ovoviviparous; Orton, 1949), *Nimbaphrynoides* (viviparous; Lamotte and Xavier, 1972), *Oreophrynella* (direct development; McDiarmid and Gorzula, 1989), and *Pelophryne* (nidicolous; Alcala and Brown, 1982). Others are also suspected to have endotrophic larvae or direct development: *Crepidophryne*, *Dendrophryniscus*, *Frostius*, *Metaphryniscus*, *Osornophryne*, *Rhamphophryne*, *Truebella*, and *Wolterstorffina* (Peixoto, 1995; Thibaudeau and Altig, 1999). Unfortunately, our inability to sample any of these taxa other than *Didynamipus*, *Necto-*

[16] The study by Pauly et al. (2004) appeared during the writing phase of this study and therefore did not influence our taxon sampling. We comment on that paper in the Taxonomy section.

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phryne, *Nectophrynoides*, *Osornophryne*, *Pelophryne*, *Rhamphophryne*, and *Wolterstorffina* prevents us from elucidating the details of the evolution of life history in this group or the considerable morphological variation in bufonid larvae, including such things as fleshy accessory respiratory structures on the head (e.g., on *Stephopaedes*, *Mertensophryne*, *Bufo taitanus*) and flaps on the head (*Schismaderma*).

Regardless of the taxa we could not include, we were able to sample a worldwide selection of 62 bufonid species: *Ansonia longidigitata*, *A. muelleri*, *Atelopus flavescens*, *A. spumarius*, *A. zeteki*, *Bufo alvarius*, *B. amboroensis*, *B. andrewsi*, *B. angusticeps*, *B. arenarum*, *B.* cf. *arunco*, *B. asper*, *Bufo aspinia*, *B. biporcatus*, *B. boreas*, *B. brauni*, *B. bufo*, *B. camerunensis*, *B. celebensis*, *B. cognatus*, *B. coniferus*, *B. divergens*, *B. galeatus*, *B. granulosus*, *B. guttatus*, *B. gutturalis*, *B. haematiticus*, *B. latifrons*, *B. lemur*, *B. maculatus*, *B. margaritifer*, *B. marinus*, *B. mazatlanensis*, *B. melanostictus*, *B. nebulifer*, *B. punctatus*, *B. quercicus*, *B. regularis*, *B. schneideri*, *B. spinulosus*, *B. terrestris*, *B. tuberosus*, *B. viridis*, *B. woodhousii*, *Capensibufo rosei*, *C. tradouwi*, *Dendrophryniscus minutus*, *Didynamipus sjostedti*, *Melanophryniscus klappenbachi*, *Nectophryne afra*, *N. batesi*, *Nectophrynoides tornieri*, *Osornophryne guacamayo*, *Pedostibes hosei*, *Pelophryne brevipes*, *Rhamphophryne festae*, *Schismaderma carens*, *Stephopaedes anotis*, *Werneria mertensi*, and *Wolterstorffina parvipalmata*. This sampling, while not dense overall given the size of Bufonidae, allows a rigorous test of the monophyly and placement of Bufonidae among anurans, as well as a minimal test of the monophyly and relationships of many groups. Most important, the results, together with the obvious deficiencies in taxon sampling, will provide an explicit reference point for future, more thorough studies of the internal phylogenetic structure of Bufonidae.

RANOIDEA: Ranoidea is an enormous group of frogs, arguably monophyletic, grouped largely on the basis of one complex morphological character of the pectoral girdle (i.e., firmisterny, the fusion of the epicoracoid cartilages), except where considered to be nonhomologous (possibly Dendrobatidae, some bufonids and pipids; see Kaplan, 1994, 1995, 2000, 2001, 2004, for discussion). In addition, most ranoids are reported as diplasiocoelous, although the definitions of amphicoely, anomocoely, procoely, diplasiocoely, as well as ectochordy (= perichordy), epichordy, holochordy, and stegochordy (= epichordy) in frogs remains controversial[17]. Ranoidea contains noncontroversially Arthroleptidae, Astylosternidae, Hemisotidae, Hyperoliidae, Mantellidae, Microhylidae, Petropedetidae, Ranidae, and Rhacophoridae. More controversially included (see above) is Dendrobatidae, which is placed by various authors within Hyloidea. Haas (2003; fig. 15) did not recover Ranoidea as monophyletic in his analysis of larval characteristics, instead finding major ranoid groups (e.g., ranids, rhacophorids, hemisotids + hyperoliids + microhylids) interspersed among various hyloid groups (e.g., *Physalaemus*, *Pleurodema*, *Odontophrynus* + *Leptodactylus*, and bufonids). Discussing the evidence that supports the monophyly of the various ranoid groups is extremely difficult, partly because of the highly contingent nature of the evidence and, more commonly because historically the groups were assembled on the basis of overall similarity or special pleading for specific characteristics.

As understood by most workers, the questions regarding Ranoidea fall into two categories: (1) What are the phylogenetic relationships within Microhylidae?; and (2) What are the phylogenetic relationships within ''Ranidae'' (sensu lato as including all other ranoid subfamilial and familial taxa). The possibility of paraphyly of ''Ranidae'' (sensu lato) with respect to Microhylidae does not seem to have been considered seriously. We know of no definitive evidence that would reject this hypothesis, although microhylids predominantly have broadly dilated sacral diapophyses, a presumed ple-

[17] Several authors (Griffiths, 1959b, 1963; Tihen, 1965; Kluge and Farris, 1969) considered the amphicoelous-anomocoelous-procoelous-diplasiocoelous conditions delimited by Nicholls (1916) to have been oversimplified and over-generalized. See Kluge and Farris (1969) for discussion, but also see comments by J.D. Lynch (1973: 140) and Haas (2003: 74), who disagreed with various statements by Kluge and Farris, including their assertion regarding the continuum of variation between epichordy and perichordy.

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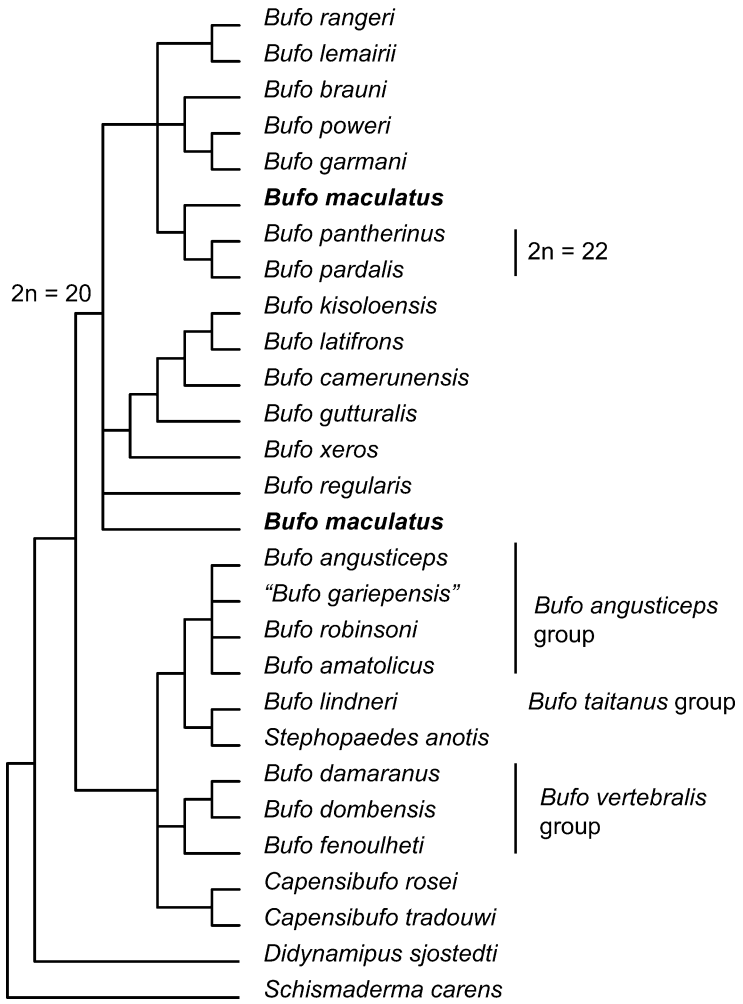

Fig. 27. Implied consensus of two most parsimonious trees of African toads studied by Cunningham and Cherry (2004), showing 22N → 20N transition point and reversal to 22N in the *Bufo pardalis* group, and alternative placements of *Bufo maculatus*. The underlying data are sequences from mtDNA (12S, 16S, ND2, and the tRNA genes flanking ND2) and nuDNA (ACTC and rhodopsin). Alignment of 12S and 16S were made initially with ClustalX (Thompson et al., 1997), costs not disclosed, and adjusted manually, guided by models of secondary structure. Alignment of coding, tRNA and intron sequences involved so few length variables that these were done manually. Gaps and missing data were treated as unknowns. Outgroups not show in tree: *Dendropsophus labialis* (Hylidae); *Euhyas cuneata* (Leptodactylidae: Eleutherodactylinae), *Limnodynastes dorsalis* (Limnodynastidae); *Heleophryne natalensis* (12S only; Heleophrynidae); *H. purcelli* (16S only; Heleophrynidae); *Nesomantis thomasetti* (Sooglossidae); *Rana temporaria* (Ranidae).

siomorphy, and ranoids predominantly have round sacral diapophyses (Noble, 1931; J.D. Lynch, 1973), although in the absence of an explicit cladogram the optimization of this transformation and the number of convergences is questionable. Nevertheless, we will restrict our comments to the ranoids, excluding microhylids, while noting that any study of ranoid phylogenetics must address the position of microhylids within the ranoid framework.

Within the nonmicrohylid ranoid group, modern progress in our understanding must be dated from the publication of Dubois

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(1981), in which he presented a discussion of ranoid nomenclature with reference to the attendant published morphological diversity of Ranidae as then understood. Although nonphylogenetic in outlook, subsequent papers by Dubois (1983, 1984b, 1987 ''1985'', 1992) provided workers with phenotypic groupings and a working taxonomy that in earlier manifestations, at least, were useful as rough approximations of phylogenetic groups. This approach was criticized for its lack of a phylogenetic rationale and overgeneralization of characters (Inger, 1996). But because there was little else with which to work, the taxonomies of Dubois have been influential. The most substantive differences between Dubois' classifications (e.g., Dubois, 1992, 2005) and those of other authors (e.g., Vences and Glaw, 2001) revolve around category-rank differences, particularly with respect to the rank and content of Rhacophoridae (variably including Mantellidae as a subfamily, or as Rhacophorinae placed as a subfamily within Ranidae or with Mantellidae and Rhacophoridae as distinct families), with the status of the various components of ''Ranidae'' left as an open question. With the exception of the recent papers by Marmayou et al. (2000) and Roelants et al. (2004), which dealt only with Asian taxa, and Van der Meijden et al. (2005), which focused on an African clade, no comprehensive attempt has been made to address the phylogenetics of the entire Ranoidea.

ARTHROLEPTIDAE, ASTYLOSTERNIDAE, AND HYPEROLIIDAE: Arthroleptidae, Astylosternidae, and Hyperoliidae are poorly understood African families that have been joined and separated by various authors (Dubois, 1981; Laurent, 1984b; Dubois, 1987 ''1985'', 1992) and even suggested to be related to at least two microhylid subgroups, Scaphiophryninae (Laurent, 1951) and Brevicipitinae (Van der Meijden et al., 2004). Ford and Cannatella (1993) regarded Arthroleptidae (sensu Dubois, 1981; including Astylosternidae) as a metataxon (Donoghue, 1985; Estes et al., 1988; Archibald, 1994), even though no evidence was suggested to support the monophyly of a group composed of Arthroleptidae and Astylosternidae and as originally proposed was considered to be paraphyletic (Laurent, 1951) with respect to Hyperoliidae (Hyperoliinae in Laurent's usage). Laurent (1986) suggested that the group composed of Arthroleptidae, Astylosternidae, and Hyperoliidae is distinguished from Ranidae (sensu lato) by having: (1) a cartilaginous metasternum without a bony style (presumably plesiomorphic at this level of generality); (2) second carpal free; (3) third distal tarsal free; (4) terminal phalanges generally hooked; (5) pupil usually vertical (usually horizontal in Hyperoliinae, although vertical in some—e.g., *Afrixalus*, *Heterixalus*, *Kassina*, *Phlyctimantis*; vertical in Leptopelinae); and (7) metatarsal tubercle absent or poorly developed. None of these characters is demonstrably synapomorphic.

ARTHROLEPTIDAE (SENSU DUBOIS, 1992; 3 GENERA, 49 SPECIES): Laurent and Fabrezi (1986 ''1985'') provided a discussion of the phylogeny of genera within this African taxon and suggested a relationship of (*Arthroleptis* + *Coracodichus*) + (*Cardioglossa* + *Schoutedenella*), although the evidence for this scenario is unclear. Like astylosternines and hyperoliids, arthroleptids possess a cartilaginous sternum, a vertical pupil (horizontal in most hyperoliines), and a free second distal carpal, all of which are questionable as to level of universality and polarity. The monophyly of this taxon has never been rigorously tested by phylogenetic analysis within a well-sampled larger group although Biju and Bossuyt (2003; fig. 21), on the basis of a relatively small sampling of frogs found Hyperoliidae to be polyphyletic, and Vences et al.'s (2003c; figs. 28, 29) analysis of mtDNA suggested that *Arthroleptis*, *Schoutedenella*, and *Cardioglossa* form a clade, either as the sister taxon of Astylosternidae + Leptopelinae, or as the sister taxon of Hyperoliinae. We sampled: *Arthroleptis tanneri*, *A. variabilis*, *Cardioglossa gratiosa*, *C. leucomystax*, *Schoutedenella schubotzi*, *S. sylvatica*, *S. taeniata*, and *S. xenodactyloides*. We were unable to sample a member of *Coracodichus* (if recognized as distinct from *Arthroleptis*). Within Arthroleptidae, *Arthroleptis*, *Schoutedenella*, and *Coracodichus* have direct development (Laurent, 1973), but *Cardioglossa* have free-living, feeding larva (Lamotte, 1961; Amiet, 1989; Altig and McDiarmid, 1999; Thibaudeau and Altig, 1999).

ASTYLOSTERNIDAE (5 GENERA, 29 SPECIES):

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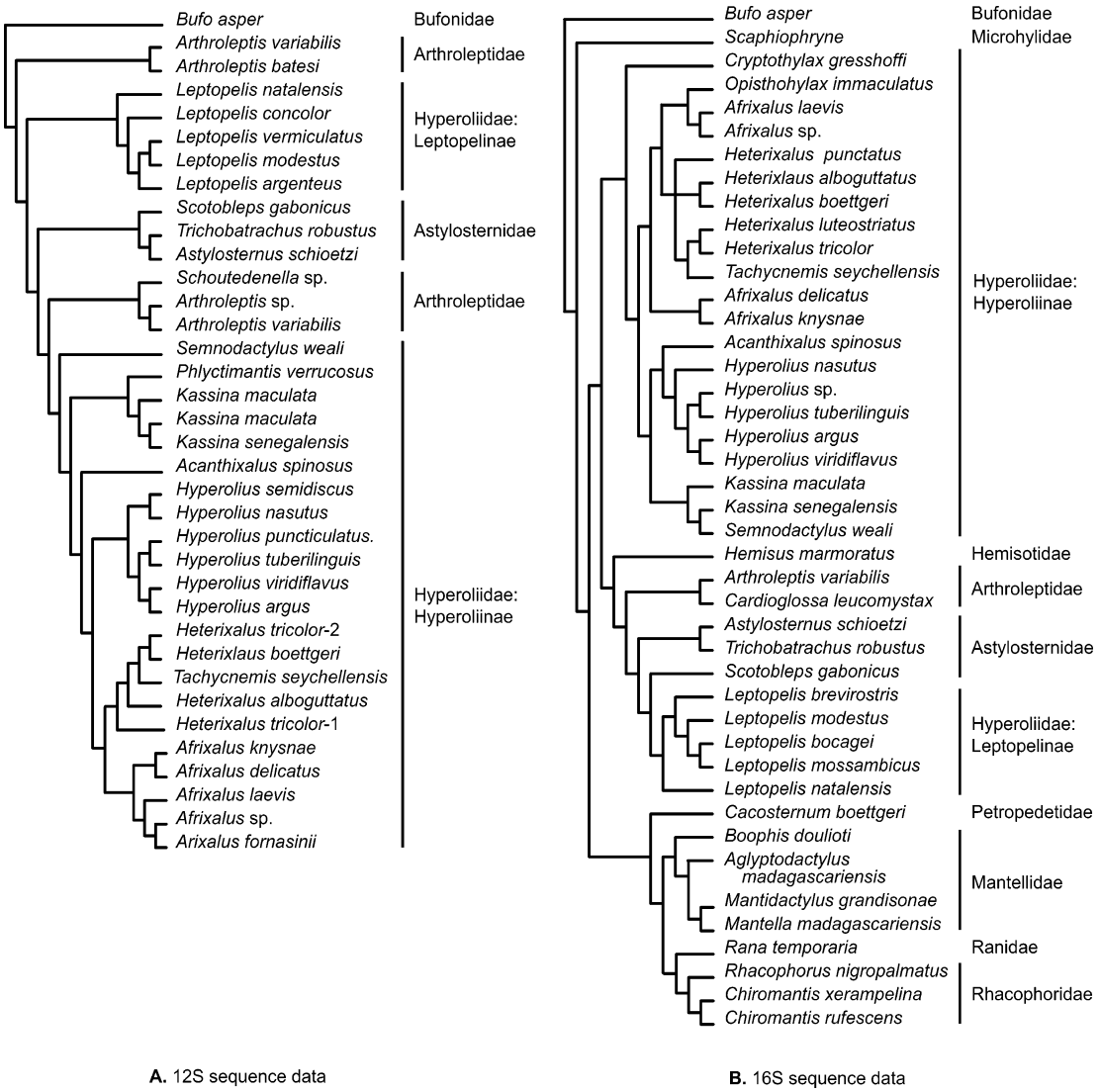

Fig. 28. Maximum-likelihood tree of hyperoliid, arthroleptid, and astylosternid frogs provided by Vences et al. (2003c). **A,** Maximum-likelihood analysis of 12S rRNA molecule (187 informative sites) analyzed under a GTR substitution model (cost functions reported) suggested by Modeltest (Posada and Crandall, 1998). Initial alignments under Clustal software, costs not disclosed, and subsequently adjusted manually. Highly variable regions and gaps were excluded as evidence. **B,** Maximum-likelihood trees based on 138 informative sites of 16S rRNA molecule under a GTR substitution model (cost functions reported) for hyperoliids, arthroleptids, and astylosternids. Initial alignments were made under Clustal, costs not disclosed, and subsequently adjusted manually. Highly variable regions and gaps sites were excluded as evidence.

The African Astylosternidae traditionally has been allied with Arthroleptidae and Hyperoliidae (see above), although the evidentiary justification for this appears to be overall similarity rather than synapomorphy. Like arthroleptines and hyperoliids, astylosternids have a cartilaginous sternum, a vertical pupil (except in *Leptodactylodon*), and a free second distal carpal, all of which are questionable as to level of universality. For our anal-

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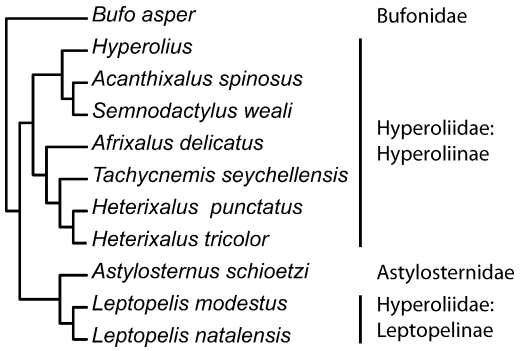

Fig. 29. Maximum-likelihood tree of Vences et al. (2003c), based on 566 informative sites of combined fragments of mitochondrial 16S, 12S rRNA, and cytochome *b*, analyzed under the assumptions of the Tamura-Nei substitution model (cost functions provided). Gaps were not treated as evidence.

ysis we sampled one species of each nominal genus: *Astylosternus schioetzi*, the presumably closely related *Trichobatrachus robustus*, and *Leptodactylodon bicolor*, *Nyctibates corrugatus*, and *Scotobleps gabonicus*. Vences et al. (2003c; figs. 28, 29) suggested on the basis of mtDNA evidence that Leptopelinae (Hyperoliidae) is either imbedded within a paraphyletic Astylosternidae or a paraphyletic Arthroleptidae, but they did not express this in the taxonomy. *Astylosternus* and *Trichobatrachus* have exotrophic aquatic larvae; in *Scotobleps*, the larva is unknown; and in *Leptodactylodon* the exotrophic aquatic larva has an upturned mouth presumably to feed on the surface film (Amiet, 1970).

HYPEROLIIDAE (18 GENERA, 2 SUBFAMILIES, 250 SPECIES): The African treefrogs of the family Hyperoliidae are currently divided into two subfamilies: Hyperoliinae, which is united by the presence of a gular gland (Drewes, 1984), and Leptopelinae, which was found by Vences et al. (2003c[18]; figs. 28, 29) to be more closely related to Astylosternidae than to Hyperoliinae. Vences et al. (2003c) further discussed some of the characters that Drewes (1984) used in his analysis of the family. Like Hyperoliinae, Leptopelinae lacks fusion of the second tarsal element and fusion of the second distal carpal (Drewes, 1984; fig. 30). Channing (1989) reanalyzed the morphological data provided by Drewes (1970; fig. 30) and provided different cladistic interpretations of these data; this reanalysis and the underlying characters were discussed in detail by J.A. Wilkinson and Drewes (2000). All hyperoliids for which it is known have free-living exotrophic larvae (Altig and McDiarmid, 1999). With the exception of a partial revision of *Hyperolius* (Wieczorek et al., 1998; Wieczorek et al., 2000, 2001), only the intergeneric relationships within Hyperoliidae have been addressed phylogenetically (Drewes, 1984; Channing, 1989; Richards and Moore, 1998) and paraphyly of *Hyperolius* and *Kassina* remain strong possibilities. Our genetic sampling included four species of the sole genus in Leptopelinae (*Leptopelis argenteus*, *L. bocagei*, *L.* sp., and *L. vermiculatus*). Of Hyperoliinae we were less complete, as we were not able to sample any member of *Callixalus*, *Chlorolius*, *Chrysobatrachus*, *Kassinula*, *Phlyctimantis*, or *Semnodactylus*. Nevertheless, we were able to obtain genetic samples of all remaining genera: *Acanthixalus spinosus*, *Afrixalus fornasinii*, *A. pygmaeus*, *Alexteroon obstetricans*, *Heterixalus* sp., *H. tricolor*, *Hyperolius alticola*, *H. puncticulatus*, *H. tuberilinguis*, *Kassina senegalensis*, *Nesionixalus thomensis* (transferred back into *Hyperolius* during the course of this study by Drewes and Wilkinson, 2004), *Opisthothylax immaculatus*, *Phlyctimantis leonardi*, and *Tachycnemis seychellensis*.

HEMISOTIDAE (1 GENUS, 9 SPECIES): Relationships of the African taxon Hemisotidae are also unclear (Channing, 1995). Like *Rhinophrynus* and *Brachycephalus*, *Hemisus* lacks a distinguishable sternum. Haas' (2003; fig. 15) study of larval morphology found it to be the sister taxon of Hyperoliidae among his exemplars. Blommers-Schlösser (1993) suggested on the basis of one morphological synapomorphy (median thyroid gland) that hemisotines should be united with brevicip-

[18] The various maximum-likelihood trees produced by this study (Vences et al., 2003c) were not shown. The authors provided trees of (1) 471 bp of the 16S rRNA; (2) combined analysis of 415 bp of the cytochrome *b* gene as well as 409 bp of the 12S and 997 bp of the 16S rRNA; and (3) 321 bp of the 12S rRNA gene. Taxon sampling among the three analyses was quite different and beyond the general conclusion that Hyperoliidae is polyphyletic, this sampling provided low resolution of intergeneric relationships.

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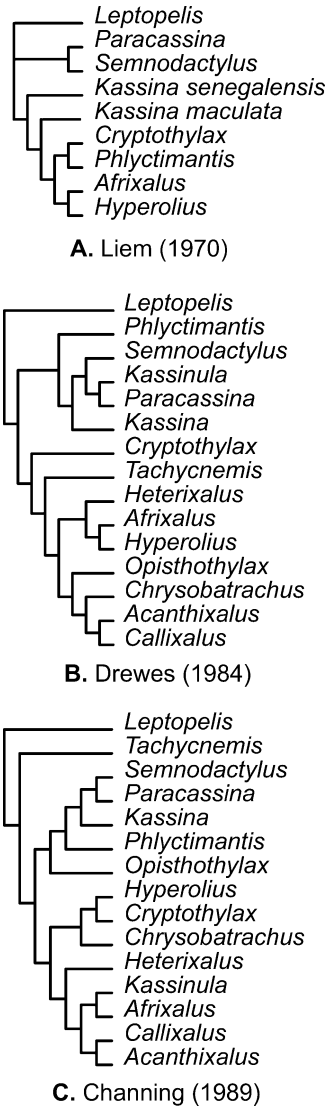

Fig. 30. Hyperoliid relationships suggested by **A,** Liem (1970) based on 36 dendritic to linear character transformations of morphology and assuming monophyly of a group composed of hyperoliids, mantellids, and rhacophorids, the tree rooted on a hypothetical ranid; **B,** Drewes' (1984) parsimony analysis of 27 morphological character transformations, rooted on a hypothetical ancestor constructed by comparison of a large number of ranids, astylosternids, and arthroleptids (*Semnodactylus* was treated as *Kassina weali* in this publication.); **C,** Channing's (1989) parsimony reanalysis (with minor modifications) of the morphological data of Drewes (1984).

itine microhylids. That hemisotines and brevicipitines are quite dissimilar cannot be disputed (Channing, 1995; Van Dijk, 2001), and the putative phylogenetic relationship between the two taxa was corroborated via molecular data only recently (Van der Meijden et al., 2004; fig. 31), although Loader et al. (2004) could not place with confidence *Hemisus* with brevicipitines on the basis of mtDNA sequence evidence. Emerson et al. (2000b) on the basis of mtDNA and a small amount of morphology also allied hemisotids with microhylids, although hemisotids retain a Type IV tadpole unlike the Type II tadpoles of microhylids (or direct development as in brevicipitines). We sampled only *Hemisus marmoratus*, one species of the single genus, of this morphologically compact taxon.

On the basis of the tree of Van der Meijden et al. (2004), Dubois (2005) recognized an enlarged family, Brevicipitidae, composed of six subfamilies: Astylosterninae, Arthroleptinae, Brevicipitinae, Hemisotinae, Hyperoliinae, and Leptopelinae. For our discussion we maintain the older, more familiar taxonomy.

MICROHYLIDAE (69 GENERA, 432 SPECIES): Microhylidae is a worldwide, arguably well-corroborated taxon (J.D. Lynch, 1973; Starrett, 1973; Blommers-Schlösser, 1975; Sokol, 1975, 1977; Wassersug, 1984; Haas, 2003; but see Van der Meijden et al., 2004 (fig. 31), who suggested that the taxon is paraphyletic with respect to the hemisotines), although the internal relationships of Microhylidae are certainly problematic (Burton, 1986; Zweifel, 1986, 2000). The subfamilial taxonomy or taxonomic differentia have not changed materially since the revision by Parker (1934), with the exception of the treatment of Phrynomeridae as a subfamily of Microhylidae by J.D. Lynch (1973), the inclusion of the Scaphiophryninae by Blommers-Schlösser (1975), and the demonstration of the evolutionary propinquity of Hemisotidae and Brevicipitinae by Van der Meijden et al. (2004; fig. 31). Beyond the isolation of brevicipitines from other microhylids, the allozyme data of Sumida et al. (2000a) suggest that the subfamilial definitions and generic assignments within nominal Genyophryninae and Asterophryninae may require change. Indeed, Savage (1973) had synonymized the

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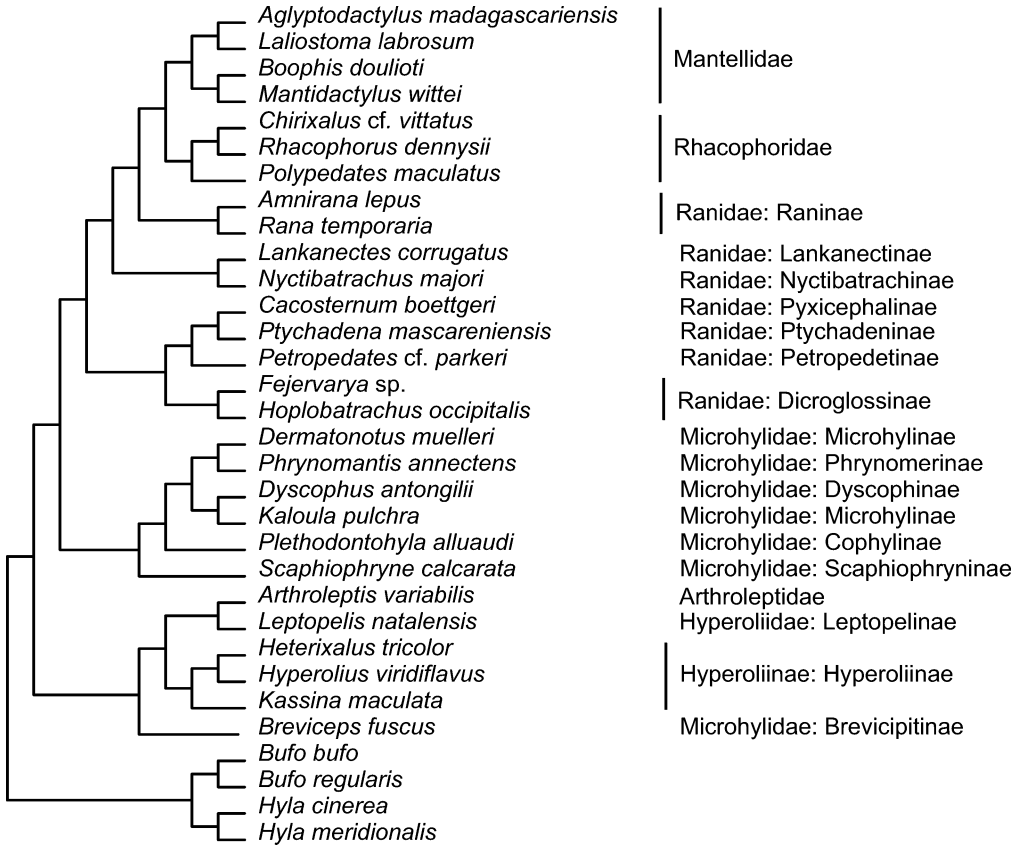

Fig. 31. Maximum-likelihood tree of various ranoids constructed by Van der Meijden et al. (2004) on the basis of 1,566 bp of the nuclear gene RAG-1. Sequence alignment was not reported. Cost functions of analysis were not provided nor which model of nucleotide evolution (as suggested by ModelTest; Posada and Crandall, 1998) was employed in the analysis. The tree was rooted on *Xenopus laevis*. We inserted the higher taxonomy on the right to allow easier comparison to other studies discussed in this section.

two subfamilies on the basis of their geographical and morphological similarity.

Savage (1973) suggested that Dyscophinae is polyphyletic, with the Asian *Calluella* more closely related to asterophryines than to the Madagascan *Dyscophus*. Blommers-Schlösser (1976) reviewed the controversy and retained *Dyscophus* and *Calluella* in Dyscophinae. Our taxon sampling allows us to test whether Dyscophinae is monophyletic or diphyletic.

Ford and Cannatella (1993) identified five larval synapomorphies for Microhylidae (although these cannot be documented in lineages with direct development such as in brevicipitines, asterophryines, and genyophrynines, so the level of universality of these characters is questionable): (1) absence of keratodonts in tadpoles; (2) ventral velum divided medially; (3) glottis fully exposed on buccal floor; (4) nares not perforate; and (5) secretory ridges of branchial food traps with only a single row of secretory cell apices. In addition, adults are characterized as having 2–3 palatal folds (palatal folds also being found in *Hemisus*). Van de Meijden et al. (2004) suggested on the basis of molecular evidence that Hemisotidae + Brevicipitinae is more closely related to Hyperoliidae, Arthroleptidae, and Astylosternidae than to an otherwise monophyletic group of microhylids (fig. 31). Therefore, the only articulated questions so far regarding the monophyly of Microhylidae are whether Hemisotidae is im-

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bedded within it (see above) or, with Brevicipitinae, more closely related to non-microhylid groups, although the definition, historical reality, and content of the various subfamilies are controversial.

SCAPHIOPHRYNINAE (2 GENERA, 11 SPECIES): The Madagascan microhylid subfamily Scaphiophryninae has no demonstrable synapomorphies in support of its monophyly, but if its monophyly is assumed it is widely considered to be the sister taxon of the remaining Microhylidae. At least some authors (e.g., Dubois, 1992) regard it as a distinct family. Ford and Cannatella (1993) suggested that larval synapomorphies that place it in association with the remaining Microhylidae (at least for those that have larvae) are (1) the possession of a median spiracle in the larvae; (2) gill filaments poorly developed or absent; (3) modifications of buccal pumping mechanisms (short lever arm on ceratohyal, small buccal floor area); (4) absence of m. suspensoriohyoideus; and (5) lack of separation of the mm. quadrato-, hyo-, and suspensorioangularis. Parker (1934) reported the taxon as diplasiocoelus like most other ranoids, although he noted Hoplophryninae (*Parhoplophryne* + *Hoplophryne*), Asterophryinae, and some members of his Microhylinae (e.g., *Melanobatrachus*, *Metaphrynella*, *Myersiella*, *Phrynella*) as procoelous. Parker (1934) noted that *Scaphiophryne* retains a complete sphenethmoid, thereby excluding it from Microhylidae, which, as he applied the name, included only those taxa where the sphenethmoid is either in two parts, or, more rarely, not ossified at all. Haas (2003) suggested on the basis of larval morphology that Scaphiophryninae is polyphyletic, with *Scaphiophryne* forming the sister taxon of the remaining microhylids, and *Paradoxophyla* more closely related to Phrynomerinae. Clearly the monophyly of this taxon is controversial, but we, unfortunately, were unable to sample *Paradoxophyla* and so could not test the monophyly of Scaphiophryninae. We were able to obtain only a representative of the other genus, *Scaphiophryne marmorata*. Our results regarding the Scaphiophryninae will therefore remain incomplete.

ASTEROPHRYINAE (8 GENERA, 64 SPECIES) AND GENYOPHRYNINAE (11 GENERA, 142 SPECIES): Zweifel (1972) and Burton (1986) last reported on phylogenetics of the Australo-Papuan Asterophryinae (fig. 32). Genyophryninae is also Australo-Papuan but extends into the Philippines and Lesser Sundas. No major revision or broad-scale phylogenetic study has appeared since Parker (1934), although Burton (1986) did suggest evidence that it is paraphyletic with respect to Asterophryinae. Sumida et al. (2000a) noted that some allozyme evidence suggested that Asterophryinae is imbedded within a paraphyletic Genyophryninae. Savage (1973) considered Genyophryninae to be part of Asterophryinae based on the dubious nature of the procoely–diplasiocoely distinction; that they share direct-development; and, in part, that

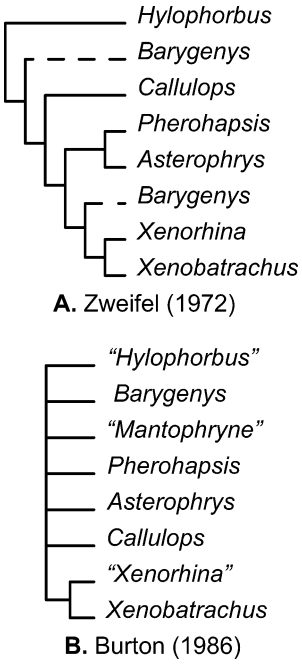

Fig. 32. Trees of Asterophryinae suggested by **A,** Zweifel (1972), based on 9 morphological transformation series and showing alternative positions of *Barygeny* (tree rooted on a generalized primitive hypothetical ancestor); and **B,** Burton (1986), based on a subjective evaluation of 54 transformation series of morphology. This tree relects our understanding of Burton's narrative summary of asterophryine relationships, with the nomenclature updated (*Callulops* replacing *Phrynomantis*). Quotation marks denote nonmonophyly.

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they are both biogeographically centered in New Guinea.

Zweifel (1971) summarized the distinction between the subfamilies as (1) maxillae often overlapping the premaxillae and usually in contact anteriorly (Asterophryinae; this presumably is apomorphic), maxillae not overlapping the premaxillae (Genyophryninae); (2) vertebral column diplasiocoelous (rarely procoelous; Asterophryinae), procoelous (Genyophryninae); and 3) tongue subcircular, entirely adherent, often with a median furrow and posterior pouch (Asterophryinae), tongue oval, half-free behind, no trace of a median furrow or pouch (Genyophryninae; shared with Cophylinae). Genyophryninae and Asterophryinae share direct development (Zweifel, 1972; Thibaudeau and Altig, 1999). Our sampling will allow us to test the hypotheses of relationship so far published and elucidate the possible paraphyly of Genyophryninae. Unfortunately, we could sample only one species of Asterophryinae, *Callulops slateri*, which will not allow us to test its monophyly. The effect of excluding representatives of *Asterophrys*, *Barygenys*, *Hylophorbus*, *Mantophryne*, *Pherohapsis*, *Xenobatrachus*, and *Xenorhina* is unknown.

Of Genyophryninae, we were able to sample *Aphantophryne pansa*, *Choerophryne* sp., *Cophixalus sphagnicola*, *Copiula* sp., *Genyophryne thomsomi*, *Liophryne rhododactyla*, *Oreophryne brachypus*, and *Sphenophryne* sp. We were unable to sample *Albericus*, *Austrochaperina*, *Oreophryne*, or *Oxydactyla*.

BREVICIPITINAE (5 GENERA, 22 SPECIES): Like the Australo-Papuan Asterophryninae and Genyophryninae, the African Brevicipitinae has direct development (Parker, 1934; Thibaudeau and Altig, 1999). Parker (1934) considered the subfamily to be distantly related to all other microhylid taxa and characterized by the retention of a medially expanded vomer. Parker (1934) reported the taxon as diplasiocoelus like most other ranoids. The species within the subfamily are closely similar and unlike all other microhylids in general habitus, although the monophyly of the group has never been tested rigorously.

Blommers-Schlösser (1993) suggested (the presence of a median thyroid gland being the sole synapomorphy) that brevicipitines should be united with hemisotids (but see Channing, 1995, who considered this change premature at the time because of the otherwise trenchant differences between them). Van der Meijden et al. (2004; fig. 31) and Loader et al. (2004) provided molecular data in support of a hemisotid–brevicipitine relationship. Of the nominal genera we were unable to sample the monotypic *Balebreviceps* and *Spelaeophryne*. The effect of excluding these taxa is unknown, although Loader et al. (2004) recovered *Spelaeophryne* in a clade with *Probreviceps* and *Callulina*, to the exclusion of *Breviceps*. We were able to sample at least one species of the remaining nominal genera: *Breviceps mossambicus*, *Callulina kisiwamitsu*, *C. kreffti*, and *Probreviceps macrodactylus*. Because there are 13 species of *Breviceps* and 3 species of *Probreviceps*, we were unable to test rigorously the monophyly of these taxa.

COPHYLINAE (7 GENERA, 41 SPECIES): The Madagascan Cophylinae is similar to Dyscophinae and Genyophryninae in retaining maxillary and vomerine teeth (except in *Stumpffia*) but differs from Dyscophinae in having procoelous vertebrae and from Dyscophinae and Genyophryninae in having a divided vomer (Parker, 1934); none of the characters is demonstrably synapomorphic. Blommers-Schlösser and Blanc (1993) provided a cladogram (fig. 33A) of the genera based on nine morphological characters, in which they suggested that *Plethodontohyla* was paraphyletic and that *Platypelis* did not have apomorphies to assure its monophyly. Andreone et al. (2004 ''2005'') recently provided a maximum likelihood analysis of 1173 bp of mtDNA (fig. 33B), in which he documented *Plethodontohyla* paraphyly. Because these sequences became available after our analyses were completed, we did not sample *Cophyla*, *Madecassophryne*, or *Rhombophryne*. The effect of this on the placement of the subfamily will remain unknown, although we did sample four species of the four remaining genera: *Anodonthyla montana*, *Platypelis grandis*, *Plethodontohyla* sp., and *Stumpffia psologlossa*. Unfortunately, because of our limited sampling we will not be able to test rigorously the results of either Blommers-Schlösser and Blanc

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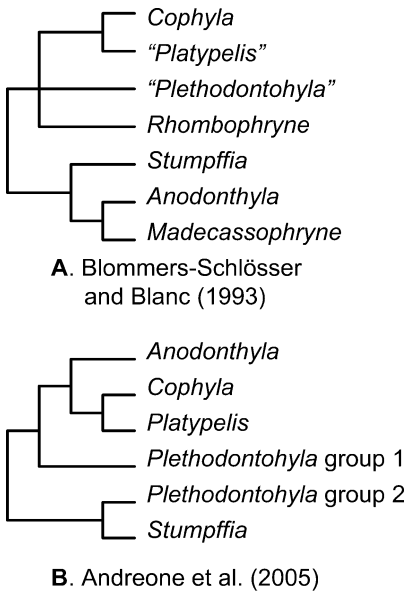

Fig. 33. Trees of Cophylinae suggested by **A,** Blommers-Schlösser and Blanc (1993), on the basis of nine morphological transformation series, rooted (by implication) on Dyscophinae and Scaphiophryninae. The figure is redrawn with branches collapsed that were unsupported by evidence in the original; **B,** Andreone et al. (2004 ''2005''), based on 1,173 bp of 12S and 16S rRNA mtDNA. This tree is redrawn to note only monophyletic genus-group taxa. Alignment was made using the Clustal option in Sequence Navigator (Applied Biosystems), with cost functions for alignment not provided. All sections that could not be aligned, including those with three of more gaps in one or more taxa, were excluded from analysis. Whether gaps were treated as unknown or evidence was not stated. The Tamura-Nei substitution model was selected for maximum-likelihood analysis of aligned data. The tree was rooted on *Scaphiophryne* (not shown). Quotation marks around names denotes nonmonophyly.

(1993) or Andreone et al. (2004 ''2005''). Species of Cophylinae have nidicolous larvae (Blommers-Schlösser and Blanc, 1991; Glaw and Vences, 1994).

DYSCOPHINAE (2 GENERA, 10 SPECIES): The Madagascan Dyscophinae is distinguished from most other microhylid subfamilies by retaining maxillary and vomerine teeth, otherwise known only in Cophylinae and Genyophryninae, both of which are procoelous rather than diplasiocoelous (Parker, 1934) as in Dyscophinae. Savage (1973) had regarded *Calluella* as associated with the direct-developing Asterophryinae and any similarities with *Dyscophus* as reflecting plesiomorphy. We sampled one species each of the two nominal genera: *Calluella guttulata* and *Dyscophus guineti*.

MELANOBATRACHINAE (3 GENERA, 4 SPECIES): On the basis of geography alone (East Africa [2 genera] and southern India [1 genus]), one would suspect that this is not a monophyletic taxon. Nevertheless, the three genera share an incomplete auditory apparatus (convergent in *Balebreviceps* [Brevicipitinae]; Largen and Drewes, 1989) and fusion of the sphenethmoid with the parasphenoid (Parker, 1934). Savage (1973), followed by Laurent (1986) and Dubois (2005), placed *Melanobatrachus* in Microhylinae and retained *Hoplobatrachus* and *Parhoplophryne* in Hoplophryninae, but did so only by discarding absence of the auditory apparatus and fusion of the sphenethmoid to the parasphenoid, as convergences, without offering specific characters that conflicted with these as synapomorphies. Although we are suspicious of the monophyly of this taxon, we stick with the most parsimonious hypothesis (monophyly of Melanobatrachinae, sensu lato) until alternative evidence emerges.

Apparently based on information provided for *Hoplophryne* by Barbour and Loveridge (1928) and Noble (1929), Parker (1934) generalized that all members of his Melanobatrachinae lack a free-swimming tadpole, the larvae with ''metamorphosis taking place on land, but not in an egg''. No reproductive or developmental data on *Parahoplophryne* or *Melanobatrachus* have been published (Daltry and Martin, 1997). Thibaudeau and Altig (1999) listed *Melanobatrachus* and *Parhoplophryne* as having endotrophic larvae, presumably because of the earlier statement by Parker (1934). McDiarmid and Altig (1999: 13), however, listed *Hoplophryne* as exotrophic, because Barbour and Loveridge (1928: 256) reported vegetable matter in the guts of larvae and because R. Altig examined AMNH larvae of *Hoplophryne* and inferred that they could feed (R.W. McDiarmid, personal commun.). Laurent (1986) reported the taxon (*Parhoplophryne* and *Hoplophryne* in his Hoplophrynnae; *Melanobatrachus* in his Microhylinae) as procoelous, unlike most

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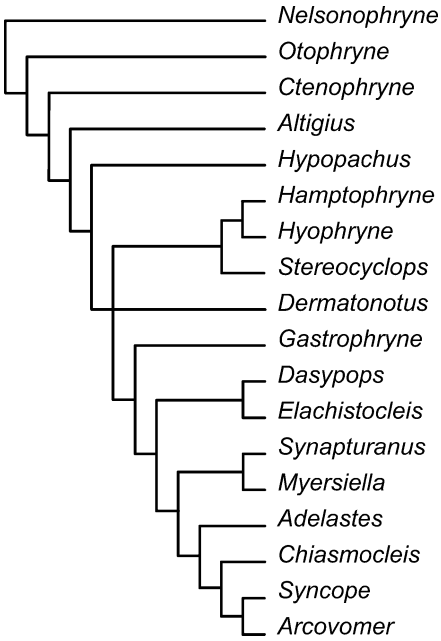

Fig. 34. Tree of New World microhylids by Wild (1995) based on a parsimony analysis of 14 morphological transformations series, outgroups and evidence for ingroup monophyly not specified.

other ranoids so this may also be synapomorphic. Unfortunately, we were able to sample only *Hoplophryne rogersi* and so will not be able to comment on the monophyly of Melanobatrachinae.

MICROHYLINAE (30 GENERA, 133 SPECIES): The American and tropical Asian Microhylinae have free-swimming tadpoles (except for a few species, such as *Myersiella microps*, that have direct development; Izecksohn et al., 1971). Although microhylines can be morphologically characterized, they have no known synapomorphies, and their monophyly is deeply suspect. According to Parker (1934), maxillary and vomerine teeth are absent (as in several other extra-Madagascar subfamilies); the vomer is much reduced and usually divided; the sphenethmoid is divided or absent; and the vertebrae are diplasiocoelous (or rarely procoelous). Wild (1995) provided a cladogram of New World genera (fig. 34), but this assumed that the New World group is monophyletic and was unclear about the outgroup(s) used to polarize the transformations. Laurent (1986) treated the Old World and New World components separately, implying some kind of taxonomic division. This was followed, without discussion, by Dubois (2005), who recognized Gastrophryninae for the New World component and Microhylinae for the Old World component. We are not aware of any evidence in support of this arrangement so we retain the old taxonomy. Of the 30 nominal genera we were able to sample representatives of 14: *Chaperina fusca*, *Ctenophryne geayei*, *Dasypops schirchi*, *Dermatonotus muelleri*, *Elachistocleis ovalis*, *Gastrophryne elegans*, *G. olivacea*, *Hamptophryne boliviana*, *Kalophrynus pleurostigma*, *Kaloula pulchra*, *Microhyla heymonsi*, *Microhyla* sp., *Micryletta inornata*, *Nelsonophryne aequatorialis*, *Ramanella obscura*, and *Synapturanus mirandaribeiroi*). We were not able to sample *Adelastes*, *Altigius*, *Arcovomer*, *Chiasmocleis*, *Gastrophrynoides*, *Glyphoglossus*, *Hyophryne*, *Hypopachus*, *Metaphrynella*, *Myersiella*, *Otophryne*, *Phrynella*, *Relictovomer*, *Stereocyclops*, *Syncope*, and *Uperodon*. Most of these appear to be clustered with sampled taxa. The exclusion of *Otophryne* and *Uperodon*, however, is particularly regrettable. Our sampling will not allow detailed elucidation of the evolution of life-history strategies. *Adelastes*, *Altigius*, *Gastrophrynoides*, *Hyophryne*, *Kalophrynus* (nidicolous), *Myersiella* (direct development), *Phrynella*, *Synapturanus* (nidicolous), and *Syncope* (nidicolous) have endotrophic larvae that exhibit (or are suspected to exhibit) various degrees of truncation of larval development (Thibaudeau and Altig, 1999). That we lack representatives of about half of these is lamentable, but our results will provide an explicit starting point for future, more detailed studies. The remaining genera have exotrophic larvae of typical microhylid morphology (Altig and McDiarmid, 1999).

PHRYNOMERINAE (1 GENUS, 5 SPECIES): The African Phrynomerinae is diagnosable from Microhylinae solely by possessing intercalary cartilages between the ultimate and penultimate phalanges (Parker, 1934). Like most other ranoids it is diplasiocoelous. Of this small taxon we sampled *Phrynomantis bifasciatus*. *Phrynomantis* typically has aquatic, exotrophic microhylid larvae (Altig and McDiarmid, 1999).

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''RANIDAE'' (CA. 54 GENERA, 772 SPECIES): Ranidae is a large ranoid taxon, that is likely paraphyletic with respect to Mantellidae and Rhacophoridae—at least on the basis of molecular evidence (Vences and Glaw, 2001; Roelants et al., 2004; Van der Meijden et al., 2005). Ford and Cannatella (1993; fig. 14) suggested that the group is paraphyletic, or, at least, that it does not have recognized synapomorphies. Nevertheless, Haas (2003; fig. 15) suggested the following to be synapomorphies for Ranidae, excluding other ranoids: (1) cartilaginous roofing of the cavum cranii present as taenia transversalis and medialis; (2) free basihyal present; and (3) firmisterny (convergent elsewhere in Haas' tree).

Laurent (1986) included the mantellines and rhacophorids in his Ranidae, a content that allows at least two other characters (distinctly notched tongue and bony sternal style) to be considered as possible synapomorphies (Ford and Cannatella, 1993). (These are, however, incongruent with characters suggested by Haas, 2003).

Dubois and coauthors (Dubois, 1992; Dubois and Ohler, 2001; Dubois et al., 2001; Dubois, 2005) suggested a taxonomy of 11–14 subfamilies of uncertain monophyly or relationship with respect to each other. For discussion, we recognize Dubois' subfamilies, except as noted. As discussed by Inger (1996), the diagnostic features supporting Dubois' (1992) classification at the time of that writing frequently reflected overgeneralized and postfacto approximations for clusters that were aggregated with overall similarity, not synapomorphy, as the organizing principle. The relationships suggested by this taxonomy (and Dubois, 2005, as well) can be at variance with evidence of monophyly, notably evidence from DNA sequences (Emerson and Berrigan, 1993; Bossuyt and Milinkovitch, 2000; Emerson et al., 2000b; Marmayou et al., 2000; Biju and Bossuyt, 2003; Roelants et al., 2004), so this taxonomy requires careful evaluation.

CERATOBATRACHINAE (6 GENERA, 81 SPECIES): Ceratobatrachinae is composed of direct-developing species found from western China (i.e., *Ingerana*) to the Indo-Australian archipelago (*Batrachylodes*, *Discodeles*, *Palmatorappia*, *Platymantis*, and the monotypic *Ceratobatrachus*). Ceratobatrachinae represents the direct-developing part of Cornuferinae sensu Noble (1931) and Platymantinae of later authors (e.g., Savage, 1973; Laurent, 1986). Those taxa formerly included in Cornuferinae or Platymantinae that exhibit unforked omosterna and/or free-living tadpoles (what are now *Amolops*, *Huia*, *Meristogenys*, *Staurois*, *Hylarana* [sensu lato], and *Micrixalus*) are now placed in Raninae or Micrixalinae. *Batrachylodes* is inferred to have direct development (Noble, 1931; Brown, 1952; Duellman and Trueb, 1986; Thibaudeau and Altig, 1999), but unlike other members of Ceratobatrachinae, *Batrachylodes* has an entire omosternum (rather than being forked). Noble (1931) regarded *Batrachylodes* as derived from his *Cornufer* (= *Platymantis*) and, by inference, exhibiting direct development. Because of the character conflict of omosternum shape and life-history, Brown (1952) regarded *Batrachylodes* as related either to ''*Hylarana*'' (exotrophic, entire omosternum) or to the *Ceratobatrachus* group (direct-developing, forked omosternum). Laurent (1986) treated *Batrachylodes* as a member of Raninae, although Boulenger (1920) had noted the intraspecific plasticity of omosternum shape, the only evidence supporting placement of *Batrachylodes* in Raninae. This arrangement was accepted by Dubois (1987 ''1985''), although subsequently, Dubois (2005) transferred *Batrachylodes* out of Raninae and into Ceratobatrachinae, presumably on the basis of the direct development. Our analysis should provide more evidence on the placement of this taxon.

Dubois (1992) recognized Ceratobatrachini within his Dicroglossinae, but later (Dubois et al., 2001) considered it to be a subfamily, of unclear relationship to Dicroglossinae. Even later, Dubois (2003) stated, on the basis of unpublished molecular data, that Ceratobatrachini is a tribe within Dicroglossinae. Van der Meijden et al. (2005) presented DNA sequence evidence that *Ceratobatrachus* is outside of Dicroglossinae, and on that basis (Dubois, 2005) once again embraced the subfamilial rank Ceratobatrachinae. Roelants et al. (2004; fig. 35), in a study of predominantly Indian taxa, provided molecular evidence that suggest that *Ingerana* is

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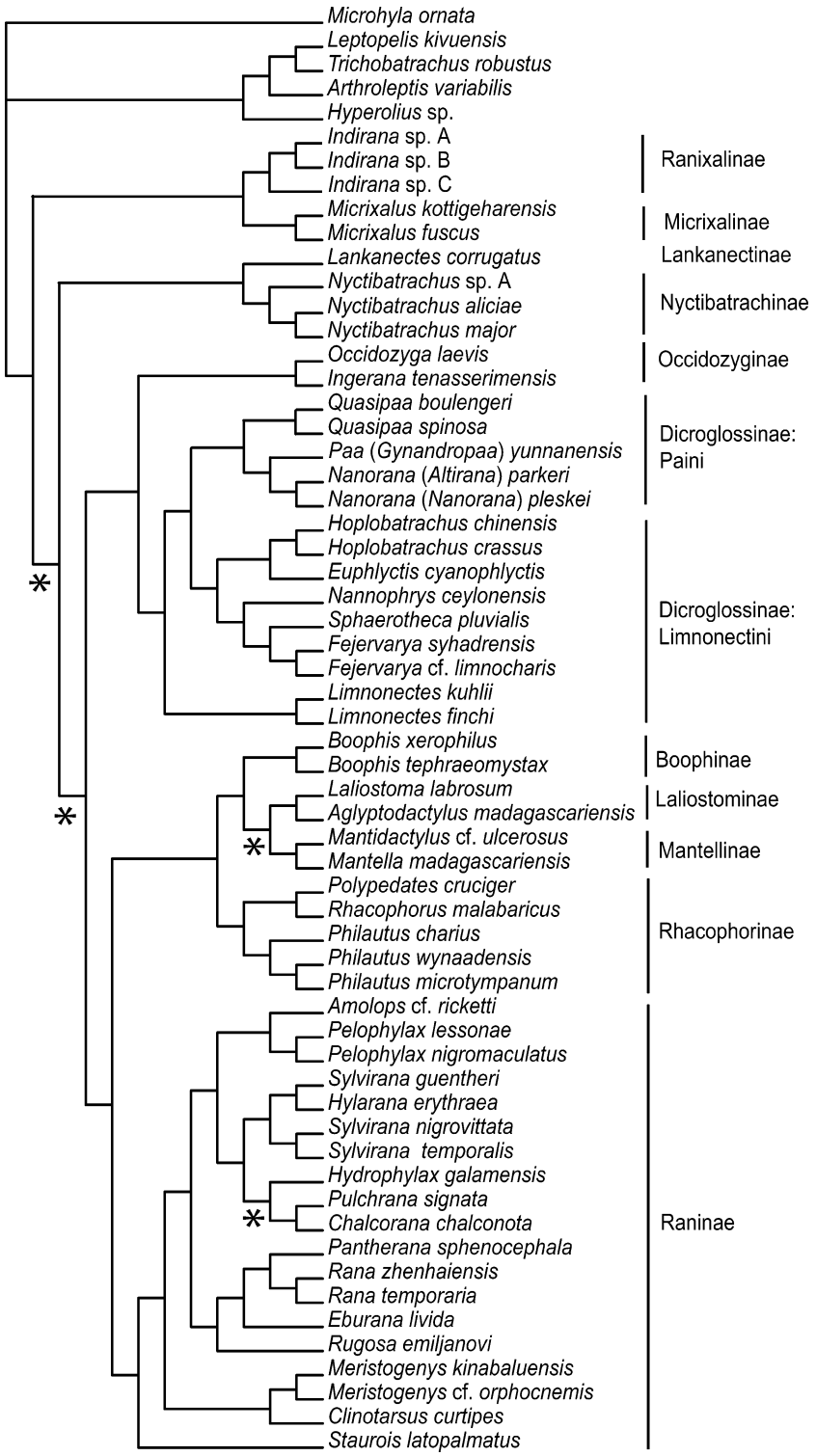

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in Occidozyginae, rather than in Ceratobatrachinae, although Dubois (2005), without discussion, did not accept this.

Of this group we sampled *Batrachylodes vertebralis*, *Discodeles guppyi*, *Ceratobatachus guentheri*, *Platymantis pelewensis*, *P. weberi*, and *Ingerana baluensis*. Thus, we only lack *Palmatorappia* from this group[19]. Although we obviously cannot test the monophyly of these individual genera (except *Platymantis*), our taxon sampling is adequate to test the monophyly of the inclusive group.

CONRAUINAE (1 GENUS, 6 SPECIES): Until the recent publication by Dubois (2005), this genus (*Conraua*) had been placed on the basis of overall similarity in a monotypic tribe, Conrauini, in Dicroglossinae (Dubois, 1992). Conrauini was proposed (Dubois, 1992) for the West African genus *Conraua*, the diagnostic characters being the retention of a free-living tadpole stage (plesiomorphic), with a larval keratodont formula of 7–8/6–11 (see Dubois, 1995, for the definition of keratodont formula) and lateral line not retained into adulthood (plesiomorphic). Van der Meijden et al. (2005; fig. 36), on the basis of DNA sequence data, showed that *Conraua* is not close to Dicroglossinae but the sister taxon to a taxonomically heterogeneous group of southern African ranoids, including *Afrana*, *Cacosternum*, *Natalobatrachus*, *Petropedetes*, *Pyxicephalus*, *Strongylopus*, and *Tomopterna*. Kosuch et al. (2001; figs. 38, 39), on a relatively small amount of evidence, had previously placed *Conraua* alternatively as either the sister taxon of *Limnonectes* (based on 16S alone) or as the sister taxon of *Tomopterna* + *Cacosternum* (based on combined 12S and 16S). The latter result was suggestive of the more complete results of Van der Meijden et al. (2005). Although characters have not been suggested that are clearly synapomorphic, the group is morphologically compact and monophyly is likely. Of the six species we sampled two: *Conraua robusta* and *C. goliath*.

DICROGLOSSINAE (12 GENERA, 152 SPECIES): Recounting the taxonomic history of Dicroglossinae is difficult inasmuch as it was originally formed on the basis of overall similarity, and the content has varied widely, even by the same authors. Only recently has its concept begun to be massaged by phylogenetic evidence. Dubois (1987 ''1985'', 1992) diagnosed Dicroglossinae (in the sense of including Conrauinae and excluding Paini) as having the omosternum moderately or strongly bifurcate at the base and the nasals usually large and in contact with each other and with the frontoparietal, although none of these characters is demonstrably synapomorphic. The most recent taxonomy of Dicroglossinae (Dubois, 2005) recognized four tribes: Dicroglossini (for *Euphlyctis*, *Fejervarya*, *Hoplobatrachus*, *Minervarya*, *Nannophrys*, and *Sphaerotheca*), Limnonectini (for *Limnonectes*, as well as some taxa considered by most authors to be synonyms of *Limnonectes*), Occidozygini (for *Occidozyga*

[19] The status of *Liurana* Dubois, 1987, is unclear. Dubois (1987 ''1985'') named *Liurana* as a subgenus of *Ingerana* (Ceratobatrachinae) but, without discussing evidence, Dubois (2005: 4) subsequently considered *Liurana* to be a synonym of *Taylorana* (= *Limnonectes*, Dicroglossinae). Similarly, Dubois (2005), with minimal discussion, placed *Annandia* Dubois, 1992, in his tribe Limnonectini, although he had named this taxon as a subgenus of *Paa*, in his Paini. Because these statements are not associated with evidence, they do not merit further discussion.

←

Fig. 35. One of 24 most parsimonious trees of ranoids of Roelants et al. (2004) that corresponds, except for branches marked with an asterisk (*), to their maximum-likelihood tree, based on 698 informative sites out of 1,895 bp of: (1) 750 bp covering part of 12S rRNA gene, complete $tRNA^{Val}$ gene, and part of the 16S rRNA gene; (2) 550 bp of the 16S rRNA gene; (3) ca. 530 bp of exon 1 of the nuclear tyronsinase gene; (4) ca. 315 bp of exon 1 of the rhodopsin gene; (5) ca. 175 bp of exon 4 of the nuclear rhodopsin gene. Alignment was made using the programs SOAP v. 1.0 (Löytynoja and Milinkovitch, 2000) and ClustalX (Thompson et al., 1997). Cost functions were not specified, and alignment was subsequently adjusted manually. Sequence segments considered to be ambiguously aligned were excluded from analysis (508 bp). Substitution model assumed for analysis was GTR + Γ+ I. It was not stated whether gaps were treated as missing data or as evidence.

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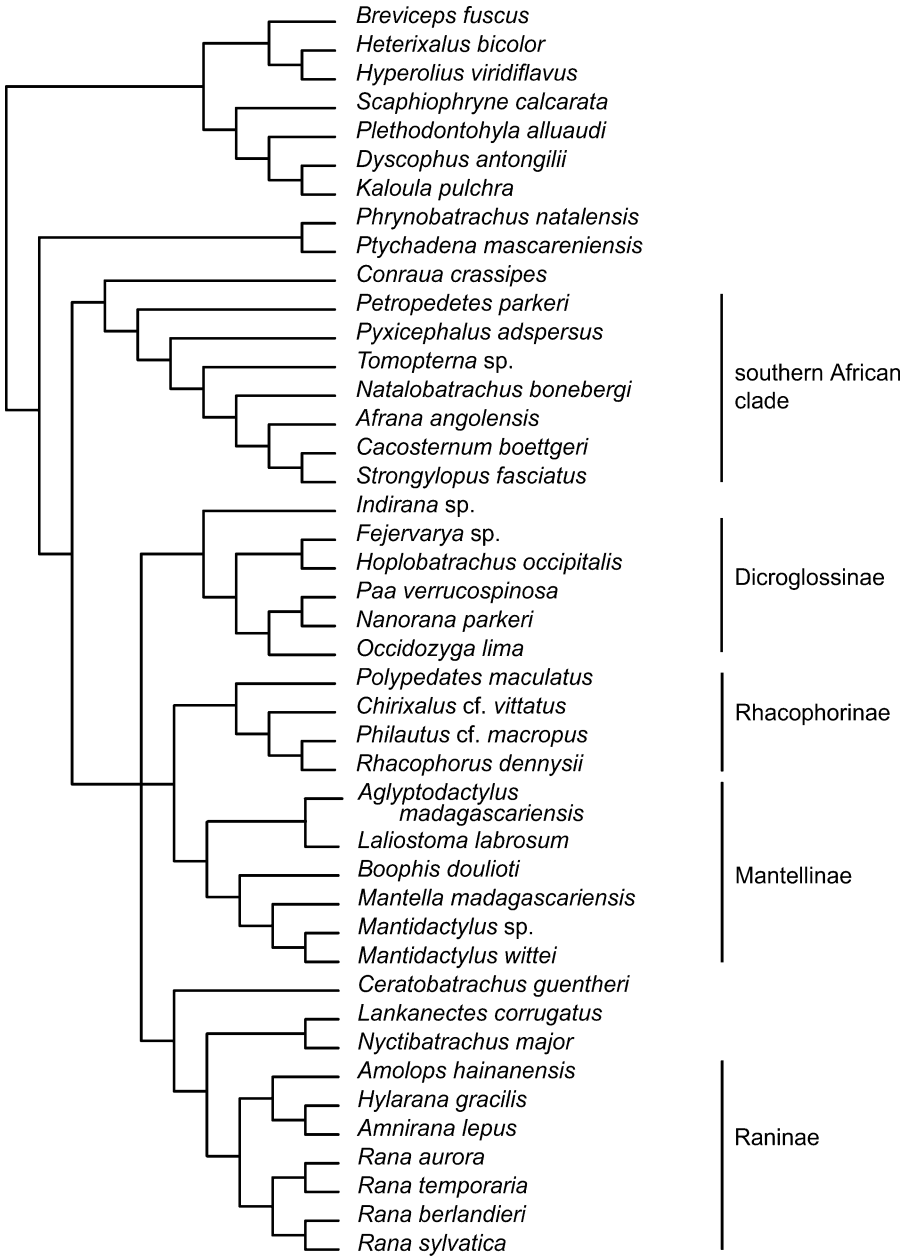

Fig. 36. Maximum likelihood tree of exemplars of Ranoidea, with a focus on African taxa, by Van der Meijden et al. (2005), based on mt DNA (12S and 16S rRNA) and nu DNA (RAG-1, RAG-2, rhodopsin), for 2,995 bp of sequence. Alignment was made using ClustalW (Thompson et al., 1994), with costs not disclosed and gaps and highly variable sites excluded from analysis. The model assumed for maximum-likelihood analysis was TrN + I + G. The tree was rooted on an hierarchical outgroups (not shown in original) composed of *Latimeria*, *Homo*, *Gallus*, *Lyciasalamandra*, *Alytes* (2 spp.), *Agalychnis*, and *Litoria*. The ''southern African clade'' represents Pyxicephalinae as subsequently redelimited by Dubois (2005).

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and *Phrynoglossus*), and Paini (for *Chaparana*, *Nanorana*, and *Quasipaa*).

Dicroglossini was diagnosed by Dubois (1992; in the sense of including Occidozyginae) as retaining a free-living tadpole (plesiomorphic) and having a lateral line system that usually is retained into adulthood (presumably apomorphic, but not present in *Occidozyga*, sensu stricto). As conceived by Dubois (1992), the taxon contained *Euphlyctis*, *Occidozyga*, and *Phrynoglossus*. Fei et al. (1991 ''1990'') and, subsequently, Dubois et al. (2001) on the basis of published and unpublished molecular evidence (Marmayou et al., 2000—fig. 37; Kosuch et al., 2001—figs. 38; Delorme et al., 2004—fig. 40) placed *Occidozyga* and *Phrynoglossus* in the subfamily Occidozyginae, and transferred without discussion into Dicroglossini *Fejervarya* and *Hoplobatrachus* (from Limnonectini) and *Sphaerotheca* (from Tomopterninae), and *Nannophrys* (from Ranixalinae).

Grosjean et al. (2004), building on the earlier work of Kosuch et al. (2001) suggested on the basis of several mtDNA and nuDNA loci that *Euphlyctis* is the sister taxon of *Hoplobatrachus* with *Fejervarya*, *Sphaerotheca*, *Nannophrys*, and *Limnonectes* forming more distant relations, a result that is consistent with the tree of Roelants et al. (2004; fig. 35).

Dubois (1992) also recognized a tribe Limnonectini diagnosed nearly identically with Conrauini (Conrauinae of this review), differing only in the larval keratodont formula of 1–5/2–5, which is arguably plesiomorphic. Nominal genera contained in this group occur from tropical Africa to tropical Asia with most taxonomic diversity being in Asia: *Hoplobatrachus*, *Limnonectes*, and *Fejervarya* (which was considered a subgenus of *Limnonectes* at the time). In addition Marmayou et al. (2000; fig. 37) and Delorme et al. (2004; fig. 40) suggested on the basis of mtDNA evidence that *Sphaerotheca* (formerly in Tomopterninae; Dubois, 1987 ''1985'') and *Taylorana* (now a synonym of *Limnonectes*; originally considered to be a member of Limnonectini [Dubois, 1987 ''1985''] but subsequently transferred to Ceratobatrachinae by Dubois, 1992) are in Limnonectini.

Sphaerotheca, therefore, is likely not to be closely related to *Tomopterna*, as one would have expected given that the species of *Sphaerotheca* were long placed in *Tomopterna* (Pyxicephalinae). Roelants et al. (2004; fig. 35) also placed *Nannophrys* in Dicroglossinae (by implication) on the basis of mtDNA and nuDNA evidence, substantiating the earlier assessment by Kosuch et al. (2001; figs. 38) which was made on less evidence. It was previously assigned to Ranixalini by Dubois (1987 ''1985'') and to Dicroglossini by Dubois et al. (2001). Dubois et al. (2001: 55) implied on the basis of various published and unpublished mtDNA data that *Euphlyctis* (formerly in his Dicroglossini), *Fejervarya*, *Hoplobatrachus*, *Minervarya*, *Nannophrys*, and *Sphaerotheca* (formerly in his Limnonectini) should be included in a reconstituted Dicroglossini.

Delorme et al. (2004; fig. 40) demonstrated—as had Roelants et al. (2004; fig. 35)—that *Lankanectes* is phylogenetically distant from *Limnonectes*.

Of these taxa we sampled rather broadly: *Euphlyctis cyanophlyctis*; *Fejervarya cancrivorus*, *F. kirtisinghei*, *F. limnocharis*, and *F. syhadrensis*; *Hoplobatrachus occipitalis* and *H. rugulosus*; *Limnonectes acanthi*, *L. grunniens*, *L. heinrichi*, *L. kuhlii*, *L. limborgi* (formerly *Taylorana limborgi*), *L. poilani*, and *L. visayanus*; *Nannophrys ceylonensis*; *Sphaerotheca breviceps* and *S. pluvialis*. On the basis of this sampling we should be able to evaluate the reality of this taxon and, at least to some degree, the monophyly of the contained genera.

Occidozygini is a tropical Asian group of arguable position. Marmayou et al. (2000; fig. 40) presented mtDNA evidence that *Occidozyga* and *Phrynoglossus* are not within Dicroglossinae but are outside of a clade composed of Rhacophoridae and other members of a paraphyletic Ranidae. Fei et al. (1991 ''1990'') had already transferred *Occidozyga* (sensu lato) out of Dicroglossinae and into its own subfamily on the basis of larval characters and this evidence supported the view that Dicroglossinae, as previously conceived, is polyphyletic. Roelants et al.'s (2004) greater sampling of Asian ranoids suggested that *Ingerana* (nominally in Ceratobatrachinae) is in this clade and together form the sister taxon of a reformulated Dicroglossinae (fig. 35), which together are the

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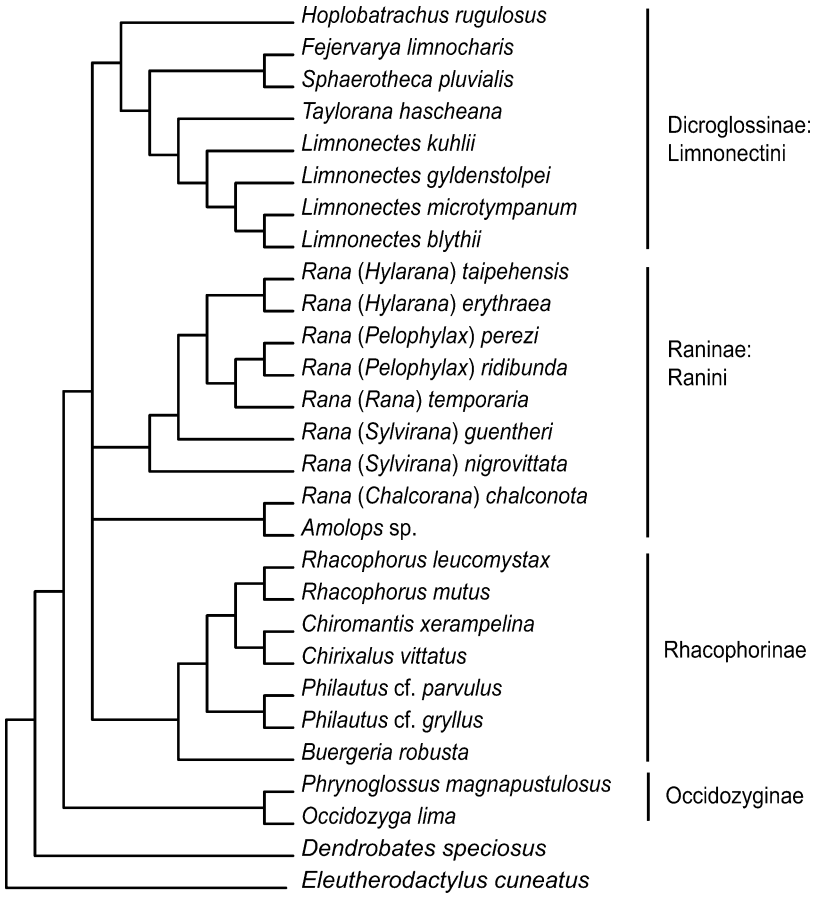

Fig. 37. Consensus of two equally parsimonious trees from Marmayou et al. (2000) of exemplars of Ranidae and Rhacophoridae (Ranidae: Rhacophorinae in their usage) based on 305 bp (151 informative sites) of 12S mtDNA, aligned using the program MUST (Philippe, 1993) and subsequently manually modified with reference to secondary structure models. Cost functions for alignment were not stated, nor whether gaps were treated as missing data or as evidence (ci = 0.382, ri = 0.429). Tree rooted on *Eleutherodactylus cuneatus* (= *Euhyas cuneata*).

sister taxon of a clade composed of Mantellidae, Rhacophoridae, and Raninae. No African taxa were examined by Marmayou et al. (2000; fig. 37), Roelants et al. (2004; fig. 35), or Delorme et al. (2004; fig. 40), so the relative position and monophyly of Occidozyginae and Dicroglossinae needed to be further elucidated. This issue was addressed by Van der Meijden et al. (2005; fig. 36), who did analyze Asian and African taxa simultaneously and found *Occidozygya lima* to sit within their Dicroglossinae. Dubois (2005), on the strength of the evidence produced by Van der Meijden et al. (2005), returned Occidozyginae to Dicroglossinae as a tribe. We sampled *Phrynoglossus baluensis*, *P. borealis*, *P. martensii*, and *Occidozyga lima*.

Paini is a montane Asian tribe diagnosed among ranids by having an unforked omosternum (and was therefore formerly included in Raninae by Dubois, 1987 ''1985'', 1992) and males having black, keratinous ventral spines (presumably a synapomorphy with *Nanorana*; Jiang et al., 2005: 357). Paini according to Dubois (1992) was composed of two genera, each with four subgenera: genus *Chaparana* with subgenera *Annandia*, *Chaparana*, *Feirana*, and *Ombrana*; genus *Paa* with subgenera *Eripaa*, *Gynandropaa*, *Paa*, and *Quasipaa*. Dubois et al. (2001), citing

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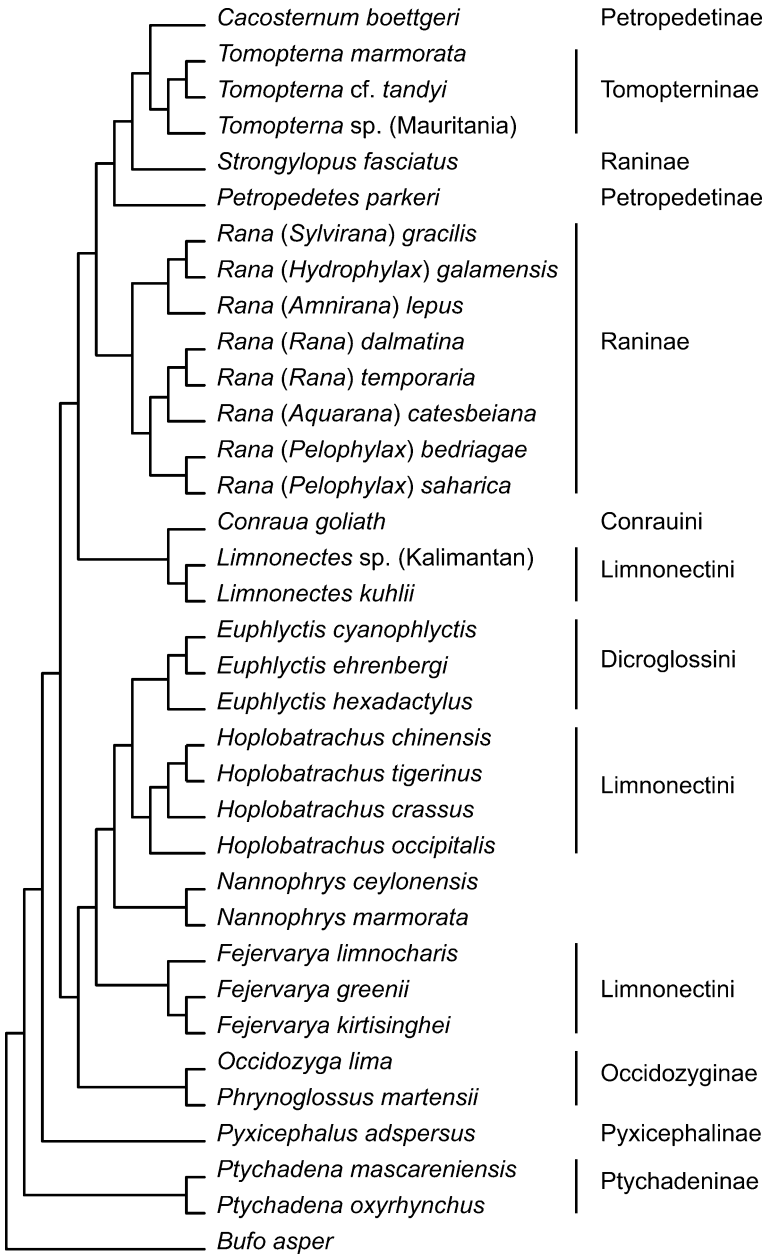

Fig. 38. Neighbor-joining tree of ranoid exemplars of Kosuch et al. (2001), which ''agreed well'' with the consensus of four equally parsimonious trees (ci = 0.51). Underlying data were 572 bp of aligned 16S mtDNA sequences of which 221 are parsimony-informative. Alignment was done manually using Sequencher (Applied Biosystems). Indels were treated as missing data. Taxon assignments on the right reflect the taxonomy as it existed at the time.

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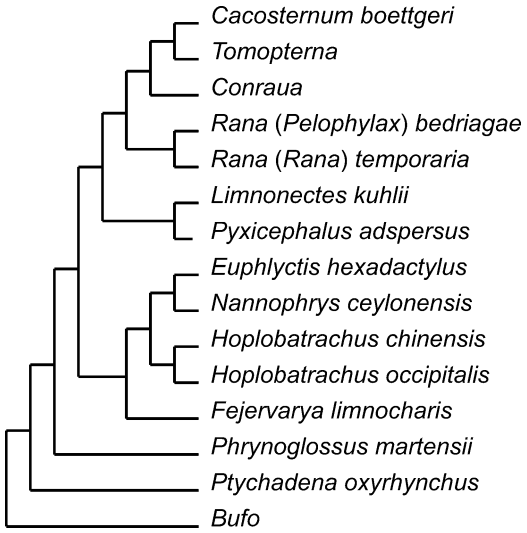

Fig. 39. Neighbor-joining tree of ranoid exemplars of Kosuch et al. (2001). Underlying data were 16S data (see figure 38) and 12S mtDNA (331 bp). Alignment was done manually using Sequencher (Applied Biosystems). Gaps treated as missing data.

unpublished DNA sequence, suggested that Paini be transferred from Raninae to Dicoglossinae. Jiang and Zhou (2001, 2005; fig. 41), Jiang et al. (2005; fig. 42), Roelants et al. (2004; fig. 35), and Van der Meijden (2005; fig. 36) on the basis of published DNA sequence evidence, suggested that Dicroglossinae, with a forked omosternum, is paraphyletic with respect to Paini, with an unforked omosternum. For this reason Roelants et al. (2004) and Jiang et al. (2005) transferred Paini out of Raninae and into Dicroglossinae. Larvae in the group are exotrophic and aquatic (Altig and McDiarmid, 1999).

Jiang et al. (2005) recently provided a phylogenetic study (fig. 42) of Paini on the basis of 12S and 16S rRNA fragments. Unfortunately, that study appeared too late to guide our choice of terminals, but their results are important in helping us interpret our own results. They found *Paa* to be paraphyletic with respect to *Chaparana* and *Nanorana*; *Chaparana* to be polyphyletic with the parts imbedded within ''*Paa*''; and *Nanorana* to be deeply imbedded within ''*Paa*''. Within Paini they recognized two groups: (1) Group 1, composed of ''*Chaparana*'', several species of ''*Paa*'', and *Nanorana*, characterized by spines forming two patches on the chest (save *C. quadranus*, the type of subgenus *Feirana*, which does not have spines on the chest); and (2) Group 2, composed of ''*Paa*'' species associated previously with the subgenera *Quasipaa* Dubois, 1992 (*P. robertingeri*), and one species nominal of the genus *Chaparana*, subgenus *Feirana* Dubois, 1992 (*Paa yei*). The second group is characterized by having spines as a single group, more or less over the entire venter, but this characteristic is sufficiently variable among subgroups as not to be diagnostic practically except in the not-*Nanorana* group sense. These authors recommended that the generic name *Quasipaa* be applied to Group 2, but for unstated reasons hesitated to resolve taxonomically the nonmonophyly of *Chaparana* and *Paa* in their Group 1. *Nanorana* Günther, 1896, is the oldest available name for their first group.

Three nominal genera are definitely included in Paini: ''*Chaparana*'' (polyphyletic; see above); *Nanorana*; and ''*Paa*'' (paraphyletic with respect to ''*Chaparana*'' and *Nanorana*[20]). We sampled *Nanorana pleskei*, *Quasipaa exilispinosa* and *Q. verrucospinosa* but did not sample ''*Chaparana*'' or ''*Paa*'' (sensu stricto).

Jiang et al. (2005) did not mention or address three supraspecific taxa usually associated with Paini. The first is *Eripaa* Dubois, 1992, whose type and only species is *Rana fasciculispina* Inger, 1970. *Eripaa* Dubois, 1992, was named and is currently treated as a subgenus of *Paa*. Although *Eripaa* exhibits spines on the entire chest and throat, such as in group 2 of Jiang et al. (2005), they are uniquely distinct from all other ''*Paa*'', ''*Chaparana*'', and *Nanorana* species in that these spines are clustered in groups of 5–10 on circular whitish tubercles. We cannot hazard a guess as to how *Eripaa* is related to the rest of Paini. The second is *Annandia*

[20] Without mentioning content, Dubois (2005) recognized three genera: *Chaparana*, *Nanorana*, and *Quasipaa*. In light of the phylogenetic study by Jiang et al. (2005), it is not clear how *Chaparana* and *Nanorana* were intended to be delimited or what the content of these taxa would be. We presume that Dubois' (2005) intention was to recognize a paraphyletic *Chaparana* within which a monophyletic *Nanorana* is imbedded.

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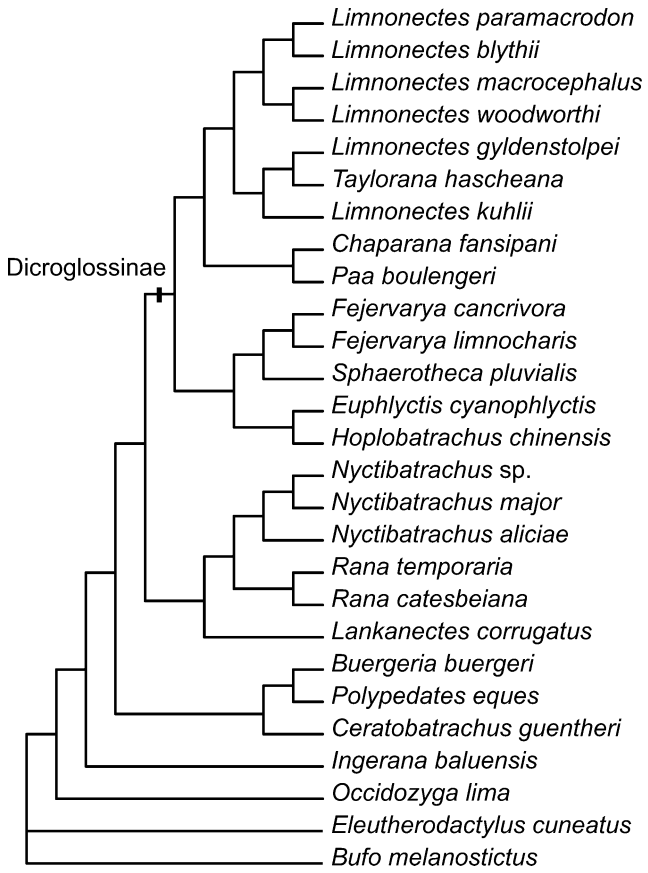

Fig. 40. Maximum-likelihood tree of ranoids of Delorme et al. (2004), based on sequences from 12S and 16S rRNA for a total of 1198 bp. Alignment was made using the program Se-Al (Rambaut, 1995; cost functions not provided) and by comparison with models of secondary structure. Gaps were treated as missing data. The maximum-likelihood nucleotide substitution model accepted was TrN + I + G.

Dubois, 1992, whose type and only species is *Rana delacouri* Angel, 1928. *Annandia* was originally named as a subgenus of *Chaparana* Bourret, 1939, but recently, Dubois (2005), without discussion of evidence, treated *Annandia* as a genus in Limnonectini. Perhaps this was done because this species bears a smooth venter, with spinules only clustering around the anus (Dubois, 1987 ''1986''). Regardless, this is a large taxonomic change (from Paini to Limnonectini) and because no evidence was produced or discussed to justify this change, we must consider the status of this taxon questionable. The third is *Ombrana* Dubois, 1992, whose type and only species is *Rana sikimensis* Jerdon, 1870). *Ombrana* Dubois, 1992, was originally proposed as a subgenus of *Chaparana*. This species also posseses spinules only around the anus, prompting Dubois (1987, ''1986'') to consider it evidence of a unique reproductive mode, and thus a close relative of *Annandia delacouri*. Unfortunately, we did not sample any of these three taxa, so their status will remain questionable.

LANKANECTINAE (1 GENUS, 1 SPECIES): This subfamily was named for *Lankanectes corrugatus* of Sri Lanka by Dubois and Ohler (2001). Its distinguishing features are (1) forked omosternum (plesiomorphy); (2) vomerine teeth present (presumed plesiomorphy); (3) median lingual process absent (likely plesiomorphy); (4) femoral glands absent (likely plesiomorphy); (5) toe tips not en-

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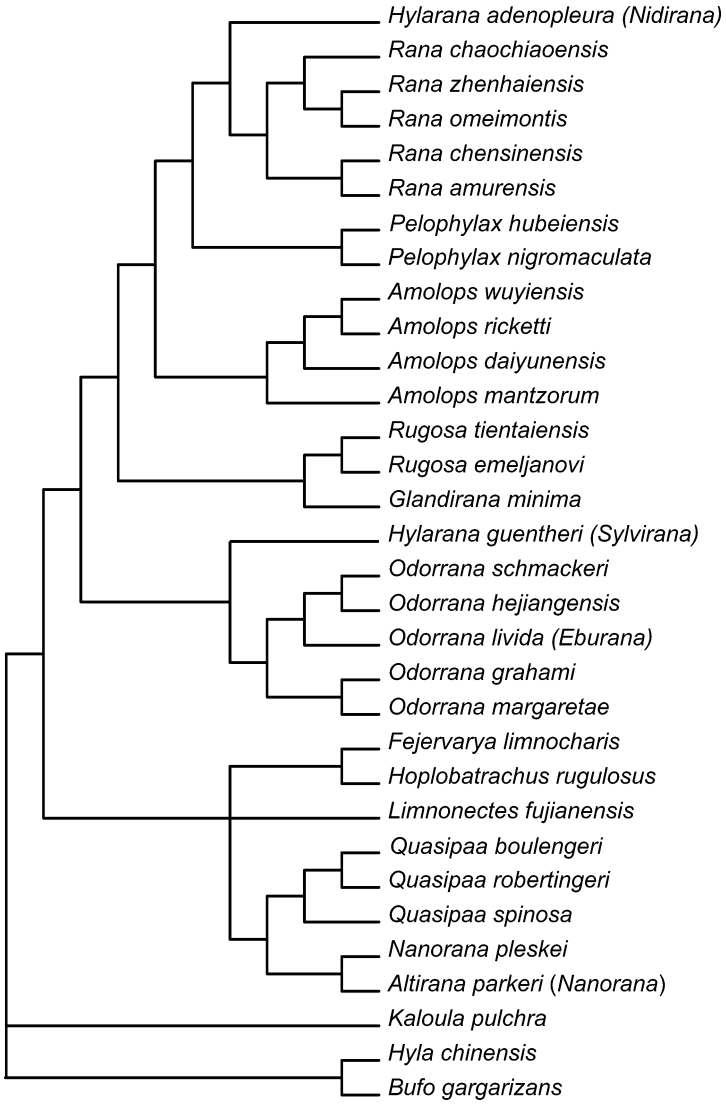

Fig. 41. Consensus of two parsimony trees of Chinese ranids from Jiang and Zhou (2005). Data were 1,005 bp of the mtDNA sequences of the 12S and 16S rRNA gene fragments (tree length = 1485, ci = 0.449). Sequences were aligned using ClustalX (Thompson et al., 1997), with manual modifications made subsequently. Gaps and ambiguously aligned sequences excluded from analysis. Generic names in parentheses reflect alternative usages. Generic taxonomy is updated to recognize *Quasipaa* (Jiang et al., 2005).

larged (arguable polarity); (6) tarsal fold present (likely plesiomorphy at this level); and (7) lateral line system present in adults (also in *Phrynoglossus* and *Euphlyctis*, but presumably apomorphic). Roelants et al. (2004; fig. 35) and Delorme et al. (2004; fig. 40) subsequently suggested on the basis of mtDNA and nuDNA evidence that *Lankanectes* is far from *Limnonectes*, where it had been placed by Dubois (1992). Roelants et al. (2004) placed it as the sister taxon of Nyctibatrachinae, and Delorme et al. (2004) placed it as the sister taxon of Nyctibatrachinae + Raninae. We sampled the sole species, *Lankanectes corrugatus*.

MICRIXALINAE (1 GENUS, 11 SPECIES): Trop-

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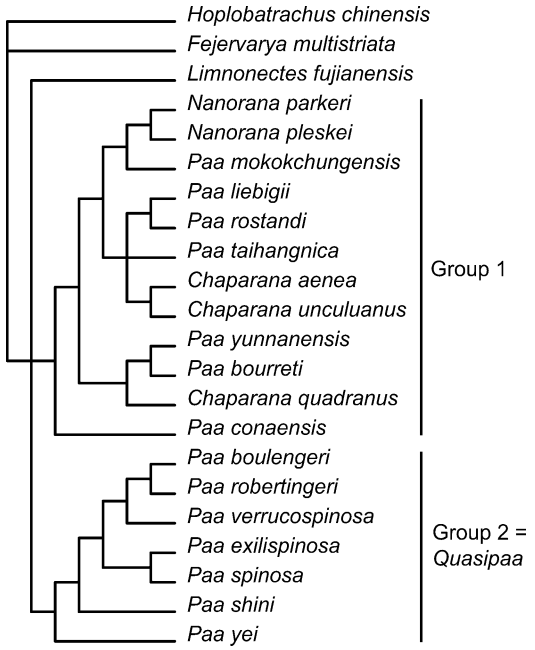

Fig. 42. Consensus of four parsimony trees of Paini by Jiang et al. (2005), based on 796 bp (of which 174 were parsimony informative) of the 12S and 16S rRNA framents of mtDNA. Sequences were aligned using ClustalW (Thompson et al., 1994), cost functions not disclosed, with subsequent manual modifications. Gaps and ambiguously aligned sequences were excluded from analysis (ci = 0.584, ri = 0.571). The trees were rooted on *Hoplobatrachus chinensis* and *Fejervarya fujianensis*. A conclusion of Jiang et al. (2005) is that their Group 2 was recognized as *Quasipaa*.

ical Asian *Micrixalus* (11 species) is the sole member of this taxon, diagnosed by Dubois (2001) as differing from Dicroglossinae in lacking a forked omosternum (possibly apomorphic), lacking vomerine teeth, having digital discs (present in some limnonectines and otherwise widespread in Ranoidea) and having a larval keratodont formula in its aquatic tadpoles of 1/0 (likely apomorphic) (Dubois et al., 2001). On the basis of mtDNA and nuDNA evidence, Roelants et al. (2004; fig. 35) considered Micrixalinae to be the sister taxon of Ranixalinae. We were able to sample *Micrixalus fuscus* and *M. kottigeharensis*. Although this provides only a minimal test of the monophyly of *Micrixalus*, it allows us to place the taxon phylogenetically.

NYCTIBATRACHINAE (1 GENUS, 12 SPECIES): Nyctibatrachinae contains the Indian taxon *Nyctibatrachus* and is characterized by having a forked omosternum (likely plesiomorphic), vomerine teeth present, digital discs present, femoral glands present (shared with Ranixalinae and some Dicroglossinae) and an aquatic tadpole with a keratodont formula of 0/0 (likely apomorphic; Dubois et al., 2001). Of this taxon we sampled *Nyctibatrachus* cf. *aliciae* and *N. major*.

PETROPEDETINAE (2 GENERA, 10 SPECIES); PHRYNOBATRACHINAE (4 GENERA, 72 SPECIES) AND PYXICEPHALINAE (13 GENERA, 57 SPECIES): Until recently, members of Petropedetinae and Phrynobatrachinae, as well as several genera now assigned to Pyxicephalinae (e.g., *Anhydrophryne*, *Arthroleptella*, *Cacosternum*, *Microbatrachella*, *Natalobatrachus*, *Nothophryne*, and *Poyntonia*) were considered members of ''Petropedetidae'' (sensu lato), aggregated on the basis of overall similarity, with no evidence for its monophyly ever suggested. Noble (1931) recognized his Petropedetinae (*Arthroleptides* and *Petropedetes*), as united by the possession of dermal scutes on the upper surface of each digit and otherwise corresponding osteologically and morphologically with Raninae. Noble (1931) also recognized Cacosterninae for *Cacosternum* and *Anhydrophryne*, united by lacking a clavicle and having palatal ridges. He related the cacosternines to brevicipitines, and the remainder of the genera then named he allocated to Raninae.

Laurent (1941 ''1940'') addressed the confusion between *Arthroleptis* and *Phrynobatrachus* and transferred *Petropedetes*, *Anhydrophryne*, *Phrynobatrachus* (including *Natalobatrachus*), *Dimorphognathus*, and *Arthroleptella* into his Phrynobatrachinae. Laurent (1941) subsequently provided an anatomical characterization of the group.

Laurent (1951) transferred Cacosterninae into Ranidae and moved *Microbatrachella* into Cacosterninae. Poynton (1964a) suggested that *Phrynobatrachus* is deeply paraphyletic with respect to Cacosterninae and therefore considered Laurent's Phrynobatrachinae (= Petropedetinae) and Cacosterninae to be synonyms. Subsequent authors (e.g., Dubois, 1981; Frost, 1985) uncritically followed this unsupported suggestion, although

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there have been significant instances of workers continuing to recognize Cacosterninae and Petropedetinae as distinct (e.g., Liem, 1970; J.D. Lynch, 1973).

Another morphologically compact African group was Pyxicephalinae (Dubois, 1992), composed of *Pyxicephalus* (2 species) and *Aubria* (2 species). The taxon was diagnosed by at least four synapomorphies (Clarke, 1981): (1) cranial exostosis; (2) occipital canal present in the frontoparietal; (3) zygomatic ramus being much shorter than otic ramus; and (4) sternal style a long bony element tapering markedly from anterior to posterior. Dubois' (1992) reasoning for excluding this taxon from Dicroglossinae is not clear, but presumably had to do with the distinctive appearances of *Pyxicephalus* and *Aubria*.

Dubois (1992) also recognized a subfamily Tomopterninae, for *Tomopterna* (sensu lato, at the time including *Sphaerotheca*, now in Dicroglossinae, Limnonectini). The diagnosis provided by Clarke (1981) presumably applies inasmuch as he examined only African species (*Tomopterna*, sensu stricto), even though the optimization of these characters on his cladogram may well be contingent on being compared only with other African ranids: (1) zygomatic ramus much shorter than otic ramus; (2) outline of anterior end of cultriform process pointed, with lateral borders tapering to a point; (3) distal end of the anterior pterygoid ramus overlapping the dorsal surface of the posterior lateral border of the palatine; (4) no overlap of the anterior border of the parasphenoid ala by the medial ramus of the pterygoid in the anterior–posterior plane; (5) sternal style short, tapering posteriorly; (6) dorsal protuberance of the ilium not or only slightly differentiated from the spikelike dorsal prominence; and (7) terminal phalanges of the fingers and toes reduced, almost conelike.

In 2003 this untidy, but familiar arrangement began to unravel. Dubois (2003), removed Cacosterninae from ''Petropedetidae'' without discussion, apparently anticipating evidence to be published elsewhere, although Kosuch et al. (2001; fig. 38) had suggested earlier that *Cacosternum* was more closely related to *Tomopterna* and *Strongylopus* than it was to *Petropedetes*. The content of this taxon was stated to be *Anhydrophryne*, *Arthroleptella*, *Cacosternum*, *Microbatrachella*, *Nothophryne*, *Poyntonia* (from Petropedetidae), and, possibly *Strongylopus* and *Tomopterna* (from Ranidae).

Van der Meijden et al. (2005; fig. 36) suggested *Phrynobatrachus* to be the sister taxon of *Ptychadena*. On this basis Dubois (2005) recognized a ranid subfamily Phrynobatrachinae, containing *Phrynobatrachus*, but also allocated to this subfamily, without discussion, *Dimorphognathus*, *Ericabatrachus*, and *Phrynodon*. *Petropedetes* and *Conraua* formed successively more distant outgroups of the southern African clade of Van der Meijden et al. (2005), so Dubois (2005) removed Conrauini (*Conraua*) from Dicoglossinae and placed it in its own subfamily, Conrauinae, and recognized Petropedetinae for *Petropedetes*, as well as the presumably closely allied *Arthroleptides*. The southern African clade of Van der Meijden et al. (2005; fig. 36) was composed of *Cacosternum* (formerly of Petropedetidae), *Afrana* and *Strongylopus* (formerly of Raninae), *Natalobatrachus* (formerly of Petropedetidae), *Tomopterna* (Tomopterninae), and *Pyxicephalus* (Pyxicephalinae), a group that Dubois (2005) allocated to an enlarged Pyxicephalinae. *Aubria* was asserted by Dubois (2005) to be in this group because it was grouped by morphological evidence with *Pyxicephalus*. *Amietia* he transferred into the group without discussion, but presumably because they appeared to him to be related to *Strongylopus* and *Afrana*. He transferred *Arthroleptella*, *Microbatrachella*, *Nothophryne*, and *Poyntonia* into Pyxicephalinae, presumably because he thought that they were more likely to be here than close to either Petropedetinae or Phrynobatrachinae.

Of Dubois' (2005) Petropedetinae (which presumably is diagnosed as by Noble, 1931) we were able to sample both genera: *Arthroleptides* sp. and *Petropedetes cameronensis*, *P. newtoni*, *P. palmipes*, and *P. parkeri*.

Of the newly constituted Phrynobatrachinae, we were also able to sample species from three of four genera: *Dimorphognathus africanus*, *Phrynobatrachus auritus*, *P. calcaratus*, *P. dendrobates*, *P. dispar*, *P. mababiensis*, *P. natalensis*, and *Phrynodon sandersoni*. We did not sample *Ericabatrachus*,

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an unfortunate omission, inasmuch as we are unaware of the evidence for Dubois' (2005) association of *Ericabatrachus* with Phrynobatrachinae, other than the statement that it is ''*Phrynobatrachus*-like'' (Largen, 1991). *Phrynobatrachus*, at least for the species which it is known, have exotrophic larvae. Larvae are unknown in *Dimorphognathus* and *Ericabatrachus*, and *Phrynodon* is endotrophic (Amiet, 1981; Altig and McDiarmid, 1999).

Of the reformulated Pyxicephalinae we were able to sample *Aubria* (*Aubria subsigillata* [2 samples[21]]) and *Pyxicephalus* (*Pyxicephalus edulis*) as well as several of the taxa recently transferred into this taxon including *Anhydrophryne rattrayi*, *Arthroleptella bicolor*, *Cacosternum platys*, and *Natalobatrachus bonebergi*. We also sampled members of *Afrana* (*A. angolensis* and *A. fuscigula*), *Tomopterna* (*T. delalandii*), *Strongylopus* (*S. grayii*), and *Amietia* (*A. vertebralis*), but for reasons having to do with the evidentiary basis and history of taxonomy in Raninae, considerable discussion of these genera is presented there. We did not sample *Microbatrachella*, *Nothophryne*, or *Poyntonia*. Pyxicephalines have exotrophic larvae, with the exception of *Anhydrophryne* and *Arthroleptella*, which are endotrophic; unknown in *Nothophryne* (Hewitt, 1919; Procter, 1925; DeVilliers, 1929; Altig and McDiarmid, 1999). This selection should allow us to test the phylogenetic results of Van der Meijden et al. (2005).

PTYCHADENINAE (3 GENERA, 51 SPECIES): Ptychadeninae is a morphologically compact group of sub-Saharan ranids diagnosed (Clarke, 1981; Dubois, 1987 ''1985'', 1992) by having: (1) an otic plate of the squamosal covering the crista parotica in dorsal view and extending mesially to overlap the otoccipital; (2) palatines absent; (3) clavicles reduced; (4) sternal style a short compact element tapering anteriorly to posteriorly; (5) eighth presacral vertebra fused with sacral vertebra; and (6) the dorsal protuberance of ilium smooth-surfaced and not prominent. The three nominal genera in the taxon are *Ptychadena* (47 species), *Hildebrandtia* (3 species), and *Lanzarana* (1 species) of which we sampled only *Ptychadena anchietae*, *P. cooperi*, and *P. mascareniensis*. Because we did not sample *Hildebrandtia* and *Lanzarana*, we did not adequately test the monophyly of this group. Nevertheless, assuming the group to be monophyletic, our three species of *Ptychadena* allow us to test the placement of Ptychadeninae within Ranoidea. For his analysis Clarke (1981) assumed that Ptychadeninae is imbedded within other African ranids, although a lack of comparison with Asian members of the group makes this assumption questionable. Van der Meijden et al. (2005; fig. 36) suggested that *Ptychadena* is the sister taxon of *Phrynobatrachus* among his exemplars, thereby implying that Ptychadeninae is the sister taxon of Phrynobatrachinae.

''RANINAE'' (CA. 8 GENERA, 309 SPECIES): ''Raninae'' is a catch-all largely Holarctic and tropical Asian taxon united because the members do not fit into the remaining subfamilies and have unforked omosterna. Until recently, ''Raninae'' included two tribes: Paini and Ranini (Dubois, 1992). However, Paini and *Nanorana* of Ranini were transferred to Dicroglossinae on the basis of mtDNA and nuDNA evidence (Roelants et al., 2004—fig. 35; Jiang et al., 2005—fig. 42), so Raninae, as we use it, is coextensive with Ranini of Dubois (1992), itself dubiously monophyletic[22].

''Raninae'' is distributed on the planet coextensively with the family and is united by the lack of putative apomorphies, either in the adult or in the larvae. There does not appear to be any reason to suggest that this nominal taxon is monophyletic.

The starting point of any discussion of Ranini must be Dubois (1992), who provided an extensive, and controversial, taxonomy. Because the distinction between ranks (sec-

[21] We included two specimens of *Aubria subsigillata* as separate terminals in the analysis because the identity of one of the specimens was not determined conclusively until after the analyses were complete.

[22] Van der Meijden et al. (2005; fig. 36), provided evidence from DNA sequences that suggests strongly that ''Raninae'' is polyphyletic, with at least *Afrana* and *Strongylopus* in a southern African clade (along with *Pyxicephalus*, *Tomopterna*, *Natalobatrachus*, and *Cacosternum*), far from other ranines, and in Pyxicephalinae of Dubois (2005). We therefore treat ''Raninae'' in the following discussion as dubiously monophyletic.

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tion, subsection, genus, and subgenus) in Dubois' system appears to rest primarily on subjective perceptions of similarity and difference, the evidentiary basis of this taxonomy is unclear, even though we accepted his system as a set of bold phylogenetic hypotheses. Nevertheless, most of these taxa are imperfectly or incompletely diagnosed and to lay the foundation for our results and concomitant taxonomic remedies, we discuss this taxonomy in greater depth than we do most of the remainder of current amphibian taxonomy. Suffice it to say that we think that we sampled ''*Rana*'' diversity sufficiently to provide at least a rudimentary phylogenetic understanding of the taxon as a starting point for future, more densely sampled studies.

Within his Ranini, Dubois (1992) recognized six genera: *Amolops*, *Batrachylodes*, *Nanorana*, *Micrixalus*, *Rana*, and *Staurois* (table 4). Of these, two continue to be placed in this taxon (*Amolops* and *Rana* [sensu lato]) (Dubois, 2005). *Staurois*, *Nanorana* and *Micrixalus* have subsequently been transferred out of Ranini, *Staurois* to a new tribe, Stauroini (Dubois, 2005), *Nanorana* to Dicroglossidae (Roelants et al., 2004; fig. 35), and *Micrixalus* to a distant Micrixalinae (Dubois et al., 2001). *Batrachylodes* was provisionally transferred, without substantial discussion, by Dubois (2005) to Ceratobatrachinae.

Within both *Amolops* and *Rana*, Dubois recognized several subgenera, that other authors (e.g., Yang, 1991b) considered to be genera, as we do, although we arrange the discussions by Dubois' genera and subgenera. Dubois (2003) arranged Raninae into two tribes (Amolopini for the taxa with cascade-adapted tadpoles, i.e., *Amo*, *Amolops*, *Huia*, *Meristogenys*, *Chalcorana*, *Eburana*, *Odorrana*) and Ranini (for everything else). This system represents typical nonevolutionary A and not-A groupings, although Amolopini in this form is testable. Dubois (2005) subsequently did not embrace Amolopini, because it was too poorly understood, but he did erect Stauroini for *Staurois*, because Roelants et al. (2004) placed *Staurois* as the putative sister taxon of other ranines.

Amolops, *Amo*, *Huia*, and *Meristogenys*: *Amolops* has been recognized in some form since Inger (1966) noted the distinctive tadpole morphology (presence of a raised, sharply defined abdominal sucker). Like other cascade-dwelling taxa, larvae of *Amolops* (sensu lato) all share high numbers of keratodont rows. Subsequently, Yang (1991b) recognized two other genera from within *Amolops*: *Meristogenys* and *Huia*. *Amolops* (sensu stricto) has one possible synapomorphy (short first metacarpal, also found in *Huia*), and three synapomorphies joining *Huia* and *Meristogenys* to the exclusion of *Amolops* (lateral glands present in larvae; four or more uninterrupted lower labial keratodont rows; and longer legs).

Subsequently, Dubois (1992) treated *Meristogenys* and *Huia* as subgenera of *Amolops*, and added a fourth subgenus, *Amo* (including only *Amolops larutensis*). *Amo* was diagnosed (Boulenger, 1918) as having a digital disc structure similar to species of *Staurois* (i.e., having a transverse groove or ridge on the posteroventral side of the disc continuous with a circummarginal groove to define a hemisphere; Boulenger, 1918) and as having axillary glands (after Yang, 1991b) that are otherwise unknown in *Amolops*.

Although Dubois (1992) considered *Amolops* (sensu stricto), *Amo*, *Huia*, and *Meristogenys* to be subgeneric parts of a monophyletic genus *Amolops*, other authors (e.g., Yang, 1991b) considered at least *Amolops*, *Huia*, and *Meristogenys* as genera. For consistency we treat as genera *Amo*, *Amolops*, *Huia*, and *Meristogenys*. Our samples were *Amolops* (*A. chapaensis*, *A. hongkongensis*), *Huia* (*H. nasica*), and *Meristogenys* (*M. orphocnemis*). We were unable to sample *Amo larutensis*.

Staurois: The definition of *Staurois* (digital discs broader than long; T-shaped terminal phalanges in which the horizontal part of the T is longer than the longitudinal part; outer metatarsals separated to base but joined by webbing; small nasals separated from each other and frontoparietal; omosternal style not forked [Boulenger, 1918]) has also been used to define *Hylarana* (Boulenger, 1920; see below). Although some larval characters are shared among species of *Staurois* (deep, cup-like oral disc in the tadpole, no glands or abdominal disc in tadpole; Inger, 1966), the diagnostic value of these characters is unknown due to the large number

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of ranid species whose adults are morphologically similar to those of *Staurois*, but whose larvae remain undescribed. Our single exemplar of *Staurois*, *S. tuberilinguis*, is not sufficient to test the monophyly of the genus. Although no one has suggested that *Staurois* is polyphyletic, or that it is paraphyletic with respect to any other group, both of these remain untested possibilities. Roelants et al. (2004; fig. 35) provided evidence that *Staurois* is the sister taxon of remaining ranines.

Rana (sensu Dubois, 1992)[23]: *Rana* of Dubois (1992) is diagnostically coextensive with his Ranini (our ''Raninae''), and no features provided in his paper exclude ''*Rana*'' from being paraphyletic with respect to *Staurois*, *Amolops* (sensu Dubois, 1992), or *Batrachylodes*. So, as we discuss the internal taxonomy of ''*Rana*'' as provided by Dubois, readers should bear in mind that *Amolops* (sensu lato), *Batrachylodes*, and *Staurois*, as discussed by Dubois (1992), must be regarded as potential members of all infrageneric taxa that do not have characters that specifically exclude them. (And, at least with respect to Dubois', 1992, *Rana* subgenera, *Strongylopus* and *Afrana*, DNA sequence data have been published that suggest that they have little relationship with other ranines [Van der Meijden et al., 2005; fig. 36].) With respect to ''*Rana*'' specifically, Dubois (1992) provided a system of sections, subsections, and subgenera that has posed serious challenges for us: Rather than a synapomorphy scheme, or even a system of carefully-evaluated characteristics, the various taxa appear to represent postfacto character justifications of decidedly nonphylogenetic and subjectively arrived-at groups. We found Dubois' (1987 ''1985'', 1992) arrangement to be inconsistent with the preponderance of evidence in certain instances (see the discussion of inclusion of *Aquarana* in his section *Pelophylax*, below) and the underlying diagnostic basis of the system to contain overly-generalized statements from the literature (Inger, 1996) that are not based on any comprehensive comparative study of either internal or external morphology. For instance, larvae may have dorsal dermal glands, lateral dermal glands, or ventral dermal glands in various combinations (e.g., Yang, 1991b). These characters have become larval dermal glands present or absent in Dubois' (1992) diagnoses, thereby conflating the positional homology of these features. Although we address deficiencies here and in the Taxonomy section, for other critiques see Emerson and Berrigan (1993), Matsui (1994), Matsui et al. (1995), Inger (1996), Bain et al. (2003), and Matsui et al. (2005).

As noted earlier, several, if not most taxa recognized by Dubois within his ''*Rana*'' are effectively undiagnosed in a utilitarian sense (i.e., they are diagnosed sufficiently only to make the names available under the International Code; ICZN, 1999). In addition, several are demonstrably nonmonophyletic (Matsui, 1994; Matsui et al., 1995; Inger, 1996; Tanaka-Ueno et al., 1998a; Emerson et al., 2000a; Marmayou et al., 2000; Vences et al., 2000a; B.J. Evans et al., 2003; Roelants et al., 2004; Jiang and Zhou, 2005). Unlike the superficially similar situation in *Eleutherodatylus* (sensu lato) where it is straightforward to get specific information on individual species and where the nominal subgenera and most related genera, even if they do not rise to the level of synapomorphy schemes, have been diagnosed largely comparatively, the subgeneric (and generic, in part) diagnoses of ranids are not comparable, and the purported differentiating characters frequently do not bear up to specimen examination (e.g., Tschudi, 1838; Boulenger, 1920; Yang, 1991b; Fei et al., 1991 ''1990''; Dubois, 1992).

Historically, taxonomists approached *Rana* (sensu lato) as being composed of two very poorly defined similarity groupings: (1) those that have expanded toe tips (likely plesiomorphic) that at one time or another have been covered by the name *Hylarana*; and (2) those that lack expanded toe tips, and that have more-or-less always been associated with the generic name *Rana*. Most authors since Boulenger (1920) recognized the lack of definitive ''breaks'' between the two groups, and Dubois was the first to attempt

[23] Although *Afrana*, *Amietia*, and *Strongylopus* (now in Pyxicephalinae), *Batrachylodes* (now in Ceratobatrachidae), *Micrixalus* (now in Micrixalinae), and *Nanorana* (now in Dicroglossinae) have been transferred out of Raninae, we address them as part of the general discussion of ranine systematics prior to 2004. (See table 4)

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TABLE 4

Generic and Subgeneric Taxonomy of Dubois' (1992) Ranini

Nanorana transferred to Paiini by Roelants et al. (2004); *Batrachylodes* transferred to Ceratobatrachinae, without discussion of evidence by Dubois (2005); *Micrixalus* transferred to a new subfamily, Micrixalinae, by Dubois (2001); *Afrana* and *Strongylopus* transferred to Pyxicephalinae by Dubois (2005), based on evidence presented by Van der Meijden et al. (2005); and *Staurois* transferred to a new tribe, Stauroini, by Dubois (2005).

Genus	Section	Subsection	Subgenus	Number of species	Species sampled (reflecting nomenclature used in this work)
Amolops			*Amolops*	22	*Amolops chapaensis, A. hongkongensis*
Amolops			*Amo*	1	Not sampled
Amolops			*Huia*	4	*Huia nasica*
Amolops			*Meristogenys*	8	*Meristogenys orphnocnemis*
Batrachylodes				8	*Batrachylodes vertebralis*
Micixalus				6	*Micrixalus fuscus, M. kottigeharensis*
Nanorana			*Altirana*	1	Not sampled
Nanorana			*Nanorana*	2	*Nanorana pleskei*
Rana	*Amerana*		*Amerana*	2	*Amerana muscosa*
Rana	*Amerana*		*Aurorana*	4	*Aurorana aurora*
Rana	*Amietia*		*Amietia*	2	*Amietia vertebralis*
Rana	*Babina*		*Babina*	2	Not sampled
Rana	*Babina*		*Nidirana*	6	*Nidirana adenopleura, N. chapaensis*
Rana	*Hylarana*	*Hydrophylax*	*Amnirana*	9	*Amnirana albilabris*
Rana	*Hylarana*	*Hydrophylax*	*Humerana*	3	Not sampled
Rana	*Hylarana*	*Hydrophylax*	*Hydrophylax*	2	*Hydrophylax galamensis*
Rana	*Hylarana*	*Hydrophylax*	*Papurana*	11	*Papurana daemeli*
Rana	*Hylarana*	*Hydrophylax*	*Pulchrana*	10	Not sampled
Rana	*Hylarana*	*Hydrophylax*	*Sylvirana*	21	*Sylvirana guentheri, S. maosonensis, S. nigrovittata, S. temporalis*
Rana	*Hylarana*	*Hylarana*	*Chalcorana*	9	*Chalcorana chalconata*
Rana	*Hylarana*	*Hylarana*	*Clinotarsus*	1	*Clinotarsus curtipes*
Rana	*Hylarana*	*Hylarana*	*Eburana*	5	*Eburana chloronota*
Rana	*Hylarana*	*Hylarana*	*Glandirana*	1	*Glandirana minima*
Rana	*Hylarana*	*Hylarana*	*Hylarana*	3	*Hylarana erythraea, H. taipehensis*
Rana	*Hylarana*	*Hylarana*	*Nasirana*	1	Not sampled
Rana	*Hylarana*	*Hylarana*	*Odorrana*	10	*Odorrana grahami*
Rana	*Hylarana*	*Hylarana*	*Pterorana*	1	Not sampled
Rana	*Hylarana*	*Hylarana*	*Sanguirana*	2	Not sampled
Rana	*Hylarana*	*Hylarana*	*Tylerana*	2	*Tylerana arfaki*
Rana	*Lithobates*		*Lithobates*	3	*Lithobates palmipes*
Rana	*Lithobates*		*Sierrana*	3	*Sierrana maculata*
Rana	*Lithobates*		*Trypheropsis*	2	*Trypheropsis warszewitschii*
Rana	*Lithobates*		*Zweifelia*	5	Not sampled
Rana	*Pelophylax*		*Aquarana*	7	*Aquarana catesbeiana, A. clamitans, A. grylio, A. heckscheri*
Rana	*Pelophylax*		*Pantherana*	22	*Pantherana berlandieri, P. capito, P. chiricahuensis, P. forreri, P. pipiens, P. yavapaiensis*
Rana	*Pelophylax*		*Pelophylax*	17	*Pelophylax nigromaculata, P. ridibunda*
Rana	*Pelophylax*		*Rugosa*	3	Not sampled
Rana	*Pseudorana*		*Pseudorana*	3	*Pseudorana johnsi*
Rana	*Rana*		*Rana*	27	*Rana japonica, R. sylvatica, R. temporaria*
Rana	*Strongylopus*		*Afrana*	8	*Afrana angolensis, Afrana fuscigula*
Rana	*Strongylopus*		*Strongylopus*	6	*Strongylopus grayii*
Staurois				4	*Staurois tuberlinguis*

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to summarize the relevant taxonomic literature and to divide *Rana* (sensu lato) into enough groups to allow some illumination of the problem. Our issue with his system is that it is impossible to tell from the relevant publication (Dubois, 1992) which species have actually been evaluated for characters and which have merely been aggregated on the basis of overall similarity or erected on the basis of specially-favored characters.

Dubois' primary division of *Rana* was into eight sections of arguable phylogenetic propinquity to each other or to other ranine genera (see table 4). We discuss these with reference to his diagnoses and other literature relevant to their recognition:

(1) Section *Amerana*. Dubois (1992) erected his subgenera *Amerana* and *Aurorana* for parts of the *Rana boylii* group of Zweifel (1955), which he placed in their own section, *Amerana*. Most previous work (e.g., Case, 1978; Farris et al., 1979; Post and Uzzell, 1981; Farris et al., 1982b; Uzzell and Post, 1986) had placed these frogs from western North American close to, or within, the Eurasian *Rana temporaria* group. Nevertheless, section *Amerana* was recognized by Dubois (1992) on the basis of a combination of characters, none unique but corresponding to the *Rana boylii* group identified by ribosomal data by Hillis and Davis (1986; fig. 43). This group had been suggested by Hillis and Davis (1986) to be in a polytomy with what Dubois regarded as his section *Rana* (*R. temporaria* and *R. sylvatica* were the exemplar species in their analysis), a group composed of a part of Dubois' section *Pelophyax* (*Aquarana*), and his sections *Lithobates* and *Pantherana*. Moreover, Hillis and Davis' (1986; fig. 43) results suggested that neither of the groups subsequently identified by Dubois (1992) as the subgenera *Aurorana* and *Amerana* are monophyletic. Subsequent work (Hillis and Wilcox, 2005; fig. 44) has provided substantial amounts of evidence in support of the nominal subgenus *Aurorana* being polyphyletic, and the subgenus *Amerana* being paraphyletic. Hillis and Wilcox (2005) used the section *Amerana* + *Rana temporaria* to root the remainder of their tree, so their overall tree cannot be taken as additional evidence of evolutionary propinquity of the section *Amerana* being in a monophyletic group with *Rana temporaria*, to the exclusion of all other North American *Rana*, inasmuch as this was an assumption of their analysis, based on earlier work (e.g., Case, 1978).

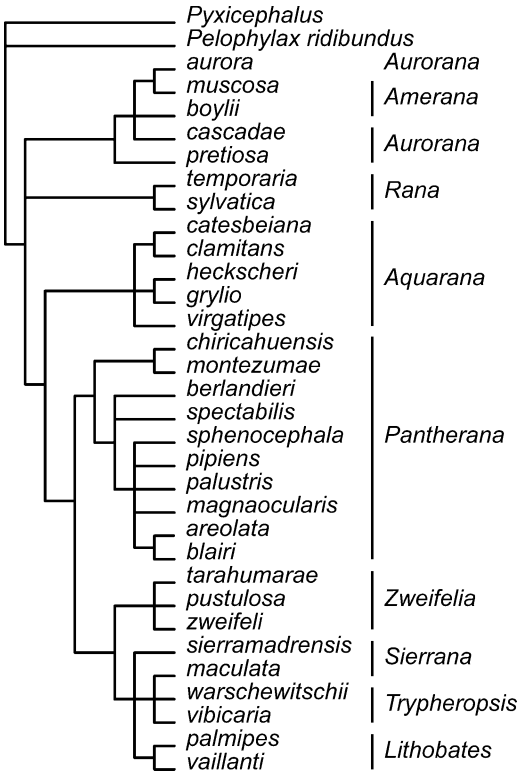

Fig. 43. Restriction-site tree of exemplars of Holarctic *Rana* of Hillis and Davis (1986). Underlying data were restriction sites of the nuclear rDNA gene; presence was considered to be evidence of relationship, absence was not. The tree was rooted on *Pyxicephalus* and *Pelophylax* (as *Rana ridibunda*). The original figure treated all species, save *Pyxicephalus*, as members of *Rana*. We have noted on the right the nominal subgenera of Dubois (1992; which we have treated as genera), to clarify discussion.

Dubois (1992) provided no unique morphological features to diagnose section *Amerana*, and because of his use of present-or-absent as a characteristic, the characters provided in his table 1 fail to rigorously distinguish section *Amerana* from sections *Hylarana*, *Lithobates*, *Pelophylax*, *Rana*, or *Strongylopus* (now in Pyxicephalinae on the basis of DNA sequence evidence—Dubois, 2005; Van der Meijden et al., 2005). Within

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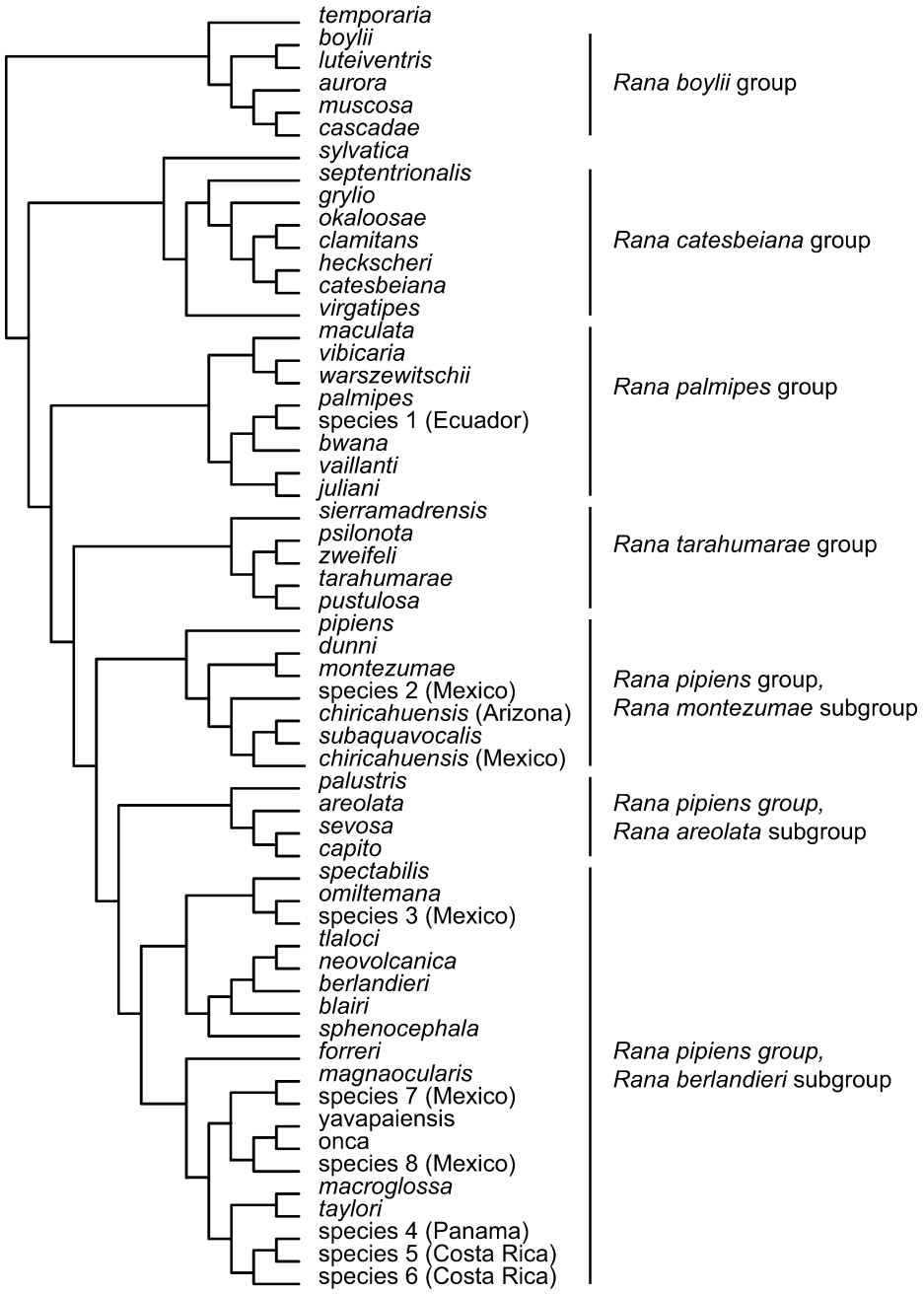

Fig. 44. Maximum-likelihood tree of Holarctic *Rana* of Hillis and Wilcox (2005). The underlying data are ca. 2kb of mtDNA of the 12S–16S region (spanning the $tRNA^{Val}$ gene). Sequence alignment was done initially using Clustal W (Thompson et al., 1994), costs not disclosed, and manually adjusted, guided by assumed secondary structure, ambiguously aligned sequences discarded. It was not stated whether gaps were treated as data, but we presume not. Substitution model GTR + Γ+ PINVAR was assumed for the maximum-likelihood analysis. On the basis of previous research, the root was assumed to be between the *Rana temporaria* + *Rana boylii* group and the remainder of New World *Rana*.

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Amerana, Dubois recognized two subgenera, *Amerana* and *Aurorana*, differing in the expansion of toe tips (mildly expanded in *Amerana*; not expanded in *Aurorana*), rows of larval keratodonts (4–7/4–6 in *Amerana*; 2–3/3–4 in *Aurorana*) karyotype (derived in *Amerana*; primitive in *Aurorana*). This subgeneric distinction is not phylogenetically consistent with the results of Hillis and Davis (1986; fig. 43), who presented evidence suggesting that Dubois' *Aurorana* is paraphyletic with respect to his *Amerana* (making one wonder what the purpose was in naming two subgenera). Macey et al. (2001) subsequently provided additional molecular evidence for paraphyly of *Aurorana* with respect to *Amerana*. Examples of this section in our analysis are *Amerana muscosa* and *Aurorana aurora* (see table 4).

(2) Section *Amietia* (including a single subgenus, *Amietia*, for two species in the Lesotho Highlands of southern Africa). The sole synapomorphy of *Amietia* is the umbraculum over the eye in the larva. The diagnosis of section *Amietia* is otherwise phylogenetically indistinguishable on the basis of the table of characters provided by Dubois (1992), from *Amerana*, *Hylarana*, *Lithobates*, *Rana*, or *Strongylopus*. We sampled *Amietia vertebralis*. *Amietia* was transferred into Pyxicephalinae by Dubois (2005) on the apparent but undiscussed assumption that it is closely related to *Strongylopus*, which was placed by Van der Meijden et al. (2005) in that group on the basis of DNA sequence evidence.

(3) Section *Babina* (for the *Rana holsti* and *Rana adenopleura* groups). The unique synapomorphy for this group is a large ''suprabrachial'' gland (sensu Dubois, 1992) on the sides of reproductive males (which can be difficult to assess in nonreproductive animals). The diagnosis of section *Babina* does not otherwise allow it to be practically separated from the sections *Amerana*, *Hylarana*, *Lithobates*, *Pelophylax*, *Rana*, or *Strongylopus*. Within section *Babina*, Dubois recognized two subgenera, *Babina* (with a large fingerlike prepollical spine, an apomorphy) and *Nidirana* (members of the *Babina* section *lacking* the apomorphy of the subgenus *Babina*). Fei et al. (2005) considered *Nidirana* to be a subgenus of their *Hylarana*, but their taxonomy was presented for only the Chinese fauna, so the wider implication of this action is not known. Of this section we sampled no member of the subgenus *Babina*, although we did sample *Nidirana adenopleura* and *N. chapaensis*. *Babina* and *Nidirana* have also been associated with ''*Hylarana*'' (see below), so Dubois' (1992) reason for recognizing this as a section distinct from section *Hylarana* is unclear.

(4) Section *Lithobates*. This section is not rigorously diagnosable by the features presented by Dubois' (1992: his table 1) from sections *Amerana*, *Hylarana*, *Rana*, or *Strongylopus*. However, *Lithobates* is consistent with the phylogenetic tree of American *Rana* provided by Hillis and Davis (1986; fig. 43), presumably the source of the concept of this section. Hillis and Davis placed this taxon, on the basis of DNA substitutions, as the sister taxon of part of Dubois' section *Pelophylax*, the subgenus *Pantherana*. Within section *Lithobates*, Dubois recognized four subgenera: *Lithobates* (*Rana palmipes* group), *Sierrana* (*Rana maculata* group), *Trypheropsis* (*Rana warszewitschii* group), and *Zweifelia* (*Rana tarahumarae* group). All of them are consistent with the tree provided by Hillis and Davis (1986). Dubois (1992) offered the following morphological characters which may be synapomorphies: *Lithobates* differs from other members of the section by having tympanum diameter larger or equal to the diameter of the eye; *Sierrana* without diagnostic characters that differentiate it from the section diagnosis; *Trypheropsis* by having an outer metatarsal tubercle (unusual in American ranids); and *Zweifelia* with sacrum not fused with presacral vertebrae. Hillis and Wilcox (2005; fig. 44) presented evidence that suggests that section *Lithobates* of Dubois (1992) is paraphyletic, with part of Dubois' subgenera *Sierrana* (*R. maculata*), and all of his subgenera *Trypheropsis*, and *Lithobates* falling within one monophyletic group, but *Zweifelia* (the *Rana tarahumarae* group) and another part of *Sierrana* (*R. sierramadrensis*) forming the sister taxon of Dubois' subgenus *Pantherana*, the *Rana pipiens* group of Hillis and Wilcox (2001).

Our exemplars of this section are *Lithobates palmipes*, *Sierrana maculata*, and *Try-*

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pheropsis warszewitschii. We did not sample *Zweifelia*.

(5) Section *Pelophylax*. The characters provided by Dubois for his section *Pelophylax* will not rigorously diagnose it from *Amerana*, *Hylarana*, *Rana*, or *Strongylopus*. Further, the association of his subgenera *Aquarana* (former *Rana catesbeiana* group), *Pantherana* (former *Rana pipiens* group), *Pelophylax* (former *Rana* ''*esculenta*'' group), and *Rugosa* (*Rana rugosa* group) is curious inasmuch as we are unaware that anyone had previously suggested such a relationship. All published evidence that was available to Dubois at the time of his writing (e.g., Case, 1978; Post and Uzzell, 1981; Hillis and Davis, 1986; Pytel, 1986; Uzzell and Post, 1986) suggested that this section is polyphyletic, with Dubois' subgenus *Pantherana* (of his section *Pelophylax*) more closely related to his section *Lithobates*, than to any other member of section *Pelophylax*. Indeed, the subgenera *Aquarana* and *Pantherana* of *Pelophylax* are both more closely related to both the sections *Lithobates*, *Rana*, and *Amerana*, than they are to the Old World members of section *Pelophylax* according to the evidentiary literature (i.e, Case, 1978; Post and Uzzell, 1981; Hillis and Davis, 1986; Pytel, 1986; Uzzell and Post, 1986). There never was any evidence for the monophyly of section *Pelophylax* sensu Dubois, while there was considerable evidence against it. Recently, Hillis and Wilcox (2005; fig. 44) have provided molecular evidence that *Aquarana* (their *Rana catesbeiana* group) is the sister taxon of *Rana sylvatica*, and together the sister taxon of all other American *Rana*, with the exception of the section *Amerana* (their *Rana boylii* group).

The subgenera recognized by Dubois within section *Pelophylax* have more justification for their monophyly. *Aquarana* is distinct on the basis of its large snout–vent length and its tympanum diameter, which is greater than eye diameter in males. *Rugosa* is separated by its ''small'' adult snout–vent length. *Pantherana* and *Pelophylax* are separated from *Aquarana* and *Rugosa* by their ''medium'' size and spots on the dorsum, but are otherwise undiagnosable from each other by features presented by Dubois (1992). Fei et al. (1991 ''1990'', 2005) consistently considered *Pelophylax* and *Rugosa* to be a distinct genera, but these authors generalized solely over the Chinese fauna rather than attempting to draw global distinctions. From *Aquarana* (*Rana catesbeiana* group) we sampled *Aquarana catesbeiana*, *A. clamitans*, *A. grylio*, and *A. heckscheri*. Of *Pantherana* (*Rana pipiens* group) we sampled *Pantherana berlandieri*, *P. capito*, *P. chiricahuensis*, *P. forreri*, *P. pipiens*, and *P. yavapaiensis*. Of *Pelophylax* we sampled *R. nigromaculata* and *P. ridibunda*. We did not sample *Rugosa*.

(6) Section *Pseudorana*. This section cannot be rigorously diagnosed on the basis of information given by Dubois (1992) from section *Hylarana*. *Pseudorana* was named by Fei et al. 1991 ''1990'') as a distinct genus for *Rana sauteri*, *R. sangzhiensis*, and *R. weiningensis*. Subsequently, Fei et al. (2000) coined *Pseudoamolops* for *Rana sauteri*, suggesting, on the basis of its having a large ventral sucker on the tadpole, that it is more closely related to *Amolops* (sensu lato) than to *Pseudorana*. Although the ventral sucker found in *Pseudoamolops* is associated with the oral disc of the tadpole, in *Amolops* the ventral sucker sits posterior to the oral disc. Fei et al. (2000) suggested that *Pseudoamolops* is the sister taxon of the remainder of their Amolopinae (*Amo*, *Amolops*, *Huia*, and *Meristogenys*) and derived with respect to a paraphyletic *Hylarana*, although Tanaka-Ueno et al. (1998a) had previous suggested on the basis of DNA sequence analysis that *Pseudorana sauteri* is imbedded within the brown frog clade (*Rana temporaria* group), although that analysis had addressed no member of nominal Amolopinae. We were able to sample *Pseudoamolops sauteri* and *Pseudorana johnsi* to test the placement of these species.

(7) Section *Rana*. This section cannot be diagnosed rigorously from sections *Amerana*, *Hylarana*, *Lithobates*, *Pelophylax*, or *Strongylopus* on the basis of characters presented by Dubois (1992). The association of *Rana sylvatica* with the *Rana temporaria* group has been controversial, with Hillis and Davis (1986) providing weak evidence for its placement with *Rana temporaria*, and Case (1978) suggesting that *Rana sylvatica* is phylogenetically within other North American

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Rana (sensu lato). Hillis and Wilcox (2005; fig. 44) recently provided molecular evidence in support of *Rana sylvatica* being the sister taxon of the *Rana catesbeiana* group (*Aquarana* of Dubois, 1992). In addition to noncontroversial members of the *Rana temporaria* group (*Rana japonica* and *R. temporaria*) we sampled *Rana sylvatica* to test whether it was a member of the *Rana temporaria* group or, as suggested previously, imbedded within a North American clade.

(8) Section *Strongylopus*. This section also is not phylogenetically diagnosable on the basis of Dubois' (1992) suggested evidence from sections *Amerana*, *Hylarana*, *Lithobates*, *Pelophylax*, or *Rana*. If the autapomorphies of *Babina* and *Amietia* are not considered, there also is nothing in the diagnosis of section *Strongylopus* that would prevent it from being paraphyletic with respect to *Babina* or *Amietia*. Nevertheless, DNA sequence evidence of Van der Meijden et al. (2005; fig. 36) places *Strongylopus* in Pyxicephalinae, and Dubois (2005) presumed that *Afrana* and *Amietia* also should be so allocated. Section *Strongylopus* is seemingly a geographically determined unit, not a phylogenetically determined one. Within section *Strongylopus*, Dubois recognized two subgenera that differ in size and color of larvae (long and dorsally black in *Afrana*; modest length and entirely black in *Strongylopus*), foot length (short in *Afrana*; long in *Strongylopus*), and webbing (less webbing in *Afrana* than in *Strongylopus*).

Van der Meijden (2005; fig. 36) provided a phylogenetic tree, based on mtDNA and nuDNA sequence data, that placed *Strongylopus* and *Afrana* in a heterogeneous clade (which they termed the ''southern African ranid clade'', and which Dubois, 2005, considered as an expanded Pyxicephalinae), along with *Tomopterna* (Tomopterninae), *Cacosternum* and *Natalobatrachus* (''Petropedetidae''), and *Pyxicephalus* (Pyxicephalinae). Because the evidence of Van der Meijden et al. (2005; fig. 36) is the first phylogenetic evidence that bears on this issue, we follow that taxonomy, but note that nothing in morphology so far supports this arrangement.

We sampled *Afrana angolensis*, *A. fuscigula*, and *Strongylopus grayii*.

(9) Section *Hylarana*. We have left section *Hylarana* to the end of this discussion because it represents the heart of the problem of ''*Rana*'' systematics. The name *Hylarana* has had an historically unstable application, alternatively being considered synonymous with *Rana*, or treated as a distinct subgenus or genus with an ill-defined content, and diagnosed in several different, even contradictory ways (e.g., Tschudi, 1838; Günther, 1859 ''1858''; Boulenger, 1882, 1920; Perret, 1977; Poynton and Broadley, 1985; Laurent, 1986; Fei et al., 1991 ''1990''; Dubois, 1992), although it is almost always associated with frogs that exhibit expanded toe tips. The original diagnostic character of the genus *Hylarana* Tschudi, 1838 (type species: *Rana erythraea* Schlegel, 1827) is the presence of a dilated disc on the tips of the toes (a character that can now be seen to encompass many of the species of Ranidae and its immediate outgroups). Günther (1859 ''1858'') revised the diagnosis to include ''males with an internal subgular vocal sac'' (i.e., lacking gular pouches) as a character, and increased the composition to five Asian and African species (including *Hylarana albolabris* and *H. chalconota*).

Because of the ambiguity of the diagnostic character of dilated toe disc, Boulenger (1882, 1920) believed *Hylarana* to be a ''group of polyphyletic origin'', but suggested that it was a subgenus of *Rana*, removing vocal sac condition as a diagnostic character and expanding its definition: dilated digital discs with circummarginal grooves, T-shaped terminal phalanges, and an unforked omosternal style (Boulenger, 1920: 123; as *Hylorana*). All of his putatively diagnostic characters have greater levels of generality than ''*Hylarana*''. He listed 62 species from Australasia, including *Rana curtipes*, *R. guentheri*, and *R. taipehensis* (the latter implicit, as he synonomized it with *R. erythraea*; Boulenger, 1920: 152–155).

Perret (1977: 842) listed ten African species of the genus *Hylarana* (including *H. galamensis*), revising the diagnosis as follows: precoracoids ossified, transverse, approaching each other medially; metasternum ossified, elongated; males with or without gular pouches; males with brachial (humeral) glands. Poynton and Broadley (1985: 139) revised the diagnosis in their account of Af-

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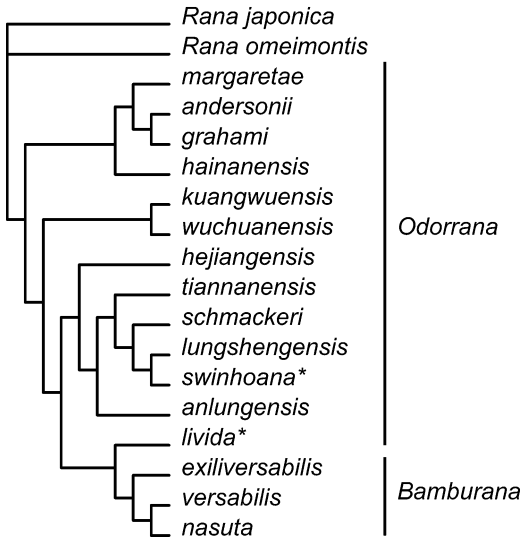

Fig. 45. Tree of Chinese species of *Odorrana* of Ye and Fei (2001), based on 29 character transformations of morphology (ci = 0.507). Tree rooted on *Rana japonica* and *Rana omeimontis*. The subgenera *Odorrana* and *Eburana* of Fei et al. (2005) are noted on the right and the terminals noted with an asterisk (*) are members of Dubois' (1992) subgenus *Eburana*.

rican *Hylarana*: only some species with expanded digital discs; broad brown to golden band from head to urostyle; upper lip white; males with single or paired baggy gular pouches. Laurent (1986: 761) further revised the diagnosis of *Hylarana*: without transverse grooves on finger discs.

Fei et al. (1991 ''1990'') moved some species from *Hylarana* into a new genus *Odorrana*. They diagnosed their new genus *Odorrana* by having: omosternum extremely small, colorless spines present on chest of male in breeding condition. Despite the etymology of the generic name, Fei et al. (1991 ''1990''), did not include odoriferous secretions as one of the characters uniting the genus. In addition, they included six species (*O. anlungensis*, *O. kwangwuensis*, *O. swinhoana*, *O. tiannanensis*, *O. versabilis*, and *O. wuchuanensis*) known not to have colorless spinules on the chest of the male. Subsequently, Ye and Fei (2001; fig. 45), on the basis of a phylogenetic study of Chinese *Odorrana* (including *Eburana* in their sense), suggested that only the *Odorrana andersoni* group (*O. andersoni*, *O. grahami*, *O. hainanensis*, and *O. margaretae*) have large chest spines, with small spines otherwise only in *O. schmackeri*. Chest spines were reported as absent in all other species of *Odorrana* that they studied: *O. anlungensis*, *O. exiliversabilis*, *O. hejiangensis*, *O. kuangwuensis*, *O. livida*, *O. lungshengensis*, *O. nasuta*, *O. swinhoana*, *O. tiannanensis*, *O. versabilis*, and *O. wuchuanensis*.

Fei et al. (1991 ''1990'': 138–139) further divided *Hylarana* into two subgenera, *Hylarana* and *Tenuirana* based on the following characters (*Tenuirana* in parentheses): anterior process of hyoid long, curved outwards (long, straight); tips of digits with or without a horizontal groove (always present on toes); feet almost fully webbed (half webbed); body not long or slender (long, slender); snout blunt and rounded (long, pointed); limbs moderate (long, slender); dorsolateral folds distinct to extremely broad (narrow); humeral gland or shoulder gland present in males (absent); gular pouches present in male (absent); and tadpole vent tube dextral (medial). As part of the Chinese fauna, they included *R. nigrovittata* and *R. guentheri* (under the subgenus *Hylarana*) and *R. taipehensis* (the type species of the subgenus *Tenuirana*) in *Hylarana*. Although they did not discuss *R. erythraea* (the type species of *Hylarana*), its inclusion in the subgenus *Hylarana* was implied.

As noted earlier, Dubois (1992) partitioned species formerly associated with one or more of the historical manifestations of *Hylarana* into several sections, subsections, and subgenera (see table 4) of which the sections *Babina* (subgenera *Babina* and *Nidirana*) and *Hylarana* (subsections *Hydrophylax* and *Hylarana*) are particularly relevant to this discussion of ''*Hylarana*''-like frogs (although the section *Hylarana*, in Dubois' system was not precluded by any evidence from being paraphyletic to any or all of the other sections defined by him). Sections *Babina* and *Hylarana* are distinguishable in Dubois' system solely by the possession of a suprabrachial gland (apomorphy) in section *Babina*. This gland is not found in section *Hylarana* which at least as portrayed by Dubois (1992) and noted above, has no apomorphies.

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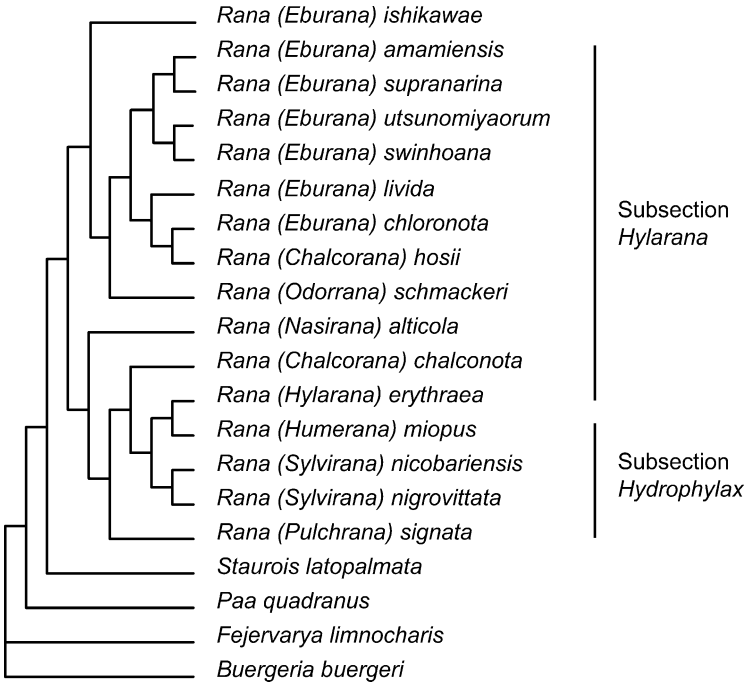

Fig. 46. Maximum-likelihood tree of Matsui et al. (2005) for East Asian ranids, based on mitochondrial 12S and 16S rRNA sequences (total of 1,283 bp). Sequence alignment was done under ClustalX (Thompson et al., 1997) with cost functions not disclosed and subsequently adjusted manually, guided by secondary structure models as suggested by Kjer (1995). Modeltest 3.06 (Posada and Crandall, 1998) was used to select nucleotide evolutionary model (GTR) assumed for analysis. *Fejervarya* and *Buergeria* were used to root the tree.

All other characters overlap or are identical between the two sections.

Dubois placed the collection of subgenera that he aggregated under section *Hylarana* into two subsections: a humeral gland-bearing group (subsection *Hydrophylax*) and a group characterized by having indistinct or absent humeral glands (subsection *Hylarana*). The presence of a humeral gland is an apomorphy, so at least prior to analysis we considered this single character as evidence of monophyly of Dubois' subsection *Hydrophylax*, leaving the condition ''humeral glands indistinct or absent'' as plesiomorphic (although we would have liked to know the distribution of ''indistinct'' humeral glands within the groups where Dubois reported them as indistinct or absent). During analysis, however, Matsui et al. (2005; fig. 46) provided DNA sequence evidence suggesting that that the subsection *Hydrophylax* is paraphyletic at least with respect to *Chalcorana chalconota* and (subgenus) *Hylarana* (subsection *Hylarana*) and that subsection *Hylarana* is polyphyletic with *Hylarana* (subgenus) and *Chalcorana chalconota* being independently derived of the main group of subsection *Hylarana*, which included all of their exemplars of subgenera *Eburana* and *Odorrana*, as well as *Chalcorana hosii*.

Within the apomorphic subsection *Hydrophylax* (well-developed humeral gland-bearing group) Dubois (1992) recognized several weakly or undiagnosed (except in the nomenclatural sense) subgenera: *Amnirana*, *Humerana*, *Hydrophylax*, *Papurana*, *Pulchrana*, and *Sylvirana*. According to Dubois (1992; his table II), *Humerana* is distinguished from other members of the subsection by the absence of an outer metatarsal tubercle; *Amnirana* and *Pulchrana* are not rigorously diagnosable from each other; *Papurana* and *Pulchrana* are not rigorously diagnosable from each other; and *Hydrophylax*

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can be diagnosed from *Sylvirana* only on the basis of the absence of an expanded disc and lateral groove on finger III and toe IV. Marmayou et al. (2000; fig. 37) presented DNA sequence evidence that *Sylvirana* (a humeral gland-bearing taxon) is paraphyletic with respect to *Hylarana* (subgenus) and *Pelophylax*, both of which lack humeral glands, suggesting that his subsection *Hydrophylax* (of section *Hylarana*) is paraphyletic. We sampled *Amnirana albilabris*, *Hydrophylax galamensis*, *Papurana daemeli*, *Sylvirana guentheri*, *S. maosonensis*, *S. nigrovittata*, and *S. temporalis*. We were unable to sample any member of *Pulchrana*, although Matsui et al. (2005; fig. 46) provided evidence that it is related to a group of subsection *Hydrophylax*, including *Sylvirana*, as well as an imbedded piece of subsection *Hylarana*, *Chalcorana chalconota*.

The ''indistinct or absent'' humeral-gland group (subsection *Hylarana*) is not rigorously diagnosable on the basis of apomorphies from any of the other sections of *Rana* (except for *Amietia* [now in Pyxicephalinae] and *Babina*) or from other genera of Ranidae. We, therefore, must assume that it is a mixture of groups with no necessary phylogenetic propinquity or to the exclusion of other ranid groups. The subgenera coined and aggregated under subsection *Hylarana* by Dubois (1992) are variably diagnosable. Marmayou et al. (2000; fig. 37) provided DNA sequence evidence for the polyphyly of subsection *Hylarana* (as well as for the paraphyly of the other subsection, *Hydrophylax*; see above), by placing *Hylarana* (subgenus) and *Chalcorana* very distant from each other evolutionarily.

Subgenus *Chalcorana* (*Chalcorana chalconota* being our exemplar, and the type of the taxon) is a morphologically very poorly diagnosed subgenus within the subsection *Hylarana*, with dermal glands present or not in the larvae, outer metatarsal tubercle present or not, male with paired subgular vocal pouches present or not, animal pole of egg pigmented or not, and the only likely synapomorphy is the relative size of the fingers (I < II; Dubois, 1992). Matsui et al. (2005; fig. 46) provided evidence that *Chalcorana* is broadly polyphyletic, with *Chalcorana chalconota* close to subsection *Hydrophylax* and *C. hosii* close to members of *Eburana*. Matsui et al. (2005) suggested that this was not surprising as *Chalcorana chalconota* lays pigmented eggs and has a larval keratodont formula of 4–5/3 (Inger, 1966), whereas *Chalcorana hosii* has pigmentless eggs and larvae with a keratodont formula of 5–6/4. Matsui et al. (2005) transferred *Chalcorana hosii* into *Odorrana* (sensu lato, as including *Eburana*), with the status of the remaining species of nominal *Chalcorana* left questionable.

Clinotarsus is a monotypic taxon (*Clinotarsus curtipes*) that is also poorly diagnosed, with larvae attaining a large size and having a somewhat high (but not exclusively) larval keratodont formula of 8/6–8 (Chari, 1962; Dubois, 1992), both characteristics found in *Nasirana* as well. We sampled the single species, *Clinotarsus curtipes*.

Subgenera *Eburana* and *Odorrana* (sensu Dubois, 1992) are putatively distinguished from each other by *Eburana* having (1) discs with a circumlateral groove on finger III and toe IV (present or absent in *Odorrana*); (2) external metatarsal tubercle present or absent (absent in *Odorrana*); (3) gular pouches (variable, including the *Eburana* condition, in *Odorrana*); (4) no unpigmented spines on the chest in males (putatively present in *Odorrana*, according to Dubois, 1992, but absent in most species, being present in *Odorrana* only in the *Odorrana andersoni* group [see above] and two species of the *Odorrana schmackeri* group [*O. schmackeri* and *O. lungshuengensis*]; see C.-C. Liu and Hu, 1962; Hu et al., 1966, 1973; Yang and Li, 1980; L. Wu et al., 1983; Fei, 1999; Fei and Ye, 2001, Ye and Fei, 2001; see also Bain et al., 2003; Bain and Nguyen, 2004); (5) animal pole of egg unpigmented (pigmented in *Odorrana*, except *O. anlungensis*, *O. exiliversabilis*, *O. hejiangensis*, *O. kwangwuensis*, *O. lungshengensis*, *O. nasuta*, *O. tiannanensis*, *O. versabilis* [C.-C. Liu and Hu, 1962; Hu et al., 1966; Yang and Li, 1980; Fei, 1999; Fei and Ye, 2001; Fei et al., 2001; Ye and Fei, 2001; see also Bain et al., 2003; Bain and Nguyen, 2004]).

Ye and Fei (2001; fig 45) on the basis of morphology, and Jiang and Zhou (2005; fig. 41), on the basis of DNA sequence evidence have demonstrated that recognition of *Ebur-*

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ana renders *Odorrana* paraphyletic. With a different sampling of species of *Eburana* and *Odorrana*, Matsui et al. (2005; fig. 46) provided DNA sequence evidence that nominal *Eburana* is paraphyletic with respect to at least one member of *Odorrana* (*O. schmackeri*) and one species of *Chalcorana* (*C. hosii*). On this basis Matsui et al. (2005) considered *Eburana* to be part of *Odorrana* (along with *Chalcorana hosii*).

As noted above, a number of characters suggested by Dubois (1992) to diagnose various taxa have taxonomic distributions to suggest more widespread occurrence. Colorless chest spinules (a putative character of *Odorrana*) are also present in *Huia nasica* (B.L. Stuart and Chan-ard, 2005), *Nidirana adenopleura*, and the holotype of *N. caldwelli* (R. Bain, personal obs.). The one putative apomorphy of *Eburana* is character 5 (lacking a pigmented animal pole on the egg) which is known from at least three other genera: *Odorrana* (see above), *Amolops* (e.g., *A. chunganensis*), and *Chalcorana* (e.g. *C. hosii*) (Bain et al., 2003; Bain and Nguyen, 2004).

Bain et al. (2003) transferred *Rana chloronota* (which they thought Dubois, 1992, had in hand as his exemplar of ''*Rana livida*'') from *Eburana* to *Odorrana* on the following bases: it has odoriferous skin secretions (implied to be characteristic of *Odorrana* by way of the formulation of the name by Fei et al., 1991 ''1990''); its chromosomes have submetacentric pairs and positions of secondary constrictions more similar (in some cases almost identical) to other species of *Odorrana* than to other species of *Eburana* (Li and Wang, 1985; Wei et al., 1993; Matsui et al., 1995); and molecular data (Murphy and Chen, unpublished), although it has unpigmented eggs and lacks pectoral spinules. The implication is that (1) odoriferous skin secretions may be unreported for other *Eburana* species, or (2) odoriferousness, presence of spinules, and egg color may be homoplastic. We sampled *Eburana chloronota* and *Odorrana grahami*. Although this will not allow us to test the monophyly of *Eburana* or *Odorrana*, it will help illuminate the extent of the problem.

Fei et al. (2005; fig. 45) have since divided *Odorrana* (sensu Fei et al., 1991 ''1990'') into two subgenera: *Bamburana* and *Odorrana*. *Bamburana* was distinguished from subgenus *Odorrana* (sensu Fei et al., 2005) by the following characters: dorsolateral folds present (absent in *Odorrana*), upper lip with sawtooth spinules (absent in *Odorrana*); xiphisternum without notch (deeply notched in *Odorrana*); sternum widened posteriorly (sternum not widened posteriorly in *Odorrana*). *Odorrana* (*Bamburana*) *versabilis* (the type species) and *O.* (*Bamburana*) *nasuta* do not have white spines on the chest of the male, but the other species, *O.* (*Bamburana*) *exiliversabilis* does. According to this diagnosis, *Bamburana* should also include *O. trankieni* (Orlov et al., 2003). Nevertheless, Ye and Fei (2001; fig. 45) provided a cladogram based on 29 character transformations of morphology that suggest strongly that *Bamburana* renders the subgenus *Odorrana* as paraphyletic. We did not sample any species of nominal *Bamburana*, but on the basis of the study of Ye and Fei (2001) we can reject its recognition.

Glandirana was coined by Fei et al. (1991 ''1990'') as a genus, a position they have maintained consistently (Fei et al., 2005). Nevertheless, *Glandirana* was placed by Dubois (1992) within subsection *Hylarana*, where it was diagnosed by Dubois as lacking digital and toe pads, although it retains a lateral groove on the toe tips as found in other groups that do have enlarged digital pads. With the exception of the lateral toe grooves in *Glandirana*, we are unaware of any morphological character that would prevent assignment of *Glandirana* to sections *Amerana*, *Pelophylax*, or *Rana*. Jiang and Zhou (2005), on the basis of DNA sequence evidence, placed *Glandirana* as the sister taxon of *Rugosa* and together as the sister taxon of a group composed of *Amolops*, *Nidirana*, *Pelophylax*, and *Rana* (fig. 41). We sampled *Glandirana minima*.

Subgenus *Hylarana* is also weakly diagnosed by comparative characters, with the only morphological apomorphies suggested by Dubois (1992) being the low number of rows of labial keratodonts in larvae (shared with *Glandirana* and sections *Amerana*, *Pelophylax*, and *Rana*; tadpoles unknown in *Pterorana* and *Tylerana*). We sampled *Hylarana erythraea* and *H. taipehensis*. Matsui

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et al. (2005; fig. 46) suggested, on the basis of DNA sequence evidence that *Hylarana* (a member of Dubois', 1992, subsection *Hylarana*) is imbedded within his subsection *Hydrophylax*.

Subgenus *Tylerana* is diagnosed from the remaining *Hylarana*-like taxa by having a large oval gland on the inner side of the arm in males (Boulenger, 1920; Dubois, 1992). We sampled *Tylerana arfaki*.

Subgenera *Sanguirana*, *Pterorana*, and *Nasirana*, which we did not study, were reported by Dubois (1992) to have dermal glands on the larvae (unknown in *Pterorana*), well-developed digital discs, and outer metatarsal tubercles (unknown in *Pterorana*). Two of the three subgenera, *Nasirana* and *Pterorana*, contain single species that have distinctive autapomorphies. *Nasirana alticola* can be distinguished from other *Hylarana*-like frogs by the large size of its larvae (shared with *Clinotarsus*), the ocellated color pattern on the larval tail (larvae of *Pterorana* and *Tylerana* unknown), the fleshy prominence on the nose of the adult, and the relatively high 7–9/8–9 keratodont formula (Dubois, 1992), which may suggest that it is a member of one of the cascade-dwelling clades. Similarly, *Pterorana khare* is distinguished from other ranid frogs by the fleshy folds on the flanks of the adult. Matsui et al. (2005) did not study *Sanguirana* or *Pterorana*, but suggested that *Nasirana* is the sister taxon of a group composed of subsection *Hydrophylax* and *Chalcorana chalconota* (nominally part of subsection *Hylarana*).

RANIXALINAE (1 GENUS, 10 SPECIES): Ranixalinae is another Indian endemic. It contains only *Indirana*, and is characterized by terrestrial tadpoles with a keratodont formula of 3–5/3–4. Otherwise, it is diagnostically identical to Nyctibatrachinae (Dubois et al., 2001). Dubois (1999a: 89) doubted that Nyctibatrachinae was distinguishable from Ranixalinae and suggested that Blommers-Schlösser's (1993) distinction between Ranixalinae (as Indiraninae), Nyctibatrachinae, and *Nannophrys* (which Blommers-Schlösser placed in the otherwise African Cacosterninae and Dubois placed in Ranixalinae) might be substantiated by additional evidence.

Van der Meijden (2005; fig. 36), recently placed, weakly, *Indirana* as the sister taxon of Dicroglossinae on the basis of mtDNA and nuDNA sequence data.

We sampled two species of *Indirana* (*Indirana* sp. 1 and *Indirana* sp. 2).

RHACOPHORIDAE (10 GENERA, 267 SPECIES) AND MANTELLIDAE (5 GENERA, 157 SPECIES): Some authors consider Afro-Asian Rhacophoridae and Madagascan Mantellidae to be families (e.g., Vences and Glaw, 2001; Van der Meijden et al., 2005). Others consider them subfamilies of Ranidae (e.g., J.D. Lynch, 1973; Dubois, 1987 ''1985'', 1992; Roelants et al., 2004) or subfamilies of a larger Rhacophoridae (e.g., J.A. Wilkinson and Drewes, 2000; J.A. Wilkinson et al., 2002). Regardless, their taxonomic histories are deeply entwined and we treat them in our discussion as families.

Liem (1970) provided the first character-analysis-based study of phylogeny of the group (including the mantellids in his sense) in which the mantellids were considered basal to the remaining rhacophorids (fig. 47A). Channing (1989) followed with a more rigorous analysis of Old World treefrogs and proposed that *Buergeria* is the sister taxon of the remaining rhacophorids (including the mantellines; fig. 47B), which he called Buergeriinae and Rhacophorinae, respectively. In his arrangement the mantellids were included as basal members of Rhacophorinae. Ford and Cannatella (1993) noted at least four synapomorphies that distinguish Rhacophoridae + Mantellidae from other ranoids: (1) presence of intercalary elements (presuming that hyperoliids are not the sister taxon); (2) one slip of the m. extensor digitorum communis longus inserts on the distal portion of the fourth metatarsal; (3) outermost slip of the m. palmaris longus inserts on the proximolateral rim of the aponeurosis palmaris; and (4) possession of a bifurcate terminal phalanx. J.A. Wilkinson and Drewes (2000) discussed the analyses by Liem (1970) and reanalysis of these data by Channing (1989) and suggested further analytical refinements but noted considerable instability in the morphological evidence (fig. 47C).

More recent work has suggested that mantellids are the sister taxon of rhacophorids (e.g., Emerson et al., 2000b; Richards et al., 2000; Roelants et al., 2004; Delorme et al., 2005), with this group imbedded within Ran-

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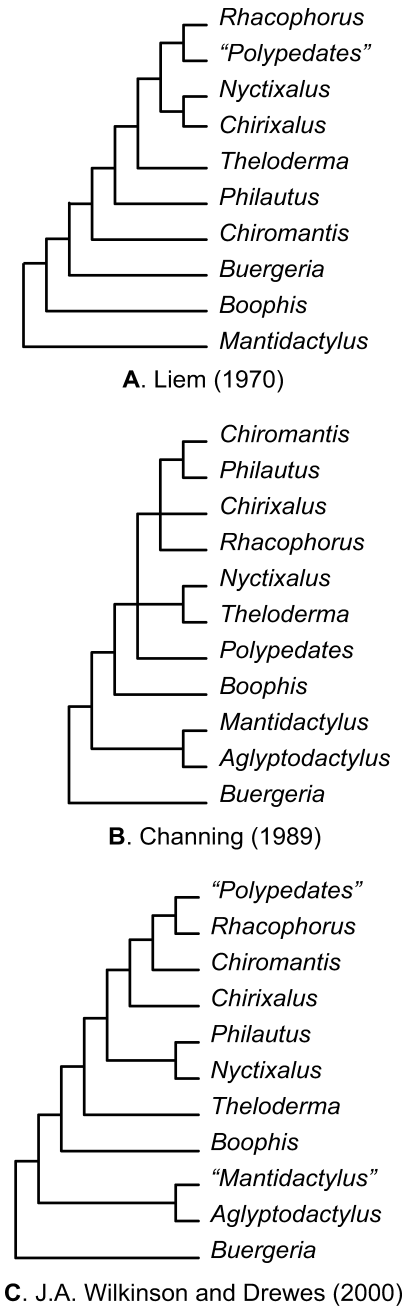

idae. Vences and Glaw (2001) suggested that Mantellidae is composed of three subfamilies: Boophinae (*Boophis*), Laliostominae (*Aglyptodactylus* and *Laliostoma*), and Mantellinae (*Mantella* and ''*Mantidactylus*''). Vences et al. (2003d) arranged these subfamilies as Boophinae + (Laliostominae + Mantellinae), with ''*Mantidactylus*'' deeply paraphyletic with respect to *Mantella*, and several of the subgenera of ''*Mantidactylus*'' paraphyletic or polyphyletic.

J.A. Wilkinson et al. (2002; fig. 48) proposed a phylogeny of rhacophorines, based on mtDNA sequence data. They found mantellines to be the sister taxon of rhacophorines, and that within rhacophorines, that Buergeria is the sister taxon of all others. They also found *Chirixalus* to be polyphyletic, a problem that was addressed, in part, by the recognition of *Kurixalus* by Ye, Fei, and Dubois (*In* Fei, 1999), for ''*Chirixalus*'' *eiffingeri*. Some other taxonomic problems were left open by J.A. Wilkinson et al. (2002): the recognition of ''*Chirixalus*'' *palbebralis*, which is isolated phylogenetically from the majority of rhacophorids; the monophyletic grouping of the type species of *Chirixalus* (*Chirixalus doriae*) with that of *Chiromantis* (*Chiromantis xerampelina*); and the weakly supported sister clade of *Chirixalus*-*Chiromantis* of *Chirixalus vittatus*, with the type species of *Polypedates*, *P. leucomystax*.

Delorme et al. (2005) have since proposed a taxonomy of Philautini (Rhacophoridae;

←

Fig. 47. **A,** Rhacophorid and mantellid tree of Liem (1970) based on 36 direct to dendritic morphological transformation series, rooted on a hypothetical generalized ranid ancestor. This is one of six equally parsimonious trees constructed under the Combinatorial Method (Sharrock and Felsenstein, 1975) that Liem considered to be the ''best''; **B,** Tree of Rhacophoridae (including Mantellidae) by Channing (1989) based on a reinterpretation and reanalysis of character transformations from Liem (1970); **C,** Rhacophorid section of consensus tree of J.A. Wilkinson and Drewes (2000; their fig. 14), based on reanalysis of Liem and Channing's data, as well as reinterpretation of some characters on the basis of specimen study. Quotation marks denote nonmonophyly.

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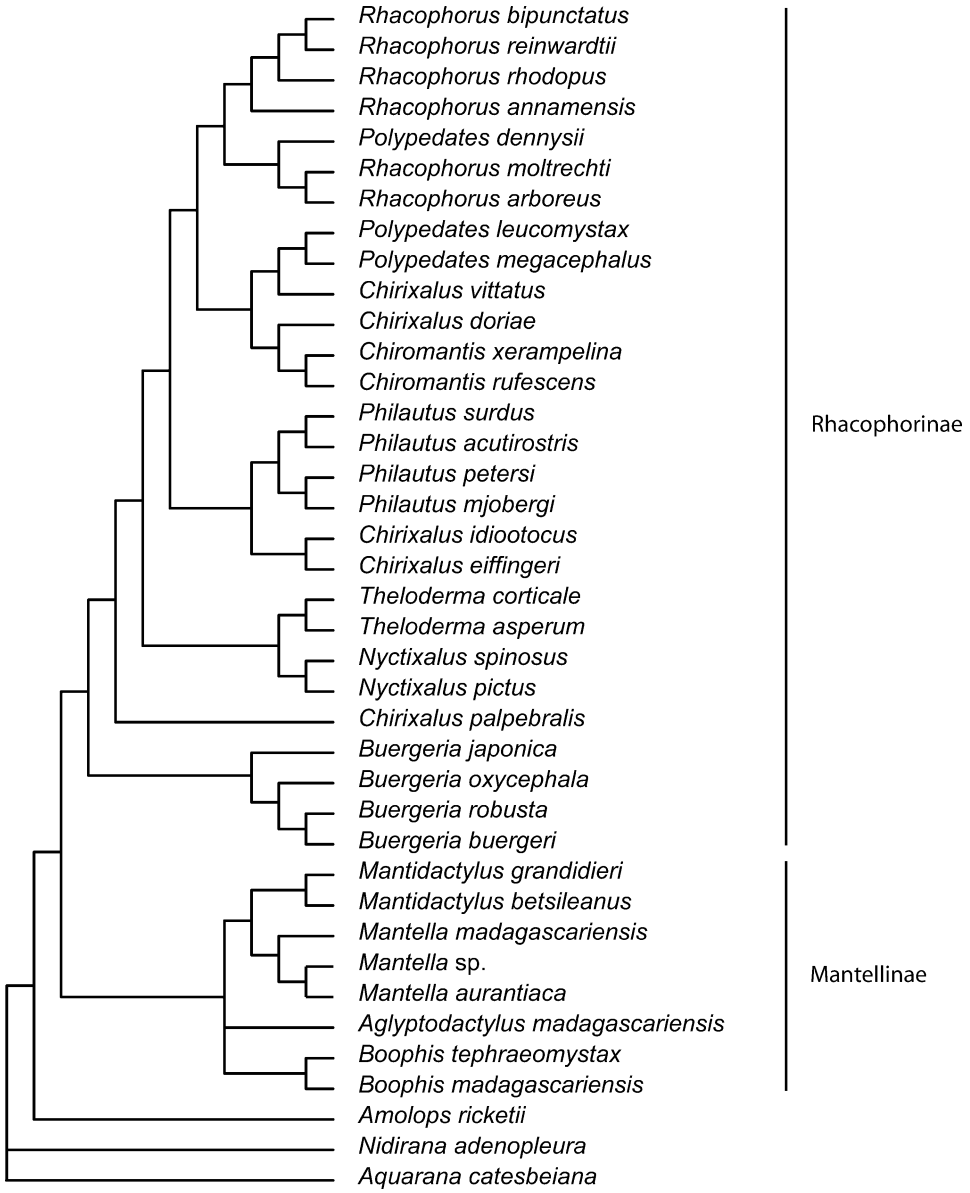

Fig. 48. Consensus of weighted parsimony trees of Rhacophoridae suggested by J.A. Wilkinson et al. (2002), with their subfamily taxonomy on right. (This is Mantellidae and Rhacophoridae of other authors.) The tree was based on 2kb (of 12S and 16S mt rRNA as well as $tRNA^{Val}$). Alignment was manual, guided by models of secondary structure with ambiguously aligned segments discarded. In analysis, transversions were weighted twice transitions. Whether reatment of gaps were treated as evidence of relationship or as missing data was not stated. *Chirixalus eiffingeri* was placed in *Kurixalus* by Ye, Fei, and Dubois (*In* Fei, 1999), and *Chirixalus idiootocus* was transferred into an explicitly polyphyletic/paraphyletic *Aquixalus* by Delorme et al. (2005). The tree was rooted on *Nidirana adenopleura* and *Aquarana catesbeiana*.

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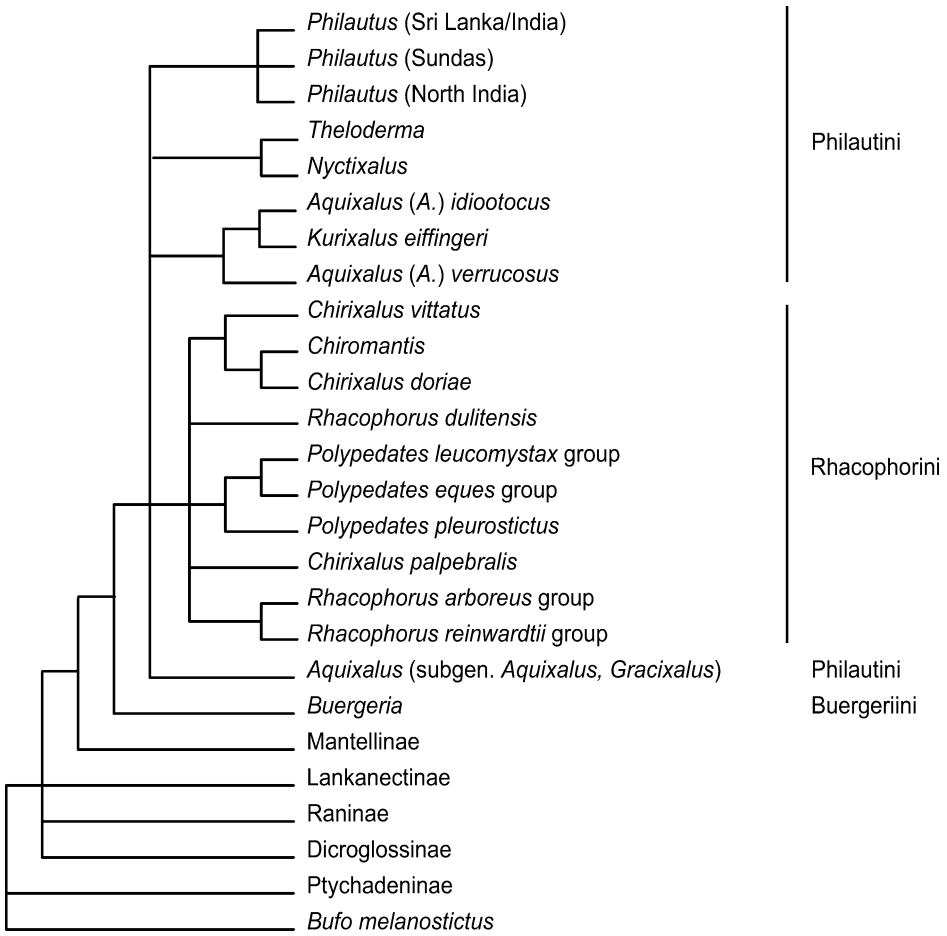

Fig. 49. Delorme et al.'s (2005) dendrogram of rhacophorids, based on undisclosed molecular and morphological data (although characters were summarized for some genera and suprageneric groups), redrawn to illuminate the paraphyly of groupings.

fig. 49). Although a tree was provided, the evidence (molecular or morphological) that provided the tree structure was not provided, and inasmuch as phylogenetic propinquity was not the organizing principle of their proposed taxonomy, their taxonomy is not consistent with the phylogeny they proposed. Although reported to be based largely on the same data set as the rhacophorid study of J.A. Wilkinson et al. (2002; 12S and 16S rRNA), the tree proposed by Delorme et al. (2005) also included data from rhodopsin and from morphology (number and content of transformations undisclosed), but Delorme et al. (2005) did not include the $tRNA^{Valine}$ gene included by J.A. Wilkinson et al. (2002). Because none of the underlying data were formally provided, methods of alignment and analysis were also not provided. Substantially less resolution is evident in the Delorme et al. (2005) tree (fig. 49) than in the J.A. Wilkinson et al. (2002) tree (fig. 48), although they agree that (1) mantellines are the sister taxon of rhacophorines; (2) *Buergeria* is the sister taxon of all remaining rhacophorids; (3) *Theloderma* and *Nyctixalus* are sister taxa; (4) *Chirixalus* is paraphyletic with respect to *Chiromantis* and likely polyphyletic (see points 6 and 7); (5) *Rhacophorus* may be paraphyletic with respect to a possibly nonmonophyletic *Polypedates*; (6) a monophyletic unit exists that is composed of

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Kurixalus eiffingeri and *Aquixalus idiootocus* and *A. verrucosus* (the latter two were transferred, respectively, by Delorme et al., 2005, from ''*Chirixalus*'' and ''*Rhacophorus*'' into an explicitly paraphyletic or polyphyletic *Aquixalus*, without disclosure of phylogenetic evidence; see comment below); (7) ''*Chirixalus*'' *palpebralis* is demonstrably not in a monophyletic group with remaining *Chirixalus*.

Delorme et al. (2005) recognized a paraphyletic/polyphyletic *Aquixalus* containing two nominal subgenera: (1) *Aquixalus* (paraphyletic/polyphyletic if *Aquixalus idiootocus* and *A. verrucosus* are included; if they are excluded from *Aquixalus* the monophyly of the remaining subgenus *Aquixalus* remains arguable); (2) *Gracixalus* (type species: *Philautus gracilipes* Bourret, 1937) for the ''*Chirixalus*'' *gracilipes* group, which they treated as phylogenetically distant from ''*C.*'' *palpebralis*, thereby suggesting that the *palpebralis* group of Fei (2001), composed, in Fei's usage, of *Philautus palpebralis*, *P. gracilipes*, *P. medogensis*, *P. ocellatus*, and *P. romeri*, is nonmonophyletic. Nevertheless, because J.A. Wilkinson et al. (2002) and Delorme et al. (2005) presumably had so much underlying evidence in common, the fact of their substantial topological differences between their results is surprising, although many of the internal branches of the J.A. Wilkinson et al. (2002) tree are weakly supported and possibly could be modified by the undisclosed rhodopsin and morphology data of Delorme (2005). Nevertheless, a tree without associated evidence (that of Delorme et al., 2005) cannot test a tree that has evidence attached to it (the tree of J.A. Wilkinson et al., 2002).

Because Delorme et al. (2005; fig. 49) do not accept (apparently) phylogenetic propinquity as the organizing principle in taxonomy, they (1) created a new paraphyletic genus, *Aquixalus* (including *Chirixalus idiootocus* and *Rhacophorus verrucosus*, which they simultaneously figured to be closer evolutionarily to *Kurixalus eiffingeri* than to other members of their *Aquixalus*), (2) retained a nonmonophyletic *Chirixalus* (with respect to *Chiromantis* and ''*Chirixalus*'' *palpebralis*), and (3) recognized Philautini (*Philautus* + *Theloderma* + *Nyctixalus* + ''*Aquixalus*''), for which the predominance of their own evidence, as demonstrated by their tree, does not reject paraphyly. In particular, it is not clear why these authors transferred *Chirixalus idiootocus* into a paraphyletic ''*Aquixalus*'', so for our overall discussion, we will not follow the transfer of ''*Chirixalus*'' *idiootocus* into a paraphyletic/polyphyletic ''*Aquixalus*'', because this taxonomic change disagrees with the phylogenetic tree (albeit, data free) proposed in the same publication.

In our analysis we sampled Boophinae (*Boophis albilabris*, *B. tephraeomystax*); Laliostominae (*Aglyptodactylus madagascariensis*, *Laliostoma labrosum*); Mantellinae (*Mantella aurantiaca*, *M. nigricans*, *Mantidactylus* cf. *femoralis*, *M. peraccae*); Buergeriinae (*Buergeria japonica*); Rhacophorinae (''*Aquixalus*'' (*Gracixalus*) *gracilipes* [formerly in *Chirixalus* or *Philautus*], ''*Chirixalus*'' *idiootocus*, *Chirixalus doriae*, *C. vittatus*, *Chiromantis xerampelina*, *Kurixalus eiffingeri*, *Nyctixalus pictus*, *N. spinosus*, *Philautus rhododiscus*, *Polypedates cruciger*, *P. leucomystax*, *Rhacophorus annamensis*, *R. bipunctatus*, *R. calcaneus*, *R. orlovi*, and *Theloderma corticale*).

RESULTS

Sequence Length Variation and Notes on Analysis

Length variation among the four nuclear protein coding genes was minimal. Following trimming of primers, all histone H3-complete products were 328 bp, and all SIA-complete products were 397 bp. All but one of the rhodopsin-complete products were 316 bp; the sequence for *Alytes obstetricans* was 315 bp, as was the sequence of this species deposited previously on GenBank (AY364385). Most tyrosinase products were 532 bp, exceptions being *Xenophrys major* and *Ophryophryne hansi*, which were 538 bp. Tyrosinase was by far the most difficult fragment to amplify (tyrosinase sequences were sampled for only 38% of the terminals), and this difficulty impedes understanding of the significance of this length variation. The ''closest'' taxa for which we were able to obtain sequences for this locus were *Xenopus laevis* (from GenBank AY341764) and *Hem-*

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isus marmoratus (both of which are 532 bp), so it is unclear whether the greater length of this tyrosinase fragment is characteristic of some megophryids or a more inclusive clade. The homologous tyrosinase sequence for *Petropedetes parkeri* downloaded from GenBank (AY341757) was 535 bp. As with the megophryids, the generality of this length is unclear. However, the length of *Arthroleptides* sp. is 532, so it is likely that the increased length is restricted to some or all species of *Petropedetes*.

Length variation was much more extensive and taxonomically widespread in the ribosomal loci. Among complete H1 sequences, the shortest length of 2269 bp was found in *Afrana fuscigula*. The longest sequence was that of the outgroup terminal *Latimeria chalumnae* (2530 bp), followed by *Ptychadena mascareniensis* (2494 bp) and *Silurana tropicalis* (2477 bp). Length variation was too extensive for clear phylogenetic patterns to emerge. However, although extensive variation in the length of the 28S sequences occurred even among closely related species (e.g., 744 bp in *Schoutedenella schubotzi* and 762 bp in *S. xenodactyloides*), numerous clades may be characterized by their 28S length. For example, of the 20 salamander 28S fragments with no missing data, all had a length of 694 bp, except *Pseudoeurycea conanti* and *Desmognathus quadramaculatus*, which were 695 bp. The only other species of 694 bp in this study were the two turtles (*Pelomedusa subrufa* and *Chelydra serpentina*) and the pelodryadine frog, *Nyctimystes dayi*. Length variation in 28S is greater among caecilians (683–727 bp), but it is still more restricted than in anurans (685–830 bp).

Among the sampled anurans, this 28S fragment is > 700 bp in all but six species (appendix 3). *Mantella nigricans* and *M. aurantiaca* differ from all other taxa in that their 28S sequence is 685 bp (28S sequences were not generated for *Mantidactylus*, but they were for *Laliostoma*, *Aglyptodactylus*, and numerous rhacophorids, which have 28S sequences of 709–712 bp). As mentioned earlier, the 28S sequence of *Nyctimystes dayi* is 694 bp, and that of the related *Litoria genimaculata* is 690. The remaining outliers are *Bufo punctatus* (700 bp) and *Microhyla* sp. (698 bp) which differ from close relatives by > 50 bp and > 25 bp, respectively. *Ascaphus truei*, *Leiopelma archeyi*, and *L. hochstetteri* are all 703 bp, as are the included species of *Pelodytes* and *Spea*. Similarly, *Alytes* and *Discoglossus* are the only sampled species with a 28S fragment of 706 bp.

Although these variations in length do not provide evidence of phylogeny independent of the underlying indel and nucleotide transformation events, their phylogenetic conservativeness makes them useful diagnostic tools, and we therefore note 28S sequence length, where relevant, in the taxonomic sections that follow.

Parsimony analysis by POY of the combined data set resulted in a single most parsimonious solution of 127019 steps. Although optimizing the implied alignment on the topology found in POY verified the length reported in POY, ratcheting of the implied alignment in NONA spawned from Winclada resulted in four most parsimonious trees of length 127,017 steps, and these are our preferred hypotheses. The only differences between the POY and NONA solutions involve the placement of (1) *Glandirana* and (2) *Brachytarsophrys feae*. This conflict is also seen among the four 127017-step trees, resulting in the polytomies seen in the strict consensus (fig. 50 [provided as a multipage insert]).

Topological Results and Discussion

A consensus of the four equally most parsimonious trees is shown in figure 50 (insert). Most clades are highly corroborated by molecular evidence (and in some places by morphological evidence). Although only an imperfect surrogate for a measure of support (something that so far eludes us), the Bremer (= decay index) and jackknife values all speak to a highly corroborated tree. (See ap-

Figure 50 is the taxonomy tree of life, inserted under the back cover.

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pendix 4 for branch length, Bremer support, and jackknife values.) Because this study rests on the largest amount of data ever applied to the problem of the relationships among amphibians, we think that the obtained tree is a step forward in the understanding of the evolutionary history of amphibians. We do, of course, have reservations about parts of the overall tree. But, upon reflection, we realized that most of the parts of the tree that concerned us were those that (1) we considered insufficiently sampled relative to known species and morphological diversity (e.g., Bufonidae); or (2) are groups for which no other evidence-based suggestions of phylogeny had ever been provided (e.g., parts of traditionally recognized Ranoidea). Nevertheless, familiarity has much to do with notions of plausibility, the root of the problem of social conservatism in amphibian systematics.

We discuss results under two headings and with reference to several different figures. The primary focus in this first section, ''Results'', is to address issues of relationship among, and monophyly of, major groups (nominal families and subfamilies and nomenclaturally unregulated taxa). We also make general taxonomic recommendations in this section. Under the second heading, ''Taxonomy'', we discuss further results and various taxonomic issues under the appropriate taxonomic category. Bremer and jackknife values are reported for each branch in figure 50 (insert; as well as in other figures, where relevant) but are otherwise only occasionally mentioned in text.

The general tree shown in figure 50 (insert), with 532 terminals, is obviously too complex and detailed for easy discussion, so we will refer to subtrees in different figures. Relevant taxa (branches) have the molecular data summarized by name and/or number in appendix 4. We first discuss the results relative to the Review of Current Taxonomy at or above the nominal family-group level, with reference to families that appear to be monophyletic and those that are paraphyletic and polyphyletic. In the case of paraphyly and polyphyly we offer remedies in this section that are paralleled in more detail in the Taxonomy section, where we propose a monophyletic taxonomy for all but a few problematic amphibian groups and discuss aspects of our results that are relevant to the systematics of that particular group, such as monophyly of nominal genera and various taxonomic remedies to problems that our results highlighted.

Outgroup Relationships

In our results, *Latimeria* is outside of the tetrapod clade, and amniotes form the sister taxon of amphibians. This topology was conventional, at least for paleontologists and morphologists (e.g., Gauthier et al., 1988a, 1988b; fig. 2A). Within Amniota, we found turtles to be the sister taxon of diapsids (archosaurs + lepidosaurs) and this inclusive group to be the sister taxon of mammals. Our molecular data do not support the suggestion by Rieppel and de Braga (1996), based on morphology, that turtles are more closely related to lepidosaurs than to archosaurs. Our molecular results disagree with the results of Mannen and Li (1999), Hedges and Poling (1999), and Iwabe et al. (2005), in which turtles were found to be closely related to archosaurs, with lepidosaurs, and mammals as successively more distant relations. An analysis of why our molecular results are congruent with the conventional tree of morphology (fig. 2A) and not with previous molecular results is largely outside the scope of this paper. Nevertheless, our analysis was a parsimony analysis, as were the studies of Gauthier et al. (1988a; 1988b). The molecular study of Hedges and Poling (1999) rested on a large amount of DNA evidence (ca. 5.2kb), but their alignment was made under a different set of evolutionary assumptions from that used in their phylogenetic analysis. A stronger test of amniote relationships will be made by combining morphology and all available DNA evidence and analyzing these data under a common set of assumptions.

Amphibia (Lissamphibia) and Batrachia

Our results (figs. 50 [insert], 51) corroborate the monophyly of amphibians (Lissamphibia of Parsons and Williams, 1963; Amphibia of Cannatella and Hillis, 1993) with reference to other living taxa, although our data obviously cannot shed any light on the placement of the lissamphibians among fossil

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Fig. 51. Basal structure of our consensus tree (fig. 50 [insert]) with respect to outgroups and major amphibian taxa.

groups. We also found the three groups of lissamphibians to be strongly supported (fig. 50 [insert], branches 7, 24, 74). Furthermore, our DNA sequence data indicate that the caecilians are the sister taxon of the clade composed of frogs plus salamanders (Batrachia; fig. 50 [insert], branch 23), the topology preferred by Trueb and Cloutier (1991). Our data reject (1) that living amphibians are paraphyletic with respect to Amniota (Carroll and Currie, 1975; J.S. Anderson, 2001); (2) that salamanders are paraphyletic with respect to caecilians (Laurin, 1998a, 1998b, 1998c); and (3) the hypothesis, based on smaller amounts of evidence, that caecilians and salamanders are closest relatives (Feller and Hedges, 1998). Our data suggest strongly that the arrangement favored by morphologists (e.g., Trueb and Cloutier, 1991; Iordansky, 1996; Zardoya and Meyer, 2000, 2001; Schoch and Milner, 2004) is also the arrangement favored by the preponderance of the molecular evidence (e.g., San Mauro et al., 2005), that living amphibians form a monophyletic group with respect to Amniota, and that frogs and salamanders are more closely related to each other than either is to the caecilians (contra Feller and Hedges, 1998). The effect of including fossils and a much more complete morphological data set are not known, but we note that our molecular data are consistent with the preponderance of morphological data so far published.

Salamanders (Caudata) and frogs (Anura) are each also monophyletic, a result that will surprise no one, even though the morphological evidence for monophyly of the salamanders, in particular, is weak (Larson and Dimmick, 1993).

Gymnophiona

In general form our cladogram (fig. 50 [insert], fig. 52) agrees with the conventional

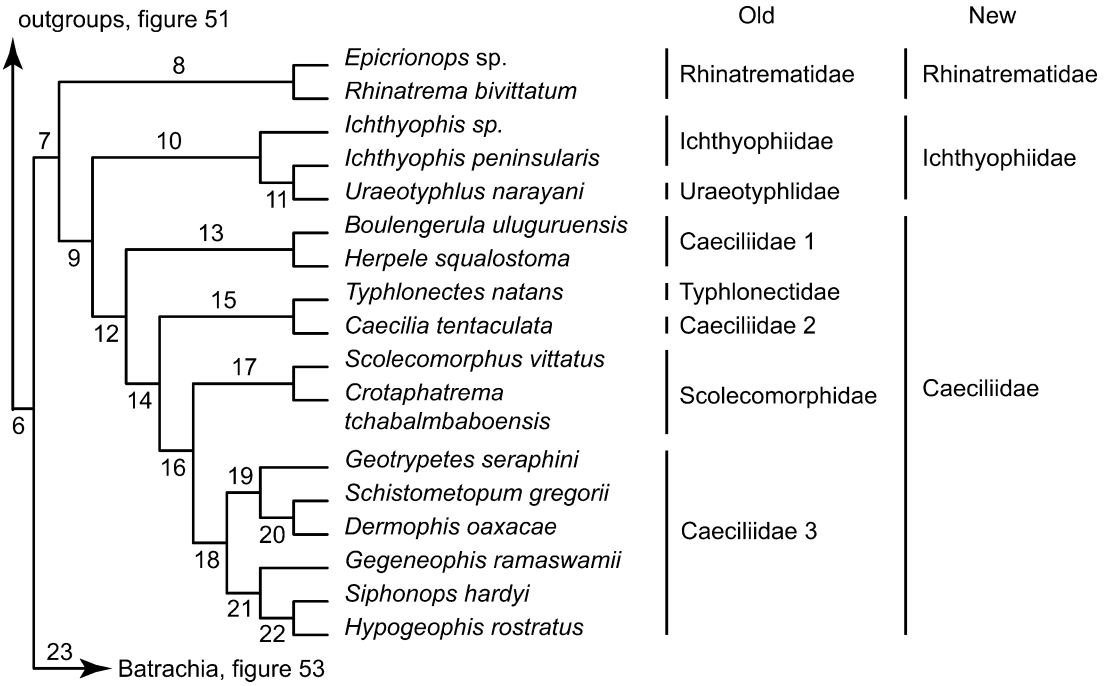

Fig. 52. Caecilian section of general tree (fig. 50 [insert]).

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view of caecilian relationships (fig. 3). Like Nussbaum (1977, 1979) and later authors (e.g., Duellman and Trueb, 1986; San Mauro et al., 2004; San Mauro et al., 2005) we find that Rhinatrematidae is the monophyletic sister taxon of the remaining caecilians. This placement appears well-corroborated on both morphological and molecular grounds.

Ichthyophiidae is paraphyletic with respect to Uraeotyphlidae (this being highly corroborated by our molecular data), and can be restated as *Ichthyophis* is paraphyletic with respect to *Uraeotyphlus*. This outcome was arrived at previously by Gower et al. (2002). There is a single morphological character, angulate annuli anteriorly, that supports the monophyly of the ichthyophiids (sensu stricto, excluding *Uraeotyphlus*), but the amount of molecular evidence in support of *Uraeotyphlus* being nested within *Ichthyophis* indicates that this character was either reversed in *Uraeotyphlus* or independently derived in different lineages of ''*Ichthyophis*''. Under these circumstances, *Uraeotyphlus* must be transferred to Ichthyophiidae, and although treatment of ''*Ichthyophis*'' is beyond the scope of this study, we expect subsequent work (denser sampling of ichthyophiids and addition of new data) to delimit the nature of this paraphyly and reformulate infrafamilial taxonomy. The effect of this change is minimal, because Uraeotyphlidae contains a single genus, and no hierarchical information is lost by placing Uraeotyphlidae in the synonymy of Ichthyophiidae.

As expected from previously published DNA sequence (M. Wilkinson et al., 2003) and morphological evidence (M.H. Wake, 1993; M. Wilkinson, 1997), we found Scolecomorphidae to be imbedded within Caeciliidae. The evidence for this is strong (appendix 4, branches 12, 14, 16), and we therefore consider Scolecomorphidae to be a subsidiary taxon (Scolecomorphinae) within Caeciliidae. Similarly, Typhlonectidae is deeply imbedded within Caeciliidae, a result previously noted (M.H. Wake, 1977; Nussbaum, 1979; M. Wilkinson, 1991; Hedges et al., 1993). Typhlonectidae is here regarded as a subsidiary taxon (as Typhlonectinae) within a monophyletic Caeciliidae, although the genera of the former ''Caeciliinae'' remain incertae sedis within the Caeciliidae.

Our results differ slightly from those presented by M. Wilkinson et al. (2003), which were based on a smaller amount of sequence data (mt rRNA only). Like us, M. Wilkinson et al. (2003) found Scolecomorphidae and Typhlonectidae to be imbedded within ''Caeciliidae'', although in a different and less strongly corroborated placement. Our placement of *Siphonops* (South America) as the sister taxon of *Hypogeophis* (Seychelles) and together the sister taxon of *Gegeneophis* (India), is the only unanticipated result. In light of the strong support it received in our analysis, this conclusion deserves to be evaluated carefully.

CAUDATA

Among previously published cladograms our results (fig. 53) most resemble the tree of salamander families suggested by Gao and Shubin (2001; fig. 5) and diverge slightly from the results presented by Larson and Dimmick (1993; fig. 4) and Wiens et al. (2005; fig. 7) in placing sirenids (which lack spermatophore-producing organs) as the sister taxon of Proteidae (which, like other salamandroid salamanders has spermatophore-producing organs), rather than placing the sirenids as the sister taxon of all other salamander families. (The Bayesian analysis of Wiens et al., 2005, however, placed cryptobranchoids as the sister taxon of remaining salamanders, suggesting that there is internal conflict within their data set.) Other recent results found, on the basis of RAG-1 DNA sequence evidence (Roelants and Bossuyt, 2005; San Mauro et al., 2005), and on the basis of RAG-1, nuRNA, and morphology (Wiens et al., 2005), Sirenidae to be the sister taxon of remaining salamanders, the traditional arrangement. Because our molecular evidence did not overlap with theirs, and with the arguable example of Wiens et al. (2005), their amount of evidence is smaller than ours, these results require additional testing. Our results do not reject the monophyly of any of the nominal families of salamanders, a result that is consistent with previous studies. Except as noted later, the remaining results are conventional.

HYNOBIIDAE AND CRYPTOBRANCHIDAE: Unlike the results of Larson and Dimmick

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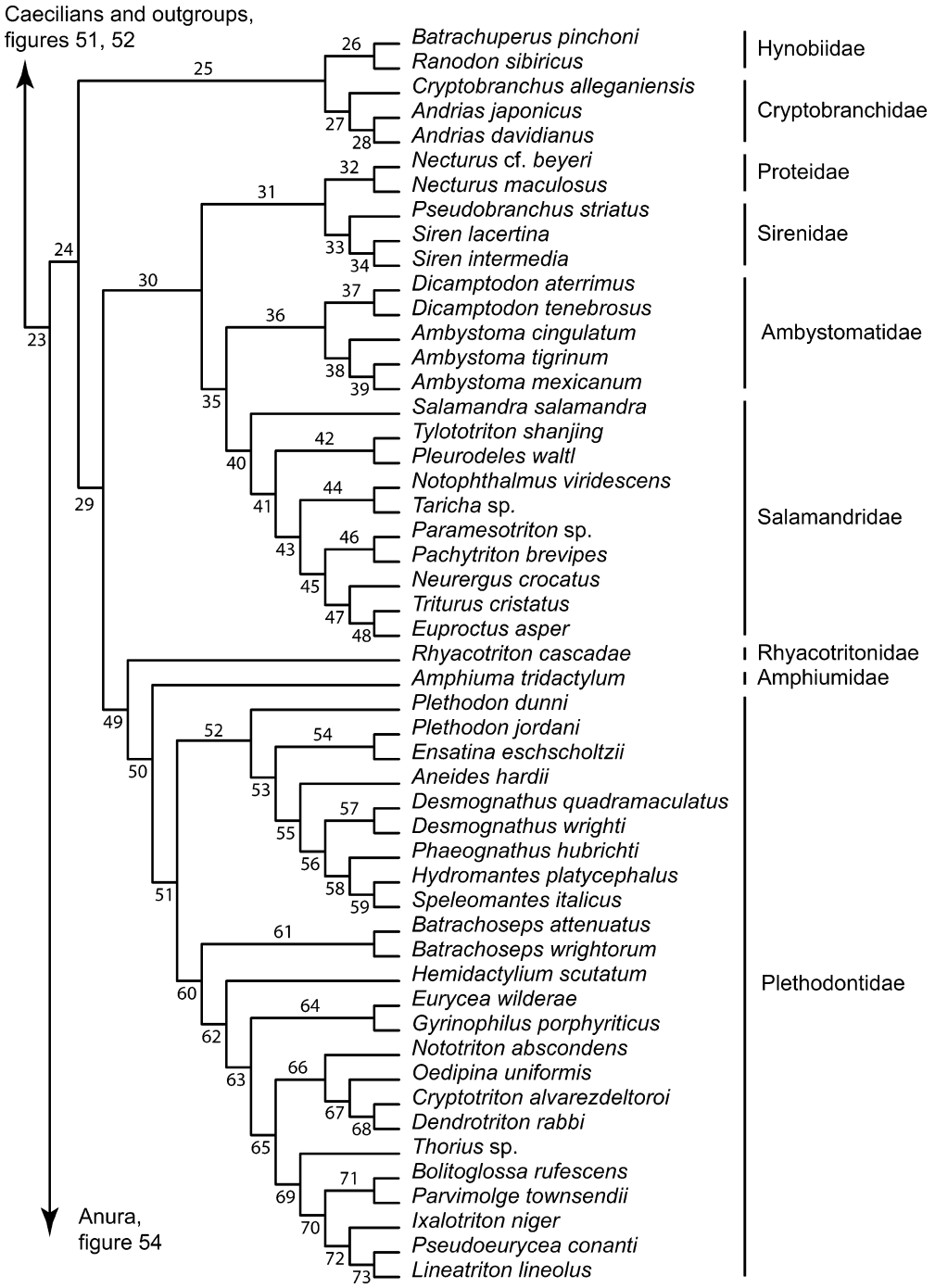

Fig. 53. Salamander section of general tree (fig. 50 [insert]). See discussion in ‘‘Taxonomy’’ for subfamilies of Plethodontidae and Salamandridae. New taxonomy is on right.

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(1993; fig. 4), San Mauro et al. (2005; fig. 17), Roelants and Bossuyt (2005; fig. 16), and Wiens et al. (2005; fig. 7) our results place these taxa as the sister taxon of all other salamanders, and not as the sister taxon of all salamanders excluding sirenids (the relationship recovered by Larson and Dimmick, 1993, San Mauro et al., 2005, and Roelants and Bossuyt, 2005). The monophyly of hynobiids plus cryptobranchids is not controversial, nor is that of Cryptobranchidae. In the case of Hynobiidae, as noted in the taxonomic review, our sampling is insufficient to address any of the generic controversies (summarized by Larson et al., 2003: 43–45) and is only a minimal test of the monophyly of Hynobiidae.

SIRENIDAE AND PROTEIDAE: Unlike Larson and Dimmick (1993) and more recent morphological and molecular studies (Roelants and Bossuyt, 2005; San Mauro et al., 2005; Wiens et al., 2005), but like Gao and Shubin (2001; fig. 5), we recovered Sirenidae not as the sister taxon of all other salamanders but as the sister taxon of Proteidae. Our highly corroborated results and the results of Gao and Shubin (2001) suggest that the perennibranch characteristics of Proteidae and Sirenidae are homologous. On this topology the cloacal apparatus for spermatophore formation is a synapomorphy at the level of all salamanders, excluding Cryptobranchidae and Hynobiidae, with a loss in Sirenidae. Alternatively, it is a convergent development in Proteidae and in the ancestor of Salamandridae, Rhyacotritonidae, Dicamptodontidae, Plethodontidae, Amphiumidae, and Ambystomatidae. The effect of combining the morphological data presented by Wiens et al. (2005) with all of their and our molecular data remains an open question, although we note that their morphological-only data set produced a result in which Sirenidae + Proteidae form a monophyletic group. Thus, it is not clear that this is a simple morphology-versus-molecules issue. Rather than oversimplify and misrepresent that paper, we leave the question open as to what the result will be when all molecular and morphological data are combined.

As noted earlier, our results reject a monophyletic Salamandroidea (all salamanders, excluding Cryptobranchidae, Hynobiidae, and Sirenidae). This taxon was diagnosed by internal fertilization through the production of spermatophores (produced by a complex system of cloacal glands) and having angular and prearticular bones fused (also found in Sirenidae). The hypothesis that sirenids and proteids form a taxonomic group is quite old: It was first suggested by Rafinesque (1815; as Meantia; see the discussion in appendix 6).

RHYACOTRITONIDAE AND AMPHIUMIDAE: We resolved the polytomy found in the tree of Gao and Shubin (2001) of Plethodontidae, Rhyacotritonidae, and Amphiumidae into Rhyacotritonidae + (Amphiumidae + Plethodontidae), a conclusion also of Wiens et al (2005). Although we did not test the monophyly of either *Rhyacotriton* or *Amphiuma*, in neither case is this seriously in question. As noted earlier, the position of *Amphiuma* with respect to plethodontids is conventional (Larson, 1991; Larson and Dimmick, 1993).

PLETHODONTIDAE: Our tree differs trenchantly from those of authors prior to 2004 (e.g., D.B. Wake, 1966; Lombard and Wake, 1986), but is similar in general form to those of Mueller et al. (2004) on the basis of complete mtDNA genomes, Macey's (2005) reanalysis of those data, and the tree of Chippindale et al. (2004), based on 123 characters of morphology and about 2.9 kb of mtDNA and nuDNA. In those studies and in ours Amphiumidae and Rhyacotritonidae were obtained as successively more distant outgroups of Plethodontidae. In the three previous studies (Chippindale et al., 2004; Mueller et al., 2004; Macey, 2005) as well as in ours, the desmognathines are in a clade with the plethodontines (*Ensatina*, and *Plethodon*). Our data (as well as those of Mueller et al., 2004, and Macey, 2005) also found *Hydromantes* and *Speleomantes* to be in this plethodontine clade, not with ''other'' bolitoglossines.

In our results, as well as those of Mueller et al. (2004) and Chippindale et al. (2004), all other plethodontids (the old Hemidactyliinae and Bolitoglossini) are placed in a group that forms the sister taxon of the first group. The evidence for these groupings is strong (appendix 4; fig. 53). The placement of *Hydromantes* and *Speleomantes* in the first group by our data is strongly corroborated,

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being placed within the desmognathines (a result that runs counter to the morphological evidence as presented by Schwenk and Wake, 1993). Mueller et al. (2004) obtained *Hydromantes* (including *Speleomantes*) in the same general group as we did, but placed as the sister taxon of *Aneides*. In the details of placement of *Batrachoseps*, *Hemidactylium*, and our few overlapping bolitoglossine genera, we differ mildly. Our differences from the tree of Macey (2005) are difficult to explain. The amount of evidence marshalled by Macey (the same aligned data set as Mueller et al., 2004), is on the order of 14kb of aligned mtDNA sequence. Our mtDNA set is a subset of that, but analyzed differently, particularly with respect to alignment. Alignment of the data set of Mueller et al. (2004) was done with different transformation costs than used in analysis, and this alignment was accepted for reanalysis by Macey (2005). Further, a number of our exemplars (i.e., *Plethodon dunni*, *P. jordani*, *Desmognathus quadramaculatus*, *Phaeognathus*, *Hydromantes platycephalus*, *Eurycea wilderae*, *Gyrinophilus porphyriticus*, *Thorius* sp., *Bolitoglossa rufescens*, and *Pseudoeurycea conanti*) are represented in our analysis by sequences that are not part of the mtDNA genome. Although we provisionally accept the results of Macey (2005; fig. 10) as based on a much larger amount of data than our results, it may be that the single biggest cause of different results between our analysis and his is the method of alignment. One will know only when that data set is analyzed using direct optimization.

Chippindale et al. (2004; fig. 11) suggested a taxonomy, consistent with their tree, for Plethodontidae. Plethodontinae in their sense corresponds to the group composed of the former Desmognathinae and former Plethodontini. Within the second group composed of hemidactyliines and bolitoglossines they recognized Hemidactyliinae (*Hemidactylium*), Spelerpinae Cope, 1859 (*Eurycea* [sensu lato], *Gyrinophilus*, *Stereochilus*, and *Pseudotriton*), and Bolitoglossinae (for all of the bolitoglossine genera studied). Macey (2005) came to the same taxonomy, but placed Hemidactyliinae as the sister taxon of remaining plethodontids, the relative position of the other groups remaining the same. He also placed *Hydromantes* (including *Speleomantes*) in Plethodontinae. These two genera had previously been associated with Bolitoglossini (D.B. Wake, 1966; Elias and Wake, 1983).

Our results regarding placement of *Hydromantes* and *Speleomantes* imply either that the morphological synapomorphies of the Desmognathinae, mostly manifestations of the bizarre method of jaw opening in which the lower jaw is held in a fixed position by ligaments extending to the atlas–axis complex, are reversed in the hydromantine clade or that this peculiar morphology is convergent in *Desmognathus* and *Phaeognathus*.

Previous to the study of Mueller et al. (2004), who found *Plethodon* to be monophyletic on the basis of analysis of mtDNA sequence data, all published evidence pointed to paraphyly of *Plethodon* with respect to *Aneides* (e.g., Larson et al., 1981; Mahoney, 2001). Our analysis of a variety of DNA sequence data suggests also that the eastern and western components of *Plethodon* do not have a close relationship, being united solely by symplesiomorphy. Had it not been for the appearance of the recent paper by Chippindale et al. (2004), we would have erected a new generic name for western *Plethodon* (for which no name is currently available). But, the denser sampling of plethodons and different selection of genes in the Chippindale et al. (2004) paper suggests that a study including all of the available data and a denser sampling is required before making any taxonomic novelties.

We recovered former Bolitoglossini as polyphyletic, with the traditional three main components (supergenera *Batrachoseps*, *Hydromantes*, and *Bolitoglossa*; D.B. Wake, 1966) being found to have little in common with each other. Our tree of bolitoglossines (sensu stricto) is not strongly corroborated. Nevertheless, that the three groups of bolitoglossines should be recovered as polyphyletic is not shocking inasmuch as the amount of evidence that traditionally held them together was small.

SALAMANDRIDAE: Our results largely correspond to those of Titus and Larson (1995) and especially with those presented by Larson et al. (2003). Our tree differs from the topology suggested by Larson et al. (2003),

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which was based on more extensive taxon sampling but less DNA evidence, in that we get additional resolution of the group *Neurergus* + (*Triturus* + *Euproctus*), where in the tree provided by Larson et al. (2003) these taxa are in a polytomy below the level of *Paramesotriton* + *Pachytriton*.

DICAMPTODONTIDAE AND AMBYSTOMATIDAE: *Dicamptodon* is recovered as the sister taxon of Ambystomatidae, the same phylogenetic arrangement found by previous authors (Sever, 1992; Larson and Dimmick, 1993; Wiens et al., 2005). The monophyly of *Dicamptodon* was only minimally tested, although *Dicamptodon* monophyly is not seriously in doubt (Good and Wake, 1992). Inasmuch as Dicamptodontidae was recognized on the basis of its hypothesized phylogenetic distance from Ambystomatidae (Edwards, 1976), a hypothesis now rejected, we propose the synonymy of Dicamptodontidae with Ambystomatidae, which removes the redundancy of having two family-group names, each containing a single genus. The reformulated Ambystomatidae contains two sister genera, *Dicamptodon* and *Ambystoma*.

Ambystomatidae was found to be monophyletic, at least with reference to our exemplar taxa, and the sister taxon of former Dicamptodontidae. Although we have not severely tested the monophyly of *Ambystoma*, others have done so (e.g., Shaffer et al., 1991; Larson et al., 2003), and its monophyly is well corroborated.

ANURA

As mentioned earlier and in the taxonomic review, the amount of morphological and DNA sequence evidence supporting the monophyly of Anura is overwhelming. We think that our data make a strong case for a new understanding of frog phylogeny. Even though most of our results are conventional with respect to understanding of frog phylogenetics, our purpose is not to conceal this understanding, but to bring the taxonomy of frogs into line with their phylogenetic relationships. For discussion we adopt the Ford and Cannatella (1993) tree (fig. 14) as the traditional view of phylogeny (although not of nomenclature). We first discuss the non-neobatrachian frogs (fig. 54).

ASCAPHIDAE AND LEIOPELMATIDAE: Ascaphidae and Leiopelmatidae are recovered in our analysis as parts of a monophyletic group, mirroring the results of Green et al. (1989), Báez and Basso (1996), and more recent authors (Roelants and Bossuyt, 2005; San Mauro et al., 2005). The paraphyly of this grouping, as suggested by Ford and Cannatella (1993), is rejected. If our results are accurate, the five morphological synapomorphies suggested by Ford and Cannatella (1993) of *Leiopelma* plus all frogs excluding *Ascaphus* must be convergences or synapomorphies of all living frogs that were lost in *Ascaphus*. Nevertheless, the hypothesis of Ford and Cannatella (1993) was based largely on the unpublished dissertation of Cannatella (1985; cited by Ford and Cannatella, 1993), who rooted his analysis of primitive frogs on *Ascaphus* on the basis of two plesiomorphic characters found among frogs uniquely in *Ascaphus*: (1) facial nerve passes through the anterior acoustic foramen and into the auditory capsule while still fused to the auditory nerve; (2) salamander-type jaw articulation in which there is a true basal articulation. All other characters placing *Leiopelma* as more closely related to all non-*Ascaphus* frogs were optimized by this assumption, requiring their polarity to be verified. Furthermore, the support for the *Ascaphus* + *Leiopelma* branch is very high (Bremer = 41, jackknife = 100%), so it is unlikely that five morphological characters (of which three have not been rigorously polarized) can reverse this. Placing *Ascaphus* and *Leiopelma* as sister taxa allows some characters to be explained more efficiently. Thus, the absence of the columella in these two taxa can be seen to be a synapomorphic loss. Ritland's (1955) suggestion that the m. caudalipubois-chiotibialis in *Leiopelma* and *Ascaphus* may not be homologous with the tail-wagging muscles of salamanders, and the more traditional view of homology with these muscles are both consistent with our results. To remove the redundancy of the family-group names with the two genera (*Ascaphus* and *Leiopelma*), we assign *Ascaphus* to Leiopelmatidae (as did San Mauro et al., 2005). Roelants and Bossuyt (2005) retained Ascaphidae and Leiopelmatidae as separate families and resurrected the name Amphicoela Noble,

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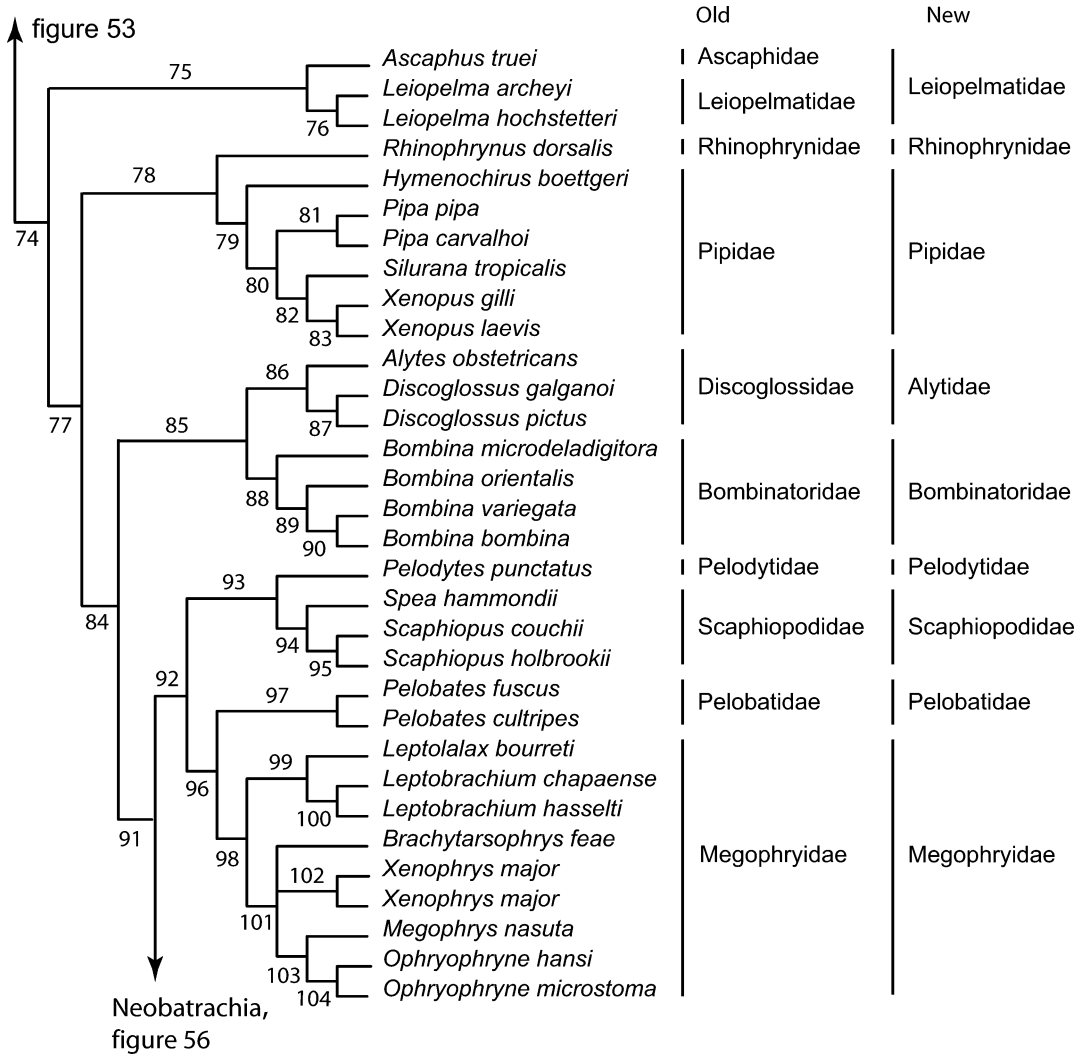

Fig. 54. Part 1 of anurans from the general tree (fig. 50 [insert]): non-neobatrachian frogs.

1931, for this taxon. Amphicoela is redundant with Leiopelmatidae (sensu lato) when Ascaphidae and Leiopelmatidae are regarded as synonymous, as we do.

PIPIDAE AND RHINOPHRYNIDAE: We found, as did Haas (2003) and San Mauro et al. (2005), and as was suggested even earlier by Orton (1953, 1957), Sokol (1975), and Maglia et al. (2001) that Rhinophrynidae + Pipidae is the sister taxon of all non-leiopelmatid frogs. This result is strongly supported by our evidence (fig. 54; appendix 4, branches 77, 78, 84). Recent suggestions had alternatively placed Pipoidea as the sister taxon of Pelobatoidea (Ford and Cannatella, 1993; their Mesobatrachia) or as the sister taxon of all other frogs (Maglia et al., 2001; Pugener et al., 2003). All three of these arrangements are supported by morphological characters, although Haas' arrangement is more highly corroborated. Haas (2003) suggested nine apomorphies that exclude Pipoidea and Ascaphidae from a clade composed of all other frogs. Pugener et al. (2003) suggested three synapomorphies for all frogs excluding pipoids. (This statement is based on examination of their figure 12; they provided no comprehensive list of synapomorphies.) Ford and

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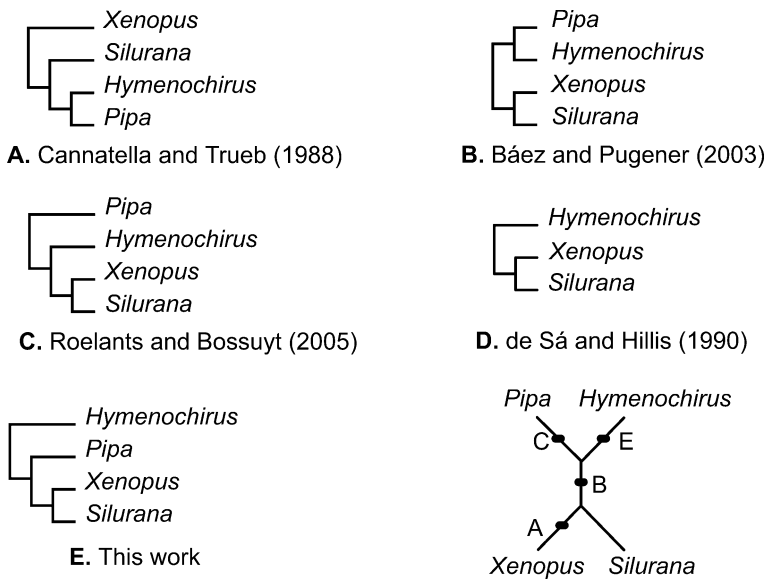

Fig. 55. Trees of intergeneric relationships within Pipidae (from fig. 19). **A,** Cannatella and Trueb (1988). **B,** Báez and Pugener (2003); **C,** Roelants and Bossuyt (2005); **D,** De Sá and Hillis (1990; results consistent with B, C, and E); **E,** This work. (Undirected network on lower right shows rooting points of each result, except for D.)

Cannatella (1993) suggested that four characters support Mesobatrachia: (1) closure of the frontoparietal fontanelle by juxtaposition of the frontoparietal bones (not in *Pelodytes* or *Spea*); (2) partial closure of the hyoglossal sinus by the ceratohyals; (3) absence of the taenia tecti medialis; and (4) absence of the taenia tecti transversum. However, on the basis of Haas' (2003) morphological data alone, these characters are rejected as synapomorphies. However, the mtDNA molecular results presented by García-París et al. (2003) support the recognition of Mesobatrachia (Pelobatoidea + Pipoidea). Nevertheless, these authors included only three non-pipoid, non-pelobatoid genera (*Ascaphus*, *Discoglossus*, and *Rana*) as outgroups, which did not provide a strong test of mesobatrachian monophyly. Placement of Pipoidea as the sister taxon of all other non-leiopelmatid frogs requires rejection of Discoglossanura, Bombinatanura, and Mesobatrachia of Ford and Cannatella (1993), a rejection that is strongly supported by our study.

In our analysis, as well as in all recent ones (Ford and Cannatella, 1993; Báez and Pugener, 2003; Haas, 2003), Pipoidea (Rhinophrynidae + Pipidae) is monophyletic, as are the component families. A novel arrangement in our tree is *Hymenochirus* being placed as the sister taxon of *Pipa* + (*Silurana* + *Xenopus*). This result differs from the cladograms of Cannatella and Trueb (1988), de Sá and Hillis (1990), Báez and Pugener (2003), and Roelants and Bossuyt (2005; fig. 16). Although our results are highly corroborated by our data, a more complete test would involve the simultaneous analysis of all of the sequence data with the morphological data of all relevant living and fossil taxa. As noted in figure 55, the rooting point of the pipid network appears to be more important to the estimates of phylogeny than differences among networks.

The placement of Pipidae + Rhinophrynidae as the sister taxon of all frogs, save Leiopelmatidae + Ascaphidae, suggests strongly that the fusion of the facial and trigeminal ganglia (Sokol, 1977) found in pelobatoids, pipoids, and neobatrachians, but not in Discoglossidae and Bombinatoridae is homoplastic. Similarly, the absence of free ribs in the adults of pelobatoids, neobatrachians, and pipoids, but their presence in *Leiopelma*, *Ascaphus*, and Discoglossidae, requires either independent losses in pipoids

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and pelobatoids + neobatrachians, or an independent gain in discoglossids + bombinatorids. Roelants and Bossuyt (2005) noted fossil evidence that would support the independent loss in pipoids and Acosmanura (Pelobatoidea + Neobatrachia).

DISCOGLOSSIDAE AND BOMBINATORIDAE: Ford and Cannatella (1993) partitioned the former Discoglossidae (sensu lato) into Discoglossidae (sensu stricto) and Bombinatoridae because their evidence suggested that former Discoglossidae was paraphyletic, with Bombinatoridae and Discoglossidae forming a graded series between the Ascaphidae and Leiopelmatidae on one hand, and all other frogs on the other hand. As noted in the taxonomic review, this partition was based on two characters shared by discoglossines and all higher frogs and absent in the bombinatorines. Haas (2003) rejected this topology with six character transformations supporting the monophyly of Bombinatoridae and Discoglossidae. In addition to Haas' characters, we have strong molecular evidence in support of the monophyly of this taxon (Discoglossidae + Bombinatoridae), as well as the subsidiary families.

Unlike Haas (2003), but like recent molecular studies (Roelants and Bossuyt, 2005; San Mauro et al., 2005), we did not recover *Alytes* as the sister taxon of the remaining discoglossines and bombinatorines. We included Haas' six characters supporting that topology in our analysis, and the taxon sampling for this part of the tree is nearly identical in the two studies, so it appears that molecular evidence in support of a topology of *Alytes* + *Discoglossus* is decisive. The only rationale for considering Discoglossidae and Bombinatoridae as separate families rested on the assertion of paraphyly of the group (Ford and Cannatella, 1993), a position now rejected. Nevertheless, we retain the two-family arrangement because this reflects the state of the literature and is consistent with recovered phylogeny.

PELOBATOIDEA: Haas (2003) did not recover Pelobatoidea (Megophryidae, Pelobatidae, Pelodytidae, Scaphiopodidae) as monophyletic. Although we included his morphological data in our analysis, we find Pelobatoidea to be highly corroborated, which suggests very interesting convergences in tadpole morphology. García-París et al. (2003; fig. 18) also found Pelobatoidea to be monophyletic, on the basis of their DNA evidence, and suggested a topology of Scaphiopodidae + (Pelodytidae + (Megophryidae + Pelobatidae)), with relatively low Bremer values on the branch tying Scaphiopodidae to the remaining taxa. In our results we recover all of these family-group units as monophyletic and highly supported. But, our data show strongly a relationship of (Pelodytidae + Scaphiopodidae) + (Pelobatidae + Megophryidae) (fig. 54).

NEOBATRACHIA: As in all previous studies, we found Neobatrachia to be highly corroborated by many transformations (figs. 50 [insert], 56, 58, 59, 60). What is particularly notable in the broad structure of Neobatrachia is the dismemberment of Leptodactylidae and Hylidae as traditionally formulated, as well as the placement of Heleophrynidae outside of the two major monophyletic components, for our purposes referred to here as (1) Hyloidea, excluding Heleophrynidae and (2) Ranoidea.

HELEOPHRYNIDAE: Haas (2003) suggested that *Heleophryne* may be related to Pelobatoidea, a suggestion that is not borne out by our simultaneous analysis of Haas' data and our molecular data. Earlier authors (e.g., J.D. Lynch, 1973) addressed the phylogenetic position of *Heleophryne* and associated it with Limnodynastidae on the basis of overall similarity, or with Limnodynastidae + Myobatrachidae on the basis of DNA sequence data (Biju and Bossuyt, 2003). But recently San Mauro et al. (2005) suggested, on the basis of DNA sequence evidence, that Heleophrynidae is the sister taxon of remaining Neobatrachia. We obtained the same placement of Heleophrynidae as did San Mauro et al. (2005).

HYLOIDEA, EXCLUDING HELEOPHRYNIDAE: Hyloidea, as traditionally composed, consists of all arciferal groups of neobatrachians and was expected (on the basis of absence of morphological evidence) to be broadly paraphyletic with respect to Ranoidea, or firmisternal frogs (Microhylidae, Ranidae, and their satellites, Mantellidae, Rhacophoridae, Hyperoliidae, Arthroleptidae, Astylosternidae, and Hemisotidae), or monophyletic on the basis of molecular data (Ruvinsky and

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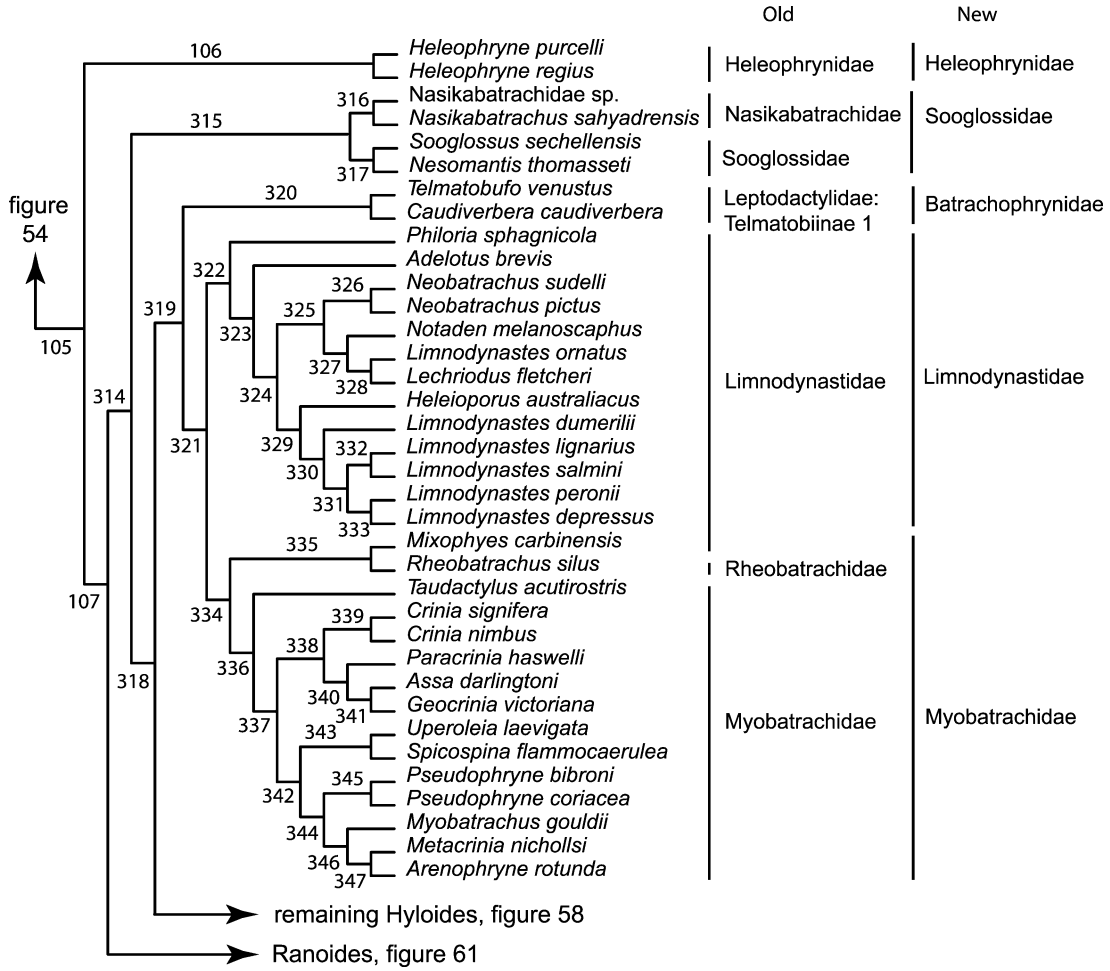

Fig. 56. Part 2 of anurans from the general tree (fig. 50 [insert]): Heleophrynidae and basal hyloids (Sooglossidae, Batrachophrynidae, Limnodynastidae, and Myobatrachidae).

Maxson, 1996; Feller and Hedges, 1998; Faivovich et al., 2005; San Mauro et al., 2005). In our results, Hyloidea is only narrowly paraphyletic, with the bulk of the hyloids forming the sister taxon of ranoids and only Heleophrynidae outside of this large clade (a conclusion also reached by San Mauro et al., 2005). Within the restricted (non-heleophrynid) Hyloidea, a unit composed of Sooglossidae and the newly discovered Nasikabatrachidae forms the sister taxon of the remaining hyloids (cf. Biju and Bossuyt, 2003; San Mauro et al., 2005). For the most part, the traditional family-group units within Hyloidea were found to be monophyletic, the exceptions being predictable from preexisting literature: Leptodactylidae was found to be composed of several only distantly related groups, and Hylidae (in the sense of including Hemphractinae) was confirmed to be paraphyletic or polyphyletic (see below).

SOOGLOSSIDAE AND NASIKABATRACHIDAE: The South Indian *Nasikabatrachus* and the Seychellean sooglossids form an ancient taxon united by considerable amounts of molecular evidence (fig. 56). Biju and Bossuyt (2003) placed *Nasikabatrachus* as the sister taxon of the sooglossids and our results corroborate this. We are unaware of any historical (in the sense of history of systematics) or other reason to regard *Nasikabatrachus* as being in a family distinct from Sooglossidae,

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and on the basis of the molecular evidence we consider *Nasikabatrachus* to be the sole known mainland member of Sooglossidae. The antiquity of this united group is evident in its placement as the sister taxon of all other non-heleophrynid hyloids. Its phylogenetic position as well as its presence both in India and in the Seychelles suggests that the taxon existed before the final breakup of Pangaea in the late Mesozoic.

MYOBATRACHIDAE, LIMNODYNASTIDAE, AND RHEOBATRACHIDAE: Because of the absence of morphological synapomorphies uniting the Australo-Papuan groups Myobatrachidae, Limnodynastidae, and Rheobatrachidae (in our usage), and because of the suggestion of a special relationship between Myobatrachidae and Sooglossidae and between Limnodynastidae and Heleophrynidae (J.D. Lynch, 1973), we were surprised that the preponderance of evidence corroborates a monophyletic Myobatrachidae + Limnodynastidae + Rheobatrachidae (fig. 56). Nevertheless, there is only one morphological character involved in these alternatives (condition of the cricoid ring: complete or incomplete), so, in retrospect, our surprise was unwarranted.

With respect to Myobatrachidae (sensu stricto; Myobatrachinae of other authors), our results are largely congruent with those of Read et al. (2001). The positions of *Metacrinia* and *Myobatrachus* are reversed in the two studies. The trenchant difference between our results is in the placement of *Paracrinia*. Our results placed it strongly as the sister taxon of *Assa* + *Geocrinia*, whereas Read et al. (2001) placed it as the sister taxon of the myobatrachids that they studied, with the exception of *Taudactylus*. Conclusive resolution of this problem will require all available evidence to be analyzed simultaneously.

We include *Mixophyes* (formerly in Limnodynastidae) and *Rheobatrachus* (sole member of former Rheobatrachidae) in Myobatrachidae (sensu stricto); Read et al. (2001) did not include those taxa in their study. We obtain a sister-taxon relationship between *Mixophyes* and *Rheobatrachus* (although this is only weakly corroborated) and association of *Mixophyes* (and *Rheobatrachus*) with Myobatrachinae, inasmuch as *Mixophyes* has traditionally been assigned to Limnodynastinae. Further discussion can be found in the Taxonomy section.

''LEPTODACTYLIDAE'': The paraphyly and polyphyly of ''Leptodactylidae'' is starkly exposed by this analysis, being paraphyletic with respect to all hyloid taxa except Heleophrynidae and Sooglossidae (fig. 57). Because of the extensiveness of the paraphyly and the complexity of the reassortment of the subsidiary groupings, the various units of a paraphyletic/polyphyletic ''Leptodactylidae'' must be dealt with before the remainder of Hyloidea can be addressed. Specifically the following nominal families are imbedded within ''Leptodactylidae'': Allophrynidae, Brachycephalidae, Bufonidae, Centrolenidae, Dendrobatidae, Hylidae, Limnodynastidae, Myobatrachidae, and Rhinodermatidae. To provide the tools to allow us to discuss the remainder of the hyloid families, we here provide a new familial taxonomy with reference to the old taxonomy provided in figure 50 (insert). We start at the top of figure 56 and address the subfamilies of ''Leptodactylidae'' as we come to them.

''TELMATOBIINAE'': ''Telmatobiinae'' is found to be polyphyletic (figs. 56, 57, 58, 59), with the austral South American Calyptocephalellini (Telmatobiinae-1: *Telmatobufo* + *Caudiverbera*) forming the sister taxon of the Australo-Papuan Myobatrachidae, Limnodynastidae, and Rheobatrachidae; Telmatobiinae-2 being paraphyletic with respect to *Batrachyla* (Telmatobiinae-3: Batrachylini); and Ceratophryini (*Lepidobatrachus* (*Ceratophrys* + *Chacophrys*)); and Telmatobiinae-4 (*Hylorina*, *Alsodes*, *Eupsophus*) being the sister taxon of a taxon composed of part of the polyphyletic Leptodactylinae (*Limnomedusa*) and Odontophrynini (*Proceratophrys* and *Odontophrynus*; part of nominal Ceratophryinae). As noted in the taxonomic review, Telmatobiinae was united by overall plesiomorphic similarity (e.g., exotrophic tadpoles, non-bony sternum). That the molecular data show Telmatobiinae to be polyphyletic is neither surprising nor unconventional.

The Chilean and Peruvian telmatobiine clade composed of *Caudiverbera* and *Telmatobufo* is monophyletic on both molecular and morphological grounds; is highly corroborated as the sister taxon of the Australo-

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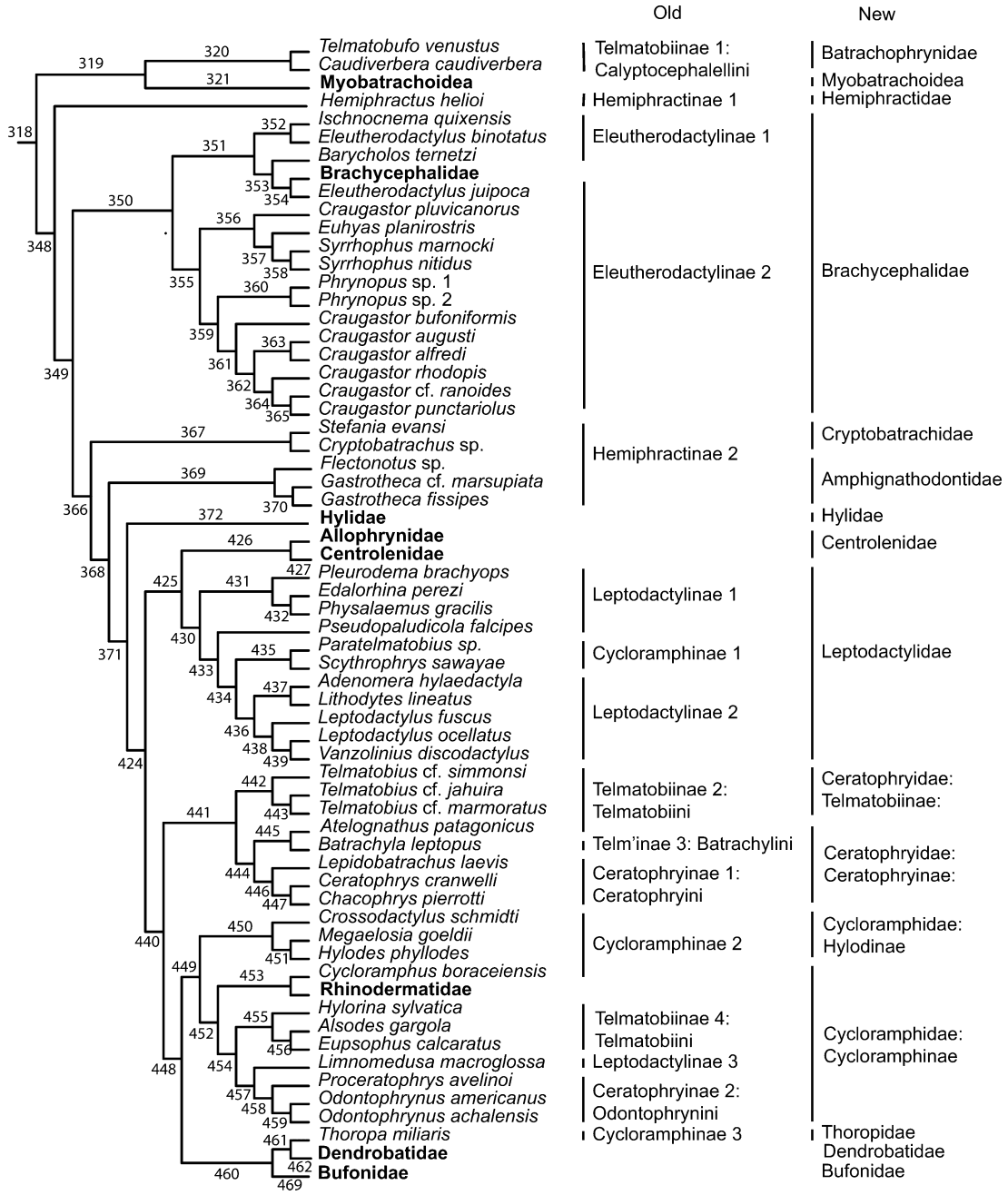

Fig. 57. Fate of former Leptodactylidae (sensu lato) on our general tree (fig. 50 [insert]). Imbedded non-leptodactylid taxa are in **bold.**

Papuan Myobatrachidae + Limnodynastidae + Rheobatrachidae; and is phylogenetically distant from all other telmatobiine ''leptodactylids'' (see also San Mauro et al., 2005; fig. 17). (The inclusion of *Batrachophrynus* is discussed under Batrachophrynidae in the Taxonomy section.) This result is not unexpected as calyptocephallelines have long

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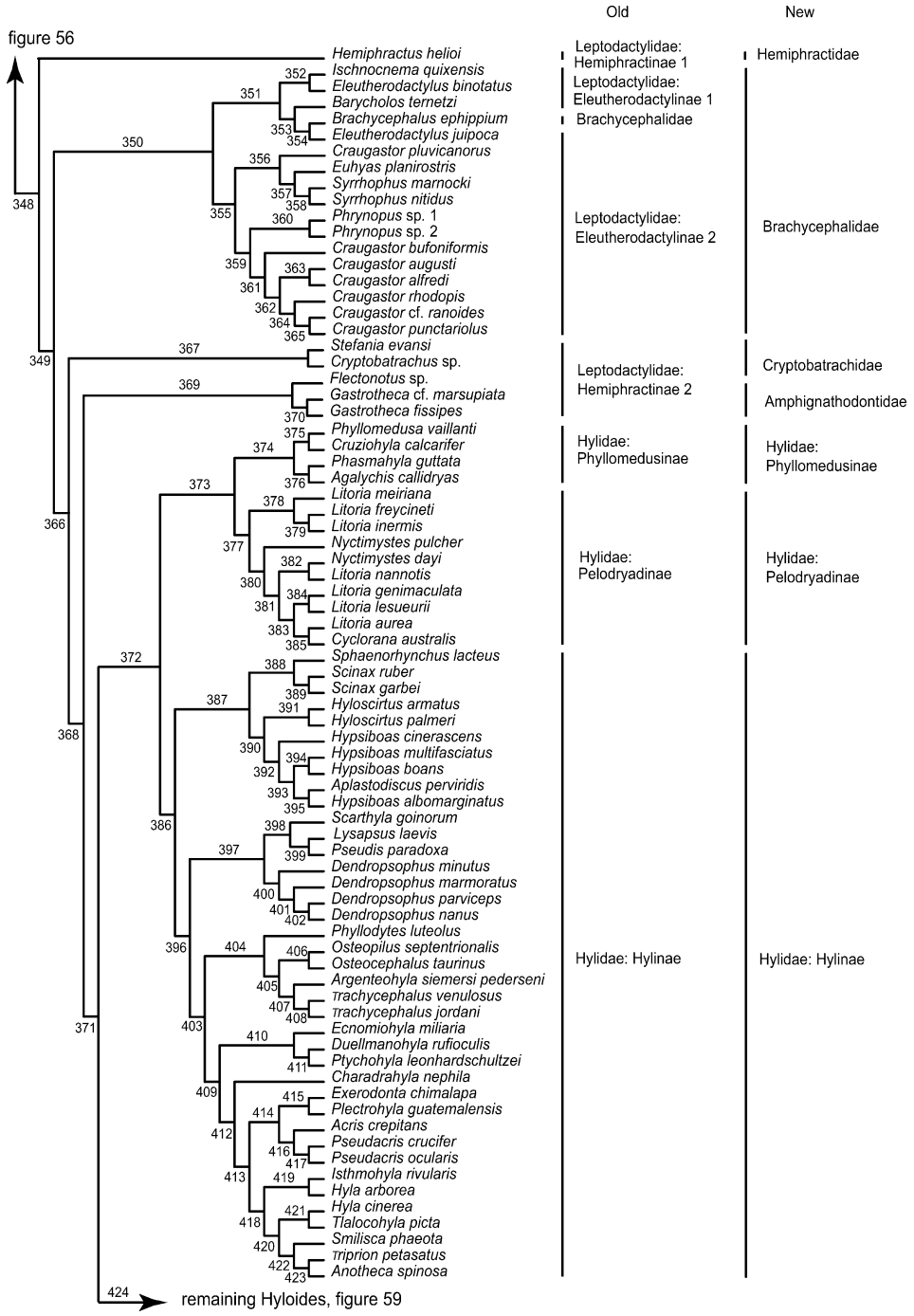

Fig. 58. Part 3 of anurans from the general tree (fig. 50 [insert]): Hemiphractidae, Brachycephalidae, Cryptobatrachidae, Amphignathodontidae, and Hylidae.

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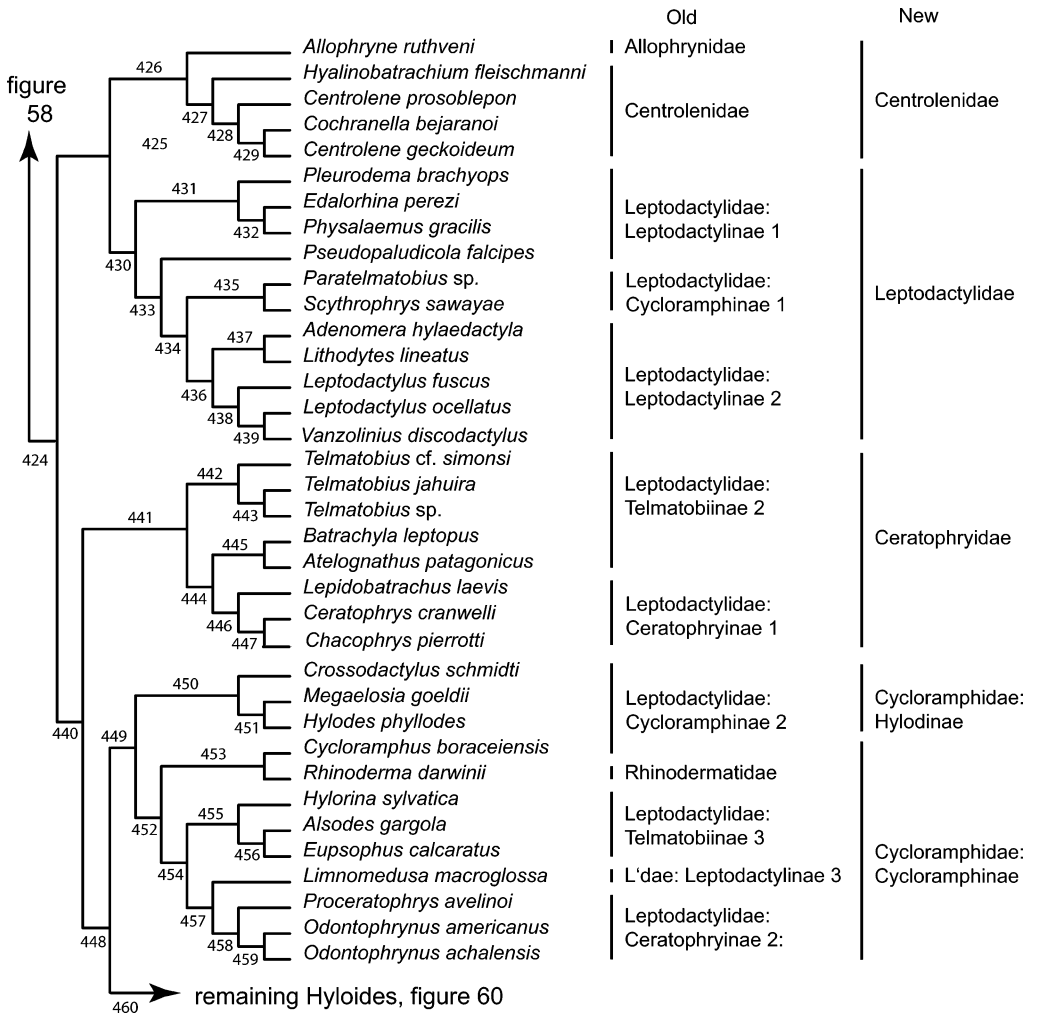

Fig. 59. Part 4 of anurans from the general tree (fig. 50 [insert]): Centrolenidae, Leptodactylidae, Ceratophryidae, and Cycloramphidae.

been suspected to be only distantly related to other telmatobiine leptodactylids (Cei, 1970; Burton, 1998a). Moreover, the region they inhabitat is also home to *Dromiciops*, a marsupial mammal most closely related to some groups of Australian marsupials and not to other South American marsupials (Aplin and Archer, 1987; Kirsch et al., 1991; Palma and Spotorno, 1999). The previous association of Calyptocephalellini with the South American Telmatobiinae was based on overall similarity with geographically nearby groups. As the sister taxon of the Australian Myobatrachidae + Limnodynastidae, it would be acceptable to place Calyptocephallelinae within some larger familial group, but to maintain familiar usage (and because we have resolved Limnodynastidae, Myobatrachidae, and Rheobatrachidae into redefined Limnodynastidae and Myobatrachidae) we consider it as the family Batrachophrynidae (the oldest available name for calyptocephallelines as currently understood; see ''Taxonomy'' and appendix 6 for discussion of application of this name).

As suggested by Lynch (1978b), one part of Telmatobiinae-2; (fig. 59), Telmatobiini, is paraphyletic with respect to Batrachylini (*Batrachylus*) as well as to Ceratophryinae-1 (Ceratophryini). The oldest name for the

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clade Telmatobiinae-2 (*Telmatobius*, *Batrachyla*, *Atelognathus*) + Ceratophryinae-1 (*Ceratophrys*, *Chacophrys*, and *Lepidobatrachus*) is Ceratophryidae. Within this family we recognize two subfamilies, Telmatobiinae (*Telmatobius*) and Ceratophryinae (for all remaining genera). Within Ceratophryinae we recognize two tribes: Batrachylini (*Batrachyla* + *Atelognathus*) and Ceratophryini (for *Ceratophrys*, *Chacophrys*, and *Lepidobatrachus*). (See the Taxonomy section for further discussion.)

As noted earlier, another former component of Telmatobiinae (Telmatobiinae-3; see figs. 57, 59) is recovered as the sister taxon of one piece of ''Leptodactylinae'' (*Limnomedusa*) plus Odontophrynini (Ceratophryinae-2, formerly part of Ceratophryinae). (The polyphyly of ''Leptodactylinae'' will be addressed under the discussion of that subfamilial taxon.) Because no documented morphological synapomorphies join the two groups of nominal Ceratophryinae (Odontophrynini and Ceratophrynini), and they had previously been shown to be distantly related (Haas, 2003), this result does not challenge credibility. (See further discussion in the Taxonomy section.)

''HEMIPHRACTINAE'': ''Hemiphractinae'', which was transferred out of Hylidae and into Leptodactylidae by Faivovich et al. (2005), is united by possessing bell-shaped gills in developing embryos and bearing eggs on the dorsum in shallow depressions to extensive cavities. The subfamily has not been found to be monophyletic by any recent author (Darst and Cannatella, 2004; Faivovich et al., 2005). In our results (figs. 57, 58) we found (1) *Hemiphractus* is the sister taxon of hyloids, excluding Batrachophrynidae, Myobatrachidae (including Rheobatrachidae), Limnodynastidae, Sooglossidae (including Nasikabatrachidae), and Heleophrynidae; (2) *Flectonotus* + *Gastrotheca*; and (3) *Stefania* + *Cryptobatrachus* are successively more distant from a clade [branch 371] bracketed by Hylidae and Bufonidae. The evidence for this polyphyly is quite strong, so we recognized three families to remedy this: Hemiphractidae (*Hemiphractus*), Cryptobatrachidae (*Cryptobatrachus* + *Stefania*), and Amphignathodontidae (*Flectonotus* + *Gastrotheca*).

ELEUTHERODACTYLINAE AND BRACHYCEPHALIDAE: Eleutherodactylinae is paraphyletic with respect to Brachycephalidae (*Brachycephalus*) (fig. 57, 58). There is nothing about *Brachycephalus* being imbedded within *Eleutherodactylus* (sensu lato) that requires any significant change in our understanding of morphological evolution, except to note that this allows the large eggs and direct development of *Brachycephalus* to be homologous with those of eleutherodactylines. This result was suggested previously (Izecksohn, 1971; Giaretta and Sawaya, 1998; Darst and Cannatella, 2004), and no evidence is available suggesting that we should doubt it. Further, to impose a monophyletic taxonomy, we follow Dubois (2005: 4) in placing Eleutherodactylinae Lutz, 1954, into the synonymy of Brachycephalidae Günther, 1858. All ''eleutherodactyline'' genera are therefore assigned to Brachycephalidae. Previous authors (e.g., Heyer, 1975; J.D. Lynch and Duellman, 1997) have suggested that *Eleutherodactylus* (and eleutherodactylines) is an explosively radiating lineage. Our results, which places brachycephalids as the sister taxon of the majority of hyloid frogs refocuses this issue. The questions now become (as suggested by Crawford, 2003): (1) Why are the ancient brachycephalids morphologically and reproductively conservative as compared with their sister taxon (composed of Cryptobatrachidae, Amphignathodontidae, Hylidae, Centrolenidae, Dendrobatidae, and Bufonidae, as well as virtually all other ''leptodactylid'' species)? (2) Why are there so few species in the brachycephalid (eleutherodactyline) radiation relative to their sister group (the former composed of some 700 species, mostly in nominal *Eleutherodactylus*, and the latter consisting of more than twice as many species)? Additional comments on this taxon will be found under Brachycephalidae in the Taxonomy section.

''LEPTODACTYLINAE'': Although ''Leptodactylinae'' has at least one line of evidence in support of its monophyly (bony sternum), the molecular data unambiguously expose its polyphyly, with its species falling into two units (fig. 57, 59). The first of these (Leptodactylinae 1–2), is paraphyletic with respect to the cycloramphine unit, called Cycloramphinae-1 in figures 57 and 59, *Paratelmato-*

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bius and *Scythrophrys* (an arrangement partially consistent with the suggestion of J.D. Lynch, 1971, that at least *Paratelmatobius* belongs in Leptodactylinae). The second unit (Leptodactylinae-3, *Limnomedusa*) is the sister taxon of Odontophrynini (Ceratophryinae-2). *Limnomedusa* was previously united with other leptodactylines solely by its possession of a bony sternum, but it lacks the foam-nesting behavior found in most other leptodactylines (exceptions being *Pseudopaludicola*, *Paratelmatobius*, and some species of *Pleurodema*). Regardless, the association of *Limnomedusa* with Leptodactylinae has always been tentative (Heyer, 1975). So, our discovery (corroborating the results of Faivovich et al., 2005) that *Limnomedusa* is not part of Leptodactylinae is not unexpected; nor does it require extensive homoplasy in the morphological data that are available. We recognize this unit (Leptodactylinae-1 + Cycloramphinae-1 + Leptodactylinae-2; figs. 57, 59, branch 430) as Leptodactylidae (sensu stricto), a taxon that is much diminished compared with its previous namesake but that is consistent with evolutionary history. Further discussion is found under Leptodactylidae in the Taxonomy section.

''CERATOPHRYINAE'': ''Ceratophryinae'' (sensu lato) is polyphyletic, with its two constituent tribes, Odontophrynini (Ceratophryinae-2) and Ceratophryninae (Ceratophryinae-1) (sensu Laurent, 1986) being only distantly related (figs. 57, 59, branches 446, 458). As noted elsewhere in this section, there has never been any synapomorphic evidence to associate these two groups. Thus, their distant relationship is not surprising or even unconventional, inasmuch as Barrio (1963; 1968) and Lynch (1971) suggested that these two units are distantly related. Ceratophryini is imbedded in a taxon (figs. 57, 59: Telmatobiinae-2; branch 441) that is weakly corroborated, but is here recognized as a family Ceratophryidae. Odonotophrynini is resolved as the sister taxon of *Limnomedusa* (formerly in Leptodactylinae), together residing in a group composed largely of former cycloramphines.

''CYCLORAMPHINAE'' AND RHINODERMATIDAE: ''Cycloramphinae'' (sensu Laurent, 1986) was also found to be polyphyletic (figs. 57, 59) in three distantly related groups. Our molecular data overcome the few morphological characters that might be considered synapomorphies of the relevant group. The first of these groups, labeled Cycloramphinae-1, is composed of *Scythrophrys* and *Paratelmatobius* and is imbedded within Leptodactylidae (sensu stricto; as part of Leptodactylinae, as discussed earlier.) The second unit, which is labelled Cycloramphinae-2, is Elosiinae (= Hylodinae) of Lynch (1971); although it is relatively weakly corroborated by molecular evidence, it is united by morphological evidence suggested by Lynch (1971, 1973). *Cycloramphus* (part of Cycloramphinae-2) is tightly linked to *Rhinoderma* (Rhinodermatidae), one of the points of paraphyly of former Leptodactylidae. Cycloramphinae-2 forms a paraphyletic group with respect to Rhinodermatidae, Telmatobiinae-2, Leptodactylinae-3, and Odontophrynini (Ceratophryinae-2). Because no morphological characteristics that we are aware of would reject this larger grouping, we place these five units into a single family, for which the oldest available name is Cycloramphidae. Within this, we recognize two subfamilies: Hylodinae (for *Crossodactylus*, *Megaelosia*, and *Hylodes*) and Cycloramphinae for the remainder of this nominal family-group taxon.

Our DNA sequence evidence places *Thoropa* (Cycloramphinae-3) as the sister taxon of the monophyletic Dendrobatidae (figs. 57, 60). We were surprised by this result, because none of the morphological characters that had been suggested to ally Hylodinae with Dendrobatidae are present in *Thoropa* (T. Grant, personal obs.), and *Thoropa* most recently has been associated with *Batrachyla* (J.D. Lynch, 1978b). Nevertheless, our molecular data support this arrangement, and *Thoropa* has never been more than tentatively associated with the grypiscines (= cycloramphines; Heyer, 1975). Furthermore, manual rearrangements of hylodines and *Thoropa* used as starting trees for further analysis inevitably led to less parsimonious solutions or returned to this solution as optimal (as implied by the Bremer values). Our first inclination was to place *Thoropa* into Dendrobatidae, so as not to erect a monotypic family. However, Dendrobatidae, as traditionally conceived, is monophyletic and has a large

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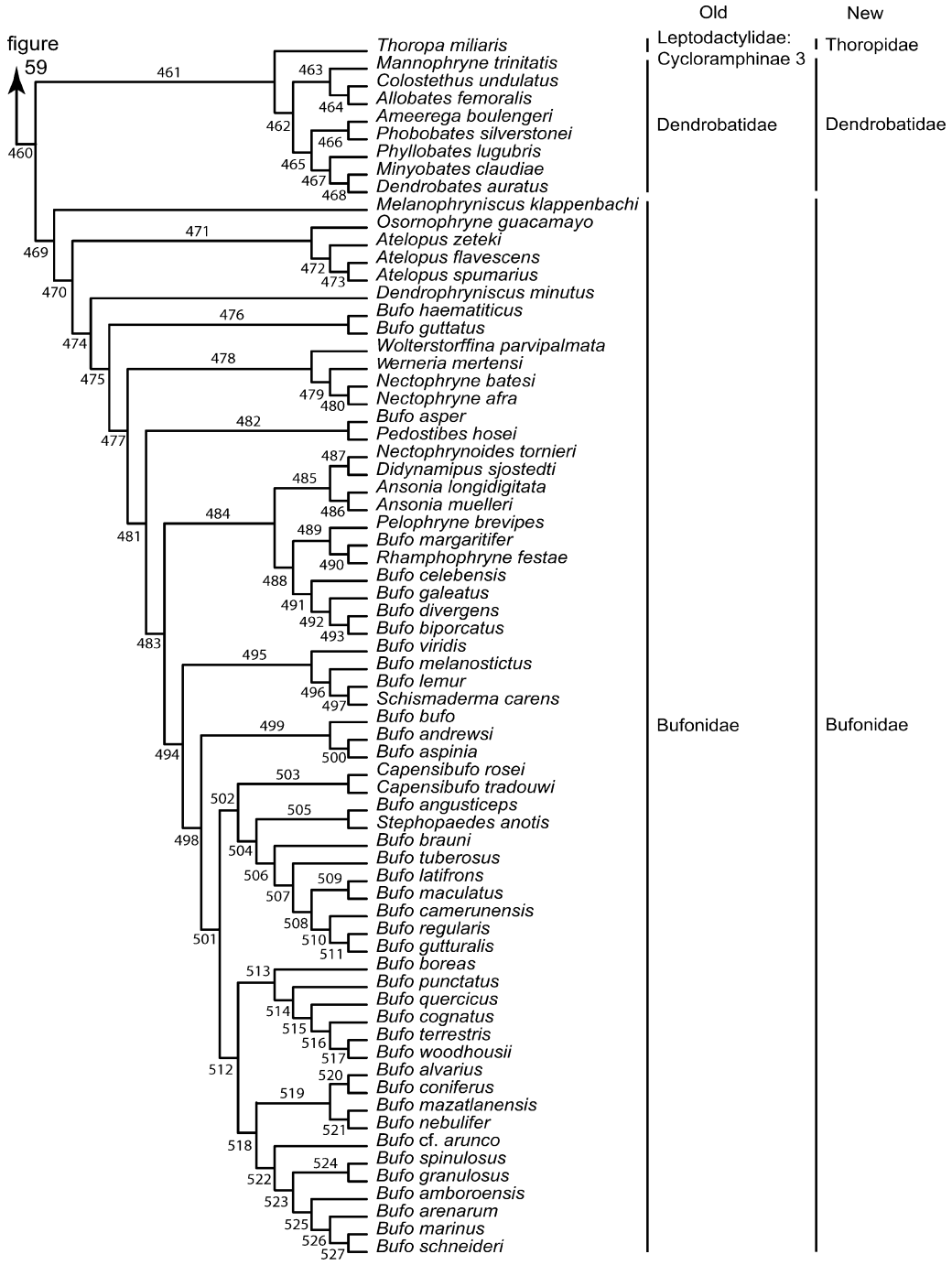

Fig. 60. Part 5 of anurans from the general tree (fig. 50 [insert]): Thoropidae, Dendrobatidae, and Bufonidae.

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literature associated with it that addresses a certain content and diagnosis that remained largely unchanged for nearly 80 years. For this reason, we place *Thoropa* into a monotypic family, Thoropidae, to preserve the core diagnostic features of Dendrobatidae for the large number of workers that are familiar with the taxon.

CENTROLENIDAE AND ALLOPHRYNIDAE: As suggested by Noble (1931), Austin et al. (2002), and Faivovich et al. (2005), *Allophryne* is closely related to Centrolenidae, together forming a monophyletic group that is the sister taxon of a group composed of most of the former Leptodactylinae (fig. 59; branch 426). Our data reject a close relationship of Centrolenidae to Hylidae, as well as the suggestion by Haas (2003), made on the basis of larval morphology, that Centrolenidae may not be a member of Neobatrachia. *Allophryne* shares with the centrolenids T-shaped terminal phalanges (J.D. Lynch and Freeman, 1966), which is synapomorphic at this level. We regard *Allophryne* as a part of Centrolenidae, the sister taxon of a taxon composed of *Centrolene* + *Cochranella* + *Hyalinobatrachium* (which has as a morphological synapomorphy intercalary phalangeal elements).

BRACHYCEPHALIDAE: Our study found *Brachycephalus* to be imbedded within Eleutherodactyinae, indeed, within *Eleutherodactylus* (sensu lato; fig. 57, 58). Previous authors (e.g., Izecksohn, 1971; Giaretta and Sawaya, 1998) suggested that *Brachycephalus* is allied with *Euparkerella* (Eleutherodactylinae) on the basis of sharing the character of digital reduction. We did not sample *Euparkerella*, which could be imbedded within a paraphyletic *Eleutherodactylus*. This proposition remains to be tested. As noted earlier, Brachycephalidae and Eleutherodactylinae are synonyms, with Brachycephalidae being the older name.

RHINODERMATIDAE: We found *Rhinoderma* to be imbedded within a clade composed largely of South American cycloramphine leptodactylids (figs. 57, 59), more specifically as the sister taxon of *Cycloramphus*. Because the only reason to recognize Rhinodermatidae has been its autapomorphic life history strategy of brooding larvae in the vocal sac, we place Rhinodermatidae into the synonymy of Cycloramphidae.

DENDROBATIDAE: We found Dendrobatidae to be monophyletic and the sister taxon of *Thoropa*. The former statement is conventional, the latter, surprising. Nevertheless, the highly corroborated nature of this placement (cladistically in the same neighborhood as hylodines, with which it was considered closely allied by some authors, e.g., Noble, 1926, and Lynch, 1973) should close discussion of whether the firmisternal dendrobatids are derived from some austral South American arciferal group (here strongly supported; for dendrobatid girdle architecture see Noble, 1926; Kaplan, 1995) or related to some ranoid or ranid group, a conclusion suggested by some lines of morphological evidence (Blommers-Schlösser, 1993; Ford, 1993; Grant et al., 1997). *Thoropa* + Dendrobatidae form the sister taxon of Bufonidae. This phylogenetic arrangement is highly corroborated and suggests that *Ameerega* Bauer, 1986 (a senior synonym of *Epipedobates* Myers, 1987; see Walls, 1994) is polyphyletic, a result that is consistent with previous studies (e.g., Santos et al., 2003; Vences et al., 2003b). Taxon sampling was limited in all studies to date, however, and we leave it to more exhaustive analyses to assess the details of the relationships within Dendrobatidae.

HYLIDAE: If hylids are considered to contain Hemiphractinae (see above), then Hylidae would be catastrophically paraphyletic with respect to leptodactylids (excluding the former calyptocephalellines [Batrachophrynidae]), dendrobatids, bufonids, *Allophryne*, and centrolenids (figs. 57, 58, 59). This arrangement suggests that the claw-shaped terminal phalanges and intercalary cartilages taken previously to be synapomorphies of Hylidae (sensu lato) are homoplastic and not synapomorphic for Hylidae. Because Hylidae (sensu lato) is broadly para- or polyphyletic, we adopt the concept of Hylidae adopted by Faivovich et al. (2005), that is Hylinae + Phyllomedusinae + Pelodryadinae.

Hylidae (sensu stricto, excluding ''Hemiphractinae'') is monophyletic and highly corroborated. Our results are largely congruent with the results of Faivovich et al. (2005), which were based on more sequence evi-

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dence and denser sampling of hylids. Faivovich et al. (2005) should be referenced for the evidentiary aspects of hylid phylogenetics. The only significant difference between our results and theirs is that our exemplars of *Hyla* form a paraphyletic group with respect to *Isthmohyla* and *Charadrahyla*, and *Hypsiboas* is paraphyletic with respect to *Aplastodiscus*, and the tribe Dendropsophini is not monophyletic as delimited by Faivovich et al. (2005). However, because our density of sampling and evidence is less than in that study, our results do not constitute a test of those results, and we leave their taxonomy unchanged.

Hylinae has long been suspected of being paraphyletic, but our results and those of Faivovich et al. (2005) strongly corroborate the notion that Hylinae is monophyletic and the sister taxon of Pelodyradinae + Phyllomedusinae, both of which are also strongly corroborated as monophyletic.

The apparent polyphyly of *Nyctimystes* in our results may be real, although our paucity of sampling prevents us from delimiting the problem precisely. Similarly, the long-recognized (Tyler and Davies, 1978; King et al., 1979; Tyler, 1979; Maxson et al., 1985; Hutchinson and Maxson, 1987; Haas, 2003; Faivovich et al., 2005), pervasive paraphyly of *Litoria* in Pelodryadinae with respect to both *Cyclorana* and *Nyctimystes* has obviously been a major problem in understanding relationships among pelodryadines. Ongoing research by S. Donnellan and collaborators aims to rectify these issues in the near future.

BUFONIDAE: That Bufonidae is a highly corroborated monophyletic group is not surprising; that we have a reasonably well-corroborated phylogenetic structure within Bufonidae *is* a surprise (figs. 50 [insert], 60). Like Graybeal (1997; fig. 25), we found *Melanophryniscus* (which lacks Bidder's organs) to form the sister taxon of the remaining bufonids (which, excluding *Truebella*, have Bidder's organs). Within this clade, *Atelopus* + *Osornophryne* forms the sister taxon of the remaining taxa.

The paraphyly of *Bufo* with respect to so many other bufonid genera had previously been detected (e.g., Graybeal, 1997; Cunningham and Cherry, 2004), but some associations are unconventional. The relationship of *Bufo margaritifer* with *Rhamphophryne* conforms with their morphological similarity, but the nesting of this clade within a group of Asian *Bufo* was unexpected. The association of *Bufo lemur* (a species of former *Peltophryne* in the Antilles) with *Schismaderma* (Africa) is novel, as is the placement of this group with *Bufo viridis* and *Bufo melanostictus*, although Graybeal (1997), at least in her parsimony analysis of molecular data, suggested that *Peltophryne* was associated with *Bufo melanostictus*, an Asian taxon.

Obviously, denser sampling will be required to resolve bufonid relationships, but the current topology provides an explicit hypothesis for further investigation. Clearly, *Bufo* must be partitioned into several genera to remedy its polyphyly/paraphyly with respect to several other nominal genera and to provide a reasonable starting place from which to make progress. For more discussion and the beginnings of this partition, see Bufonidae in the Taxonomy section.

RANOIDEA: Monophyly of Ranoidea (in the sense of excluding Dendrobatidae) was strongly corroborated in our analysis, as well as by other recent analyses (Roelants and Bossuyt, 2005; San Mauro et al., 2005). Ranoidea in our analysis is divided into two major groups (see figs. 50 [insert], 56, 61, 62, 63, 65), which correspond to (1) a group composed of a para- or polyphyletic Microhylidae, Hemisotidae, Hyperoliidae, paraphyletic Astylosternidae, and Arthroleptidae (figs. 61, 62); and (2) a giant paraphyletic ''Ranidae'' and its derivative satellites, Mantellidae and Rhacophoridae (fig. 63, 65). This is summarized on the general tree (fig. 50 [insert]).

MICROHYLIDAE AND HEMISOTIDAE: Our results (figs. 50, 61, 62) do not support the traditional view of subfamilies and relationships suggested by Parker (1934) in the last revision of the family. The notion of polyphyletic Microhylidae falling into two monophyletic groups—(1) Brevicipitinae (as the sister taxon of Hemisotidae); and (2) the remaining microhylids—extends from the suggestion by Blommers-Schlösser (1993) that Hemisotidae and Brevicipitinae are closely related. Because the Type II tadpole that was considered a synapomorphy in microhylids (Star-

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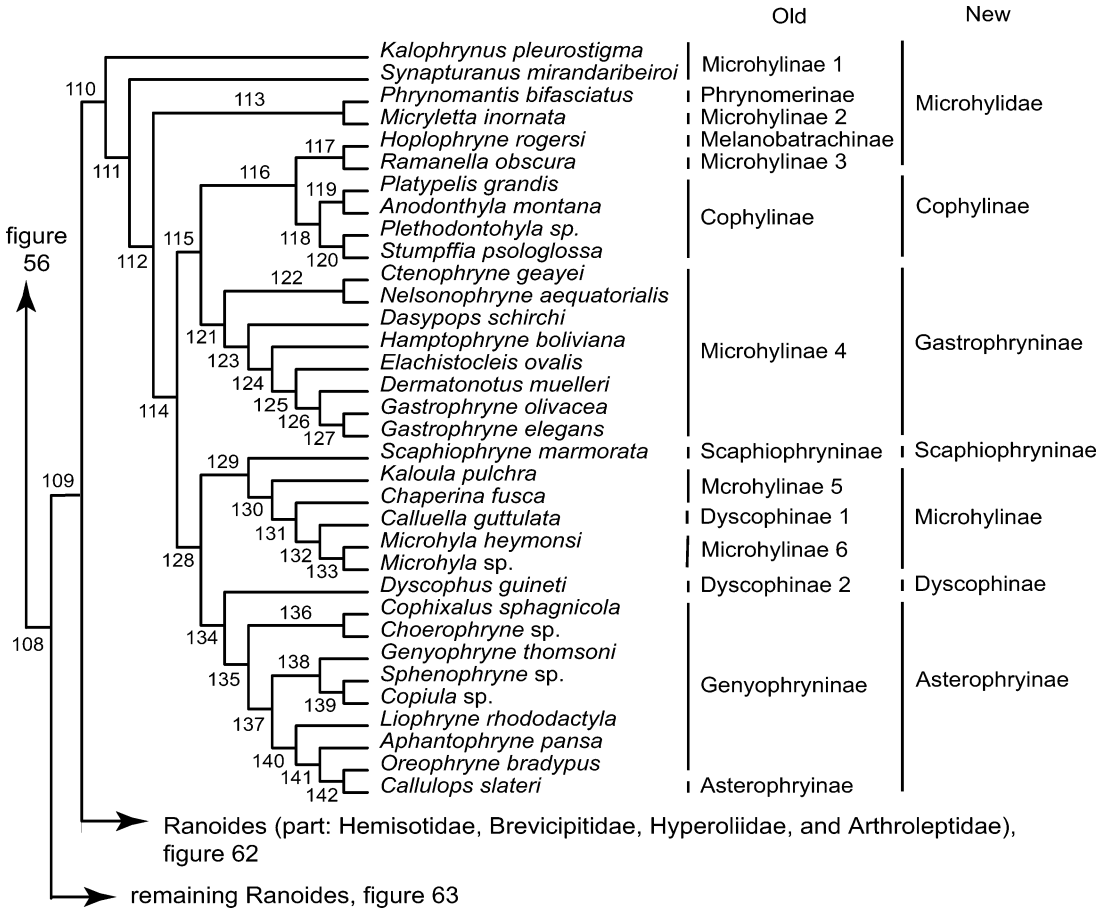

Fig. 61. Part 6 of anurans from the general tree (fig. 50 [insert]): Microhylidae.

rett, 1973) is not present in brevicipitines (which have direct development) and hemisotids have a Type IV tadpole, there was never any particular evidence tying brevicipitines to the remaining microhylids. Moreover, only a single synapomorphy tied brevicipitines to hemisotines (Channing, 1995), so the evidence for paraphyly/polyphyly of microhylids also was not strong. As suggested by Van der Meijden et al. (2004; and consistent with the results of Biju and Bossuyt, 2003, and Loader et al., 2004, but contrary to the Scoptanura hypothesis of Ford and Cannatella, 1993), we find Brevicipitinae and Hemisotidae to form a monophyletic group, and this taxon to be more closely related to Arthroleptidae, Astylosternidae, and Hyperoliidae than to remaining Microhylidae. For this reason we regard brevicipitines as a distinct family, Brevicipitidae. (We find Dubois', 2005, proposal that Arthroleptidae, Astylosternidae, Brevicipitidae, Hemisotidae, and Hyperoliiidae be considered subfamilies of an enlarged Brevicipitidae, to be an unnecessary perturbation of familiar nomenclature.)

Within the larger group of ''microhylids'', Microhylinae is broadly paraphyletic with respect to the remaining subfamilies, with *Phrynomantis* (Phrynomerinae) being situated near the base of our sampled microhylines, *Hoplophryne* (Melanobatrachinae) placed weakly next to *Ramanella* (Microhylinae), and Cophylinae (based on our exemplars of *Anodonthyla*, *Platypelis*, *Plethodontohyla*, and *Stumpffia*) being found to be monophyletic and placed as the sister taxon of *Ramanella* (Microhylinae) + *Hoplophry-*

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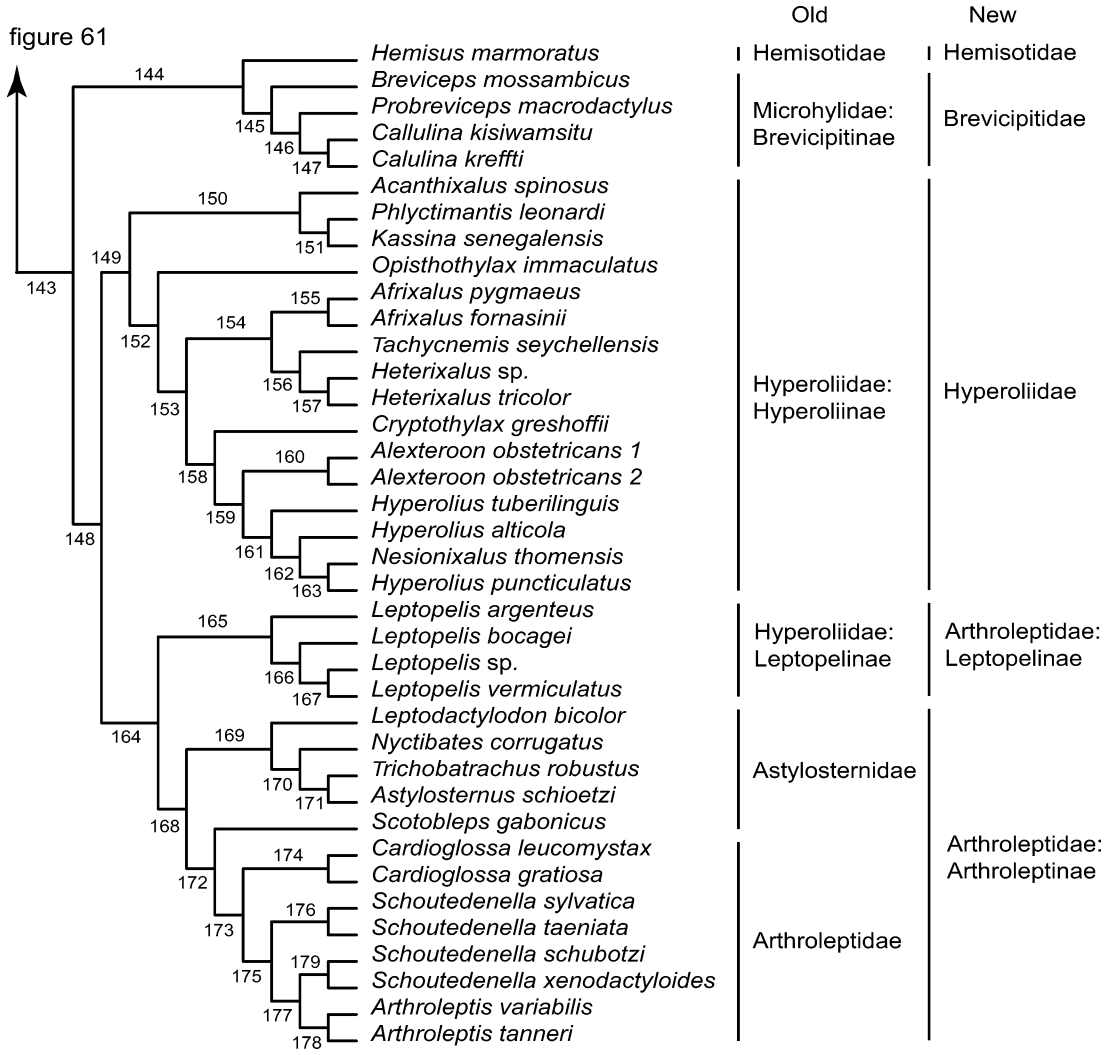

Fig. 62. Part 7 of anurans from the general tree (fig. 50 [insert]): Hemisotidae, Hyperoliidae, and Arthroleptidae.

ne (Melanobatrachinae). Surprisingly, *Scaphiophryne* (Scaphiophryninae) is deeply imbedded among the microhylids and the sister taxon of part of ''Microhylinae'' (branch 130, subtending *Kaloula*, *Chaperina*, *Calluella*, and *Microhyla*). Ford and Cannatella (1993) and Haas (2003) had considered *Scaphiophryne* to form the sister taxon of the remaining microhylids on the basis of larval features, but because we included Haas' (2003) morphological data in our analysis, we can see that these features must be homoplastic.

Microhylinae is nonmonophyletic, with (1) some taxa clustered around the base of the Microhylidae and weakly placed (e.g., *Kalophrynus*, *Synapturanus*, *Micryletta*); (2) a group of Asian taxa (e.g., *Kaloula–Microhyla*) forming the sister taxon of *Scaphiophryne*; and (3) a New World clade (i.e., the group composed of *Ctenophryne*, *Nelsonophryne*, *Dasypops*, *Hamptophryne*, *Elachistocleis*, *Dermatonotus*, and *Gastrophryne*) placed as the sister taxon of Cophylinae + Melanobatrachinae + *Ramanella*.

Our picture of ''Microhylinae'' runs coun-

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ter to the little phylogenetic work that has been done so far, especially with respect to the cladogram of New World taxa by Wild (1995). Wild's (1995; fig. 34) cladogram assumed New World monophyly, was rooted on a composite outgroup, and is strongly incongruent with our topology. Our solution is to (1) recognize Gastrophryninae for the New World taxa that do form a demonstrably monophyletic group (including *Ctenophryne*, *Nelsonophryne*, *Dasypops*, *Hamptophryne*, *Elachistocleis*, *Dermatonotus* and *Gastrophryne*); and (2) restrict Microhylinae to a monophyletic group including *Calluella*, *Chaperina*, *Kaloula*, and *Microhyla*. The genera that we have not assigned to either Gastrophryninae or Microhylinae (sensu stricto), or that are clearly outside of either group (e.g., *Synapturanus* or *Kalophrynus*), we treat as incertae sedis within Microhylidae. The arrangement asserted without evidence by Dubois (2005), of an Old World Microhylini and New World Gastrophrynini, within his Microhylinae, is specifically rejected by the basal position in our tree of *Kalophrynus* and *Synapturanus*, far from our Microhylinae and Gastrophryninae.

As suggested by Savage (1973), Dyscophinae is polyphyletic, with *Calluella* deeply imbedded within Asian microhylines and *Dyscophus* placed as the sister taxon of a group composed of members of Asterophryinae (*Cophixalus*, *Choerophryne*, *Genyophryne*, *Sphenophryne*, *Copiula*, *Liophryne*, *Aphantophryne*, *Oreophryne*) and Asterophryinae (*Callulops*). Genyophryninae is clearly paraphyletic with respect to Asterophryinae, as suggested by Savage (1973) and Sumida et al. (2000a). For this reason we regard Asterophryinae and Genyophryninae as synonyms, with Asterophryinae being the older name for this taxon. This allows the optimization of direct development as a synapomorphy for the combined taxon.

ARTHROLEPTIDAE, ASTYLOSTERNIDAE AND HYPEROLIIDAE: We found an African group composed of Hyperoliidae, Astylosternidae, and Arthroleptidae to constitute a highly corroborated clade, the sister taxon of Hemisotidae + Brevicipitidae (fig. 62). This existence of this group was suggested previously but has not been substantiated by synapomorphies (Laurent, 1951; Dubois, 1981; Laurent, 1984b; Dubois, 1987 ''1985'', 1992). Within this group we found Hyperoliidae (excluding *Leptopelis*) to form a monophyletic group.

Phylogenetic structure within Hyperoliidae has been contentious, with various arrangements suggested by different authors. Our results differ significantly from all previously published hyperoliid trees (Drewes, 1984; Channing, 1989; Vences et al., 2003c). Like Vences et al. (2003c), we found *Leptopelis* (Hyperoliidae) to form a monophyletic group that is separate from the remainder of Hyperoliidae and placed with a group composed of the Astylosternidae + Arthroleptidae. The consideration of Leptopelinae as a subfamily of Hyperoliidae cannot be continued because it renders Hyperoliidae (sensu lato) paraphyletic. We restrict the name Hyperoliidae to the former Hyperoliinae, which in addition to our molecular data, is supported by the synapomorphic presence of a gular gland (Drewes, 1984).

We found Astylosternidae to be paraphyletic with respect to Arthroleptidae, with *Scotobleps* (Astylosternidae) being the sister taxon of Arthroleptidae (fig. 62). No previous hypotheses of relationship within Astylosternidae or Arthroleptidae have been rigorously proposed (Vences et al., 2003c), so our results are the first to appeal to synapomorphy. Our finding that *Schoutendenella* is paraphyletic with respect to *Arthroleptis* is particularly noteworthy because recognition of *Schoutedenella* as distinct from *Arthroleptis* has been contentious (e.g., Laurent, 1954; Loveridge, 1957; Schmidt and Inger, 1959; Laurent, 1961; Poynton, 1964b; Laurent, 1973; Poynton, 1976; Poynton and Broadley, 1985; Poynton, 2003). Laurent and Fabrezi (1986 ''1985'') suggested that *Schoutedenella* is more closely related to *Cardioglossa* than to *Arthroleptis*, an hypothesis rejected here.

RANIDAE, MANTELLIDAE, AND RHACOPHORIDAE: Our results for this group are similar in some respects to those presented by Van der Meijden et al. (2005; fig. 36). Differences in results may be due to our denser taxon sampling, to their greater number of analytical assumptions, their inclusion of RAG-1 and RAG-2, which we did not include, or their lack of 28S, seven in absentia, histone H3,

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tyrosinase, and morphology, which we did include. Final resolution will require analysis of all of the data under a common assumption set.

We found a taxon composed of a broadly paraphyletic ''Ranidae'', and monophyletic Mantellidae + Rhacophoridae to form the sister taxon of Microhylidae + Hemisotidae + Hyperoliidae + Arthroleptidae + Astylosternidae (fig. 50 [insert], 61, 63). The results are complex but are comparable to a group of smaller studies that dealt overwhelmingly with Asian taxa (Tanaka-Ueno et al., 1998a, 1998b; Bossuyt and Milinkovitch, 2000; Emerson et al., 2000a; Marmayou et al., 2000; Bossuyt and Milinkovitch, 2001; Kosuch et al., 2001; Grosjean et al., 2004; Roelants et al., 2004; Jiang and Zhou, 2005). This overall result varies widely from Bossuyt and Milinkovitch (2001), who found Mantellinae + Rhacophorinae as the sister taxon of Nyctibatrachinae + Raninae; this clade sister to Dicroglossinae + Micrixalinae, and Ranixalinae sister to them all.

We find Ptychadeninae (*Ptychadena* being our exemplar genus) to be the sister taxon of the remaining ''Ranidae'', a highly corroborated result (fig. 63). The sister taxon of Ptychadeninae is composed of Ceratobatrachinae (*Ingerana*, *Discodeles*, *Ceratobatrachus*, *Batrachylodes*, and *Platymantis*) and the remaining ''ranids''. Here we differ significantly from Roelants et al. (2004), inasmuch as they considered *Ingerana* to be an occidozygine, whereas we find *Ingerana* to be in Ceratobatrachinae, where it had originally been placed by Dubois (1987 ''1985'').

We find a major African clade (fig. 63; branch 192), similar to the results of Van der Meijden et al. (2005). One clade (branch 193) is Phrynobatrachinae of Dubois (2005), composed of a paraphyletic *Phrynobatrachus*, within which *Phrynodon* and *Dimorphognathus* are imbedded. A second component (branch 200) is composed of Conrauinae (*Conraua*), Ranixalinae (*Indirana*), Petropedetinae, and Pyxicephalinae sensu Dubois (2005). Petropedetinae of Dubois (2005) (*Petropedetes* + *Arthroleptides*, subtended by branch 205), forms the sister taxon of *Indirana* (Ranixalinae of Dubois, 2005). *Pyxicephalus* + *Aubria* (branch 210) form the sister taxon of the Pyxicephalinae of Dubois (2005), the ''southern African clade'' of Van der Meijden et al. (2005): *Tomopterna*, *Arthroleptella*, *Natalobatrachus*, *Afrana*, *Amietia*, *Strongylopus*, *Cacosternum*, and *Anhydrophryne*. We place (1) *Phrynobatrachus* (and its satellites *Phrynodon* and *Dimorphognathus*) in Phrynobatrachidae; (2) *Arthroleptides*, *Conraua*, *Indirana*, and *Petropedetes* in Petropedetidae; (3) *Afrana*, *Amietia*, *Anhydrophryne*, *Arthroleptella*, *Aubria*, *Cacosternum*, *Natalobatrachus*, *Pyxicephalus*, *Strongylopus*, and *Tomopterna* in Pyxicephalidae, as had Dubois (2005). (See fig. 63 and further discussion of these groups in the Taxonomy section.)

Roelants et al. (2004), who did not include any African taxa in their study, proposed *Indirana* to be the sister taxon of Micrixalinae, although their evidence did not provide resolution beyond a polytomy with (1) the *Lankanectes–Nyctibatrachus* clade; and (2) the ranine-rhacophorine-mantelline clade. However, we found *Indirana* to be deeply imbedded in an African clade otherwise composed of *Conraua*, *Arthroleptides*, and *Petropedetes* (a clade we consider a family, Petropedetidae). Dissimilarly, Van der Meijden et al. (2005) found, albeit weakly, *Indirana* as the sister taxon of Dicroglossinae. Nevertheless, our result is highly corroborated, although it is based on less overall evidence than that of Van der Meijden et al. (2005), although as noted previously, analyzed differently. Our sequence evidence for *Indirana* is the same 12S and 16S GenBank sequences produced/used by Roelants et al. (2004), so contamination or misidentification is not an issue.

Like Roelants et al. (2004), we find occidozygines to form the sister taxon of Dicroglossinae, with the latter containing Paini (our exemplares being members of *Nanorana* and *Quasipaa*), which had been transferred from Raninae into Dicroglossinae by Roelants et al. (2004). Unlike their data, ours place *Nanorana* not within *Paa*, but as the sister taxon of a clade composed of *Fejervarya* (which we show to be paraphyletic), *Sphaerotheca*, *Nannophrys*, *Euphlyctis*, and *Hoplobatrachus*.

Our results are broadly consistent with several other studies showing that *Hoplobatrachus* (Limnonectini) is the sister taxon of *Euphlyctis* (Dicroglossini) (Bossuyt and Mil-

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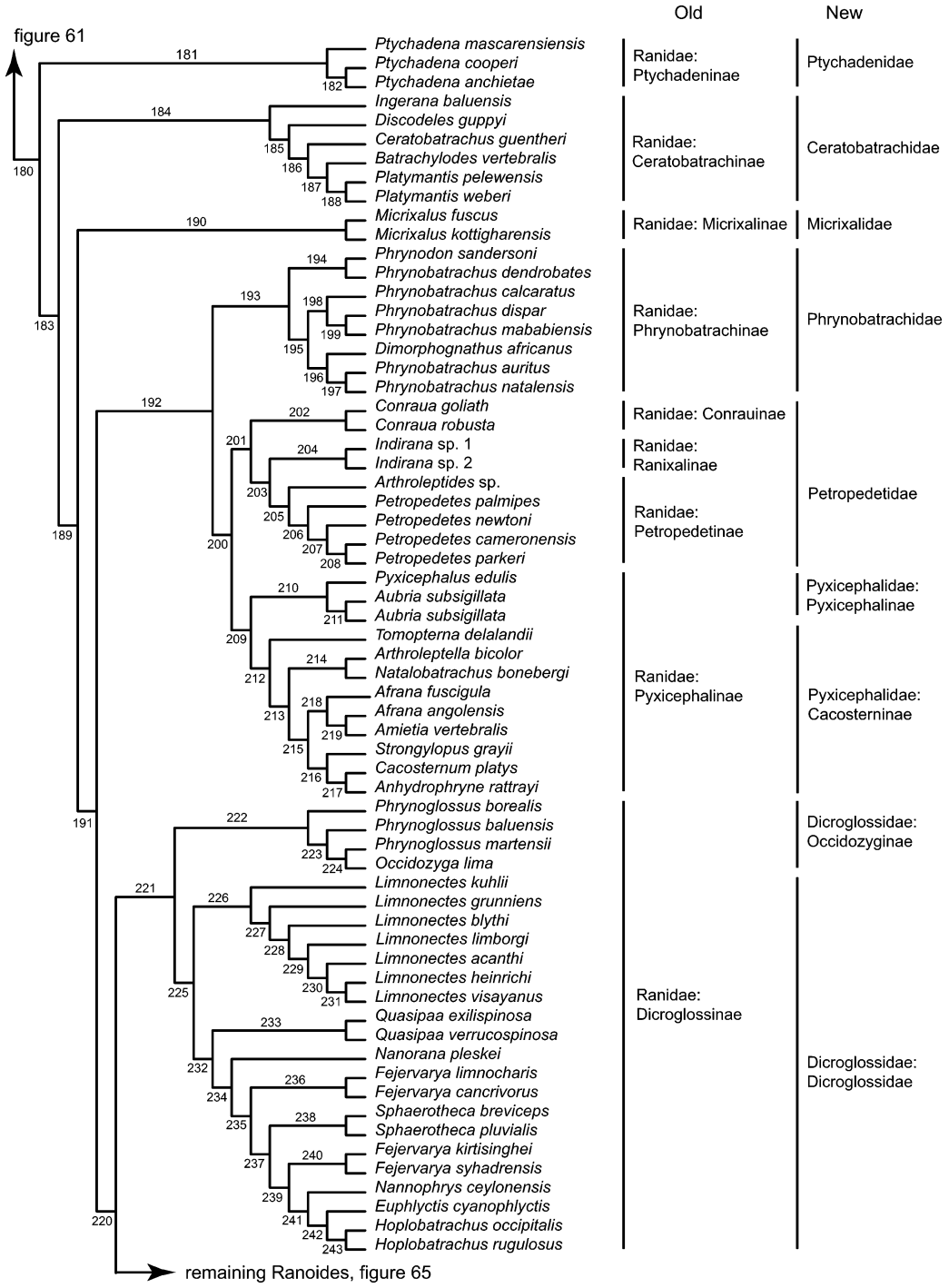

Fig. 63. Part 8 of anurans from the general tree (fig. 50 [insert]): Ptychadenidae, Ceratobatrachidae, Micrixalidae, Phrynobatrachidae, Petropedetidae, Pyxicephalidae, and Dicroglossidae.

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inkovitch, 2001; Kosuch et al., 2001; Grosjean et al., 2004; Roelants et al., 2004). Limnonectini (sensu Dubois, 1992) is therefore rejected as nonmonophyletic. *Limnonectes* (including *Taylorana* Dubois, 1987 ''1986'', as a synonym; a result congruent with Emerson et al., 2000a) forms the sister taxon of a clade formed by Paini (*Quasipaa*), *Nanorana*, *Nannophrys*, and the remaining members of ''Limnonectini'' (*Fejervarya*, *Sphaerotheca*, and *Hoplobatrachus*) and Dicroglossini (*Euphlyctis*), a result congruent with Grosjean et al. (2004). Marmayou et al. (2000) found *Fejervarya* + *Sphaerotheca* to form the sister taxon of a monophyletic *Limnonectes* + *Hoplobatrachus*, but they did not include *Euphlyctis* in their study. Roelants et al. (2004; fig. 35), and Jiang et al. (2005; fig. 42), and Jiang and Zhou (2005; fig. 41) found Paini to be imbedded within this group (Dicroglossinae), and our results confirm their result. This suggests that a character that has been treated as of particular importance to ranoid systematics, forked or entire omosternum, is considerably more variable than previously supposed (see Boulenger, 1920: 4), regardless of the weight placed on this character by some taxonomists (e.g., Dubois, 1992).

Our topology is not consistent with that of Roelants et al. (2004), Jiang et al. (2005), and Van der Meijden et al. (2005) in that we do not recover a monophyletic Paini, instead finding our exemplars (2 species of *Quasipaa* and 1 of *Nanorana*) to form a pectinate series leading to ''*Fejervarya*'' + *Hoplobatrachus* (*Euphlyctis* and *Nannophrys* were pruned for this discussion because they were not part of the study of Jiang et al., 2005; fig. 42). Although our topological differences from the results of Roelants et al. (2004) apparently reflect differences in evidence and sampling, we have more of both. The difference between our results and those of Jiang et al. (2005) seemingly do not reflect differences at the level of descriptive efficiency at the level of unrooted network. We do have a bit more resolution between their groups 1 and 2 as a paraphyletic grade, rather than as a polytomy. By treating *Hoplobatrachus* and *Fejervarya* as their outgroups on which to root a tree of *Limnonectes* + Paini, the study by Jiang et al. (2005) inadvertantly forced Paini to appear monophyletic. Examination of the trees and associated unrooted networks (fig. 64) support this view. That *Euphlyctis*, *Hoplobatrachus*, and *Nannophrys* lack spines on the forearms and belly as in Paini is incongruent evidence. Nevertheless, it does strengthen our view that Group 1 of Jiang et al. (2005) deserves generic recognition, and that Paini, as nonmonophyletic, must be placed into the synonymy of Dicroglossinae. (See the account of Dicroglossinae in the Taxonomy section.)

A trenchant difference between our results and those of Roelants et al. (2004; but the same as found by Van der Meijden et al., 2005) is in the placement of *Lankanectes* + *Nyctibatrachus*. Roelants et al. (2004) placed this taxon outside of most of ''Ranidae'' (excepting Micrixalinae and Indiraninae, which we also found to be placed elsewhere). We find *Lankanectes* + *Nyctibatrachus* to be the sister taxon of Raninae, excluding *Amietia*, *Afrana*, and *Strongylopus* (and *Batrachylodes*, transferred to Ceratobatrachidae, as discussed earlier).

Dubois' (1992) *Amolops* (containing the subgenera *Amo* [which we did not study], *Amolops*, *Huia*, and *Meristogenys*) is demonstrated to be polyphyletic (a result congruent with Roelants et al., 2004; who did not study *Huia*; fig. 65). At least with respect to our exemplars, the character of a ventral sucker on the larva is suggested by our results to be convergent in *Amolops* (in the sense of including *Amo*), *Huia*, and *Meristogenys* (as well as in *Pseudoamolops*).

As expected, the genus *Rana* (sensu Dubois, 1992) is shown to be wildly nonmonophyletic, with Dubois' sections *Strongylopus* (*Afrana* and *Strongylopus*) and *Amietia* (*Amietia*) being far from other ''*Rana*'' in our results. (This result is consistent with that of Van der Meijden et al., 2005, and was anticipated by Dubois, 2005.) In this position, Section *Strongylopus* is paraphyletic with respect to *Cacosternum* + *Anhydrophyne* (fig. 63). As noted earlier, we transfer Sections *Strongylopus* and *Amietia* out of Ranidae and into a newly recognized family, Pyxicephalidae, as was done by Dubois (2005). (See the Taxonomy section for further discussion.)

As noted in the Review of Current Taxonomy, understanding the phylogeny of *Hy-*

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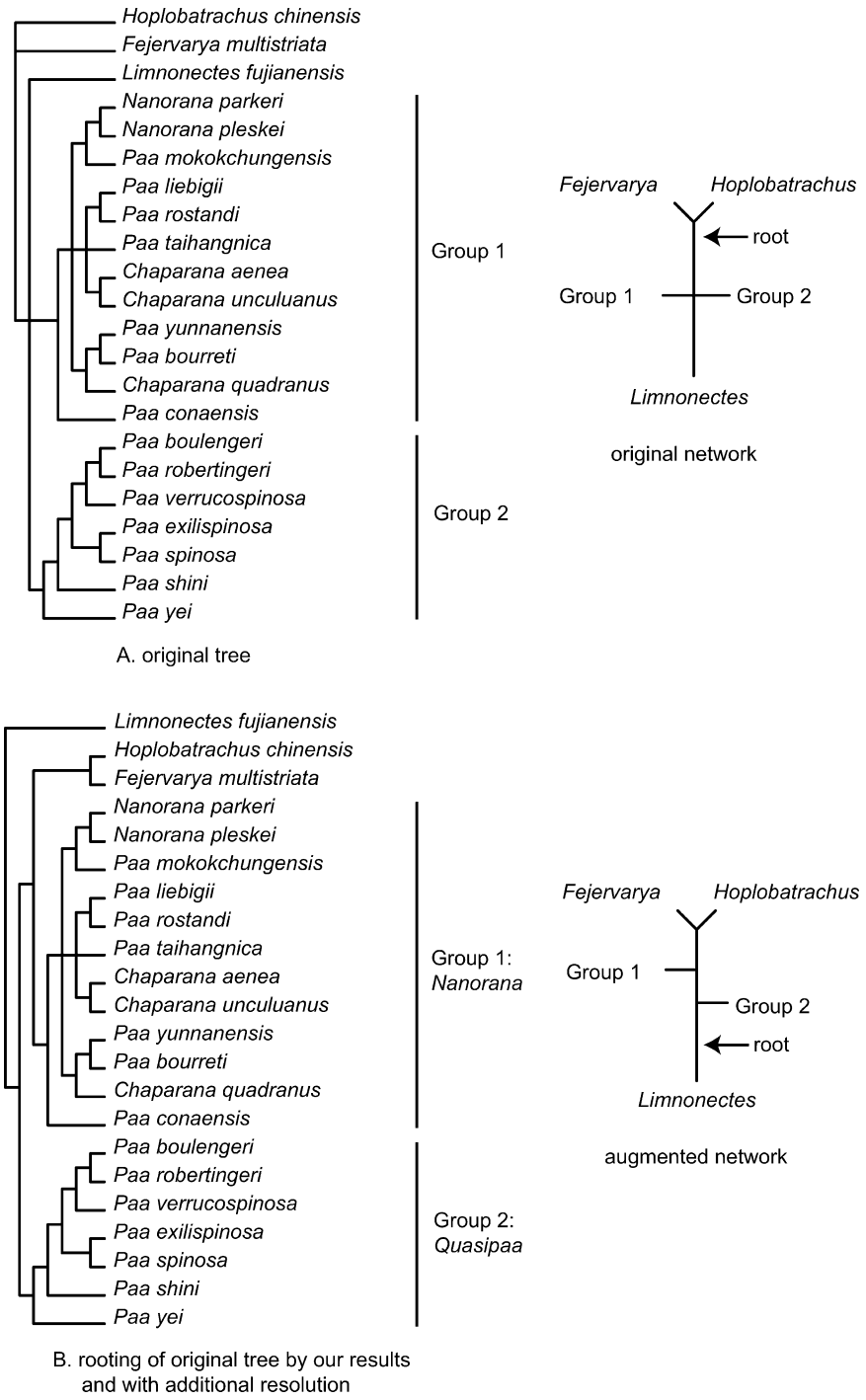

Fig. 64. **A,** Original tree of Jiang et al. (2005; from fig. 42) of Paini and (on right) its equivalent undirected network; **B,** Tree rerooted and with augmented resolution as implied by our general results, and, at right, its equivalent undirected network. We have applied the name *Nanorana* to Group 1 of Jiang et al. (2005); *Quasipaa* was applied by Jiang et al. (2005) for their Group 2.

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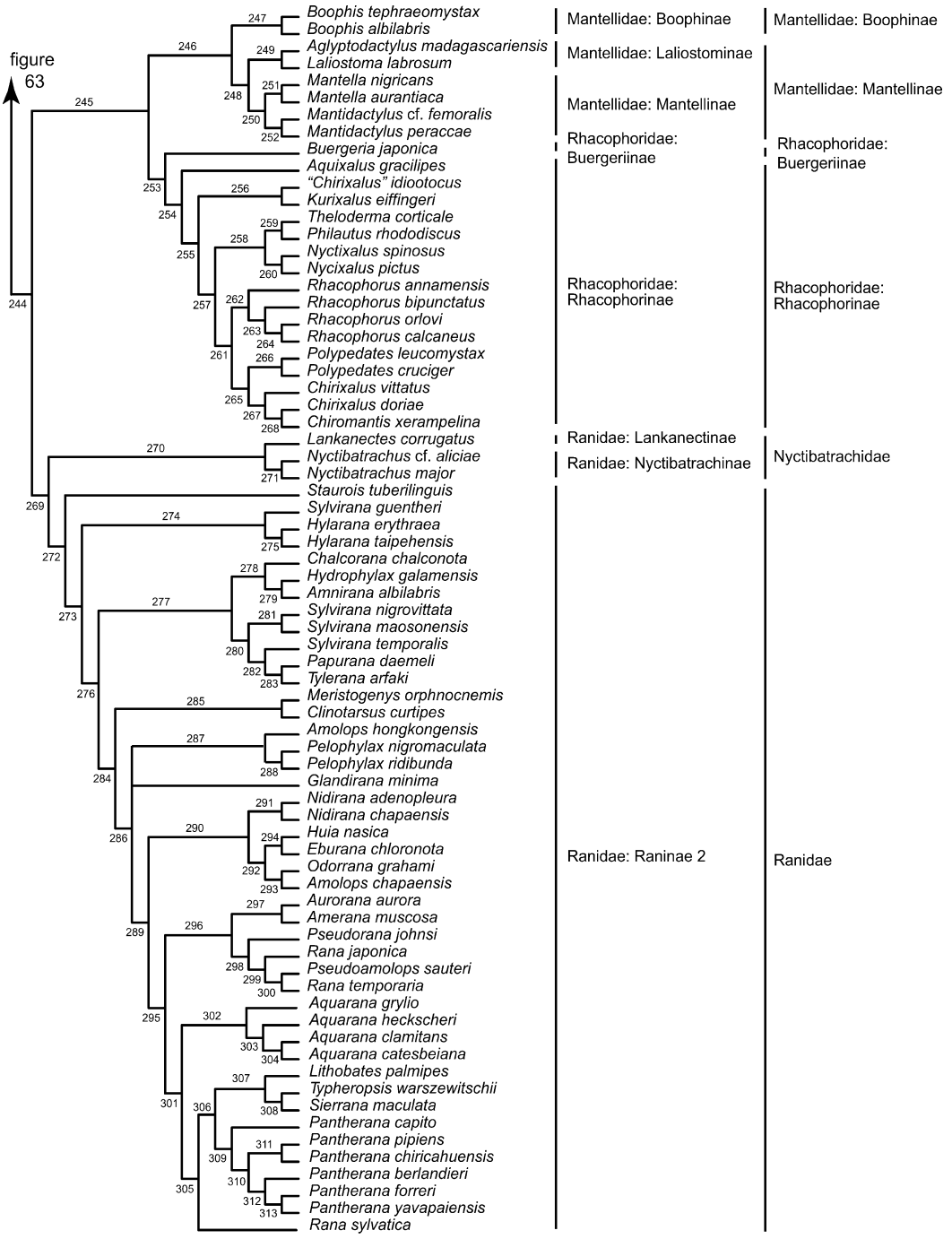

Fig. 65. Part 9 of anurans from the general tree (fig. 50 [insert]): Mantellidae, Rhacophoridae, Nyctibatrachidae, Ranidae.

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larana-like frogs (Dubois' sections *Babina* and *Hylarana*) is critical to understanding ranid systematics. Our results show that Boulenger (1920) was correct that ''*Hylarana*'' (sensu lato) is polyphyletic, or at least wildly paraphyletic. The plesiomorphic condition in Ranidae is to have expanded toe digits, as in Rhacophoridae + Mantellidae and farther outgroups, so this discovery merely illuminates that ''*Hylarana*'' was constructed on the basis of plesiomorphy. Dubois' (1992) Section *Hylarana* is paraphyletic with respect to *Amolops*, *Meristogenys*, and *Huia*, as well as most of sections *Babina*, *Amerana*, *Rana*, *Pelophylax*, and *Lithobates*. Further, the *Hylarana* subsection *Hydrophylax* (his humeral-gland group) is polyphyletic (as hinted at by the results of Matsui et al., 2005; fig. 46), in our results placing this group in two places: (1) *Sylvirana guentheri* forms the sister taxon of subgenus *Hylarana* (in the non-humeral-gland group) and (2) in a group containing *Hydrophylax galamensis* and *Papurana daemeli*. Our findings are largely congruent with the results of Roelants et al. (2004), who suggested ''*S.*'' *guentheri* as sister to *H. erythraea*, but who also suggested that this ''*erythraea* clade'' is sister to a clade containing *Sylvirana nigrovittata*. Marmayou et al. (2000; fig. 37) found strong support for *H. erythraea* and *H. taipehensis* as sisters, and weak support for ''*S.*'' *guentheri* to be part of that clade. They did show, weakly but consistently, that *Sylvirana* is polyphyletic with respect to *Hylarana* (Marmayou et al., 2000). Kosuch et al. (2001) found *Amnirana* to be the sister taxon of *Hydrophylax galamensis* + *Sylvirana gracilis*. Differences in data size and taxon sampling may account for differences in tree topology among these studies, but the substantial results are similar. Roelants et al. (2004) included exemplars of subgenus *Hydrophylax* sensu Dubois and subgenus *Hylarana* sensu Dubois, but not *Amnirana* as in our study. Kosuch et al. (2001) included exemplars of *Hydrophylax* and *Amnirana*, but not *Hylarana*, as was done for our study; but Roelants et al. (2004), Kosuch et al. (2001), and Marmayou et al. (2000) did not include species of *Papurana* or *Tylerana*.

The subsection *Hylarana* (the non-humeral-gland group) is polyphyletic as well. (This is not surprising, as subsection *Hylarana* never did have any suggested synapomorphies; again, this is consistent with the results of Matsui et al., 2005.) The component subgenus *Hylarana* is most closely related to *Sylvirana guentheri* (subsection *Hydrophylax*); subgenus *Chalcorana* (subsection *Hylarana*) is most closely related to *Hydrophylax* + *Amnirana* (subsection *Hydrophylax*); *Tylerana* (subsection *Hylarana*) is most closely related to *Papurana* (subsection *Hydrophylax*); and *Clinotarsus* (subsection *Hylarana*) forms the sister taxon of *Meristogenys* (subgenus of *Amolops* sensu Dubois, 1992). *Glandirana* (subsection *Hylarana*) is the sister taxon of *Pelophylax* (section *Pelophylax*). *Eburana* (subsection *Hylarana*) is the sister taxon of *Huia* (subgenus of *Amolops* sensu Dubois), and our exemplar of *Odorrana* (subsection *Hylarana*) is the sister taxon of ''*Amolops*'' *chapaensis*, a result similar to those of Jiang and Zhou (2005; fig. 41), who found *Eburana* nested within *Odorrana* (see the Taxonomy section for further discussion).

As suggested by Hillis and Davis (1986) and confirmed by Hillis and Wilcox (2005), Dubois' (1992) Section *Pelophylax* is polyphyletic, with one part, *Pelophylax* (sensu stricto), being found most closely related to *Glandirana* (section *Hylarana*) and the part composed of *Aquarana* and *Pantherana* being paraphyletic with respect to Dubois' Section *Lithobates*, as well as one species in his Section *Rana* (*R. sylvatica*). Our results do not conflict with Roelants et al. (2004), who found *Pelophylax* (*P. lessonae*, *P. nigromaculata*) to be the sister taxon of *Amolops* cf. *ricketti* (*A. ricketti* and *P. lessonae* not included in our study). Roelants et al. (2004) also found that the *Amolops–Pelophylax* clade is sister to a ''*Sylvirana*''*–Hylarana–Chalcorana–Hydrophylax–Pulchrana* clade, which is largely consistent with our findings. (We did not study *Pulchrana*.) Jiang and Zhou (2005) had results that were only partly congruent with ours and with those of Roelants et al. (2004). Jiang and Zhou (2005; fig. 41) found *Pelophylax* to form a monophyletic group with *Nidirana* and *Rana*, and this group formed the sister taxon of *Amolops*. The next more inclusive group was found to include the *Rugosa–Glandirana* clade.

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Dubois' (1992) Section *Amerana* is recovered as monophyletic and the sister taxon of *Pseudorana* + *Rana* + *Pseudoamolops*. Section *Rana* (our exemplars being *Rana japonica*, *R. temporaria*, and *R. sylvatica*) is recovered as polyphyletic, with one component (*Rana japonica* and *R. temporaria*) being paraphyletic with respect to *Pseudoamolops*, and another (*R. sylvatica*) forming the sister taxon of *Pantherana* (section *Pelophylax*) + Section *Lithobates*.

Excluding Dubois' (1992) section *Amerana*, we find American *Rana* (i.e., *Aquarana*, *Lithobates*, *Trypheropsis*, *Sierrana*, *Pantherana*, and *Rana sylvatica*) to form a monophyletic group, a conclusion reached previously by Hillis and Wilcox (2005; fig. 44). Section *Amerana* (subgenera *Aurorana* plus *Amerana* [former *Rana aurora* and *R. boylii* groups]) is most closely related to the *Rana temporaria* group (including *Pseudorana* and *Pseudamolops*), an arrangement that suggests the results of Case (1978) and Post and Uzzell (1981). Further discussion and generic realignments are provided in the Taxonomy section.

MANTELLIDAE AND RHACOPHORIDAE: We find Mantellidae and Rhacophoridae to be monophyletic sister taxa deeply imbedded within the traditional ''Ranidae'', together placed as the sister taxon of Raninae + Nyctibatrachinae (fig. 65). The monophyly of the combined Mantellidae and Rhacophoridae is not controversial and was suggested by a number of authors on the basis of DNA sequence data (e.g., Emerson et al., 2000b; Richards et al., 2000; J.A. Wilkinson et al., 2002; Roelants et al., 2004; Roelants and Bossuyt, 2005; Van der Meijden et al., 2005) as well as the morphological data of Liem (1970).

For mantellids, the phylogenetic structure we obtained is identical to that obtained by Vences et al. (2003d): *Boophis* ((*Aglyptodactylus* + *Laliostoma*) + (*Mantidactylus* + *Mantella*)), but different from that of Van der Meijden (2005) ((*Aglyptodactylus* + *Laliostoma*) + (*Boophis* + (*Mantella* + *Mantidactylus*)). Although Vences et al. (2003d) demonstrated that *Mantidactylus* is deeply paraphyletic with respect to *Mantella*, our limited taxon sampling did not allow us to test that result rigorously.

The basal dichotomy of Rhacophoridae is as suggested by Channing (1989), with *Buergeria* forming the sister taxon of the remaining rhacophorids. But beyond that level, however, our results are quite different. This is not surprising, given the inherent conflict and lack of resolution in the morphological data gathered so far, as discussed by J.A. Wilkinson and Drewes (2000). We will not discuss in detail the minor differences between our results and those of J.A. Wilkinson et al. (2002) because, although our taxon sampling was somewhat different, we included all of the same genes used in that study, as well as our own.

Our tree suggests polyphyly of *Chirixalus*, a conclusion to which others had previously arrived (e.g., J.A. Wilkinson et al., 2002): (1) one relatively basal clade (our *Kurixalus eiffingeri* and ''*Chirixalus*'' *idiootocus*) noted previously by J.A. Wilkinson et al.'s (2002) study for which the name *Kurixalus* Ye, Fei, and Dubois (*In* Fei, 1999) is available; (2) the group associated with the name *Chirixalus* (*Chirixalus doriae* and *C. vittatus*) forming a paraphyletic grade with respect to *Chiromantis* (also illustrated by Delorme et al., 2005; fig. 49); and (3) our ''*Chirixalus*'' *gracilipes*, except for *Buergeria*, being the sister taxon of all rhacophorids. We, unfortunately, did not sample ''*Chirixalus*'' *palpebralis*, which J.A. Wilkinson et al. (2002; fig. 48) found in a similar, basal, position, although as shown by the dendrogram published by Delorme et al. (2005; fig. 49), ''*Chirixalus*'' *palpebralis*, which we did not study, will likely be found to be quite distant from *Aquixalus* (*Gracixalus*) *gracilipes*, once *Aquixalus* is adequately sampled for molecular analysis.

A TAXONOMY OF LIVING AMPHIBIANS

The taxonomy that we propose is consistent with the International Code of Zoological Nomenclature (ICZN, 1999). It will appear to some that we have adopted an unranked taxonomy. This is partially true, but only for above-family-group nomenclature unregulated by the Code. Regardless of widespread perception, the Code does not govern nomenclature above the family

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group. In fact, it barely mentions the existence of Linnaean nomenclature above the rank of the family group, and it does not specify particular ranks above that category. Our suggested taxonomy is predicated on the recognition that the community of taxonomists has largely discarded its concerns regarding ranks above the family-group level. For example, one no longer hears arguments regarding whether Aves is a class, coordinate with a Class Amphibia, or whether it is at most a family within Archosauria. The reason for this withering of concerns about ranks is that the concerns do not constitute an empirical issue. Notions of rank equivalency are always based on notions of levels of divergence, age, content, or size that are bound to fail for a number of theoretical or empirical reasons[24]. But, because nominal families and the ranks below them have been regulated by a more or less universally accepted rulebook for more than 160 years (Stoll, 1961), we are not inclined to easily throw out that rulebook or the universal communication that it has fostered. Even though several of the criticisms of Linnaean nomenclature are accurate, the alternatives so far suggested have their own drawbacks. The International Code can be changed, and we expect that changes will be made to meet the needs of modern-day problems.

All taxonomies are rough and ready in the sense that, except for the most general level of communication, they must be qualified implicitly or explicitly with respect to variation in taxon content according to various authors, controversies regarding diagnosis, or, more subtly, the taxon sampling regime (Delorme et al., 2004) and underlying data used to infer the existence of particular taxa. In other words, taxonomies are constructions for verbal and written communication that are inherently limited because they represent sets of theories of relationship and do not communicate information on underlying data or assumptions of analysis. *Precision* in communication is enhanced by background knowledge on the part of those using the system for communication or, even better, having the relevant tree(s) and data set(s) available from which the taxonomy was derived. For an example of how taxonomies always must be qualified, Ford and Cannatella (1993) explicitly defined Hylidae as the most recent common ancestral species of Hemiphractinae, Hylinae, Pseudinae, Pelodryadinae, and Phyllomedusinae and all of its descendants. This definition was implicitly changed by Darst and Cannatella (2004) to be the ancestor of Pelodryadinae, Phyllomedusinae, and Hylinae, and all of its descendants, because Hemiphractinae was discovered to be paraphyletic and phylogenetically distant from ''other'' hylids. A casual glance at our tree will show that an application of Ford and Cannatella's (1993) cladographic definition of Hylidae would render as hylids nearly all arciferal neobatrachians, with the exception of Batrachophrynidae, Heleophrynidae, Limnodynastidae, Myobatrachidae, and Sooglossidae—a far cry from any content familiar to any who have used these terms and certainly not promoting precision in the discussion of synapomorphies or even casual notions of similarity[25]. Furthermore, the molecular evidence that optimizes as synapomorphies for Hylidae (sensu stricto) in the study of Darst and Cannatella (2004) *must* differ from those proposed by Faivovich et al. (2005) simply because the

[24] A major underlying reason for this failure is that there are no natural classes in evolution that correspond to taxonomic ranks such as genus (contra Van Gelder, 1977; Dubois, 1982, 1988b, 2005; see Fink, 1990), family, or phylum. A related logical error is the notion that organismal characteristics are transitive to their inclusive clades, except in an operational sense that is dependent on simplifying analytical assumptions (Frost and Kluge, 1994), rendering such mistaken ideas such that there are ''generic'' or ''family'' characters (e.g., see recognition of *Taylorana* by Dubois, 2005). Further, inasmuch as no objective criteria can correspond to subjective and idiosyncratic notions of organismal similarity and difference (Ghiselin, 1966), the idea that ranks could be tied to special characters or levels of organismal divergence is seen to be particularly futile. Ranks in the Linnaean system are assigned to taxa as part of a formal nomenclatural/mnemonic system, not through discovery of Linnaean ranks.

[25] Note that this kind of instability of nomenclature and diagnosis is, in part, what Phylogenetic Nomenclature is supposed to address. Compare this with the example of Linnaean nomenclatural instability provided by de Queiroz and Gauthier (1992) to demonstrate that this kind of instability is found in both systems but apparently is more typical of Phylogenetic Nomenclature.

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ingroup and outgroup taxon sampling of the latter is so much denser than that of the former. As taxa are sampled more and more densely, more and more nonhomology will be detected, with concomitant improvements in estimates of phylogeny (W.C. Wheeler, 1992; Zwickl and Hillis, 2002). The controversy as it exists today, regardless of sloganeering, is about how to portray in words hypotheses of monophyly, and revolves not about precision of communicating tree structure or underlying data, but about how to maintain consistency of communication among authors and across studies with a minimum of qualification. All systems so far suggested have limitations; like all maps they must have limitations to be useful. Linnaean taxonomy does promote useless rank controversies, but, as noted above and discussed more fully below, rigid application of cladographic definitions of taxonomic names (such as the method proposed by de Queiroz and Gauthier, 1992) brings other kinds of nomenclatural instability as well.

It is beyond the scope of this work to discuss at length the theory and practice of taxonomy and nomenclature. The ranked and rankless alternatives to expressing phylogenetic relationships in words theoretically are endless but most recently and most clearly discussed by Kluge (2005). To oversimplify his paper, currently competing systems for expressing phylogenetic relationships in words are (1) Linnaean system (Linnaeus, 1758); (2) Annotated Linnaean system (Wiley, 1981); (3) what Kluge termed ''Descent Classification'' and proponents call ''Phylogenetic Taxonomy'' (de Queiroz and Gauthier, 1992); (4) the ''Set Theory Classification'' system of Papavero et al. (2001), as termed by Kluge; and (5) Kluge's (2005) ''Phylogenetic System''.

We have taken a sixth approach, one that we think is based on common sense, especially with respect to how systematists use taxonomies and with respect to the state of the discussion, which is still *very* preliminary and reflecting a deep ambivalence on the part of taxonomists (for all sides of the controversy see: Wiley, 1981; de Queiroz, 1988; de Queiroz and Gauthier, 1994; Cantino et al., 1997; Cantino et al., 1999; Benton, 2000; Nixon and Carpenter, 2000; Withgott, 2000; Kress and DePriest, 2001; Niklas, 2001; Papavero et al., 2001; Pennisi, 2001; Brummitt, 2002; Carpenter, 2003; Keller et al., 2003; Kojima, 2003; Nixon et al., 2003; Schuh, 2003; Kluge, 2005; Pickett, 2005). What we do think is that the conversation will continue for some time and that changes will take place, all discussed fully and not driven by the overheated sloganeering that, unfortunately, characterizes so much of the rhetoric at this time—on all sides—inasmuch as this is a political, not a scientific controversy (see Pickett, 2005, for discussion). With respect to our approach to taxonomy, we, in effect, take the easy way out, we follow the International Code of Zoological Nomenclature (ICZN, 1999) for regulated taxa (family group and down) and apply an unranked taxonomy for unregulated taxa (above family group), the hypotheses for these taxa being derived from their included content and diagnostic synapomorphies.

We expect that regulated nomenclature will increasingly be pushed toward the terminal taxa and that unregulated taxa will increasingly be rankless. The reason for this is that there really is a practical limit to the number of ranks that workers are willing to use. Systematists seemingly are not enamored of new ranks such as grandorders, hyperfamilies, epifamilies, and infratribes (e.g., Lescure et al., 1986) or of the redundancies and controversies over rank that are part and parcel of ranked nomenclature (e.g., see Dubois, 2005). So, our observation is that sociological pressures will push workers towards ever smaller families, especially because there is no scientific or sociological pressure to construct larger families. Regardless, we think that this process will correspond with enormous progress in phylogenetic understanding.

We suggest that the content of an above-family taxon as originally formed by an author renders an implied hypothesis of descent, even if the concept of that taxon predates any particular theory of descent with modification. We spent considerable time determining the original intent of various taxonomic names. Unfortunately, an examination of the original content of the groups denoted by these taxonomic names obviated the need to use many of them because they de-

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viated so widely from all but a few of our phylogenetic hypotheses (e.g., Salientia in the original sense of Laurenti, 1768, not only includes all frogs, but shares *Proteus* with his Gradientia, a novel phylogenetic hypothesis!).

In some cases (e.g., Caudata), we set aside the intent of the original author in favor of widespread current usage as suggested by subsequent authors. The wisdom of this kind of action is open for discussion (see Dubois, 2004b, 2005), but increasingly the International Commission of Zoological Nomenclature appears to be moving toward usage rather than priority as an important criterion to decide issues, so we take this to be the appropriate strategy.

As noted above, we are unconvinced that cladographic rules governing name assignment (sensu de Queiroz and Gauthier, 1992) necessarily engender enhanced stability or precision of discussion (except in the special case of the crown-group approach to delimitation). However, we do think that associating names of extant taxa with content-specific, ostensively derived concepts (cf. Patterson and Rosen, 1977) will go a long way toward reducing the ''wobble'' of diagnoses associated with extant taxa as membership changes. One need only look at the history of the use of ''Amphibia'' to see how the lack of an overarching concept of the taxon has resulted in considerable drift of content and diagnosis. As noted by Laurin (1998a: 10), until Huxley (1863), the term Amphibia applied only to Recent taxa. Haeckel (1866) and Cope (1880) rendered Amphibia paraphyletic by the addition of some fossil taxa, with other authors (e.g., Romer, 1933) continuing the trend until all fossil tetrapods that were not ''reptiles'' were considered to be members of ''Amphibia''. Amphibia was returned to monophyly only by Gauthier et al. (1989) and subsequently restricted back to the groups of original intent by de Queiroz and Gauthier (1992).

Although the discussion is generating considerable self-examination by systematists, we think that cladographically assigned taxonomic names (de Queiroz and Gauthier, 1992) introduce a new kind of nomenclatural instability by tying names, not to content, types, or diagnoses but to tree topology[26]. Avoiding this instability requires great caution in the application of that naming convention. Nevertheless, in our judgment it is unlikely that a fourth ''order'' of living amphibians will be discovered, so application of the cladographic rules suggested by de Queiroz and Gauthier (1992) governing the application of the names Anura, Caudata, and Gymnophiona could be salutary for purposes of discussing fossil relatives of these crown groups.

Our strategy in designing a taxonomy for unregulated taxa is to preserve, as nearly as practical, the originally implied phylogenetic content of named above-family-group taxa. We also attempted to apply older names for above family-group taxa, but because of the constant redefinition of many of these taxa, we could solve these only on an *ad hoc* basis, depending on use, original intent, and recency of coining of the name(s).

In several cases, we changed the ranks of some regulated taxa from subfamilies to families to provide flexibility and help workers in the future with the problems inherent in ranked hierarchies. Because all names above the regulated family group are unaddressed by the International Code of Zoological Nomenclature (ICZN, 1999) we have regarded all of these names as unranked, but within the zone normally associated with class and order (whatever that might mean to the reader). We have not been constrained by recommendations regarding name formations and endings for ranks above the level of family group simply because we believe that these are unworkable and that they merely exacerbate the previously recognized problems of taxonomic ranks (de Queiroz and Gauthier, 1992).

Although we argue that taxonomy should reflect knowledge of phylogeny as closely as possible, by eliminating all paraphyly and

[26] If the application of a name for a taxon A (B + C) is governed by the cladographic rule ''the ancestor of A and B and all of its descendants'', and if new data show that the phylogenetic structure of this taxon has to change to C (A + B), the cladographically assigned name has to apply to A + B and exclude C, even though the content of the taxon A + B + C has not changed. Linnaean nomenclature would be unaffected by this topological change.

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recognizing all clades, we focused our attention primarily on the taxonomy of clades above the ''genus level'' for three reasons. First, for the most part our taxon sampling was inadequate to test prior hypotheses of intrageneric relationships for most genera. The practical implication of this inadequacy is that we lack evidence to refer the majority of species in a more refined generic taxonomy, which would require those species to be placed as incertae sedis, a cumbersome solution with little payoff. The other alternative—expanding the content of genera to enforce monophyly is equally unsatisfactory in these cases, as it overlooks the finer-level knowledge of phylogeny that exists but, for practical reasons was not brought to bear in this analysis. Secondly, the bulk of phylogenetic research since the mid-1970s has focused primarily on ''genus-level'' diversity, which means that a considerable amount of evidence, both molecular and morphological, has been generated for those groups, most of which was not included in the present study. Third, we see the value of the present contribution to be in framing finer level problems that are better addressed by regional specialists who can achieve more exhaustive taxon and character sampling.

Our consensus tree is shown in figure 50 (insert), which also displays the current and recommended family-group taxonomy. We modify the current generic taxonomy in places in this section, but those changes are not reflected in the figure for purposes of clarity in ''Results''. With minor exceptions, all clades are highly corroborated by molecular evidence (and morphological evidence on many branches as well) as estimated by Bremer values and parsimony jackknife frequencies (see below and appendix 4 for these values by branch). Because this study rests on the largest amount of data applied to the problem of the relationships among living amphibians, we provide a new taxonomy that we think will provide a better reference for additional progress.

This taxonomy of living amphibians is based on a phylogenetic analysis of 532 terminals, on the basis of a total of 1.8 million bp of nuDNA and mtDNA sequence data ($\bar{x}$ = 3.7 kb/terminal) in addition to the morphological data from predominantly larval morphology presented by Hass (2003), the only comparable data set across all frogs. Despite the fact that this is, so far, the most data-heavy analysis of amphibians, we expect to be criticized for presenting this taxonomy for four reasons:

(1) This taxonomy will be criticized both as premature and as not conservative. However, the underlying cladogram reflects the best overall estimate of phylogeny on the most thorough dataset applied to the issue. The alternative—to stick for sociological reasons to an old taxonomy that is clearly misleading and based on relatively little evidence—certainly will not efficiently promote additional research. Some will attempt to defend as conservative the old arrangements, especially favored paraphyletic groups, but mostly this will mean *socially* conservative, not *scientifically* conservative, something detrimental to scientific progress. As revealed in the ''Review of the Current Taxonomy'', much of the existing taxonomy of amphibians stands on remarkably little evidence and has simply been made plausible through decades of repetition and reification.

A similar argument is that we should retain the status quo with respect to taxonomy until we are ''more sure'' of a number of weakly recovered relationships. This position ignores how *little* evidence underlies the existing classifications. Indeed, our taxonomy explains more of the evolution of amphibian characteristics than the existing classification(s) and has the distinction of attempting to be explicitly monophyletic over all of the evidence analyzed. We are surely mistaken in several places, but this is better than continuing to recognize taxonomic groups that are known to be inconsistent with evolutionary history, regardless of social convention. We do go beyond our data in several places (e.g., Brachycephalidae, Bufonidae) and recognize some groups whose monophyly we have not rigorously tested. The reason for this is to attempt to delimit new hypotheses and not sit idly by while major problems are concealed by convention. Critics may charge that this is no different from post facto ''diagnosis'' of subjective similarity groupings (e.g., Dubois, 1987 ''1985'', 1992). However, in each case we think there is good reason to expect our taxa to obtain as monophylet-

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ic—and that leaving the taxonomy as it exists does nothing to promote improved understanding of evolutionary history.

(2) Some will be critical of the fact that we have not included all of the morphological data that have been presented by other authors. Early in the development of this work, we made an attempt to marshal the disparate but extensive number of characters presented by such authors as J.D. Lynch (1973), Estes (1981), Duellman and Trueb (1986), Milner (1988), Nussbaum and Wilkinson (1989), Trueb and Cloutier (1991), Ford and Cannatella (1993), Larson and Dimmick (1993), Milner (1993 (1994), McGowan and Evans (1995), Shubin and Jenkins (1995), M. Wilkinson and Nussbaum (1996), Laurin and Reisz (1997), Laurin (1998a), Maglia (1998), Carroll et al. (1999), M. Wilkinson and Nussbaum (1999), Carroll (2000a), Laurin et al. (2000), Milner (2000), J.S. Anderson (2001), Gardner (2001), Kaplan (2001), Zardoya and Meyer (2001), Gardner (2002), Gower and Wilkinson (2002), Laurin (2002), Scheltinga et al. (2002), and Báez and Pugener (2003). What we found, not surprisingly, is that different studies tended to generalize across different exemplars, even if they were working on the same groups, and that in some cases putative synapomorphies had been so reified through repetition in the literature that it was difficult, if not impossible, to ascertain which taxa (much less which specimens) had actually been evaluated for which characters. We also found that many of the new characters remain in unpublished dissertations (e.g., Cannatella, 1985; Ford, 1990; S.-H. Wu, 1994; Graybeal, 1995; da Silva, 1998; Scott, 2002), where ethics dictates they not be mined for information if they are new, and prudence dictates that the information in them not be taken at face value if they are old and still unpublished.

Further, most of the paleontological literature reflects such incomplete sampling of living taxa as to oversimplify living diversity. (One does not read evolution from the rocks, but the rocks certainly are an undersampled component of our study.) Reconciling *all* morphological descriptions of characters in comparable form, obviously, is the next big step, for someone else, and in combined analysis this will constitute a test of our results and taxonomy. This problem calls for careful evaluation of all morphological characters across all taxonomic groups concomitant with the evaluation of relevant fossil groups. This is a big task, but one worth doing well. Unfortunately, this kind of infrastructural science is not flashy and therefore will not attract funding from already oversubscribed and underfinanced granting agencies. (See Maienschein, 1994, for an essay on the dangers to science from the preoccupation by administrators and funding agencies with the ''cutting edge''.)

(3) Some will criticize our analytical methods. We have been conservative with respect to analytical assumptions. Beyond attempting to maximize explanatory efficiency, some workers prefer to incorporate assumptions about the evolutionary process by the addition of particular evolutionary models. This is obviously a discussion that we think will continue for a long time because of the serious philosophical and evidentiary issues involved.

Some will be uncomfortable that such a large proportion of our data are molecular (even though most of our results are generally conventional). We believe that it is better to present a taxonomy that represents explicit, evidence-based hypotheses of relationships than to retain a taxonomy solely because we are used to it. Some will want to exclude all sequence data that require alignment. Unfortunately, this assumes that same-length sequences lack evidence of having had length variation, an assumption not supported by evidence (Grant, unpubl.). Others will want to ''correct'' alignments manually (although this is likely to increase the number of transformations required to explain sequence variation). Although such methodological choices are crucial and should continue to be debated (indeed, we urge authors and editors of empirical papers to be more explicit about both their methods of alignment and analysis and their reasons for employing them), the issue at hand is that it is time to move away from a taxonomy known to be fatally flawed and that promotes misunderstanding and into a scientific dialogue that will promote a much improved under-

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standing of the evolution of amphibian taxic, life history, and morphological diversity.

(4) We will be trivially criticized for formulating new taxonomic names with 19 authors. Times change and collaborations on this scale are necessary to answer global questions. That a new name can have 19 authors may be cumbersome, but, authorship is not part of the scientific name. And, regardless of recommendations made in the Code (ICZN, 1999) this authorship reflects accurately the extensive effort in collecting samples, sequencing, data analysis, and writing that work on this scale requires.

Although our results will undoubtedly allow considerable progress to be made, by nearly doubling the number of amphibian species for which DNA sequences are available in GenBank, projects such as this one generate questions as well as answers. Our results therefore will provide a reasonably well-tested departure point for future studies by identifying outstanding problems that are especially worthy of investigation.

Taxonomic Accounts

Below we present ancillary information and discussion to accompany the taxonomy presented in figures 50 (insert) and 66 (a reduced tree of family-group taxonomy). (Table 5 provides names of taxa/branches on the interior of the tree shown in figure 66, and figure 67 provides the taxonomy of amphibians in condensed form.) Most morphological evidence is addressed in accounts, but molecular synapomorphies are provided where relevant in appendix 5, with branch numbers corresponding with those noted in the various figures. We are *conservative* in the scientific sense in that we stick close to the preponderance of evidence and not to tradition. Genera in **bold** listed under Content represent those from which one or more species were included in our analysis (as DNA sequences either generated or by us or others and available via GenBank). A justification is provided for inclusion of taxa that were not sampled. Synonymies provided in the family group and below conform to the International Code of Zoological Nomenclature (ICZN, 1999). We include citations only to original uses and not to emendations, rank changes, or incorrect subsequent spellings. More extensive discussion of specific nomenclatural issues are dealt with in appendix 6. A summary of generic name changes is presented in appendix 7. We do not address fossil taxa, although they can be placed within this framework with relatively little effort. Dubois (2005) recently provided a taxonomy of living amphibians and their fossil relatives (Neobatrachii in his sense). Because his taxonomy appeals to a taxonomic philosophy deeply steeped in the importance of ranks and personal authority and the unimportance of evidence and logical consistency with evolutionary history, we comment on it only where necessary.

For taxa above the family group, which are not regulated by the Code, homonymy remains an unresolved issue in amphibian nomenclature because, even if the original author intended one content (i.e., one hypothesis of relationship), subsequent authors saw (and may see) little problem in redefining these names to fit revised hypotheses of relationship. For these taxa we do not provide a synonymy because in the absence of any regulatory tradition of above-family-group nomenclature, we have tried to optimize on the hypothesis of relationship intended by the author (or redefiner) of that taxon. Although we do not provide a ''synonymy'' in the accounts of unregulated taxa, we variably note in appendix 6 (''Nomenclature'') synonyms, near-synonyms, and problematic nomenclatural issues.

The structure of the taxonomic accounts is straight-forward with several categories of information: (1) the name and author of the taxon (and where appropriate and to enhance navigation among records, bracketed numbers are associated that correspond to the numbered branches in our various figures and tables in ''Results''); (2) a list of available names if application of the name is regulated by the International Code of Zoological Nomenclature; (3) an etymology if the name of a taxon is used for the first time; (4) the name and branch number of the immediately more inclusive taxon; (5) the name and branch number of the sister taxon; (6) a statement of the geographic distribution of the taxon; (7) the concept of the taxon in terms of content; and (8) a characterization

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TABLE 5

Branch Numbers and Taxon Names Corresponding to Internal Branches on Figure 50

Left side, sorted by branch number; right side, sorted by taxon name.

Branch number	Taxon name	Branch number	Taxon name
6	Amphibia	91	Acosmanura
7	Gymnophiona	192	Africanura
8	Rhinatrematidae	143	Afrobatrachia
9	Stegokrotaphia	460	Agastrorophrynia
23	Batrachia	244	Aglaioanura
24	Caudata	109	Allodapanura
25	Cryptobranchoidei	191	Ametrobatrachia
29	Diadectosalamandroidei	6	Amphibia
30	Hydatinosalamandroidei	92	Anomocoela
31	Perennibranchia	74	Anura
35	Treptobranchia	371	Athesphatanura
49	Plethosalamandroidei	319	Australobatrachia
50	Xenosalamandroidei	23	Batrachia
74	Anura	24	Caudata
77	Lalagobatrachia	440	Chthonobatrachia
78	Xenoanura	366	Cladophrynia
84	Sokolanura	85	Costata
85	Costata	25	Cryptobranchoidei
91	Acosmanura	461	Dendrobatoidea
92	Anomocoela	29	Diadectosalamandroidei
93	Pelodytoidea	425	Diphyabatrachia
96	Pelobatoidea	7	Gymnophiona
105	Neobatrachia	448	Hesticobatrachia
107	Phthanobatrachia	30	Hydatinosalamandroidei
108	Ranoides	314	Hyloides
109	Allodapanura	77	Lalagobatrachia
143	Afrobatrachia	148	Laurentobatrachia
144	Xenosyneunitanura	424	Leptodactyliformes
148	Laurentobatrachia	349	Meridianura
180	Natatanura	321	Myobatrachoidea
183	Victoranura	180	Natatanura
189	Telmatobatrachia	105	Neobatrachia
191	Ametrobatrachia	348	Nobleobatrachia
192	Africanura	318	Notogaeanura
200	Pyxicephaloidea	96	Pelobatoidea
220	Saukrobatrachia	93	Pelodytoidea
244	Aglaioanura	31	Perennibranchia
245	Rhacophoroidea	107	Phthanobatrachia
269	Ranoidea	49	Plethosalamandroidei
314	Hyloides	200	Pyxicephaloidea
318	Notogaeanura	269	Ranoidea
319	Australobatrachia	108	Ranoides
321	Myobatrachoidea	245	Rhacophoroidea
348	Nobleobatrachia	8	Rhinatrematidae
349	Meridianura	220	Saukrobatrachia
366	Cladophrynia	84	Sokolanura
368	Tinctanura	9	Stegokrotaphia
371	Athesphatanura	189	Telmatobatrachia
424	Leptodactyliformes	368	Tinctanura
425	Diphyabatrachia	35	Treptobranchia
440	Chthonobatrachia	183	Victoranura
448	Hesticobatrachia	78	Xenoanura
460	Agastorophrynia	50	Xenosalamandroidei
461	Dendrobatoidea	144	Xenosyneunitanura

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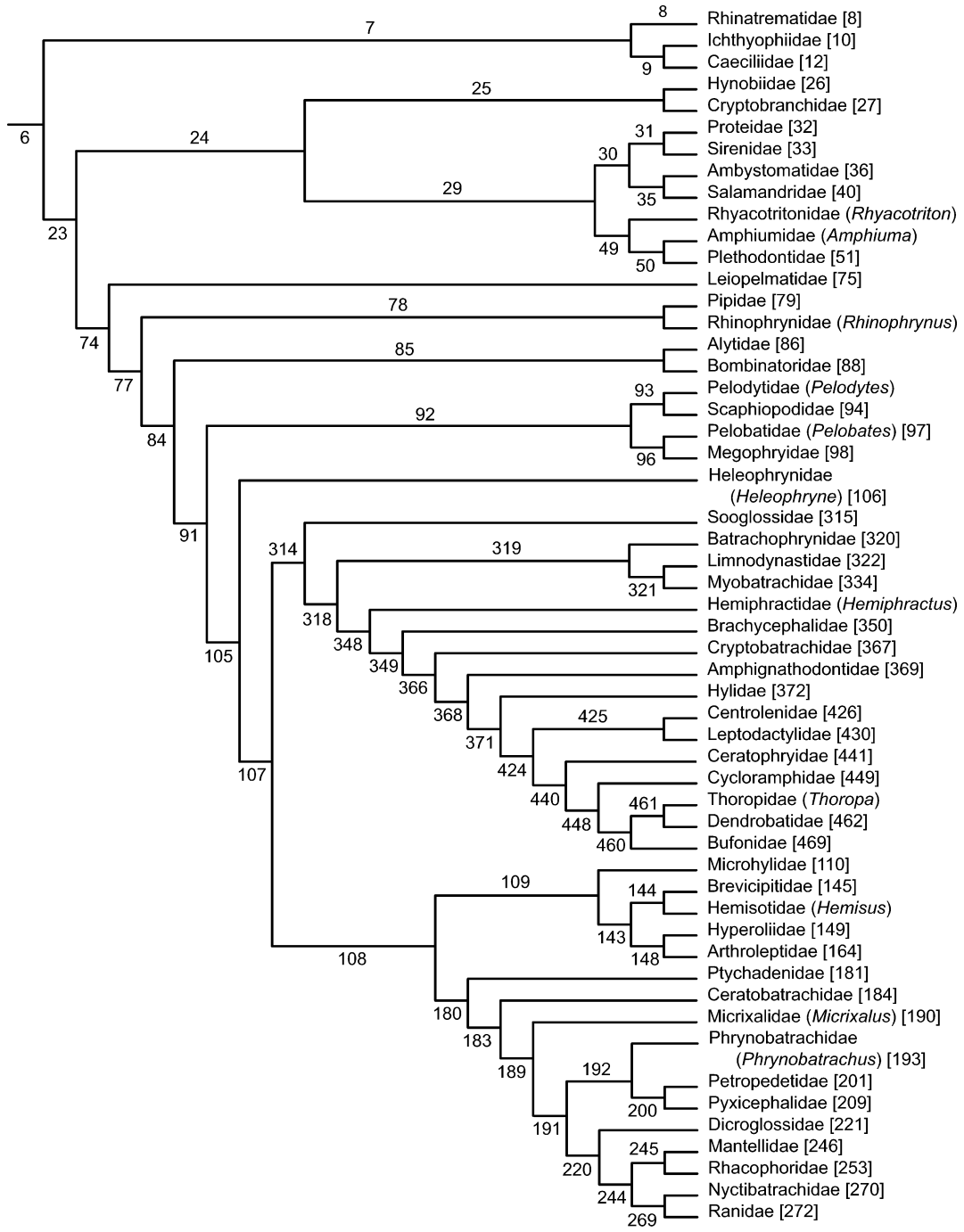

Fig. 66. A simplied tree of our results (fig. 50) tree showing families. Numbers on branches allow branch lengths, Bremer, and jackknife values, as well as molecular synapomorphies to be identified in appendices 4 and 5. See table 5 for taxon names associated with internal numbered branches and figure 67 for a complete summary of taxonomy.

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Amphibia Gray, 1825
- Gymnophiona Müller, 1832
  - Rhinatrematidae Nussbaum 1977
    - *Epicrionops* Boulenger, 1883
    - *Rhinatrema* Duméril and Bibron, 1841
  - Stegokrotaphia Cannatella and Hillis, 1993
    - Ichthyophiidae Taylor, 1968
      - *Caudacaecilia* Taylor, 1968
      - "*Ichthyophis*" Fitzinger, 1826
      - *Uraeotyphlus* Peters, 1880 "1879"
    - Caeciliidae Rafinesque, 1814
      - *Boulengerula* Tornier, 1896
      - *Brasilotyphlus* Taylor, 1968
      - *Caecilia* Linnaeus, 1758
      - *Dermophis* Peters, 1880
      - *Gegeneophis* Peters, 1880
      - *Geotrypetes* Peters, 1880
      - *Grandisonia* Taylor, 1968
      - *Gymnopis* Peters, 1874
      - *Herpele* Peters, 1880
      - *Hypogeophis* Peters, 1880
      - *Idiocranium* Parker, 1936
      - *Indotyphlus* Taylor, 1960
      - *Luetkenotyphlus* Taylor, 1968
      - *Microcaecilia* Taylor, 1968
      - *Mimosiphonops* Taylor, 1968
      - *Oscaecilia* Taylor, 1968
      - *Parvicaecilia* Taylor, 1968
      - *Praslinia* Boulenger, 1909
      - *Schistometopum* Parker, 1941
      - *Siphonops* Wagler, 1828
      - *Sylvacaecilia* Wake, 1987
      - Scolecomorphinae Taylor, 1969
        - *Crotaphatrema* Nussbaum, 1985
        - *Scolecomorphus* Boulenger, 1883
      - Typhlonectinae Taylor, 1968
        - *Atretochoana* Nussbaum and Wilkinson, 1995
        - *Chthonerpeton* Peters, 1880
        - *Nectocaecilia* Taylor, 1968
        - *Potomotyphlus* Taylor, 1968
        - *Typhlonectes* Peters, 1880

Fig. 67. Summary taxonomy of living amphibians. Quotation marks around names denote nonmonophyly.

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Batrachia Latreille, 1800
- Caudata Fischer von Waldheim, 1813
  - Cryptobranchoidei Noble, 1931
    - Cryptobranchidae Fitzinger, 1826
      - *Andrias* Tschudi, 1837
      - *Cryptobranchus* Leuckart, 1821
    - Hynobiidae Cope, 1859
      - *Batrachuperus* Boulenger, 1878
      - *Hynobius* Tschudi, 1838
      - *Onychodactylus* Tschudi, 1838
      - *Pachyhynobius* Fei, Qu, and Wu, 1983
      - *Protohynobius* Fei and Ye, 2000
      - *Ranodon* Kessler, 1866
      - *Salamandrella* Dybowski, 1870
  - Diadectosalamandroidei **new taxon**
    - Hydatinosalamandroidei **new taxon**
      - Perennibranchia Latreille, 1825
        - Proteidae Gray, 1825
          - *Necturus* Rafinesque, 1819
          - *Proteus* Laurenti, 1768
        - Sirenidae Gray, 1825
          - *Pseudobranchus* Gray, 1825
          - *Siren* Österdam, 1766
      - Treptobranchia **new taxon**
        - Ambystomatidae Gray, 1850
          - *Ambystoma* Tschudi, 1838
          - *Dicamptodon* Strauch, 1870
        - Salamandridae Goldfuss, 1820
          - Pleurodelinae Bonaparte, 1839
            - *Cynops* Tschudi, 1838
            - *Echinotriton* Nussbaum and Brodie, 1982
            - *Euproctus* Gené, 1838
            - *Lissotriton* Bell, 1838
            - *Mesotriton* Bolkay, 1927
            - *Neurergus* Cope, 1862
            - *Notophthalmus* Rafinesque, 1820
            - *Pachytriton* Boulenger, 1878
            - *Paramesotriton* Chang, 1935
            - *Pleurodeles* Michahelles, 1830
            - *Salamandrina* Fitzinger, 1826
            - *Taricha* Gray, 1850
            - *Triturus* Rafinesque, 1815
            - *Tylototriton* Anderson, 1871
          - Salamandrinae Goldfuss, 1820
            - *Chioglossa* Bocage, 1864
            - *Lyciasalamandra* Veith and Steinfartz, 2004
            - *Mertensiella* Wolterstorff, 1925
            - *Salamandra* Laurenti, 1768

Fig. 67. Continued.

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Plethosalamandroidei **new taxon**
- Rhyacotritonidae Tihen, 1958
  - *Rhyacotriton* Dunn, 1920
- Xenosalamandroidei **new taxon**
  - Amphiumidae Gray, 1825
    - *Amphiuma* Garden, 1821
  - Plethodontidae Gray, 1850
    - Hemidactyliinae Hallowell, 1856
      - *Hemidactylium* Tschudi, 1838
    - Bolitoglossinae Hallowell, 1856
      - *Batrachoseps* Bonaparte, 1839
      - *Bolitoglossa* Duméril, Bibron, and Duméril, 1854
      - *Bradytriton* Wake and Elias, 1983
      - *Chiropterotriton* Taylor, 1944
      - *Cryptotriton* García-París and Wake, 2000
      - *Dendrotriton* Wake and Elias, 1983
      - *Nototriton* Wake and Elias, 1983
      - *Nyctanolis* Elias and Wake, 1983
      - *Oedipina* Keferstein, 1868
      - *Parvimolge* Taylor, 1944
      - *Pseudoeurycea* Taylor, 1944 (including *Ixalotriton* Wake and Johnson, 1989; and *Lineatriton* Tanner, 1950)
      - *Thorius* Cope, 1869
    - Spelerpinae Cope, 1859
      - *Eurycea* Rafinesque, 1822 (including *Haideotriton* Carr, 1939)
      - *Gyrinophilus* Cope, 1869
      - *Pseudotriton* Taylor, 1944
      - *Stereochilus* Cope, 1869
    - Plethodontinae Gray, 1850
      - *Aneides* Baird, 1851
      - *Desmognathus* Baird, 1850
      - *Ensatina* Gray, 1850
      - *Hydromantes* Gistel, 1848
      - *Karsenia* Min, Yang, Bonett, Vieites, Brandon, and Wake, 2005
      - *Phaeognathus* Highton, 1961
      - *Plethodon* Tschudi, 1838
      - *Speleomantes* Dubois, 1984

Fig. 67. Continued.

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Anura Fischer von Waldheim, 1831
- Leiopelmatidae Mivart, 1869
  - *Ascaphus* Stejneger, 1899
  - *Leiopelma* Fitzinger, 1861
- Lalagobatrachia **new taxon**
  - Xenoanura Savage, 1973
    - Pipidae Gray, 1825
      - *Hymenochirus* Boulenger, 1896
      - *Pipa* Laurenti, 1768
      - *Pseudhymenochirus* Chabanaud, 1920
      - *Silurana* Gray, 1864
      - *Xenopus* Wagler, 1827
    - Rhinophrynidae Günther, 1859 "1858"
      - *Rhinophrynus* Duméril and Bibron, 1841
  - Sokolanura **new taxon**
    - Costata Lataste, 1879
      - Alytidae Fitzinger, 1843
        - *Alytes* Wagler, 1830
        - *Discoglossus* Otth, 1837
      - Bombinatoridae Gray, 1825
        - *Barbourula* Taylor and Noble, 1924
        - *Bombina* Oken, 1816
    - Acosmanura Savage, 1973
      - Anomocoela Nicholls, 1916
        - Pelobatoidea Bonaparte, 1850
          - Pelobatidae Bonaparte, 1850
            - *Pelobates* Wagler, 1830
          - Megophryidae Bonaparte, 1850
            - *Atympanophrys* Tian and Hu, 1983
            - *Brachytarsophrys* Tian and Hu, 1983
            - *Leptobrachella* Smith, 1925
            - *Leptobrachium* Tschudi, 1838
            - *Leptolalax* Dubois, 1980
            - *Megophrys* Kuhl and Hasselt, 1822
            - *Ophryophryne* Boulenger, 1903
            - *Oreolalax* Myers and Leviton, 1962
            - *Scutiger* Theobald, 1868
            - *Vibrissaphora* Liu, 1945
            - *Xenophrys* Günther, 1864
        - Pelodytoidea Bonaparte, 1850
          - Pelodytidae Bonaparte, 1850
            - *Pelodytes* Bonaparte, 1838
          - Scaphiopodidae Cope, 1865
            - *Scaphiopus* Holbrook, 1836
            - *Spea* Cope, 1866

Fig. 67. Continued.

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Neobatrachia Reig, 1958
- Heleophrynidae Noble, 1931
  - *Heleophryne* Sclater, 1898
- Phthanobatrachia **new taxon**
  - Hyloides **new taxon**
    - Sooglossidae Noble, 1931
      - *Nasikabatrachus* Biju and Bossuyt, 2003
      - *Sooglossus* Boulenger, 1906 (including *Nesomantis* Boulenger, 1909)
    - Notogaeanura **new taxon**
      - Australobatrachia **new taxon**
        - Batrachophrynidae Cope, 1875
          - *Batrachophrynus* Peters, 1873
          - *Caudiverbera* Laurenti, 1768
          - *Telmatobufo* Schmidt, 1952
        - Myobatrachoidea Schlegel, 1850
          - Limnodynastidae Lynch, 1971
            - *Adelotus* Ogilby, 1907
            - *Heleioporus* Gray, 1841
            - *Lechriodus* Boulenger, 1882
            - *Limnodynastes* Fitzinger, 1843 (including *Megistolotis* Tyler, Martin, and Davis, 1979)
            - *Neobatrachus* Peters, 1863
            - *Notaden* Günther, 1873
            - *Opisthodon* Steindachner, 1867
            - *Philoria* Spencer, 1901 (including *Kyarranus* Moore, 1958)
          - Myobatrachidae Schlegel, 1850
            - *Arenophryne* Tyler, 1976
            - *Assa* Tyler, 1972
            - *Crinia* Tschudi, 1838
            - *Geocrinia* Blake, 1973
            - *Metacrinia* Parker, 1940
            - *Mixophyes* Günther, 1864
            - *Myobatrachus* Schlegel, 1850
            - *Paracrinia* Heyer and Liem, 1976
            - *Pseudophryne* Fitzinger, 1843
            - *Rheobatrachus* Liem, 1973
            - *Spicospina* Roberts, Horwitz, Wardell-Johnson, Maxson, and Mahony, 1997
            - *Taudactylus* Straughan and Lee, 1966
            - *Uperoleia* Gray, 1841
      - Nobleobatrachia **new taxon**
        - Hemiphractidae Peters, 1862
          - *Hemiphractus* Wagler, 1828
        - Meridianura **new taxon**
          - Brachycephalidae Günther, 1858
            - *Adelophryne* Hoogmoed and Lescure, 1984
            - *Atopophrynus* Lynch and Ruiz-Carranza, 1982
            - *Barycholos* Heyer, 1969
            - *Brachycephalus* Fitzinger, 1826
            - *Craugastor* Cope, 1862
            - *Dischidodactylus* Lynch, 1979

Fig. 67. Continued.

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"*Eleutherodactylus*" Duméril and Bibron, 1841
"*Euhyas*" Fitzinger, 1843
Euparkerella Griffiths, 1959
Geobatrachus Ruthven, 1915
Holoaden Miranda-Ribeiro, 1920
Ischnocnema Reinhardt and Lütken, 1862 "1861"
"*Pelorius*" Hedges, 1989
Phrynopus Peters, 1873
Phyllonastes Heyer, 1977
Phyzelaphryne Heyer, 1977
Syrrhophus Cope, 1878
Cladophrynia **new taxon**
Cryptobranchidae **new family**
Cryptobatrachus Ruthven, 1916
Stefania Rivero, 1968 "1966"
Tinctanura **new taxon**
Amphignathodontidae Boulenger, 1882
Flectonotus Miranda-Ribeiro, 1920
Gastrotheca Fitzinger, 1843
Athesphatanura **new taxon**
Hylidae Rafinesque, 1815
Hylinae Rafinesque, 1815
Acris Duméril and Bibron, 1841
Anotheca Smith, 1939
Aparasphenodon Miranda-Ribeiro, 1920
Aplastodiscus Lutz *In* Lutz, 1950
Argenteohyla Trueb, 1970
Bokermannohyla Faivovich et al., 2005
Bromeliohyla Faivovich et al., 2005
Charadrahyla Faivovich et al., 2005
Corythomantis Boulenger, 1896
Dendropsophus Fitzinger, 1843
Duellmanohyla Campbell and Smith, 1992
Ecnomiohyla Faivovich et al., 2005
Exerodonta Brocchi, 1879
Hyla Laurenti, 1768
Hyloscirtus Peters, 1882
Hypsiboas Wagler, 1830
Isthmohyla Faivovich, et al., 2005
Itapotihyla Faivovich et al., 2005
Lysapsus Cope, 1862
Megastomatohyla Faivovich et al., 2005
Myersiohyla Faivovich et al., 2005
Nyctimantis Boulenger, 1882
Osteocephalus Steindachner, 1862
Osteopilus Fitzinger, 1843
Phyllodytes Wagler, 1830
Plectrohyla Brocchi, 1877
Pseudacris Fitzinger, 1843
Pseudis Wagler, 1830

Fig. 67. Continued.

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Ptychohyla Taylor, 1944
Scarthyla Duellman and de Sá, 1988
Scinax Wagler, 1830
Smilisca Cope, 1865 (including *Pternohyla* Boulenger, 1882)
Sphaenorhynchus Tschudi, 1838
Tepuihyla Ayarzagüena, Señaris, and Gorzula, 1993 "1992"
Tlalocohyla Faivovich et al., 2005
Trachycephalus Tschudi, 1838 (including *Phrynohyas* Fitzinger, 1843)
Triprion Cope, 1866
Xenohyla Izecksohn, 1998 "1996"
Pelodryadinae Günther, 1858
Litoria Tschudi, 1838 (including *Cyclorana* Steindachner, 1867; and *Nyctimystes* Stejneger, 1916)
Phyllomedusinae Günther, 1858
Agalychnis Cope, 1864
Cruziohyla Faivovich et al., 2005
Hylomantis Peters, 1873 "1872"
Pachymedusa Duellman, 1968
Phasmahyla Cruz, 1991 "1990"
Phrynomedusa Miranda-Ribeiro, 1923
Phyllomedusa Wagler, 1830
Leptodactyliformes **new taxon**
Diphyabatrachia **new taxon**
Centrolenidae Taylor, 1951
Allophryninae Goin et al., 1978
Allophryne Gaige, 1926
Centroleninae Taylor, 1951
"*Centrolene*" Jiménez de la Espada, 1872
"*Cochranella*" Taylor, 1951
Hyalinobatrachium Ruiz-Carranza and Lynch, 1991
Leptodactylidae Werner, 1896 (1838)
Edalorhina Jiménez de la Espada, 1871 "1870"
Engystomops Jiménez de la Espada, 1872
Eupemphix Steindachner, 1863
Hydrolaetare Gallardo, 1963
Leptodactylus Fitzinger, 1826 (including *Adenomera* Steindachner, 1867; *Lithodytes* Fitzinger, 1843; and *Vanzolinius* Heyer, 1974)
Paratelmatobius Lutz and Carvalho, 1958
Physalaemus Fitzinger, 1826
Pleurodema Tschudi, 1838
Pseudopaludicola Miranda-Ribeiro, 1926
Scythrophrys Lynch, 1971
Somuncuria Lynch, 1978
Chthonobatrachia **new taxon**
Ceratophryidae Tschudi, 1838
Ceratophryinae Tschudi, 1838
Atelognathus Lynch, 1978
Batrachyla Bell, 1843

Fig. 67. Continued.

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Ceratophrys Wied-Neuwied, 1824
Chacophrys Reig and Limeses, 1963
Insuetophrynus Barrio, 1970
Lepidobatrachus Budgett, 1899
Telmatobiinae Fitzinger, 1843
Telmatobius Wiegmann, 1834
Hesticobatrachia **new taxon**
Cycloramphidae Bonaparte, 1850
Incertae sedis: *Rupirana* Heyer, 1999
Cycloramphinae Bonaparte, 1850
Alsodes Bell, 1843
Crossodactylodes Cochran, 1938
Cycloramphus Tschudi, 1838
Eupsophus Fitzinger, 1843
Hylorina Bell, 1843
Limnomedusa Fitzinger, 1843
Macrogenioglottus Carvalho, 1946
Odontophrynus Reinhardt and Lütken, 1862 "1861"
Proceratophrys Miranda-Ribeiro, 1920
Rhinoderma Duméril and Bibron, 1841
Zachaenus Cope, 1866
Hylodinae Günther, 1858
Crossodactylus Duméril and Bibron, 1841
Hylodes Fitzinger, 1826
Megaelosia Miranda-Ribeiro, 1923
Agastorophrynia **new taxon**
Dendrobatoidea Cope, 1865
Dendrobatidae Cope, 1865
Allobates Zimmermann and Zimmermann, 1988
Ameerega Bauer, 1986 (including *Epipedobates* Myers, 1987)
Aromobates Myers, Paolillo O., and Daly, 1991
Colostethus Cope, 1866
Cryptophyllobates Lötters, Jungfer, and Widmer, 2000
Dendrobates Wagler, 1830 (including *Oophaga* Bauer, 1988; and *Ranitomeya* Bauer, 1986)
Mannophryne La Marca, 1992
Minyobates Myers, 1987
Nephelobates La Marca, 1994
Phobobates Zimmermann and Zimmermann, 1988
Phyllobates Duméril and Bibron, 1841
Thoropidae **new family**
Thoropa Cope, 1865
Bufonidae Gray, 1825
Adenomus Cope, 1861 "1860"
Altiphrynoides Dubois, 1987 "1986" (including *Spinophrynoides* Dubois, 1987 "1986")
Amietophrynus **new genus**
Anaxyrus Tschudi, 1845
Andinophryne Hoogmoed, 1985

Fig. 67. Continued.

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Ansonia Stoliczka, 1870
Atelophryniscus McCranie, Wilson, and Williams, 1989
Atelopus Duméril and Bibron, 1841
Bufo Laurenti, 1768
Bufoides Pillai and Yazdani, 1973
Capensibufo Grandison, 1980
Chaunus Wagler, 1828
Churamiti Channing and Stanley, 2002
Cranopsis Cope, 1875 "1876"
Crepidophryne Cope, 1889
Dendrophryniscus Jiménez de la Espada, 1871 "1870"
Didynamipus Andersson, 1903
Duttaphrynus **new genus**
Epidalea Cope, 1865
Frostius Cannatella, 1986
Ingerophrynus **new genus**
Laurentophryne Tihen, 1960
Leptophryne Fitzinger, 1843
Melanophryniscus Gallardo, 1961
Mertensophryne Tihen, 1960 (including *Stephopaedes* Channing, 1979 "1978")
Metaphryniscus Señaris, Ayarzagüena, and Gorzula, 1994
Nannophryne Günther, 1870
Nectophryne Buchholz and Peters, 1875
"*Nectophrynoides*" Noble, 1926
Nimbaphrynoides Dubois, 1987 "1986"
Oreophrynella Boulenger, 1895
Osornophryne Ruiz-Carranza and Hernández-Camacho, 1976
Parapelophryne Fei, Ye, and Jiang, 2003
Pedostibes Günther, 1876 "1875"
Pelophryne Barbour, 1938
Peltophryne Fitzinger, 1843
Phrynoidis Fitzinger, 1843
Poyntonophrynus **new genus**
Pseudobufo Tschudi, 1838
Pseudepidalea **new genus**
Rhaebo Cope, 1862
Rhamphophryne Trueb, 1971
Rhinella Fitzinger, 1826
Schismaderma Smith, 1849
Truebella Graybeal and Cannatella, 1995
Vandijkophrynus **new genus**
Werneria Poche, 1903
"*Wolterstorffina*" Mertens, 1939

Fig. 67. Continued.

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Ranoides **new taxon**
- Allodapanura **new taxon**
  - Microhylidae Günther, 1858 (1843)
    - *Adelastes* Zweifel, 1986
    - *Altigius* Wild, 1995
    - *Arcovomer* Carvalho, 1954
    - *Chiasmocleis* Méhely, 1904
    - *Gastrophrynoides* Noble, 1926
    - *Glyphoglossus* Günther, 1869 "1868"
    - *Hyophryne* Carvalho, 1954
    - *Hypopachus* Keferstein, 1867
    - *Kalophrynus* Tschudi, 1838
    - *Metaphrynella* Parker, 1934
    - *Micryletta* Dubois, 1987
    - *Myersiella* Carvalho, 1954
    - *Otophryne* Boulenger, 1900
    - *Paradoxophyla* Blommers-Schlösser and Blanc, 1991
    - *Phrynella* Boulenger, 1887
    - *Phrynomantis* Peters, 1867
    - *Ramanella* Rao and Ramanna, 1925
    - *Relictivomer* Carvalho, 1954
    - *Stereocyclops* Cope, 1870 "1869"
    - *Syncope* Walker, 1973
    - *Synapturanus* Carvalho, 1954
    - *Uperodon* Duméril and Bibron, 1841
    - Asterophryinae Günther, 1858
      - *Albericus* Burton and Zweifel, 1995
      - *Aphantophryne* Fry, 1917 "1916"
      - *Asterophrys* Tschudi, 1838
      - *Austrochaperina* Fry, 1912
      - *Barygenys* Parker, 1936
      - *Callulops* Boulenger, 1888
      - *Choerophryne* Kampen, 1914
      - *Cophixalus* Boettger, 1892
      - *Copiula* Méhely, 1901
      - *Genyophryne* Boulenger, 1890
      - "*Hylophorbus*" Macleay, 1878
      - *Liophryne* Boulenger, 1897
      - "*Mantophryne*" Boulenger, 1897
      - *Oreophryne* Boettger, 1895
      - *Oxydactyla* Kampen, 1913
      - *Pherohapsis* Zweifel, 1972
      - *Sphenophryne* Peters and Doria, 1878
      - *Xenorhina* Peters, 1863 (including *Xenobatrachus* Peters and Doria, 1878)

Fig. 67. Continued.

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Cophylinae Cope, 1889
Anodonthyla Müller, 1892
Cophyla Boettger, 1880
Madecassophryne Guibé, 1974
Platypelis Boulenger, 1882
Plethodontohyla Boulenger, 1882
Rhombophryne Boettger, 1880
Stumpffia Boettger, 1881
Dyscophinae Boulenger, 1882
Dyscophus Grandidier, 1872
Gastrophryninae Fitzinger, 1843
Ctenophryne Mocquard, 1904
Dasypops Miranda-Ribeiro, 1924
Dermatonotus Méhely, 1904
Elachistocleis Parker, 1927
Gastrophryne Fitzinger, 1843
Hamptophryne Carvalho, 1954
Nelsonophryne Frost, 1987
Melanobatrachinae Noble, 1931
Hoplophryne Barbour and Loveridge, 1928
Melanobatrachus Beddome, 1878
Parhoplophryne Barbour and Loveridge, 1928
Microhylinae Günther, 1858 (1843)
Calluella Stoliczka, 1872
Chaperina Mocquard, 1892
Kaloula Gray, 1831
Microhyla Tschudi, 1838
Scaphiophryninae Laurent, 1946
Scaphiophryne Boulenger, 1882
Afrobatrachia **new taxon**
Xenosyneunitanura **new taxon**
Brevicipitidae Bonaparte, 1850
Balebreviceps Largen and Drewes, 1989
Breviceps Merrem, 1820
Callulina Nieden, 1911 "1910"
Probreviceps Parker, 1931
Spelaeophryne Ahl, 1924
Hemisotidae Cope, 1867
Hemisus Günther, 1859 "1858"
Laurentobatrachia **new taxon**
Arthroleptidae Mivart, 1869
Arthroleptinae Mivart, 1869
Arthroleptis Smith, 1849 (including *Schoutedenella* De Witte, 1921)
Astylosternus Werner, 1898
Cardioglossa Boulenger, 1900
Leptodactylodon Andersson, 1903
Nyctibates Boulenger, 1904
Scotobleps Boulenger, 1900
Trichobatrachus Boulenger, 1900
Leptopelinae Laurent, 1972
Leptopelis Günther, 1859

Fig. 67. Continued.

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Hyperoliidae Laurent, 1943
Acanthixalus Laurent, 1944
Afrixalus Laurent, 1944
Alexteroon Perret, 1988
Arlequinus Perret, 1988
Callixalus Laurent, 1950
Chlorolius Perret, 1988
Chrysobatrachus Laurent, 1951
Cryptothylax Laurent and Combaz, 1950
Heterixalus Laurent, 1944
Hyperolius Rapp, 1842 (including *Nesionixalus* Perret, 1976)
Kassina Girard, 1853
Kassinula Laurent, 1940
Opisthothylax Perret, 1966
Paracassina Peracca, 1907
Phlyctimantis Laurent and Combaz, 1950
Semnodactylus Hoffman, 1939
Tachycnemis Fitzinger, 1843
Natatanura **new taxon**
Ptychadenidae Dubois, 1987 "1986"
Hildebrandtia Nieden, 1907
Lanzarana Clarke, 1982
Ptychadena Boulenger, 1917
Victoranura **new taxon**
Ceratobatrachidae Boulenger, 1884
Batrachylodes Boulenger, 1887
Ceratobatrachus Boulenger, 1884
Discodeles Boulenger, 1918
Ingerana Dubois, 1987 "1986"
Palmatorappia Ahl, 1927 "1926"
Platymantis Günther, 1858
Telmatobatrachia **new taxon**
Micrixalidae Dubois, Ohler, and Biju, 2001
Micrixalus Boulenger, 1888
Ametrobatrachia **new taxon**
Africanura **new taxon**
Phrynobatrachidae Laurent, 1941 "1940"
Ericabatrachus Largen, 1991
Phrynobatrachus Günther, 1862 (including *Dimorphognathus* Boulenger, 1906; and *Phrynodon* Parker, 1935)
Pyxicephaloidea Bonaparte, 1850
Petropedetidae Noble, 1931
Arthroleptides Nieden, 1911 "1910"
Conraua Nieden, 1908
Indirana Laurent, 1986
Petropedetes Reichenow, 1874

Fig. 67. Continued.

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Pyxicephalidae Bonaparte, 1850
- Pyxicephalinae Bonaparte, 1850
  - *Aubria* Boulenger, 1917
  - *Pyxicephalus* Tschudi, 1838
- Cacosterninae Noble, 1931
  - *Amietia* Dubois, 1987 "1986" (including *Afrana* Dubois, 1992)
  - *Anhydrophryne* Hewitt, 1919
  - *Arthroleptella* Hewitt, 1926
  - *Cacosternum* Boulenger, 1887
  - *Microbatrachella* Hewitt, 1926
  - *Natalobatrachus* Hewitt and Methuen, 1912
  - *Nothophryne* Poynton, 1963
  - *Poyntonia* Channing and Boycott, 1989
  - *Strongylopus* Tschudi, 1838
  - *Tomopterna* Duméril and Bibron, 1841

Saukrobatrachia **new taxon**
- Dicroglossidae Anderson, 1871
  - Dicroglossinae Anderson, 1871
    - *Annandia* Dubois, 1992
    - *Euphlyctis* Fitzinger, 1843
    - "*Fejervarya*" Bolkay, 1915
    - *Hoplobatrachus* Peters, 1863
    - *Limnonectes* Fitzinger, 1843 (including *Taylorana* Dubois, 1987 "1986")
    - *Minervarya* Dubois, Ohler, and Biju, 2001
    - *Nannophrys* Günther, 1869 "1868"
    - *Nanorana* Günther, 1896 (including *Chaparana* Bourret, 1939; and *Paa* Dubois, 1975)
    - *Ombrana* Dubois, 1992
    - *Quasipaa* Dubois, 1992
    - *Sphaerotheca* Günther, 1859 "1858"
  - Occidozyginae Fei, Ye, and Huang, 1991 "1990"
    - *Occidozyga* Kuhl and Van Hasselt, 1822 (including *Phrynoglossus* Peters, 1867)
- Aglaioanura **new taxon**
  - Rhacophoroidea Hoffman, 1932 (1858)
    - Mantellidae Laurent, 1946
      - Boophinae Vences and Glaw, 2001
        - *Boophis* Tschudi, 1838
      - Mantellinae Laurent, 1946
        - *Aglyptodactylus* Boulenger, 1919 "1918"
        - *Laliostoma* Glaw, Vences, and Böhme, 1998
        - *Mantella* Boulenger, 1882
        - "*Mantidactylus*" Boulenger, 1895

Fig. 67. Continued.

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Rhacophoridae Hoffman, 1932 (1858)
Buergeriinae Channing, 1989
Buergeria Tschudi, 1838
Rhacophorinae Hoffman, 1932 (1858)
Aquixalus Delorme, Dubois, Grosjean, and Ohler, 2005
Chiromantis Peters, 1854 (including *Chirixalus* Boulenger, 1893)
Feihyla **new genus**
Kurixalus Ye, Fei, and Dubois, 1999
Nyctixalus Boulenger, 1882
Philautus Gistel, 1848
Polypedates Tschudi, 1838
Rhacophorus Kuhl and Hasselt, 1822
Theloderma Tschudi, 1838
Ranoidea Rafinesque, 1814
Nyctibatrachidae Blommers-Schlösser, 1993
Nyctibatrachus Boulenger, 1882
Lankanectes Dubois and Ohler, 2001
Ranidae Rafinesque, 1814
Amolops Cope, 1865
Babina Thomson, 1912 (including *Nidirana* Dubois, 1992)
Clinotarsus Mivart, 1869
Glandirana Fei, Ye, and Huang, 1991 "1990" (including *Rugosa* Fei, Ye, and Huang, 1991 "1990")
Hydrophylax Fitzinger, 1843 (including *Amnirana* Dubois, 1992; and *Chalcorana* Dubois, 1992)
Hylarana Tschudi, 1838
Huia Yang, 1991 (including *Eburana* Dubois, 1992; and *Odorrana* Fei, Ye, and Huang, 1991 "1990")
Humerana Dubois, 1992
Lithobates Fitzinger, 1843 (including *Aquarana* Dubois, 1992; *Pantherana* Dubois, 1992; *Sierrana* Dubois, 1992; *Trypheropsis* Cope, 1868; and *Zweifelia* Dubois, 1992)
Meristogenys Yang, 1991
Nasirana Dubois, 1992
Pelophylax Fitzinger, 1843
Pterorana Kiyasetuo and Khare, 1986
Pulchrana Dubois, 1992
Rana Linnaeus, 1758 (including *Amerana* Dubois, 1992; *Aurorana* Dubois, 1992; *Pseudoamolops* Jiang, Fei, Ye, Zeng, Zhen, Xie, and Chen, 1997; and *Pseudorana* Dubois, 1992)
Sanguirana Dubois, 1992
Staurois Cope, 1865
Sylvirana Dubois, 1992 (including *Papurana* Dubois, 1992; and *Tylerana* Dubois, 1992)

Fig. 67. Continued.

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and diagnosis, which is merely a general summary of the salient features of the animals that are included in the taxon under discussion, and characters (either synapomorphic or not) that differentiate this taxon from others. Where a character is thought to be a synapomorphy, this is stated. If the explicit statement is not made, then the character should be assumed to be of unknown polarity. Because we included Haas' (2003) characters in the analysis, for each group we list all unambiguously optimized synapmorphies for that data set, reported using Haas' original numbering scheme (e.g., Haas 34.1). Otherwise, we have not attempted to be exhaustive nor to make these differentia explicitly comparable for the simple reason that the challenge of sorting out the published record regarding the morphological characteristics of amphibians will be enormous and, clearly, is outside of the scope of this work[27]. Regardless, that next step is an important one in elucidating the morphological evolution of amphibians. The characterization and diagnosis is followed by (9) various systematic comments and discussion. Considerable taxonomic ''sausage making'' is evident in these sections, particularly with respect to the larger and more chaotic genera, which we have not been shy about partitioning because considerable redistribution of taxonomic names needs to happen if we are going to progress towards a taxonomy that reflects evolutionary history. In some places our changes have not been successful in producing a taxonomy that is entirely monophyletic. Our rationale for failing to propose a more precise taxonomy was given earlier, and we are confident that future work will correct this shortcoming in our proposal. To that end, we emphasize and discuss the specific problems and inadequacies for each of these cases. Some workers will not appreciate the loose-ends that remain untied and will prefer the old approach of concealing these questions. Our position, however, is that unless these problems are advertised, the sociological response of the scientific community will be to let sleeping dogs lie.

In a few places in the taxonomy, we do not render taxonomic changes suggested by our tree. In the cases of ''*Eleutherodactylus*'' and ''*Centrolene*'', our sampling density is so low compared to the species diversity that our results could not be practically translated into an informative taxonomy. In two other cases, the reason is that we do not consider our results to constitute a sufficient test of a published cladogram, based on a data set that includes as a subset the data over which we generalized. The first of these is in Hylinae, where our data represent a subset of the data (and concomitant results) of Faivovich et al. (2005), meaning that our analysis does not constitute an adequate test of their results. The second is plethodontid salamanders, where the placement of certain taxa (i.e., *Hemidactylium* and *Batrachoseps*) in our tree is based on a subset of data in a published tree (Macey, 2005), which came to different conclusions regarding those critical taxa, based, at least with respect to those taxa, on a more inclusive data set (although the assumptions of analysis were subtly different). In these two cases we do not reject the conclusions of these authors, pending even more inclusive analyses.

[6] AMPHIBIA GRAY, 1825

Amphibia Gray, 1825: 213. (See appendix 6 for further nomenclatural discussion.)

RANGE: Worldwide on all continents except Antarctica and most oceanic islands, in cold-temperate to tropical habitats.

CONCEPT AND CONTENT: Amphibia is a monophyletic taxon composed of [7] Gymnophiona J. Müller, 1832, and [23] Batrachia Latreille, 1800, constituting the crown group (i.e., living) amphibians (sensu Amphibia Gray, 1825; *not* Amphibia of Linnaeus, 1758; cf. de Queiroz and Gauthier, 1992).

CHARACTERIZATION AND DIAGNOSIS: Beyond our molecular data, Amphibia is diagnosed by many morphological characters. Amphibians, like mammals, retain plesiomorphically the glandular skin of ancestral tetrapods. They do not have the apomorphy of epidermal scales found in sauropsids (turtles and diapsids).

[27] For some clades, diagnosis by nongenetic characters is not currently possible. To make molecular diagnosis more tangible and descriptively simple, we also report salient charateristics, such as length variation in 28S sequences (appendix 3), as well as unambiguous molecular transformations (appendix 5), where needed.

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Trueb and Cloutier (1991) and Ruta et al. (2003) provide extensive discussions of the synapomorphies of Amphibia (as Lissamphibia) in the context of fossil groups. Synapomorphies of Amphibia include (Trueb and Cloutier, 1991): (1) loss of the postparietal bones; (2) loss of the supratemporal bone; (3) loss of the tabular bone; (4) loss of the postorbital bones; (5) loss of the jugal bone; (6) loss of the interclavicle; (7) loss of the cleithrum; (8) papilla amphibiorum present in ear; (9) opercular element associated with the columella; (10) fat bodies present that originate from the germinal ridge associated with the gonads; and (11) pedicellate and bicuspid teeth that are replaced mediolaterally (reversed in some taxa).

SYSTEMATIC COMMENTS: Amphibia is highly corroborated as a taxon, but this only implies that all living amphibians are more closely related to each other than to any other living species and does not address the placement of amphibian groups within the larger structure of relevant fossil tetrapods. All work so far on the overall placement of amphibians (lissamphibians) among fossil groups has depended on inadequate sampling of living taxa and, with the exception of Gao and Shubin (2001), has ignored available molecular data. We hope that additional work on fossil groups, combined with the data presented here, and a better account of living diversity, will further elucidate those relationships.

[7] GYMNOPHIONA J. MÜLLER, 1832

Gymnophiona J. Müller, 1832: 198. (See appendix 6 for nomenclatural discussion.)

IMMEDIATELY MORE INCLUSIVE TAXON: [6] Amphibia Gray, 1825.

SISTER TAXON: [23] Batrachia Latreille, 1800.

RANGE: Pantropical, except for Madagascar and southeast of Wallace's Line; not yet reported from central equatorial Africa.

CONCEPT AND CONTENT: Gymnophiona is a monophyletic taxon containing the living caecilians (cf. J. Müller, 1832; Cannatella and Hillis, 1993): [8] Rhinatrematidae Nussbaum, 1977, and [9] Stegokrotaphia Cannatella and Hillis, 1993.

CHARACTERIZATION AND DIAGNOSIS: Caecilians are a bizarre group of legless amphibians, primitively oviparous with aquatic larvae (Rhinatrematidae, Ichthyophiidae), although some species are ovoviparous (with or without direct development) and burrowing, as reflected by considerable numbers of osteological modifications.

Beyond our molecular data, the following morphological characters have been suggested to be synapomorphies (Nussbaum and Wilkinson, 1989; Trueb and Cloutier, 1991): (1) lacking limbs and girdles (except for one antecedent fossil taxon not included in the crown group; Carroll, 2000b); (2) presence of a dual jaw-closing mechanism; (3) presence of an eversible phallodeum in males formed by a portion of the cloacal wall; (4) annuli encircling the body; (5) paired sensory tentacles on the snout.

SYSTEMATIC COMMENTS: M. Wilkinson has an extensive morphological matrix of more than 180 character transformations (see also Nussbaum and Wilkinson, 1995; M. Wilkinson and Nussbaum, 1996, 1999), which will appear elsewhere, analyzed in conjunction with this and additional evidence.

[8] FAMILY: RHINATREMATIDAE NUSSBAUM, 1977

Rhinatrematidae Nussbaum, 1977: 3. Type genus: *Rhinatrema* Duméril and Bibron, 1841.

IMMEDIATELY MORE INCLUSIVE TAXON: [7] Gymnophiona J. Müller, 1832.

SISTER TAXON: [9] Stegokrotaphia Cannatella and Hillis, 1993.

RANGE: Tropical northern South America from Amazonian Peru and Brazil, through eastern Ecuador, Colombia, Venezuela, and the Guianas.

CONTENT: ***Epicrionops*** Boulenger, 1883; ***Rhinatrema*** Duméril and Bibron, 1841.

CHARACTERIZATION AND DIAGNOSIS: Rhinatrematids are oviparous with aquatic larvae. They are strongly annulated with numerous secondary and tertiary grooves. Like ichthyophiids, rhinatrematids have a short tail and the eyes are visible, although they lie beneath the skin in bony sockets. The tentacle arises near the anterior edge of each eye, and the middle ear contains a stapes (Nussbaum, 1977).

Beyond the molecular evidence, the fol-

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lowing morphological characters have been suggested to be synapomorphies (Duellman and Trueb, 1986; M. Wilkinson and Nussbaum, 1996): (1) dorsolateral process of the os basale present; (2) loss or fusion of the prefrontal with the maxillopalatine; (3) secondary annulus/primary annulus greater than one; and (4) fourth ceratobranchial absent. In addition, the prefrontals are fused with the maxillopalatine as in caeciliids, but not in ichthyophiids and outgroups, rendering the optimization of this character arguable.

[9] STEGOKROTAPHIA CANNATELLA AND HILLIS, 1993

Stegokrotaphia Cannatella and Hillis, 1993: 2.

IMMEDIATELY MORE INCLUSIVE TAXON: [7] Gymnophiona J. Müller, 1832.

SISTER TAXON: [8] Rhinatrematidae Nussbaum 1977.

RANGE: Tropics of southern North America, South America, equatorial East and West Africa, islands in the Gulf of Guinea, Seychelles, and India; Philippines and India to southern China, Thailand, Indochina and the Malayan archipelago.

CONCEPT AND CONTENT: Stegokrotaphia is a monophyletic group containing [10] Ichthyophiidae Taylor, 1968, and [12] Caeciliidae Rafinesque, 1814 (cf. Cannatella and Hillis, 1993).

CHARACTERIZATION AND DIAGNOSIS: Stegokrotaphian caecilians show variation in reproductive mode (from aquatic larvae to ovoviviparity) and morphology, with some retaining tails (Ichthyophiidae) and others (Caeciliidae) having lost them (even though a pseudotail may be present). The eyes may be visible (e.g., *Ichthyophis*), completely hidden beneath bone (e.g., *Scolecomorphus*), or completely absent (*Boulengerula*). Unlike in rhinatrematids, the tentacle originates in front of the eye and may be nearly as far forward as the nostril. A stapes is generally present but is lost in some taxa (Nussbaum, 1977).

Beyond the molecular evidence, the following morphological characters have been suggested to be synapomorphies (Duellman and Trueb, 1986; M. Wilkinson and Nussbaum, 1996): (1) mouth subterminal or recessed rather than terminal; (2) tentacular opening anterior to the anterior edge of the eye; (3) frontal and squamosal articulate; (4) stegokrotaphic skull; (5) vomers in contact throughout their entire length; (6) sides of the parasphenoid converge anteriorly; (7) quadrate and maxillopalatine lack articulation; (8) squamosal and frontal in contact; (9) pterygoid reduced; (10) basipterygoid present; (11) retroarticular process long and usually curved dorsally; (12) third and fourth ceratobranchial fused; (13) anterior fibers of the m. interhyoideus do not insert on ceratohyal; (14) m. interhyoideus posterior in two bundles; (15) orientation of m. interhyoideus posterior is longitudinal rather than oblique; and (16) m. depressor mandibulae longitudinally oriented rather than vertically oriented.

[10] FAMILY: ICHTHYOPHIIDAE TAYLOR, 1968

Epicria Fitzinger, 1843: 34. Type genus: *Epicrium* Wagler, 1828. Suppressed for purposes of priority but not homonymy in favor of Ichthyophiidae by Opinion 1604 (Anonymous, 1990: 166).

Ichthyophiidae Taylor, 1968: 46. Type genus: *Ichthyophis* Fitzinger, 1826. Placed on Official List of Family-Group Names in Zoology by Opinion 1604 (Anonymous, 1990: 166–167).

Uraeotyphlinae Nussbaum, 1979: 14. Type genus: *Uraeotyphlus* Peters, 1880 ''1879''.

IMMEDIATELY MORE INCLUSIVE TAXON: [9] Stegokrotaphia Cannatella and Hillis, 1993.

SISTER TAXON: [12] Caeciliidae Rafinesque, 1814.

RANGE: India to southern China, Thailand, and through the Malayan archipelago to the Greater Sunda Islands and Philippines.

CONTENT: *Caudacaecilia* Taylor, 1968; ''***Ichthyophis***'' Fitzinger, 1826 (see Systematic Comments); ***Uraeotyphlus*** Peters, 1880 ''1879''.

CHARACTERIZATION AND DIAGNOSIS: Ichthyophiids are oviparous with aquatic larvae, both features being plesiomorphies. Like rhinatrematids, ichthyophiids plesiomorphically retain a true tail. Eyes are externally visible beneath the skin and are in bony sockets. The tentacle arises between the nostril and the eye, generally closer to the eye in *Ichthyophis* and *Caudacaecilia* and anterior near the nostril in *Uraeotyphlus*. A stapes is present (Nussbaum, 1977).

Beyond the molecular evidence supporting

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the monophyly of this group the following morphological characters have been suggested to be synapomorphies (M. Wilkinson and Nussbaum, 1996): (1) vomers in contact anteriorly (convergent in *Siphonops*, *Scolecomorphus*, and *Gegeneophis*); (2) atria divided externally; (3) anterior pericardial sac long and extensive; (4) posterior internal flexures in the m. rectus lateralis II; (5) tracheal lung present (also in *Typhlonectes*).

SYSTEMATIC COMMENTS: As noted in ''Results'', the preponderance of evidence suggests that ''*Ichthyophis*'' is paraphyletic with respect to *Uraeotyphlus*. Unfortunately, the number of species currently assigned to ''*Ichthyophis*'' is large and mostly unsampled, and the relationships among them (and *Caudacaecilia* [unsampled by us] and *Uraeotyphlus*) are unclear. Nussbaum and Wilkinson (1989: 31) suggested that *Caudacaecilia* and *Ichthyophis* might both be polyphyletic inasmuch as they are diagnosed solely on single characters of known variability. We do not place *Caudacaecilia* and *Uraeotyphlus* into the synonymy of *Ichthyophis*, although to do so would certainly render a monophyletic taxonomy. Ongoing work by M. Wilkinson, Nussbaum, and collaborators should provide a monophyletic taxonomy without resorting to that minimally informative one. In the interim we place quotation marks around ''*Ichthyophis*'' (the only ichthyophiid genus for which we have evidence of paraphyly). In the face of strong evidence of paraphyly of ''*Ichthyophis*'', maintaining a family-group name for *Uraeotyphlus* is unnecessary, and we therefore place Uraeotyphlinae in the synonymy of Ichthyophiidae. Other than assuming that the morphological synapomorphies are sufficient, stronger evidence of monophyly of Ichthyophiidae will require sampling of *Caudacaecilia* and more ''*Ichthyophis*''. Nevertheless, we make the hypothesis that Ichthyophiidae is a monophyletic taxon and trust that others will elucidate this further.

[12] FAMILY: CAECILIIDAE RAFINESQUE, 1814

Cecilinia Rafinesque, 1814: 104. Type genus: *Caecilia* Linnaeus, 1758. See Dubois (1985: 70). Authorship but not spelling to be conserved following Opinion 1830 (Anonymous, 1996: 68–69).

Caeciliadae Gray, 1825: 217. Type genus: *Caecilia* Linnaeus, 1758.

Siphonopina Bonaparte, 1850: 1 p. Type genus: *Siphonops* Wagler, 1828.

Typhlonectidae Taylor, 1968: xi, 231. Type genus: *Typhlonectes* Peters, 1880 ''1879''.

Scolecomorphidae Taylor, 1969a: 297. Type genus: *Scolecomorphus* Boulenger, 1883.

Dermophiinae Taylor, 1969b: 610. Type genus: *Dermophis* Peters, 1880 ''1879''.

Herpelinae Laurent, 1984a: 199–200. Type genus: *Herpele* Peters, 1875.

Geotrypetoidae Lescure et al., 1986: 162. Type genus: *Geotrypetes* Peters, 1880.

Grandisoniilae Lescure et al., 1986: 164. Type genus: *Grandisonia* Taylor, 1968.

Indotyphlini Lescure et al., 1986: 164. Type genus: *Indotyphlus* Taylor, 1960.

Afrocaeciliiti Lescure et al., 1986: 164. Type genus: *Afrocaecilia* Taylor, 1968.

Brasilotyphlili Lescure et al., 1986: 166. Type genus: *Brasilotyphlus* Taylor, 1968.

Pseudosiphonopiti Lescure et al., 1986: 166. Type genus: *Pseudosiphonops* Taylor, 1968.

Oscaecilioidae Lescure et al., 1986: 167. Type genus: *Oscaecilia* Taylor, 1968.

Gymnopiilae Lescure et al., 1986: 168. Type genus: *Gymnopis* Peters, 1874.

Potamotyphloidea Lescure et al., 1986: 169. Type genus: *Potamotyphlus* Taylor, 1968.

Pseudotyphlonectini Lescure et al., 1986: 170. Type genus: *Pseudotyphlonectes* Lescure, Renous, and Gasc, 1986.

IMMEDIATELY MORE INCLUSIVE TAXON: [9] Stegokrotaphia Cannatella and Hillis, 1993.

SISTER TAXON: [10] Ichthyophiidae Taylor, 1968.

RANGE: Tropics of Mexico, Central America, and South America; equatorial East and West Africa and islands in the Gulf of Guinea, Seychelles, and India.

CONTENT: *Atretochoana* Nussbaum and Wilkinson, 1995; ***Boulengerula*** Tornier, 1896; *Brasilotyphlus* Taylor, 1968; ***Caecilia*** Linnaeus, 1758; *Chthonerpeton* Peters, 1880; ***Crotaphatrema*** Nussbaum, 1985; ***Dermophis*** Peters, 1880; ***Gegeneophis*** Peters, 1880; ***Geotrypetes*** Peters, 1880; *Grandisonia* Taylor, 1968; *Gymnopis* Peters, 1874; ***Herpele*** Peters, 1880; ***Hypogeophis*** Peters, 1880; *Idiocranium* Parker, 1936; *Indotyphlus* Taylor, 1960; *Luetkenotyphlus* Taylor, 1968; *Microcaecilia* Taylor, 1968; *Mimosiphonops* Taylor, 1968; *Nectocaecilia* Taylor, 1968; *Oscaecilia* Taylor, 1968; *Parvicaecilia* Taylor,

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1968; *Potomotyphlus* Taylor, 1968; *Praslinia* Boulenger, 1909; ***Schistometopum*** Parker, 1941; ***Scolecomorphus*** Boulenger, 1883; ***Siphonops*** Wagler, 1828; *Sylvacaecilia* Wake, 1987; ***Typhlonectes*** Peters, 1880.

CHARACTERIZATION AND DIAGNOSIS: Caeciliids represent the bulk of caecilian diversity and, not surprisingly, show considerable morphological and reproductive variation. Some taxa are oviparous with aquatic larvae (e.g., *Praslinia*), whereas others are oviparous with direct development in the egg (e.g., *Hypogeophis*, *Idiocranium*, and *Boulengerula*), and others are viviparous (e.g., *Schistometopum*, *Dermophis*, and typhlonectines). Unlike Ichthyophiidae and Rhinatrematidae, no caeciliid possesses a true tail, although some (e.g., typhlonectines) have a pseudotail. Most species are terrestrial and burrowing, although some (e.g., typhlonectines) are secondarily aquatic. At least one species (*Atretochoana eiselti*: Typhlonectinae) is totally lungless (Nussbaum and Wilkinson, 1995). Most taxa have stapes, but all scolecomorphines lack them (Nussbaum, 1977).

Beyond the molecular evidence, the following morphological characters have been suggested to be synapomorphies of this group (M. Wilkinson and Nussbaum, 1996): (1) tail absent; (2) premaxillae and nasal bones fused; (3) septomaxillae reduced or absent (reversed in *Scolecomorphus*); (4) pterygoid absent; (5) basiptergygoid process large (small in *Scolecomorphus*); (6) fused third and fourth ceratobranchials greatly expanded; and (7) vent circular or transverse, not longitudinally oriented (reversed in *Scolecomorphus*).

SYSTEMATIC COMMENTS: Recognition of the nominal families Typhlonectidae (*Atretochoana*, *Chthonerpeton*, *Nectocaecilia*, *Potomotyphlus*, *Typhlonectes*) and Scolecomorphidae (*Crotaphatrema* and *Scolecomorphus*) renders Caeciliidae paraphyletic. Although we expect that ongoing work by M. Wilkinson, Nussbaum, and collaborators will provide a more refined taxonomy, these currently recognized taxa can be retained as subfamilies (Scolecomorphinae Taylor, 1969, and Typhlonectinae Taylor, 1968) with no paraphyly implied *as long as* the remaining caeciliids are not placed within a subfamily. (A Caeciliinae recognized as nomenclaturally coordinate with Scolecomorphinae and Typhlonectinae would merely push the paraphyly to the subfamily level, as was done by Hedges et al., 1993.) Although molecular evidence corroborates the monophyly of Scolecomorphinae, the following morphological characters also diagnose that taxon (Nussbaum and Wilkinson, 1989; M. Wilkinson and Nussbaum, 1996): (1) temporal fossa secondarily large (also in Typhlonectinae, though not homologously); (2) premaxillae separate; (3) septomaxilla present; (4) prefrontals present; (5) basipterygoid process small; and (6) no stapes. Similarly, for Typhlonectinae, the following apomorphic characters diagnose that taxon (Nussbaum and Wilkinson, 1989; M. Wilkinson and Nussbaum, 1996): (1) temporal fossa secondarily large (also in Scolecomorphinae, though not homologously); and (2) choanae large, with well-developed valves.

[23] BATRACHIA LATREILLE, 1800

Batrachii Latreille, 1800: xxxvii. A Latinization of Batraciens Brongniart, 1800b, emended to Batrachia by Rafinesque, 1814: 103. (See appendix 6 for nomenclatural discussion.)

IMMEDIATELY MORE INCLUSIVE TAXON: [6] Amphibia Gray, 1825.

SISTER TAXON: [7] Gymnophiona J. Müller, 1832.

RANGE: Cosmopolitan in cold-temperate to tropical habitats, except for extreme northern latitudes, Antarctica, and most oceanic islands.

CONCEPT AND CONTENT: Batrachia is a monophyletic taxon containing [24] Caudata Fischer von Waldheim, 1813, and [74] Anura Fischer von Waldheim, 1831 (cf. Cannatella and Hillis, 1993; cf. Latreille, 1800).

CHARACTERIZATION AND DIAGNOSIS: Batrachia is a taxon whose living members of the two component groups (salamanders and frogs) are so different (and mutually apomorphic) that their synapomorphies are not obviously reflected in external appearance. The annectant members of the taxon are all fossil and not well known. For practical purposes, Batrachia is composed of living amphibians that are not members of Gymnophiona.

Beyond our molecular evidence, the fol-

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lowing morphological characters have been suggested to be synapomorphies of this group (Trueb and Cloutier, 1991): (1) loss of a postfrontal bone; (2) loss of the surangular bone; (3) loss of splenial bone; (4) loss of dermal scales; (5) absence of an articulation of the anterior ptergygoid ramus with the palatine; (6) absence of an ectopterygoid; (7) absence of a stapedial foramen; (8) presence of a papilla neglecta; (9) presence of a carotid labyrinth; (10) choanal tube opens into the archenteron during development; and (11) pronephros modified for sperm transport.

SYSTEMATIC COMMENTS: Feller and Hedges (1998) coined the name Procera (for which Homomorpha Fitzinger [1835] is an available older name) for a clade composed of salamanders and caecilians that they believed to be monophyletic. Procera was supported by analysis of 2.7 kb of sequence from four mtDNA genes. We have not attempted to reanalyze the data of Feller and Hedges (1998), but we note that we also used 12S and 16S fragments of the mt rRNA genes and t-RNA^{Valine}. They also used sequences from a portion of the tRNA^{Leucine} gene, which we did not. Unlike Feller and Hedges (1998), we included substantial evidence from nuDNA sequences (see ''Materials''), with the result that we have employed almost half again as much sequence as they did and more than 43 times as many terminals. Our results strongly support the relationship corroborated by morphological evidence (Trueb and Cloutier, 1991), which is caecilians + (frogs + salamanders). This arrangement, in turn, is consistent with the recognition of Batrachia Latreille (1800) and as intended by Trueb and Cloutier (1991). Furthermore, for our data alternative topologies required considerably more steps: (1) frogs + (caecilians + salamanders) required 84 additional steps; and (2) salamanders + (caecilians + frogs) solution required an additional 85 steps.

[24] CAUDATA FISCHER VON WALDHEIM, 1813

Caudati Fischer von Waldheim, 1813: 58, an apparent latinization and reranking of Caudati A.M.C. Duméril, 1806: 95 (which was coined as a family-group taxon and is therefore unavailable for above-family-group taxonomy). Emended here to conform to the traditional spelling, Caudata (see Stejneger, 1907). *Not* Caudata Scopoli (1777), as attributed incorrectly by Stejneger, 1907: 215. (See appendix 6 for nomenclatural discussion.)

IMMEDIATELY MORE INCLUSIVE TAXON: [23] Batrachia Latreille, 1800.

SISTER TAXON: [74] Anura Fischer von Waldheim, 1831.

RANGE: Temperate Eurasia, northwestern Africa, and North America, and in disjunct populations throughout tropical America.

CONCEPT AND CONTENT: Caudata is a monophyletic group composed of all living salamanders (cf. Cannatella and Hillis, 1993), the subsidiary taxa being [25] Cryptobranchoidei Noble, 1931, and [29] Diadectosalamandroidei **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Salamanders are immediately recognizable because they are the only living amphibians to have both forelimbs and tails. Their primitive aspect is restricted only to general body plan. Salamanders show many osteological losses and morphological simplifications from their non-caudatan ancestors. Unlike the other two major clades of living amphibians, whole groups of salamanders are known for paedomorphic lineages with varying degrees of retention of larval characteristics in the aquatic adults (e.g., Cryptobranchidae, Sirenidae, Proteidae, and various members of the Ambystomatidae [e.g., *Amybystoma dumerilii*] and Plethodontidae [e.g., *Eurycea tridentifera*]). Most salamanders transfer sperm via the production of spermatophores, but like frogs and caecilians, salamanders primitively have external fertilization with free-living aquatic larvae.

Beyond our molecular evidence, Caudata is diagnosed by the following morphological characters, judged to be synapomorphies (modified from Trueb and Cloutier, 1991; Larson and Dimmick, 1993; Larson et al., 2003): (1) incomplete maxillary arcade; (2) presence of a tuberculum interglenoideum; (3) scapulocoracoid and scapula fused (reversed in sirenids); (4) no operculum and columella detached (modified in some hynobiids, plethodontids, salamandrids, and ambystomatids); and (5) male anterior ventral glands present (reversed in sirenids). In addition, Trueb and Cloutier (1991) dis-

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cussed a number of other features that may be synapomorphic but are highly contingent on cladogram topology.

[25] CRYPTOBRANCHOIDEI NOBLE, 1931

Cryptobranchoidea Noble, 1931: 473. Explicit order emended to Cryptobranchoidei by Tamarunov, 1964b: 159. (See appendix 6 for nomenclatural note.)

IMMEDIATELY MORE INCLUSIVE TAXON: [24] Caudata Fischer von Waldheim, 1813.

SISTER TAXON: [29] Diadectosalamandroidei **new taxon.**

RANGE: Eastern United States and southeastern Canada in North America; in Eurasia from Kamchatka west through Siberia to eastern European Russia to Turkmenistan, Afghanistan, and Iran and eastward through central China to Korea and Japan.

CONCEPT AND CONTENT: Cryptobranchoidei is a monophyletic taxon composed of [27] Cryptobranchidae Fitzinger, 1826, and [26] Hynobiidae Cope, 1859.

CHARACTERIZATION AND DIAGNOSIS: Cryptobranchoidei exhibits external fertilization (one genus showing a unique kind of spermatophore formation) and other features primitive for Caudata. Although one group (Cryptobranchidae) consists of paedomorphic giants with distinctive apomorphies such as lateral folds of skin, the bulk of species (Hynobiidae) are generalized forms that are similar in many ways to the ancestral salamander.

Beyond the molecular evidence, the following morphological characters are likely synapomorphies (Noble, 1931; Larson and Dimmick, 1993; Larson et al., 2003): (1) fusion of the m. pubotibialis and m. puboischiotibialis; and (2) ribs unicapitate (also in Anura).

[27] FAMILY: CRYPTOBRANCHIDAE FITZINGER, 1826

Cryptobranchoidea Fitzinger, 1826: 42. Type genus: *Cryptobranchus* Leuckart, 1821.

Menopomatidae Hogg, 1838: 152. Type genus: *Menopoma* Harlan, 1825.

Andriadini Bonaparte, 1839: 131. Type genus: *Andrias* Tschudi, 1837.

Protonopsina Bonaparte, 1840: 101 (p. 11 of offprint). Type genus: *Protonopsis* LeConte, 1824.

Salamandropes Fitzinger, 1843: 34. Type genus: *Salamandrops* Wagler, 1830.

Megalobatrachi Fitzinger, 1843: 34. Type genus: *Megalobatrachus* Tschudi, 1837.

Sieboldiidae Bonaparte, 1850: 1 p. Type genus: *Sieboldia* Gray, 1838.

Protonopsidae Gray, 1850a: 52. Type genus: "*Protonopsis* Barton, 1824" (= *Protonopsis* LeConte, 1824).

IMMEDIATELY MORE INCLUSIVE TAXON: [25] Cryptobranchoidei Noble, 1931.

SISTER TAXON: [26] Hynobiidae Cope, 1859.

RANGE: Central China; Japan; eastern temperate North America.

CONTENT: ***Andrias*** Tschudi, 1837; ***Cryptobranchus*** Leuckart, 1821.

CHARACTERIZATION AND DIAGNOSIS: Cryptobranchidae is a taxon composed of three species of giant, obligately aquatic paedomorphs. Like other cryptobranchoids, they lack internal fertilization and share a suite of internal characters primitive for Caudata. Adults lack gills and the lungs are nonfunctional, so nearly all respiration is across the extensively folded and wrinkled skin (Noble, 1931; Bishop, 1943).

Beyond the molecular evidence, the following morphological characters have been suggested to be synapomorphies (Larson and Dimmick, 1993; Larson et al., 2003): (1) dorsoventrally flattened bodies; (2) presence of folds of skin forming flaps along the lateral margins of the body; and (3) septomaxilla absent (also in some salamandrids, Amphiumidae, and Perennibranchia).

SYSTEMATIC COMMENT: The monophyly of Cryptobranchidae was never seriously in doubt, but our results (appendix 5) and those of Larson et al. (2003) demonstrate that *Cryptobranchus* is the sister taxon of *Andrias*, an arrangement suggested, but not substantiated, by Estes (1981).

[26] FAMILY: HYNOBIIDAE COPE, 1859 (1856)

Ellipsoglossidae Hallowell, 1856: 11. Type genus: *Ellipsoglossa* Duméril, Bibron, and Duméril, 1854.

Hynobiidae Cope, 1859: 125. Type genus: *Hynobius* Tschudi, 1838.

Protohynobiinae Fei and Ye, 2000: 64. Type genus: *Protohynobius* Fei and Ye, 2000.

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IMMEDIATELY MORE INCLUSIVE TAXON: [25] Cryptobranchoidei Noble, 1931.

SISTER TAXON: [27] Cryptobranchidae Fitzinger, 1826.

RANGE: Japan, Korea, and Kamchatka west through Siberia and China to eastern European Russia to Turkmenistan, Afghanistan, and Iran.

CONTENT: ***Batrachuperus*** Boulenger, 1878; *Hynobius* Tschudi, 1838; *Onychodactylus* Tschudi, 1838; *Pachyhynobius* Fei, Qu, and Wu, 1983; *Protohynobius* Fei and Ye, 2000; ***Ranodon*** Kessler, 1866; *Salamandrella* Dybowski, 1870.

CHARACTERIZATION AND DIAGNOSIS: Hynobiids are unremarkable salamanders, predominantly exhibiting a biphasic life history with external fertilization and females lacking spermathecae. Lungs are usually developed, except in *Onychodactylus*.

Beyond the molecular evidence (which is of limited value in testing the monophyly of this group; see ''Review of Current Taxonomy'' and ''Results''), the following morphological characters are likely synapomorphies (Larson and Dimmick, 1993; Larson et al., 2003): (1) first hypobranchial and first ceratobranchial fused (also in amphiumids); and (2) vomerine dentition replacement from posterior (also in *Rhyacotriton* and Ambystomatidae).

SYSTEMATIC COMMENTS: Monophyly of Hynobiidae requires additional testing, especially with respect to Cryptobranchidae. Larson et al. (2003) suggested that *Batrachuperus* is polyphyletic. Unfortunately, although the resultant tree was published, the underlying data were not, leaving the problem unaddressable at this time. The status of Protohynobiinae also requires phylogenetic corroboration to determine the placement of *Protohynobius* within the remaining hynobiids.

[29] DIADECTOSALAMANDROIDEI **NEW TAXON**

ETYMOLOGY: Diadectos (Greek: transmitter) + salamandroidei- (Greek: of the form of a salamander). (See appendix 6 for nomenclatural note.)

IMMEDIATELY MORE INCLUSIVE TAXON: [24] Caudata.

SISTER TAXON: [25] Cryptobranchoidei.

RANGE: Temperate and tropical regions of North America, tropical South America, and Palearctic Eurasia and North Africa.

CONCEPT AND CONTENT: Diadectosalamandroidei is a monophyletic group of salamanders containing [30] Hydatinosalamandroidei **new taxon** and [49] Plethosalamandroidei **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Diadectosalamandroids represent the bulk of living salamander diversity. All are characterized by internal fertilization through the use of a spermatophore. The exception is Sirenidae, which in our analysis appears to have lost this complex reproductive feature (inasmuch as the secretory structures are absent), although this is optimization-dependent, the alternative being that Proteidae gained the characteristic independently of other salamander families that have spermatophore production. Morphological diversity is enormous, from the large and obligately aquatic amphiumas to arboreal web-footed tropical bolitoglossine plethodontids to various paedomorphic perennibranch lineages such as in *Ambystoma*. All families within Diadectosalamandroidei primitively show a biphasic life history. However, because of the enormous species diversity of direct-developing plethodontids, most species within this taxon lack a free-living larval stage.

Beyond the molecular evidence (appendix 5), the following are likely synapomorphies (modified from Larson and Dimmick, 1993; Larson et al., 2003): (1) maxilla with a single center of ossification (maxilla lost in *Necturus*); (2) angular bone absent; (3) spinal nerve foramina present in at least some vertebrae; (4) spermathecae present (lost in Sirenidae); (5) posterior ventral glands present (lost in amphiumids and sirenids); (6) Kingsbury's glands present (lost in sirenids); and (7) dorsal pelvic glands present in females (lost in sirenids).

[30] HYDATINOSALAMANDROIDEI **NEW TAXON**

ETYMOLOGY: Hydatino- (Greek: of the water) + salamandroidei (Greek: of salamander form), denoting that these salamanders generally spend at least part of their lives in water.

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IMMEDIATELY MORE INCLUSIVE TAXON: [29] Diadectosalamandroidei **new taxon.**

SISTER TAXON: [49] Plethosalamandroidei **new taxon.**

RANGE: Coextensive with Caudata, excluding the Americas south of the Mexican Plateau.

CONCEPT AND CONTENT: Hydatinosalamandroidei is a monophyletic group composed of [31] Perennibranchia Latreille, 1825, and [35] Treptobranchia **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Hydatinosalamandroidei is the predominant group of transforming salamanders, with a few paedomorphic lineages in the major families. There are no morphological characters of unambiguous placement (i.e., morphological synapomorphies) of this clade. Molecular synapomorphies are summarized in appendix 5.

[31] PERENNIBRANCHIA LATREILLE, 1825

Perennibranchia Latreille, 1825: 105. (See appendix 6 for nomenclatural note.)

IMMEDIATELY MORE INCLUSIVE TAXON: [30] Hydatinosalamandroidei **new taxon.**

SISTER TAXON: [35] Treptobranchia **new taxon.**

RANGE: Extreme northeastern Mexico north through the eastern United States to southeastern Canada; Adriatic seaboard as far north as Istrian region and as far south as Montenegro; isolated population in northeastern Italy.

CONCEPT AND CONTENT: Perennibranchia Latreille, 1825, is a monophyletic group as implied by its original content, containing [32] Proteidae Gray, 1825, and [33] Sirenidae Gray, 1825.

CHARACTERIZATION AND DIAGNOSIS: Perennibranchia is a clade composed of moderate to large obligately aquatic paedomorphic species, with permanent bushy external gills, no eyelids, and laterally compressed tails. All species have well-developed forelimbs and one group has lost hindlimbs. Lungs are present, and although internal fertilization appears to be the plesiomorphic condition in this group, it may have been lost in sirenids, although this is optimization-dependent.

Beyond the molecular evidence, the following morphological characters are likely synapomorphies (from Larson and Dimmick, 1993):(1) metamorphosis absent so adults retain numerous paedomorphic characteristics, such as large bushy external gills (also in various paedomorphic lineages in Ambystomatidae and Plethodontidae); and (2) ypsiloid cartilage absent (also lacking in Amphiumidae + Plethodontidae, and the hynobiid *Onychodactylus*); (3) second ceratobranchial in three or four elements; and (4) maxilla reduced or absent (also reduced in *Batrachuperus*).

SYSTEMATIC COMMENTS: The monophyly of Perennibranchia requires additional testing although the preponderane of our evidence supports strongly its recognition. Wiens et al. (2005) did not support the monophyly of Perennibranchia in their parsimony analysis, instead placing Sirenidae as the sister taxon of all other salamanders. Their evidence included morphological and molecular evidence (from RAG-1) that we did not have, although our total amount of molecular evidence is greater. These authors treated inferred gaps as unknown characters, while we treated inferred gaps as evidence. (As noted in ''Methods'', we see gaps as a logical consequence of indels and like other characters that are consequences of deductive reasoning, such as morphological reversals, we are inclined to include them as evidence.) A strong test of Perennibranchia will involve analyzing all of the data of Wiens et al. (2005) along with our evidence, under a single analytical assumption-set (e.g., the same assumption set for alignment and analysis, inclusion as evidence of gaps and morphological reversals, and nonexclusion of morphological characters deemed paedomorphic).

[32] FAMILY: PROTEIDAE GRAY, 1825

Proteina Gray, 1825: 215. Type genus: *Proteus* Laurenti, 1768.

Phanerobranchoidea Fitzinger, 1826: 43. Type genus: *Phanerobranchus* Leuckart, 1821.

Necturi Fitzinger, 1843: 35. Type genus: *Necturus* Rafinesque, 1819.

Hypochthonina Bonaparte, 1840: 101 (p. 11 of offprint). Type genus: *Hypochthon* Merrem, 1820.

Necturina Bonaparte, 1845: 6. Type genus: *Necturus* Rafinesque, 1819.

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Hylaeobatrachidae Abel, 1919: 329–330. Type Genus: *Hylaeobatrachus* Dollo, 1884. (Whether this fossil taxon is inside the crown group is unknown and it is placed here provisionally.)
Menobranchida Knauer, 1883: 96. Type genus: *Menobranchus* Harlan, 1825.

IMMEDIATELY MORE INCLUSIVE TAXON: [31] Perennibranchia Latreille, 1825.

SISTER TAXON: [33] Sirenidae Gray, 1825.

RANGE: Eastern United States and adjacent southeastern Canada; Adriatic seaboard as far north as Istrian region and as far south as Montenegro; isolated population in northeastern Italy.

CONTENT: ***Necturus*** Rafinesque, 1819; *Proteus* Laurenti, 1768.

CHARACTERIZATION AND DIAGNOSIS: Proteidae is a group of obligately aquatic paedomorphic salamanders characterized by having bushy external gills throughout life, lacking eyelids, having laterally compressed tails. Unlike their sister taxon, Sirenidae, they exhibit internal fertilization and have hind legs (Noble, 1931). All of these characteristics are either synapomorphic with their sister taxon or plesiomorphic with respect to Perennibranchia.

Beyond our molecular evidence, the following morphological characters are likely synapomorphic (modified from Larson and Dimmick, 1993; Larson et al., 2003): (1) recessus amphibiorum with vertical orientation (also in Plethodontidae); (2) basilaris complex absent (also in plethodontids and some salamandrids); and (3) maxilla absent.

[33] FAMILY: SIRENIDAE GRAY, 1825

Sirenina Gray, 1825: 215. Type genus: *Siren* Linnaeus, 1767 (= *Siren* Österdam, 1766).
Sirenes Fitzinger, 1843: 35. Type genus: *Siren* Linnaeus, 1767 (= *Siren* Österdam, 1766).

IMMEDIATELY MORE INCLUSIVE TAXON: [13] Perennibranchia Latreille, 1825.

SISTER TAXON: [32] Proteidae Gray, 1825.

RANGE: Southeastern United States and extreme northeastern Mexico.

CONTENT: ***Pseudobranchus*** Gray, 1825; ***Siren*** Österdam, 1766.

CHARACTERIZATION AND DIAGNOSIS: Sirens are a group of slender, obligately aquatic paedomorphic salamanders that exhibit the standard suite of paedomorphic characteristics—lack of eyelids, bushy external gills, and laterally compressed tail—but also lack premaxillary teeth and have keratinized jaw pads (a synapomorphy). Unlike all other salamanders, sirens lack hind limbs; unlike near relatives they appear to have lost internal fertilization (Noble, 1931). They typically live in heavily vegetated lakes, ponds, and swamps (Bishop, 1943).

Beyond our molecular evidence, the following morphological characters have been suggested to be synapomorphies (Larson et al., 2003) or are synapomorphies in our topology: (1) hindlimbs lost; (2) scapulocoracoid and scapula separate elements (a reversal); (3) teeth absent (present in some fossil forms, outside of the crown group), replaced by keratinized beaklike pads; (5) all spinal nerves exit through foramina except for first two vertebrae (also in salamandrids); and (7) all glands and spermathecae lost that were associated with spermatophore production.

ANATOMICAL COMMENT: Sirenid nasal bones have been suggested to be nonhomologous with those in spermatophore-producing taxa (Salamandroidea sensu Duellman and Trueb, 1986) because they ossify from anlagen positioned medially to the dorsal process of the premaxillae (laterally to the paired premaxillary processes in ''salamandroids''; Larson et al., 2003). Our placement of sirenids within Diadectosalamandroidei suggests that the ossification center has moved from lateral to medial in sirenids, with the nasal bones themselves remaining homologous as nasal bones.

[35] TREPTOBRANCHIA **NEW TAXON**

ETYMOLOGY: Greek: Treptos (Greek: turned) + branchia (Greek: gill), noting that the bulk of the salamanders in this group are transforming (or a few further derived in having direct development).

IMMEDIATELY MORE INCLUSIVE TAXON: [30] Hydatinosalamandroidei **new taxon.**

SISTER TAXON: [31] Perennibranchia Latreille, 1825.

RANGE: British Isles and Scandinavia eastward to the Ural Mountains, southward into the Iberian Peninsula and Asia Minor; north-central India and China to northern Indochina; extreme northwestern Africa; southern

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Canada and southern Alaska south to the southern edge of the Mexican Plateau.

CONCEPT AND CONTENT: Treptobranchia is a monophyletic group containing Ambystomatidae Gray, 1850, and Salamandridae Goldfuss, 1820.

CHARACTERIZATION AND DIAGNOSIS: Ambystomatids and salamandrids are commonly encountered salamanders in North America and temperate Eurasia. Their life history is biphasic and they have internal fertilization. With the exception of a few paedomorphic lineages, they transform into adults that lack gills and have eyelids. Their body forms run from moderately slender to robust; the limbs are well-developed and robust.

No morphological synapomorphies have been suggested for this taxon, and although this group is uniformly characterized by several of the included morphological characters, none of them optmizes unambiguously to this taxon. Unambiguously optimized molecular synapomorphies of Treptobranchia are listed in appendix 5.

[36] FAMILY: AMBYSTOMATIDAE GRAY, 1850

Ambystomina Gray, 1850a: 32. Type genus: *Ambystoma* Tschudi, 1838.

Siredontina Bonaparte, 1850: 1 p. Type genus: *Siredon* Wagler, 1830.

Dicamptodontinae Tihen, 1958: 3. Type genus: *Dicamptodon* Strauch, 1870. **New synonymy.**

IMMEDIATELY MORE INCLUSIVE TAXON: [35] Treptobranchia **new taxon.**

SISTER TAXON: [40] Salamandridae Goldfuss, 1820.

RANGE: Alaska and southern Canada south to the southern edge of the Mexican Plateau.

CONTENT: ***Ambystoma*** Tschudi, 1838; ***Dicamptodon*** Strauch, 1870.

CHARACTERIZATION AND DIAGNOSIS: Ambystomatids are thick-bodied salamanders with well-developed limbs. They inhabit a wide variety of habitats from semidesert grassland to boreal conifer forest and deciduous forest, generally returning to water only for reproduction. Nevertheless, the most famous paedomorphic lineage, *Ambystoma mexicanum* (axolotl) of central Mexico, is in this family. Some of the paedomorphic lakeform species have assumed extreme and large forms, with the formerly recognized genus *Bathysiredon* being distinguished from *Ambystoma* on the basis of its catfish-like habitus (Dunn, 1939).

Beyond our molecular evidence, the following morphological characters have been suggested to be synapomorphies: (1) vomerine dentition replacement from posterior (also in Hynobiidae and Rhyacotritonidae; Larson and Dimmick, 1993; Larson et al., 2003); (2) presence of conspicuous folds in cloacal tube in males (also in Rhyacotritonidae; Larson and Dimmick, 1993; Larson et al., 2003); and (3) ring-shaped otoglossal cartilage (also in *Rhyacotriton*; Cope, 1887; Tihen, 1958).

SYSTEMATIC COMMENTS: We place *Dicamptodon* in Amybstomatidae, because doing so renders a more efficient taxonomy and because the reason for removing *Dicamptodon* originally from Ambystomatidae (that it was thought to be distantly related to *Ambystoma* [Edwards, 1976]) has now been rejected (Larson et al., 2003).

[40] FAMILY: SALAMANDRIDAE GOLDFUSS, 1820

Salamandrae Goldfuss, 1820: 129. Type genus: *Salamandra* Laurenti, 1768.

Tritonidae Boie, 1828: 363. Type genus: *Triton* Laurenti, 1768.

Pleurodeles Tschudi, 1838: 91. Type genus: *Pleurodeles* Michahelles, 1830.

Salamandrinae Fitzinger, 1843: 33. Type genus: *Salamandrina* Fitzinger, 1826.

Molgidae Gray, 1850a: 14. Type genus: *Molge* Merrem, 1820.

Seiranotina Gray, 1850a: 29. Type genus: *Seiranota* Barnes, 1826.

Bradybatina Bonaparte, 1850: 1 p. Type genus: *Bradybates* Tschudi, 1838.

Geotritonidae Bonaparte, 1850: 1 p. Type genus: *Geotriton* Bonaparte, 1832 (= *Triturus* Rafinesque, 1815).

IMMEDIATELY MORE INCLUSIVE TAXON: [35] Treptobranchia **new taxon.**

SISTER TAXON: [36] Ambystomatidae Gray, 1850.

RANGE: British Isles and Scandinavia eastward to the Ural Mountains, southward into the Iberian Peninsula and Asia Minor; north-central India and China to northern Indochina; extreme northwestern Africa; northeastern and extreme northwestern Mexico

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through western and eastern United States north to Alaska and southeastern Canada.

CONTENT: *Chioglossa* Bocage, 1864; *Cynops* Tschudi, 1838; *Echinotriton* Nussbaum and Brodie, 1982; ***Euproctus*** Gené, 1838 (see Systematic Comments); *Lissotriton* Bell, 1838; *Lyciasalamandra* Veith and Steinfartz, 2004; *Mertensiella* Wolterstorff, 1925; *Mesotriton* Bolkay, 1927; ***Neurergus*** Cope, 1862; ***Notophthalmus*** Rafinesque, 1820; ***Pachytriton*** Boulenger, 1878; ***Paramesotriton*** Chang, 1935; ***Pleurodeles*** Michahelles, 1830; ***Salamandra*** Laurenti, 1768; *Salamandrina* Fitzinger, 1826; ***Taricha*** Gray, 1850; ***Triturus*** Rafinesque, 1815 (see Systematic Comments); ***Tylototriton*** Anderson, 1871.

CHARACTERIZATION AND DIAGNOSIS: The salamandrid body plans range from moderately slender to robust with four well-developed limbs. Most species are periodically (e.g., *Taricha*, *Notophthalmus*) or completely (e.g., *Cynops*, *Pleurodeles*, and *Pachytriton*) aquatic and typically have biphasic life histories, except for *Mertensiella*, which has direct-development from terrestrial eggs, and some populations of *Salamandra* that have live birth. *Notophthalmus* exhibits three distinct life-history stages, an aquatic larva, terrestrial subadult (eft), and aquatic adult (Bishop, 1943). There are a few paedomorphic populations of *Notophthalmus* and *Triturus*, that, although they retain external gills, do develop eyelids (Duellman and Trueb, 1986; Zug et al., 2001).

Beyond our molecular evidence, the following morphological characters have been suggested to be synapomorphies (Larson and Dimmick, 1993; Larson et al., 2003): (1) periotic connective tissue present (also in plethodontids); (2) periotic cistern small (also in plethodontids); and (3) vomerine dentition medially replaced.

SYSTEMATIC COMMENTS: Our results, although based on less dense sampling, are broadly similar to those of Titus and Larson (1995; see ''Results''). Various authors (e.g., Risch, 1985) have recognized subfamilies, although none so far suggested has been consistent with the phylogeny of the group. Current understanding of relationships among salamandrids (e.g., Larson et al., 2003) is consistent with the recognition of two subfamilies: Salamandrinae Goldfuss, 1820, for the ''true'' salamanders (*Chioglossa*, *Lyciasalamandra*, *Mertensiella*, and *Salamandra*) and Pleurodelinae Tschudi, 1838 (for ''newts'', the remaining genera). *Salamandra* is our sole exemplar of Salamandrinae and likely some of the molecular characters for this genus (appendix 5) are synapomorphies of the subfamily. Branch 41 in appendix 5 is equivalent to Pleurodelinae as we hypothesize it.

García-París et al. (2004a: 602) suggested in brief comment that the date of publication of *Euproctus* Gené is not 1838, but 1839, rendering it a junior synonym of *Megapterna* Savi, 1838. They also suggested that ongoing molecular work will show *Euproctus* to be paraphyletic and render *Euproctus asper* as *Calotriton asper* (Dugès, 1852) as well as show that *Triturus vittatus* should not be included within *Triturus*, the oldest available name for this monotypic taxon being *Ommatotriton* Gray, 1850. Pending publication of the relevant evidence we retain the status quo.

[49] PLETHOSALAMANDROIDEI **NEW TAXON**

ETYMOLOGY: Pletho- (Greek: great number) + salamandrodei (Greek: of salamander form), to denote the large number of species in this taxon, and with passing reference to the largest contributor to this enormity, Plethodontidae.

IMMEDIATELY MORE INCLUSIVE TAXON: [29] Diadectosalamandroidei **new taxon.**

SISTER TAXON: [30] Hydatinosalamandroidei **new taxon.**

RANGE: Temperate and tropical North and tropical South America; Korea; and Mediterranean Europe.

CONCEPT AND CONTENT: Plethosalamandroidei is a monophyletic group containing Rhyacotritonidae Tihen, 1958, and [50] Xenosalamandroidei **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Plethosalamandroidei contains the vast majority of species of salamanders, being dominated by the very large family Plethodontidae. Morphological and life-history variation is extensive, from the obligately aquatic amphiumas to the arboreal species of *Bolitoglossa*. Although primitively exhibiting a bi-

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phasic life history, the bulk of the plethosalamandroids are direct-developers.

No unambiguous evidence for this taxon extends from morphology, and only molecular evidence documents the existence of this clade, summarized in appendix 5.

FAMILY: RHYACOTRITONIDAE TIHEN, 1958

Rhyacotritoninae Tihen, 1958: 3. Type genus: *Rhyacotriton* Dunn, 1920.

IMMEDIATELY MORE INCLUSIVE TAXON: [49] Plethosalamandroidei.

SISTER TAXON: [50] Xenosalamandroidei **new taxon.**

RANGE: Extreme northwestern United States.

CONTENT: ***Rhyacotriton*** Dunn, 1920.

CHARACTERIZATION AND DIAGNOSIS: Animals in this taxon are relatively small, semiaquatic transforming salamanders of stout body and limbs, resembling the ambystomatids in general aspect, a group with which they were once considered to be allied. Rhyacotritonids exhibit a biphasic life history and have internal fertilization.

Beyond our molecular evidence, the following characters have been suggested to be synapomorphies (modified from Larson and Dimmick, 1993; Larson et al., 2003): (1) vomerine dentition replacement from posterior (also in Hynobiidae and Ambystomatidae); (2) conspicuous folds present in the male cloacal tube (also in Ambystomatidae); (3) male vent gland extremely enlarged and secretes through pores lateral to the cloacal orifice rather than into the cloacal orifice as in other spermatophore-producing groups; and (4) no dorsal ossifications of the maxilla. In addition, the otoglossal cartilage is ring-shaped as in Ambystomatidae (Dunn, 1920; Tihen, 1958)

[50] XENOSALAMANDROIDEI **NEW TAXON**

ETYMOLOGY: Xenos (Greek: strange) + salamandroidei (Greek: of salamander form), to denote the fact that some of the more exotic salamanders (e.g., *Nyctanolis*, *Thorius*, and *Amphiuma*) are in this clade and that some of the stranger biogeographical distributions of vertebrates on the planet are attributed to members of this group (e.g., *Hydromantes* + *Speleomantes*).

IMMEDIATELY MORE INCLUSIVE TAXON: [49] Plethosalamandroidei **new taxon.**

SISTER TAXON: Rhyacotritonidae Tihen, 1958.

RANGE: Extreme southern Alaska and Nova Scotia (Canada) south to Amazonian Brazil and central Bolivia; southern Europe and the Korean Peninsula.

CONCEPT AND CONTENT: Xenosalamandroidei is a monophyletic group containing Amphiumidae Gray, 1825, and [51] Plethodontidae Gray, 1850.

CHARACTERIZATION AND DIAGNOSIS: Xenosalamandroids share no externally obvious synapomorphies and have widely divergent life histories and morphologies (e.g., troglobitic paedomorphs; large eel-like obligately aquatic predators; burrowers; and arboreal salamanders). The two nominal families are also dissimilar in most aspects of their biology.

Beyond our molecular evidence (appendix 5), the following characters have been suggested to be synapomorphies (Larson and Dimmick, 1993): (1) maxillae fused (also in *Notophthalmus* and some *Hynobius*); and (2) ypsiloid cartilage absent (also absent in sirenids and *Onychodactylus*).

FAMILY: AMPHIUMIDAE GRAY, 1825

Amphiumidae Gray, 1825: 216. Type genus: *Amphiuma* Garden, 1821.

IMMEDIATELY MORE INCLUSIVE TAXON: [50] Xenosalamandroidei **new taxon.**

SISTER TAXON: [51] Plethodontidae Gray, 1850.

RANGE: Southeastern United States.

CONTENT: ***Amphiuma*** Garden, 1821.

CHARACTERIZATION AND DIAGNOSIS: Amphiumas are large, obligately aquatic salamanders with cylindrical bodies up to 1.16 meters in length, tiny legs, and unpleasant dispositions. Transformation is partial, the gills being lost but eyelids never developing.

Beyond our molecular evidence, the following morphological characters have been suggested to be synapomorphies (modified from Larson and Dimmick, 1993): (1) septomaxilla absent (also absent in some salamandrids, Sirenidae, and Cryptobranchidae); (3) first hypobranchial and first ceratobranchial fused (also in hynobiids); (4) second

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ceratobranchial in four elements; and (5) posterior ventral glands absent. Beyond this, their elongate body and tiny limbs are clearly synapomorphies.

SYSTEMATIC COMMENT: Because *Amphiuma* is clearly the sister taxon of Plethodontidae, under normal circumstances it would be desirable to place them in a single family to avoid having a monotypic Amphiumidae. But, because Amphiumidae and Plethodontidae have never been considered to constitute one nominal family and there is no paraphyly to be eliminated, little is to be gained by a nomenclatural change, so we stay with traditional usage.

[51] FAMILY: PLETHODONTIDAE GRAY, 1850

Plethodontidae Gray, 1850a: 31. Type genus: *Plethodon* Tschudi, 1838.
Desmognathina Gray, 1850a: 40. Type genus: *Desmognathus* Baird, 1850.
Oedipina Gray, 1850a: 42. Type genus: *Oedipus* Tschudi, 1838.
Ensatinina Gray, 1850a: 48. Type genus: *Ensatina* Gray, 1850.
Bolitoglossidae Hallowell, 1856: 11. Type Genus: *Bolitoglossa* Duméril, Bibron, and Duméril, 1854.
Hemidactylidae Hallowell, 1856: 11. Type Genus: *Hemidactylium* Tschudi, 1838.
Spelerpinae Cope, 1859: 123. Type Genus: *Spelerpes* Rafinesque, 1832.
Thoriidae Cope, 1869: 110. Type Genus: *Thorius* Cope, 1869.
Typhlomolgidae Stejneger and Barbour, 1917: 2. Type Genus: *Typhlomolge* Stejneger, 1896.

IMMEDIATELY MORE INCLUSIVE TAXON: [50] Xenosalamandroidei **new taxon.**

SISTER TAXON: Amphiumidae Gray, 1825.

RANGE: Extreme southeastern Alaska and Nova Scotia (Canada) south to eastern Brazil and central Bolivia; Mediterreanean Europe; southwestern Korea.

CONTENT: ***Aneides*** Baird, 1851; ***Batrachoseps*** Bonaparte, 1839; ***Bolitoglossa*** Duméril, Bibron, and Duméril, 1854; *Bradytriton* Wake and Elias, 1983; *Chiropterotriton* Taylor, 1944; ***Cryptotriton*** García-París and Wake, 2000; ***Dendrotriton*** Wake and Elias, 1983; ***Desmognathus*** Baird, 1850; ***Ensatina*** Gray, 1850; ***Eurycea*** Rafinesque, 1822 (including *Haideotriton* Carr, 1939; see Systematic Comments and new combination in appendix 7); ***Gyrinophilus*** Cope, 1869; ***Hemidactylium*** Tschudi, 1838; ***Hydromantes*** Gistel, 1848; *Karsenia* Min, Yang, Bonett, Vieites, Brandon, and Wake, 2005; ***Nototriton*** Wake and Elias, 1983; *Nyctanolis* Elias and Wake, 1983; ***Oedipina*** Keferstein, 1868; ***Parvimolge*** Taylor, 1944; see Systematic Comment; ***Phaeognathus*** Highton, 1961; ***Plethodon*** Tschudi, 1838; ***Pseudoeurycea*** Taylor, 1944 (including ***Ixalotriton*** Wake and Johnson, 1989, and ***Lineatriton*** Tanner, 1950; see Systematic Comments and new combinations in appendix 7); *Pseudotriton* Taylor, 1944; *Speleomantes* Dubois, 1984; *Stereochilus* Cope, 1869; ***Thorius*** Cope, 1869.

CHARACTERIZATION AND DIAGNOSIS: Plethodontids demonstrate a spectacular radiation in the Americas, with representatives also found in Mediterranean Europe and one species on the Korean Peninsula. Plethodontids are all lungless and uniquely exhibit distinctive nasolabial grooves in transformed adults. Most species show direct development, which has arisen within the clade several times (Chippindale et al., 2004). A few lineages are perennibranch paedomorphs, but they are all contained within genera that otherwise are composed of salamanders with terrestrial adults.

Beyond our molecular evidence, the following morphological characters are likely synapomorphies (modified from Larson and Dimmick, 1993; Larson et al., 2003): (1) loss of stylus from opercular apparatus; (2) periotic connective tissue present (also in salamandrids); (3) periotic cistern small (also in salamandrids); (4) basilaris complex absent (also absent in proteids and some salamandrids); (5) recessus amphibiorum with vertical orientation (also in Proteidae); (6) palatal dentition replacement both laterally and posteriorly; and (7) loss of lungs.

SYSTEMATIC COMMENTS: Chippindale et al. (2004) suggested on the basis of their study of DNA and morphology that two major groups could be discerned within Plethodontidae: (1) Plethodontinae, including former Desmognathinae and Plethodontini (*Aneides*, *Desmognathus*, *Ensatina*, *Plethodon*, and *Phaeognathus*); and (2) an unnamed taxon composed of (a) Hemidactyliinae (*Hemidactylium*); (b) Spelerpinae (*Eurycea*, *Gyrinophilus*, *Stereochilus*, and *Pseudotriton*); and

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(c) Bolitoglossinae (*Batrachoseps*, *Bolitoglossa*, *Nyctanolis*, and *Pseudoeurycea*). Chippindale et al. (2004) assumed the following (which they had not included in their analysis) to be in Bolitoglossinae: *Chiropterotriton*, *Cryptotriton*, *Dendrotriton*, *Hydromantes*, *Nototriton*, *Oedipina*, *Speleomantes*, and *Thorius*). However, our results and those of Mueller et al. (2004) and Macey (2005) suggest that *Hydromantes* and *Speleomantes* are not bolitoglossines, but fall inside Plethodontinae. Beyond this, the placement of *Hemidactylium* is problematic. Chippindale et al. (2004) on the basis of mtDNA and nuDNA and morphology, placed it as the sister taxon of Bolitoglossinae; Mueller et al. (2004), on the basis of a Bayesian analysis of mtDNA, placed it as the sister taxon of *Batrachoseps*; Macey (2005), on the basis of a parsimony analysis of mtDNA, placed it as the sister taxon of all other plethodontids; and we place it as imbedded in a group composed of the traditional Bolitoglossinae and Hemidactyliinae. But, our placement of several of the terminals in this group (notably *Batrachoseps* and *Hemidactylium*) is based solely on a fraction of the mtDNA of Macey (2005) and barring differences due to alignment, our placement of these taxa does not constitute a strong test of Macey's (2005) placement of these taxa or, concomitantly, of the taxonomy that he adopted. A strong test, of course, would be the analysis, using direct optimization, of all of the data presented by us, Mueller et al. (2004), and by Chippindale et al. (2004) to see what the preponderance of evidence actually is. Regardless, the earlier taxonomy (e.g., D.B. Wake, 1966) has been specifically rejected.

We consider *Lineatriton* to be a junior synonym of *Pseudoeurycea*. Parra-Olea (2002) presented DNA sequence evidence for the polyphyly of *Lineatriton* and that both ''*Lineatriton*'' lineages rendered *Pseudoeurycea* paraphyletic. She also provided DNA sequence evidence that *Parvimolge* and *Ixalotriton* extended from within a paraphyletic *Pseudoeurycea*. She recommended, but did not execute, a partition of *Pseudoeurycea* to maintain ''*Lineatriton*'', *Parvimolge*, and *Ixalotrition*, that presumably would require the recognition of several new genera to preserve the two *Lineatriton* clades (one of which would require a new name). Inasmuch as a partition of *Pseudoeurycea* does not appear to be forthcoming in the near future, we prefer to recognize a monophyletic *Pseudoeurycea*, which requires the synonymy of *Lineatriton* and *Ixalotriton*. (See appendix 7 for name changes caused by these generic changes.) Although our results suggest that *Ixalotriton* and *Parvimolge* are outside of *Pseudoeurycea*, in the first case this conclusion is likely an illusion due to sparse taxon sampling. In the case of *Parvimolge*, our data place it outside of this clade and as the sister taxon to *Bolitoglossa*, a taxon not in Parra-Olea's (2002) analysis. We therefore retain *Parvimolge* and regard the clade subtended by our branch 72 to be *Pseudoeurycea*. A densely sampled study including all bolitoglossine taxa (especially *Bolitoglossa*), and all available evidence, should be the next step.

We have been unable to discern any characters (see D.B. Wake, 1966) other than those related to paedomorphy (such as those that formerly distinguished *Typhlomolge* and *Typhlotriton* from *Eurycea*) to distinguish the monotypic *Haideotriton* Carr, 1939, from *Eurycea* Rafinesque, 1822. We, like Dubois (2005), regard the former to be a synonym of the latter. Bonett and Chippindale (2004) recently placed *Typhlotriton* Stejneger, 1892, into the synonymy of *Eurycea* as well. (See appendix 7 for new combinations produced by these generic changes.) As noted in ''Results'', the status of *Plethodon* is equivocal inasmuch as our evidence suggests its paraphyly, but more densely sampled studies based on more and different assortments of evidence (Chippindale et al., 2004; Macey, 2005) suggest its monophyly.

[74] ANURA FISCHER VON WALDHEIM, 1813

Anuri Fischer von Waldheim, 1813: 58. Latinization and reranking of Anoures of A.M.C. Duméril, 1806 (which was coined explicitly as a family and therefore unavailable for regulated nomenclature). Emended to Anura by Hogg, 1839a: 270. (See appendix 6 for nomenclatural note.)

IMMEDIATELY MORE INCLUSIVE TAXON: [23] Batrachia Latreille, 1825.

SISTER TAXON: [24] Caudata Fischer von Waldheim, 1813.

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RANGE: Worldwide in tropical to cold-temperate habitats, excluding Antarctica and most oceanic islands.

CONCEPT AND CONTENT: Anura Fischer von Waldheim, 1813, is a monophyletic group containing all living frogs (i.e., [75] Leiopelmatidae Mivart, 1869, and [77] Lalagobatrachia **new taxon**).

CHARACTERIZATION AND DIAGNOSIS: Frogs are so distinctive among tetrapods that little introduction is required. Among frogs, however, there is enormous variation in morphology, behavior, reproductive mode, and life-history. Plesiomorphically, frogs exhibit the textbook amphibian biphasic life history, with an aquatic tadpole transforming to an air-breathing adult. However, many species of frogs exhibit mild to extreme variations on this theme, with many exhibiting direct development within the egg capsule (e.g., *Eleutherodactylus*) and others bearing the developing young in dermal vacuities on the dorsum (*Pipa*), in vocal sacs (*Rhinoderma*), or even in the stomach (*Rheobatrachus*).

Beyond our molecular data, the following morphological characteristics have been suggested to be synapomorphies of this group (Trueb and Cloutier, 1991; Ford and Cannatella, 1993): (1) loss of prefrontal bone; (2) loss of prearticular bone; (3) loss of a palatine (reversed in Acosmanura); (4) reduction of vertebrae to nine or fewer; (5) atlas with a single centrum; (6) first spinal nerve exits from spinal nerve canal via intervertebral foramen; (7) fusion of caudal vertebral segments into a urostyle; (8) hindlimbs significantly longer than forelimbs (with exceptions), including elongation of ankle bones; (9) fusions of radius and ulna and tibia and fibula; (6) fusion of hyobranchial elements into a hyoid plate; (10) presence of keratinous jaw sheaths and keratodonts on larval mouthparts (lost in some lineages); (11) a single median spiracle in the larva (a characteristic of Type III tadpoles—this being highly contingent on phylogenetic structure); and (12) skin with large subcutaneous lymph spaces; (13) two m. protractor lentis attached to lens (based on very narrow taxon sampling; Saint-Aubain, 1981; Ford and Cannatella, 1993).

In addition, Haas (2003) reported 19 unambiguous synapomorphies from larval morphology, several of which appear to be related to the major evolutionary step in anuran larvae—suspension feeding—whereas others have no apparent relation to feeding ecology: (1) operculum fused to abdominal wall (Haas 16.1); (2) m. geniohyoideus origin from ceratobranchials I/II (Haas 19.1); (3) m. interhyoideus posterior absent (Haas 23.0); (4) larval jaw depressors originate from palatoquadrate (Haas 42.1); (5) ramus maxillaris (cranial nerve V_2) medial to the muscle (m. levator manidbulae longus; Haas 63.1); (6) ramus mandibularis (cranial nerve V_3) anterior (dorsal) to the m. levator mandibulae longus (Haas 64.2); (7) ramus mandibularis (cranial nerve V_3) anterior (dorsal) to the externus group (Haas 65.2); (8) cartilago labialis superior (suprarostral cartilage) present (Haas 84.1; (9) two perilymphatic foramina (Haas 97.1); (10) hypobrachial skeletal parts as planum hypobranchiale (Haas 104.1); (11) processus urobranchialis short, not reaching beyond the hypobranchial plates (Haas 108.1); (12) commisura proximalis present (Haas 109.1); (13) commisura proximalis II present (Haas 110.1); (14) commisura proximalis III present (Haas 111.1); (15) ceratohyal with diarthrotic articulation present, medial part broad (Haas 115.1); (16) cleft between hyal arch and branchial arch I closed (Haas 123.0); (17) ligamentum cornuquadratum present (Haas 125.1); (18) ventral valvular velum present (Haas 128.1); and (19) branchial food traps present (Haas 134.1).

Haas (2003) also suggested that the following are nonlarval synapomorphies not mentioned as such by Ford and Cannatella (1993): (1) amplexus present (Haas 138.1); (2) vertical pupil shape (Haas 143.0); (3) clavicle overlapping scapula anteriorly (Haas 145.1); (4) cricoid as a closed ring (Haas 148.1); and (5) tibiale and fibulare elongate and fused at ends (Haas 150.1).

In addition, the following optimize as synapomorphies (Trueb and Cloutier, 1991) of Salientia (= Proanura [fossil taxon] + Anura): (1) loss of lacrimal bone; (2) presence of a frontoparietal bone; (3) long and slender ilium; and (4) ribs unicapitate (also in Cryptobranchoidei).

[75] FAMILY: LEIOPELMATIDAE MIVART, 1869

Liopelmatina Mivart, 1869: 291. Type genus: *Liopelma* Günther, 1869. Emended to Leiopelma-

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tidae by N.G. Stephenson (1951: 18–28); Liopelmatina considered an incorrect original spelling and Leiopelmatidae placed on the Official List of Family-Group Names in Zoology by Opinion 1071 (Anonymous, 1977: 167).

Ascaphidae Fejérváry, 1923: 178. Type genus: *Ascaphus* Stejneger, 1899.

IMMEDIATELY MORE INCLUSIVE TAXON: [74] Anura Fischer von Waldheim, 1813.

SISTER TAXON: [77] Lalagobatrachia **new taxon.**

RANGE: New Zealand; Pacific northwestern United States and adjacent Canada.

CONTENT: ***Ascaphus*** Stejneger, 1899; ***Leiopelma*** Fitzinger, 1861.

CHARACTERIZATION AND DIAGNOSIS: Leiopelmatidae is a group of pervasively plesiomorphic frogs, in many aspects of their anatomy, including vertical pupils (likely a synapomorphy of frogs), retention of short ribs in adults, and amphicoelous vertebrae. Nevertheless, they are apomorphic in many ways, including highly derived, high gradient-adapted tadpoles in *Ascaphus*; and nidicolous endotrophy to direct development in *Leiopelma*. *Ascaphus* is unique among frogs in having an intromittent organ.

In addition to our molecular evidence, a likely synapomorphy of Leiopelmatidae is loss of columella. Presence of an accessory coccygeal head of the m. semimembranosus (Ritland, 1955; observationally equivalent to the m. caudalipuboischiotibialis of other authors, although not homologous if so named) may be synapomorphic, but plesiomorphic retention of the m. caudalopuboischiotibialis is also consistent with our cladogram.

Larval characters in our analysis (from Haas, 2003) that optimize on the *Ascaphus* branch may be characters solely of *Ascaphus* or may be synapomorphies of Leiopelmatidae (although possibly further modified within the endotrophy of *Leiopelma*). These characters are (1) larval subdermal serous glands present (Haas 2.1); (2) three heads of the m. subarcualis obliquus originates from ceratobranchialia II, III, and IV (Haas 31.2); (3) larval m. levator mandibulae externus inserts on soft tissue (Haas 55.2); (4) larval m. levator mandibular internus inserts broadly across the jaw articulation (Haas 59.2); (5) distal end of cartilago meckeli broad and flat with processus dorsomedialis absent and without a fossa (Haas 94.3); (6) processus postcondylaris of ceratohyals present (Haas 118.1, shared with *Alytes* and *Discoglossus*); (7) intracranial endolymphatic system with anterior recessus ascendens present (Haas 122.1, also present in *Alytes*, and Acosmanura); and (8) larval lungs present and functional (Haas 133.1).

SYSTEMATIC COMMENTS: *Ascaphus* and *Leiopelma* had long been associated with each other in Leiopelmatidae (e.g., Noble, 1931), but were placed in different families by Savage (1973) on biogeographic grounds and by subsequent authors (Ford and Cannatella, 1993; Green and Cannatella, 1993) on the basis of suggested paraphyly with respect to all other frogs. We return them to the same family-group taxon (as had Roelants and Bossuyt, 2005; but against the judgment of D.M. Green) to avoid having monotypic families and to recognize that the only reason for treating *Ascaphus* and *Leiopelma* as representing separate families—that they are not each other's closest living relatives—has not survived testing.

Characters suggested by Ford and Cannatella (1993) to unite *Leiopelma* with all frogs, excluding *Ascaphus*, must be considered either convergences between *Leiopelma* and all other non-*Ascaphus* frogs, or characters that are apomorphies of Anura that have been secondarily lost in *Ascaphus*: (1) elongate arms on the sternum; (2) loss of the ascending process of the patalatoquadrate; (3) sphenethmoid ossifying in the anterior position; (4) root of the facial nerve exits the braincase through the facial foramen, anterior to the auditory capsule, rather than via the anterior acoustic foramen into the auditory capsule (Slabbert and Maree, 1945; N.G. Stephenson, 1951); and (5) palatoquadrate articulation with the braincase via a pseudobasal process, rather than a basal process (Pusey, 1943).

[77] LALAGOBATRACHIA **NEW TAXON**

ETYMOLOGY: Lalago (Greek: calling) + batrachos (Greek: frog), in reference to the fact that the frogs of the sister taxon of Lalagobatrachia, Leiopelmatidae, do not call, whereas the vast majority of the Lalagobatrachia have a wide variety of calls. Although it may be that vocal behavior is not a syna-

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pomorphy of this taxon, it certainly is characteristic.

IMMEDIATELY MORE INCLUSIVE TAXON: [74] Anura Fischer von Waldheim, 1831.

SISTER TAXON: [75] Leiopelmatidae Mivart, 1869.

RANGE: Coextensive with the range of Anura, excluding New Zealand.

CONCEPT AND CONTENT: Lalagobatrachia Fischer von Waldheim, 1813, is a monophyletic group containing [78] Xenoanura Savage, 1973, and [84] Sokolanura **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Members of Lalagobatrachia are the familiar frogs of pools and streams, forests and meadows, desert, and canyons throughout the world. As with Anura, morphological and life-history diversity is so great that it defies detailed description.

Larval characters (Haas, 2003) that optimize to this branch are (1) m. transversus ventralis IV absent (Haas 22.1, reversed elsewhere but also absent in *Heleophryne*, *Hemisus*, and hyperoliids among the taxa that Haas studied); (2) single m. subarcualis obliquus originates from ceratobranchial II (Haas 31.0); (3) insertion of the m. rectus cervicis at the processus branchiales II or III (Haas 39.1); (4) m. hyoangularis present (Haas 43.1); (5) m. levator mandibulae internus anterior (Haas 58.1); (6) m. levator mandibulae longus originates from posterior palatoquadrate (Haas 60.1); and (7) and palatoquadrate connection to trabecula cranii rostral (Haas 69.1).

The synapomorphies associated with Discoglossanura of Ford and Cannatella (1993) optimize on this branch as well (with reversal in Bombinatoridae): (1) bicondylar sacrococcygeal articulation; and (2) episternum present.

Several characters suggested by Ford and Cannatella (1993) as synapomorphies of their Pipanura would optimize on our tree alternatively as synapomorphies of Lalagobatrachia and reversed in Costata (Alytidae + Bombinatoridae), or independently derived in Xenoanura (Pipidae + Rhinophrynidae) and Acosmanura (Anomocoela + Neobatrachia). These characters are (1) torsion of carpal elements; (2) absence of free ribs in adults; (3) presence of vocal sacs; and (4) fusion of the trigeminal and facial ganglia. Ford and Cannatella (1993) had also included the Type IV tadpole as a synapomorphy of Pipanura; however, besides the fact that Orton's larval types are not characters by themselves but a complex mosaic of multiple, independent character transformations, the Type I tadpole of Xenoanura is most parsimoniously derived from the Type III tadpole of Costata and *Ascaphus*, with the Type IV tadpole a synapomorphy of Acosmanura.

In addition, Abourachid and Green (1999) noted that members of this taxon swim with coordinated thrusts of the hind legs rather than alternating sweeps, as in Leiopelmatidae. We think that this character may well be a unique and unreversed synapomorphy of Lalagobatrachia.

[78] XENOANURA SAVAGE, 1973

Xenoanura Savage, 1973: 352. (See appendix 6 for nomenclatural comment.)

IMMEDIATELY MORE INCLUSIVE TAXON: [77] Lalagobatrachia **new taxon.**

SISTER TAXON: [84] Sokolanura **new taxon.**

RANGE: Tropical Africa and South America, north to southern North America.

CONCEPT AND CONTENT: Xenoanura Savage, 1973, is a monophyletic crown taxon containing [79] Pipidae Gray, 1825, and Rhinophrynidae Günther, 1859 ''1858'' (and presumably a number of fossil taxa internal to this clade, including palaeobatrachids; Savage, 1973; cf. Ford and Cannatella, 1993).

CHARACTERIZATION AND DIAGNOSIS: The highly aquatic bizarre pipids and equally strange, but terrestrial, *Rhinophrynus* share the distinctive Type I tadpole (Orton, 1953; Starrett, 1973).

Several characters of larval morphology (originally from Haas, 2003) used in our analysis optimize on this branch: (1) eye position lateral (Haas 11.1); (2) opercular canal absent and spiracle paired (Haas 17.0); (3) m. constrictor branchialis I absent (Haas 27.0); (4) m. levator mandibulae internus anterior (Haas 58.2); (5) m. levator mandibulae longus originates exclusively from the arcus suborcularis (Haas 60.2); (6) posterolateral projections of the crista parotica are expansive flat chondrifications (Haas 67.2); (7) ar-

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cus subocularis with a distinct processus lateralis posterior projecting laterally from the posterior palatoquadrate (Haas 81.3); (8) articulation of cartilago labialis superior with cornu trabeculae fused into rostral plate (Haas 85.2); and (9) forearm erupts out of limb pouch outside peribranchial space (Haas 132.0).

Characters suggested by Ford and Cannatella (1993) in support of their Mesobatrachia (Xenoanura + Anomocoela) are on our topology required to be convergent in their Pipoidea (our Xenoanura) and their Pelobatoidea (our Anomocoela), and they are therefore independent apomorphies for each group: (1) closure of the frontoparietal fontanelle by juxtaposition of the frontoparietal bones; (2) partial closure of the hyoglossal sinus by the ceratohyals; (3) absence of the taenia tecti medialis; and (4) absence of the taenia tecti transversum (Sokol, 1981).

Characters that Ford and Cannatella (1993) listed as apomorphies of their Pipoidea also optimize on this branch: (1) lack of mentomeckelian bones; (2) absence of lateral alae of the parasphenoid; (3) fusion of the frontoparietals into an azygous element; (4) greatly enlarged otic capsule; (5) tadpole with paired spiracles and lacking keratinized jaw sheaths and keratodonts (Type I tadpole). J.D. Lynch (1973: 169) reported Rhinophrynidae to have opisthocoelous vertebrae, in which case opisthocoely may be a synapomorphy of Xenoanura (and independently of Costata), or alternatively opisthocoely may be a character of Lalagobatrachia and subsequently modified at the level of Acosmanura.

Xenoanura in our sense is coextensive with the Recent content of the redundant ranks Pipoidia Gray, 1825 (epifamily) and Pipoidea Gray, 1825 (superfamily) of Dubois (2005).

[79] FAMILY: PIPIDAE GRAY, 1825

Piprina Gray, 1825: 214. Type genus: ''*Pipra* Laurent'' (= *Pipa* Laurenti, 1768). Incorrect original spelling.

Dactylethridae Hogg, 1838: 152. Type genus: *Dactylethra* Cuvier, 1829.

Astrodactylidae Hogg, 1838: 152. Type genus: *Astrodactylus* Hogg, 1838 (= *Asterodactylus* Wagler, 1827).

Xenopoda Fitzinger, 1843: 33. Type genus: *Xenopus* Wagler, 1827.

Hymenochiridae Bolkay, 1919: 348. Type genus: *Hymenochirus* Boulenger, 1896.

Siluraninae Cannatella and Trueb, 1988: 32. Type genus: *Silurana* Gray, 1864.

IMMEDIATELY MORE INCLUSIVE TAXON: [78] Xenoanura Savage, 1973.

SISTER TAXON: Rhinophrynidae Günther, 1859 ''1858''.

RANGE: South American and Panamanian tropics; sub-Saharan Africa.

CONTENT: ***Hymenochirus*** Boulenger, 1896; ***Pipa*** Laurenti, 1768; *Pseudhymenochirus* Chabanaud, 1920; ***Silurana*** Gray, 1864; ***Xenopus*** Wagler, 1827.

CHARACTERIZATION AND DIAGNOSIS: Pipids are highly aquatic frogs that have inguinal amplexus and that vocalize using the hyoid apparatus to make clicks (Rabb, 1960), a characteristic that is likely synapomorphic. Pipids share with Rhinophrynidae the distinctive Type I tadpole (Orton, 1953, 1957; Starrett, 1973) but are highly apomorphic with respect to that group. Morphological characters (from Haas, 2003) addressed in our analysis provided a large number of larval and adult synapomorphies: (1) interbranchial septum invaded by lateral fibers of the m. subarcualis rectus I–IV (Haas 29.2); (2) anterior insertion of the m. subarcualis rectus II–IV on ceratobranchial III (Haas 37.2); (3) commissurae craniobranchiales present (Haas 75.1); (4) one perilymphatic foramen on the otic capsule (Haas 97.0); (5) ventral centra formation perichordal (Haas 99.1; but see Systematic Comment under Xenoanura); (6) free basihyal present (Haas 105.0); (7) processus urobranchialis absent (Haas 108.0); (8) ventral valvular velum absent (Haas 128.0); (9) advertisement call without airflow (Haas 140.3); (10) pupil shape round (Haas 143.3); (11) shoulder girdle with epicoracoids abutting and functionally fixed (Haas 144.2); (12) tongue absent (Haas 149.0).

Ford and Canntella (1993) provided 11 characters in support of the monophyly of this group, although we are not sure of the character optimization of all of them because these authors did not provide a character matrix and our different placement of this taxon within Anura may have resulted in some

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reoptimization: (1) lack of a quadratojugal; (2) presence of an epipubic cartilage; (3) unpaired epipubic muscle; (4) free ribs in larvae; (5) fused articulation between coccyx and sacrum; (6) short stocky scapula; (7) elongate septomaxillary bones; (8) ossified pubis; (9) a single median palatal opening of the eustachian tube; (10) lateral line organs persisting in adults; and (11) loss of tongue.

Báez and Trueb (1997) added to this list (fossil taxa pruned for purposes of this discussion): (1) the possession of an optic foramen with a complete bony margin formed by the sphenethmoid; (2) anterior ramus of the pterygoid arises near the anteromedial corner of the otic capsule; (3) parasphenoid fused at least partially with the overlying braincase; (4) vomer lacks an anterior process, if the bone is present; (5) mandible bears a broad-based, bladelike coronoid process along its posteromedial margin; (6) sternal end of the coracoid not widely expanded; (7) anterior ramus of pterygoids dorsal with respect to the maxilla; and (8) premaxillary alary processes expanded dorsolaterally.

Finally, Burton (1998a) suggested that the dorsal origin of the mm. flexores teretes III and IV relative to the corresponding mm. transversi metacarpum I and II is a synapomorphy.

SYSTEMATIC COMMENT: Our data do not support the recognition of sister-subfamilies Pipinae Günther, 1859 ''1858'' (*Hymenochirus*, *Pseudhymenochirus*, and *Pipa*) and Dactylethrinae Hogg, 1839 (*Silurana* and *Xenopus*), as found by de Sá and Hillis (1990) and Báez and Pugener (2003). Instead, our data indicate that *Hymenochirus* (a member of nominal Pipinae) is the sister taxon of the remainder of Pipinae + Dactylethrinae.

FAMILY: RHINOPHRYNIDAE GÜNTHER, 1859 ''1858''

Rhinophrynina Günther, 1859 ''1858'': xiv. Type genus: *Rhinophrynus* Duméril and Bibron, 1841.

IMMEDIATELY MORE INCLUSIVE TAXON: [78] Xenoanura Savage, 1971.

SISTER TAXON: [79] Pipidae Günther, 1859 ''1858''.

RANGE: Tropical and subtropical lowland North and Central America.

CONTENT: ***Rhinophrynus*** Duméril and Bibron, 1841.

CHARACTERIZATION AND DIAGNOSIS: Rhinophrynidae contains a single species, *Rhinophrynus dorsalis*, which is of medium-size, with a cone-shaped head and globular body, reflecting its burrowing life history. Like the pipids, it has inguinal amplexus and a Type I tadpole (Orton, 1953; J.D. Lynch, 1973).

Several larval characters in our analysis optimize as synapomorphies of this group: (1) m. geniohyoideus lost (Haas 19.5); (2) m. levator mandibulae externus present in two portions (profundus and superficialis; Haas 54.1); (3) ramus mandibularis (of cranial nerve V3; Haas 65.0); (4) larval ribs absent, the feature convergent with the condition in Lalagobatrachia (Haas 102.0); (5) processus urobranchialis reaching far beyond hyobranchial plates (Haas 108.2); (6) endolymphatic spaces extend into more than half of vertebral canal (presacral vertebrae IV or beyond; Haas 121.1); (7) branchial food traps divided and crescentic (Haas 135.1); and (8) cartilaginous cricoid ring with a dorsal gap (Haas 148.3). In addition, *Rhinophrynus* has lost ribs in the adults.

Ford and Cannatella (1993, following Henrici, 1991) suggested the following as synapomorphies of the group: (1) division of the distal condyle of the femur into lateral and medial condyles; (2) modification of the prehallux and distal phalanx of the first digit into a spade for digging; (3) tibiale and fibulare short and stocky, with distal ends fused; (4) an elongate atlantal neural arch; and (5) sternum absent. Although these characters are not available in matrix form, precluding careful evaluation of level of universality, we have no reason to doubt these suggestions.

[84] SOKOLANURA **NEW TAXON**

ETYMOLOGY: Sokol (Otto Sokol) + anoura (Greek: tailless, i.e., frog). We commemorate Otto Sokol with this name. Dr. Sokol was an anatomist of great talent who would have continued to make important contributions to comparative larval anatomy had his life not been cut short by a tragic automobile accident. (See appendix 6 for nomenclatural note.)

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IMMEDIATELY MORE INCLUSIVE TAXON: [77] Lalagobatrachia **new taxon.**

SISTER TAXON: [78] Xenoanura Savage, 1973.

RANGE: Coextensive with Anura, excluding New Zealand.

CONCEPT AND CONTENT: Sokolanura is a monophyletic taxon composed of [85] Costata Lataste, 1879, and [91] Acosmanura Savage, 1973.

CHARACTERIZATION AND DIAGNOSIS: Larval morphological synapomorphies (from Haas, 2003) optimized by our analysis on this branch are (1) m. mandibulolabialis present (Haas 48.1); upper jaw cartilages powered by jaw muscles (Haas 53.1); (2) main part of larval m. levator mandibulae externus inserts on on upper jaw cartilages (Haas 55.1); (3) insertion of the larval m. levator mandibulae internus is lateral to jaw articulation (Haas 59.1); (4) m. levator mandibulae longus in two portions (profundus and superficialis; Haas 61.1); (5) processus muscularis on the lateral margin of the palatoquadrate present (Haas 79.1); and (6) ligamentum mandibulosuprarostrale present (Haas 127.1).

[85] COSTATA LATASTE, 1879

Costati Lataste, 1879: 339. Emended to Costata by Stejneger, 1907: 49. (See appendix 6 for nomenclatural note.)

IMMEDIATELY MORE INCLUSIVE TAXON: [84] Sokolanura **new taxon.**

SISTER TAXON: [91] Acosmanura Savage, 1973.

RANGE: Western Europe, North Africa, and Israel, possibly into Syria; east to eastern Russia and Turkey, China, Korea, and northern Indochina; Borneo (western Kalimantan, Indonesia), and the Philippines.

CONCEPT AND CONTENT: Costata Lataste, 1879, is a monophyletic group containing [86] Alytidae Fitzinger, 1843, and [88] Bombinatoridae Gray, 1825.

CHARACTERIZATION AND DIAGNOSIS: Members of Costata are relatively small, unremarkable frogs in external appearance, which exhibit the typically biphasic life history via a Type III larva with postmetamorphs retaining ribs (Noble, 1931; J.D. Lynch, 1973; Zug et al., 2001). Larval characters (Haas, 2003) that optimize unambiguously in our analysis on this branch are (1) origin of m. intermandibularis restricted to the medial side of the cartilago meckeli corpus (Haas 52.1); (2) larval m. levator mandibulae externus in two parts (profundus and superficialis; Haas 54.1); (3) posterior processes of the pars alaris double (Haas 88.0); (4) vertebral central formation epichordal (Haas 99.1); and (5) processus urobranchialis absent (Haas 108.0).

Costata is also characterized by opisthocoelous vertebrae, which is found in Xenoanura (J.D. Lynch, 1973), making it either a synapomorphy of Lalagobatrachia and subsequently modified at the level of Acosmanura, or nonhomologous synapomorphies.

SYSTEMATIC COMMENTS: We could have combined Alytidae and Bombinatoridae as a single family with two subfamilies, but rather than continue an arbitrary rank controversy, we retain Alytidae and Bombinatoridae as families for the sake of continuity of discourse (but see comments by Dubois, 2005). Costata in our sense is identical in Recent content to the redundant taxa Bombinatoroidia Gray, 1825 (epifamily), Bombinatoroidea Gray, 1825 (superfamily, and Bombinatoridae (family) of Dubois (2005).

[86] FAMILY: ALYTIDAE FITZINGER, 1843

Alytae Fitzinger, 1843: 32. Type genus: *Alytes* Wagler, 1829.

Colodactyli Tschudi, 1845: 167. Type genus: *Colodactylus* Tschudi, 1845 (= *Discoglossus* Otth, 1837).

Discoglossidae Günther, 1858b: 346. Type genus: *Discoglossus* Otth, 1837. (See appendix 6 for nomenclatural comment.)

IMMEDIATELY MORE INCLUSIVE TAXON: [85] Costata Lataste, 1879.

SISTER TAXON: [88] Bombinatoridae Gray, 1825.

RANGE: Western Europe, North Africa, and Israel, possibly into Syria.

CONTENT: ***Alytes*** Wagler, 1830; ***Discoglossus*** Otth, 1837.

CHARACTERIZATION AND DIAGNOSIS: Alytidae represents small frogs that reproduce via typical Type III pond-type larvae that postmetamorphically retain ribs and are generally found around water, with *Alytes* being more terrestrial than *Discoglossus* (Noble, 1931; J.D. Lynch, 1973).

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Haas (2003) did not consider our Alytidae to have synapomorphies, because his shortest tree placed *Alytes* as the sister taxon of *Discoglossus* + *Bombina*. Nevertheless, combined with our molecular data, the larval characters from Haas study that optimize on this branch are (1) admandibular cartilage present (Haas 95.1, also found in *Heleophryne*); and (2) processus postcondylaris of ceratohyal present (Haas 118.1). As noted under Lalagobatrachia, characters suggested by Ford and Cannatella (1993) to be synapomorphies of Discoglossanura are here considered to be synapomorphies of Lalagobatrachia, with reversal of these in Bombinatoridae: (1) monocondylar sacrococcygeal articulation; and (2) episternum absent. Ford and Cannatella (1993) also suggested that V-shaped parahyoid bones (convergent in *Pelodytes*) and a narrow epipubic cartilage plate are synapomorphies of this taxon.

SYSTEMATIC COMMENTS: Haas (2003) suggested that *Alytes* is the sister taxon of *Discoglossus* + *Bombina* on the basis of three characters (epidermal melanocytes irregular in shape and not forming reticulaton [Haas 1.1], inspiratory advertisement call [Haas 140.1]; and pupil shape triangular [Haas 143.2]) considered to be synapomorphies of *Discoglossus* + *Bombina*. Nevertheless, placing *Alytes* as the sister taxon of *Discoglossus* requires only two additional steps in his data set.

[88] FAMILY: BOMBINATORIDAE GRAY, 1825

Bombinatorina Gray, 1825: 214. Type genus: *Bombinator* Merrem, 1820.
Bombitatores Fitzinger, 1843: 32. Type genus: *Bombitator* Wagler, 1830.
Bombininae Fejérváry, 1921: 25. Type genus: *Bombina* Oken, 1816.

IMMEDIATELY MORE INCLUSIVE TAXON: [85] Costata Latste, 1879.

SISTER TAXON: [86] Alytidae Fitzinger, 1843.

RANGE: France and Italy east to western Russia and Turkey; China, Korea, and northern Indochina; Borneo and the Philippines.

CONTENT: *Barbourula* Taylor and Noble, 1924; ***Bombina*** Oken, 1816.

CHARACTERIZATION AND DIAGNOSIS: Members of Bombinatoridae are distinctive aquatic frogs that are generally brightly colored ventrally (less so in *Barbourula*) and exhibit a typically biphasic life history (unknown in *Barbourula*). Like Alytidae, they have Type III larvae. Postmetamorphs retain ribs (Noble, 1931; J.D. Lynch, 1973). The only morphological synapomorphy from our analysis (originally from Haas, 2003) that optimizes on this branch is m. mandibulolabialis superior present (Haas 50.1).

The implication of our topology is that the two characters suggested by Ford and Cannatella (1993) as synapomorphies of Discoglossanura (bicondylar sacrococcygeal articulation and episternum present) optimize to Lalagobatrachia, with a loss in Bombinatoridae (*Bombina* + *Barbourula*). Bombinatoridae was suggested (Ford and Cannatella, 1993) to have as synapomorphies (1) an expanded flange of the quadratojugal; and (2) presence of enchochondral ossifications in the hyoid plate.

[91] ACOSMANURA SAVAGE, 1973

Acosmanura Savage, 1973: 354. (See appendix 6 for nomenclatural comment.)

IMMEDIATELY MORE INCLUSIVE TAXON: [84] Sokolanura **new taxon.**

SISTER TAXON: [85] Costata Lataste, 1879.

RANGE: Coextensive with Anura, excluding New Zealand.

CONCEPT AND CONTENT: Acosmanura Savage, 1973, is, as originally conceived, a monophyletic group containing [92] Anomocoela Nicholls, 1916, and [105] Neobatrachia Reig, 1958.

CHARACTERIZATION AND DIAGNOSIS: As noted by Starrett (1973), Acosmanura is characterized by a Type IV tadpole, differing from the ancestral Type III tadpole (of Leiopelmatidae and Costata) in having a sinistral spiracle in the larvae, although there are other character differences (summarized below).

Beyond the molecular synapomorphies of the group, several larval morphological characters in our analysis (from Haas, 2003) optimized on this branch: (1) labial ridge with a single row of keratodonts (Haas 4.0); (2) paired venae caudales laterales long (Haas 15.1); (3) spiracle position sinistral (Haas 18.1, also in *Scaphiophryne*); (4) m. subarcualis rectus I portion with origin from cer-

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atobranchial II present (Haas 34.1); (5) insertion site of the m. subarcualis rectus I on the ventral muscle portion lateral (Haas 35.1); (6) anterior insertion of m. subarcualis rectus II–IV on ceratobranchial II (Haas 37.1); (7) m. suspensoriohyoideus present (Haas 45.1); (8) m. interhyoideus and m. intermandibularis well separated by a gap (Haas 47.1); (9) functional larval m. levator mandibulae lateralis present (Haas 56.1; lost in *Gastrotheca*); (10) articulation of cartilago labialis superior with cornua trabeculae by pars alaris (Haas 85.1); (11) larval ribs absent (Haas 102.0; also in *Rhinophrynus*); (12) commissura proximalis I absent (Haas 109.0; 109.1 in microhylids); (13) spicula present and long (Haas 112.1; lost in *Ceratophrys* + *Lepidobatrachus* and independently gained in *Alytes*); (14) anterior processus ascendens of intracranial endolymphatic system present (Haas 122.1; also in *Ascaphus*, *Alytes*); (15) ligamentum cornuquadratum inserting on cornu trabeculae (Haas 126.1; reversed in *Ceratophrys*); (16) clavicula in adult not overlapping (Haas 145.2; see also J.D. Lynch, 1973: 147); (17) palatine bones present (Haas 146.1; independently lost in several groups, including microhylids, and dendrobatids).

SYSTEMATIC COMMENTS: Presence of a (neo)palatine bone as a synapomorphy of Acosmanura could be seen as controversial. It is not controversial that a palatine is characteristic of Neobatrachia, but its presence in Anomocoela is. Some authors favored the view that the palatine develops in pelobatids (sensu lato) but later fuses to the maxilla (Zweifel, 1956; Kluge, 1966; Estes, 1970); others have asserted that the palatine is fused with either the vomer or maxilla (Jurgens, 1971; Roček, 1981 ''1980''). Wiens (1989) suggested that the palatine never forms, at least not in *Spea*. Hall and Larsen (1998) discussed the issue and provided evidence that palatine centers of ossification do exist in *Spea* and in other anomocoelans. Without evidence that the ''palatine'' center of ossification in anomocoelans is anything other than the palatine, Hennig's auxiliary principle (Hennig, 1966) suggests that we accept it as homologous with the palatine of neobatrachians.

J.D. Lynch (1973) noted that Leiopelmatidae is notochordal/amphicoelous; that Xenoanura and Costata exhibit opisthocoelous vertebrae; and that Anomocoela and more ''basal'' groups within Hyloides have intervertebral bodies unfused to the centra, at least in subadults. (Sooglossidae most likely has amphicoelous vertebrae as an apomorphy at that level of universality.) Much work needs to be accomplished, but currently it appears that the fusion of intervertebral bodies has taken place in Hyloides and Ranoides independently.

[92] ANOMOCOELA NICHOLLS, 1916

Anomocoela Nicholls, 1916: 86.

IMMEDIATELY MORE INCLUSIVE TAXON: [91] Acosmanura Savage, 1973.

SISTER TAXON: [105] Neobatrachia Reig, 1958.

RANGE: Southern Canada and United States south to south-central Mexico; Europe and northwestern Africa; western Asia to tropical southeastern Asia southeast to the Greater Sunda Islands.

CONCEPT AND CONTENT: Anomocoela Nicholls, 1916, is here conceived as originally formed, a monophyletic group containing [96] Pelobatoidea Bonaparte, 1850, and [93] Pelodytoidea Bonaparte, 1850.

CHARACTERIZATION AND DIAGNOSIS: Only one of the morphological characters in our analysis optimized on this branch: partes corpores medially separate (Haas 87.0).

Characters suggested by Ford and Cannatella (1993) in support of their Pelobatoidea (our Anomocoela) are (1) sternum ossified into a bony style, and (2) pupil vertical (plesiomorphic for Anura and possibly here; convergent with phyllomedusine and some pelodryadine hylids and Africanura, except Brevicipitidae and Hyperoliidae).

Characters suggested by Ford and Cannatella (1993) in support of their Mesobatrachia we found to be convergent in their Pipoidea (our Xenoanura) and their Pelobatoidea (our Anomocoela), and therefore independent apomorphies for each group: (1) closure of the frontoparietal fontanelle by juxtaposition of the frontoparietal bones; (2) partial closure of the hyoglossal sinus by the ceratohyals; (3) absence of the taenia tecti medialis; and (4) absence of the taenia tecti transversum

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(Sokol, 1981). We have some reservations, however, because the characters were not presented in matrix form so we are not sure of the distribution of any of these characters away from their Mesobatrachia. J.D. Lynch (1973: 148) provided a character distribution that suggests a dorsally incomplete cricoid ring as a synapomorphy at this level (convergent in *Rhinophrynus*).

SYSTEMATIC COMMENT: The monophyly of this group seems assured and the reason for maintaining four families within it, rather than having a single larger Pelobatidae, is that no clarity is gained by changing the current taxonomy (contra Dubois [2005: 3], who aggregated the content as four subfamilies within a larger Pelobatidae).

[93] SUPERFAMILY: PELODYTOIDEA BONAPARTE, 1850

IMMEDIATELY MORE INCLUSIVE TAXON: [92] Anomocoela Nicholls, 1916.

SISTER TAXON: [96] Pelobatoidea Bonaparte, 1850.

RANGE: Southwestern Europe and the Caucasus; southern Canada and United States south to south-central Mexico.

CONTENT: Pelodytidae Bonaparte, 1850, and [94] Scaphiopodidae Cope, 1865.

CHARACTERIZATION AND DIAGNOSIS: Only one of the morphological characters in our analysis (originally from Haas, 2003) optimizes on this branch: basibranchial long (Haas 105.0). Nevertheless, the molecular data are decisive (appendix 5). The length of the 28S fragment is diagnostic for this taxon, being 703 bp (appendix 3; as in Leiopelmatidae), but differing from that taxon in all of the morphological characters of the intervening taxa.

FAMILY: PELODYTIDAE BONAPARTE, 1850

Pelodytina Bonaparte, 1850: 1 p. Type genus: *Pelodytes* Bonaparte, 1838.

IMMEDIATELY MORE INCLUSIVE TAXON: [93] Pelodytoidea Bonaparte, 1850.

SISTER TAXON: [94] Scaphiopodidae Cope, 1865.

RANGE: Southwestern Europe and the Caucasus.

CONTENT: ***Pelodytes*** Bonaparte, 1838.

CHARACTERIZATION AND DIAGNOSIS: Pelodytids are small terrestrial frogs that live in moist habitats and have a typically biphasic life history. A number of morphological characters (Haas, 2003) in our analysis optimize on this branch (although some of these may actually apply to some subset of *Pelodytes*): (1) epidermal melanocytes of irregular shape not forming reticulation (Haas 1.1, also in *Discoglossus* and *Bombina*); (2) upper labial papillae continuous (Haas 8.0); (3) interbranchial septum IV invaded by fibers of m. subarcualis rectus II–IV (Haas 29.1); (4) m. subarcualis rectus I portion with origin from ceratobranchial I absent (Haas 33.0); (5) larval m. levator mandibulae externus in two portions (profundus and superficialis; Haas 54.1); (6) dorsal connection from processus muscularis to commissura quadrato-orbitalis (Haas 78.2); (7) articulation of cartilago labialis superior with cornua trabeculae by pars corporis (Haas 85.0); (8) vertebral centra formation epichordal (Haas 99.1); (9) larval ribs present (Haas 102.1); (10) commissura proximalis II absent (Haas 110.0); (11) eggs laid in strings (Haas 141.1; (also in *Pelobates* and elsewhere in Acosmanura); (12) parahyoid ossification present (Haas 147.1); and (13) tibiale and fibulare elongate and fully fused (Haas 150.2; convergent in Neobatrachia).

[94] FAMILY: SCAPHIOPODIDAE COPE, 1865

Scaphiopodidae Cope, 1865: 104. Type genus: *Scaphiopus* Holbrook, 1836.

IMMEDIATELY MORE INCLUSIVE TAXON: [93] Pelodytoidea Bonaparte, 1850.

SISTER TAXON: Pelodytidae Bonaparte, 1850.

RANGE: Southern Canada and United States south to south-central part of the Plateau of Mexico.

CONTENT: ***Scaphiopus*** Holbrook, 1836; ***Spea*** Cope, 1866.

CHARACTERIZATION AND DIAGNOSIS: Scaphiopodids are toad-like frogs characterized by the possession of large metatarsal spades, as found in Pelobatidae, with which they burrow. Their life-history is typically biphasic with a Type IV tadpole and inguinal amplexus. Morphological characters in our analysis (from Haas, 2003) that optimize on this branch are (1) paired venae caudales laterales

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short (Haas 15.0); (2) m. subarcualis rectus I portion with origin from ceratobranchial III absent (Haas 35.0); and (3) m. mandibulolabialis superior absent (Haas 50.0). Because Haas' (2003) study included only *Spea* within Scaphiopodidae, these characters may actually be synapomorphies of *Scaphiopus* + *Spea* or some subset of *Spea*. Additional taxon sampling is needed to elucidate the appropriate level of universality of these characters.

Other possible synapomorphies at this level are (1) fusion of the sacrum and coccyx (although J.D. Lynch, 1973: 141, disagreed with this); (2) exostosed frontoparietals; and (3) presence of a metatarsal spade supported by a well-ossified prehallux (Ford and Cannatella, 1993). These appear convergently in Pelobatidae, possibly relating to their burrowing habits.

[96] SUPERFAMILY: PELOBATOIDEA BONAPARTE, 1850

IMMEDIATELY MORE INCLUSIVE TAXON: [92] Anomocoela Nicholls, 1916.

SISTER TAXON: [93] Pelodytoidea Bonaparte, 1850.

RANGE: Europe, western Asia, and northwestern Africa; Pakistan and western China, Indochinese peninsula, east to the Philippines and the Greater Sunda Islands.

CONTENT: [97] Pelobatidae Bonaparte, 1850, and [98] Megophryidae Bonaparte, 1850.

CHARACTERIZATION AND DIAGNOSIS: Morphological characters in our analysis (from Haas, 2003) that optimized on this branch are (1) m. interhyoideus posterior present (Haas 23.1); (2) m. diaphragmatopraecordialis present (Haas 25.1); (3) m. constrictor branchialis I absent (Haas 27.0); (4) m. mandibulolabialis superior present (Haas 50.1); and (5) adrostral cartilage very large and elongate (Haas 90.2). Because this generalization is based solely on *Pelobates*, *Megophrys*, and *Leptobrachium*, taxon sampling needs to be expanded for further elucidation of the distribution of these characters. J.D. Lynch (1973) noted that *Pelobates* and megophryids have a monocondylar sacrococcygeal articulation, which is likely a synapomorphy at this level.

[97] FAMILY: PELOBATIDAE BONAPARTE, 1850

Pelobatidae Bonaparte, 1850: 1 p. Type genus: *Pelobates* Wagler, 1830.

IMMEDIATELY MORE INCLUSIVE TAXON: [92] Pelobatoidea Bonaparte, 1850.

SISTER TAXON: [98] Megophryidae Bonaparte, 1850.

RANGE: Europe, western Asia, and northwestern Africa.

CONTENT: ***Pelobates*** Wagler, 1830.

CHARACTERIZATION AND DIAGNOSIS: Pelobatids are toad-like frogs, that have a distinctive metatarsal spade (as does Scaphiopodidae) and their life history is typically biphasic with inguinal amplexus and a Type IV tadpole. Morphological characters (from Haas, 2003) that optimize on this branch are (1) larval eye positioned dorsolaterally (Haas 11.1); (2) posterolateral projections of the crista parotica present (Haas 67.1); (3) arcus subocularis with an irregular margin (Haas 81.1); (4) vertebral centra epichordal (Haas 99.1); (5) processus branchialis closed (Haas 114.1); (6) endolymphatic spaces extend into more than half of vertebral canal (presacral vertebra IV or beyond; Haas 121.1); (7) eggs laid in strings (Haas 141.1; convergent elsewhere within Acosmanura).

Because this diagnosis is based solely on *Pelobates fuscus*, some of these characters may optimize on some subset of the species of *Pelobates* and not on the Pelobatidae branch. Increased density of sampling is needed.

Other possible synapomorphies at this level are (1) fusion of the sacrum and coccyx; (2) exostosed frontoparietals; and (3) presence of a metatarsal spade supported by a well-ossified prehallux (Ford and Cannatella, 1993). These appear convergently in Scaphiopodidae, possibly relating to their burrowing habits.

[98] FAMILY: MEGOPHRYIDAE BONAPARTE, 1850

Megalophreidina Bonaparte, 1850: 1 p. Type genus: *Megalophrys* Wagler, 1830 (= *Megophrys* Kuhl and Van Hasselt, 1822).

Leptobrachiini Dubois, 1980: 471. Type genus: *Leptobrachium* Tschudi, 1838.

Oreolalaxinae Tian and Hu, 1985: 221. Type genus: *Oreolalax* Myers and Leviton, 1962.

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IMMEDIATELY MORE INCLUSIVE TAXON: [96] Pelobatoidea Bonaparte, 1850.

SISTER TAXON: [97] Pelobatidae Bonaparte, 1850.

RANGE: Montane Pakistan and western China, Indochinese peninsula, east to the Philippines and the Greater Sunda Islands.

CONTENT: *Atympanophrys* Tian and Hu, 1983; ***Brachytarsophrys*** Tian and Hu, 1983; *Leptobrachella* Smith, 1925; ***Leptobrachium*** Tschudi, 1838; ***Leptolalax*** Dubois, 1980; ***Megophrys*** Kuhl and Hasselt, 1822; ***Ophryophryne*** Boulenger, 1903; *Oreolalax* Myers and Leviton, 1962; *Scutiger* Theobald, 1868; *Vibrissaphora* Liu, 1945; ***Xenophrys*** Günther, 1864.

CHARACTERIZATION AND DIAGNOSIS: Megophryids are small to large frogs that are generally found hopping in leaf litter along streams, although some species extend upwards in elevation to 5,100 meters on the southern slopes of the Himalayas (Lathrop, 2003). Reproduction is typically biphasic with inguinal amplexus and a Type IV tadpole. Although our morphological data for this group were restricted to *Megophrys montana* and *Leptobrachium hasseltii*, our preferred tree (figs. 50, 54) suggests that synapomorphies subtending these two species are likely synapomorphies of Megophryidae. Characters of morphology (from Haas, 2003) that optimize on this branch are (1) m. subarcualis rectus accessorius present (Haas 32.1); and (2) suspensorium low (Haas 71.2).

In addition, Ford and Cannatella (1993) suggested that the following are synapomorphies for Megophryidae: (1) complete or almost complete absence of ceratohyals in adults; (2) intervertebral cartilages with an ossified center; and (3) paddle-shaped tongue.

SYSTEMATIC COMMENTS: The recognition of *Xenophrys* as a genus distinct from *Megophrys* (e.g., Ohler et al., 2002) appears justified, inasmuch as *Megophrys* and *Xenophrys* do not appear to be each other's closest relatives, with *Megophrys* most closely related to *Ophryophryne*. The subfamilies [101] Megophryinae Bonaparte, 1850, and Leptobrachiinae Dubois, 1980, were not rejected by our molecular data (fig. 54). Nevertheless, although Megophryinae has apomorphies (an umbelliform oral disc in larvae and a very large tubercle starting at the base and extending out and onto the first finger [Lathrop, 2003]), ''Leptobrachiinae'' is recognized solely on the basis of plesiomorphies (lacking the umbelliform mouth and the large tubercle extending out on the finger), so there is little point in recognizing these taxa. Moreover, Delorme and Dubois' (2001; fig. 20) own analysis rejects leptobrachiine monophyly. Beyond rejecting the monophyly of Leptobrachiinae, Delorme and Dubois' (2001; fig. 20) cladogram suggests that the currently recognized nominate subgenus of the genus *Scutiger*, *Scutiger* (paraphyletic with respect to *Aelurophryne*), must be rejected, as must the monotypic subgenus *Aelurolalax* of genus *Oreolalax* that renders the subgenus *Oreolalax* paraphyletic.

[105] NEOBATRACHIA REIG, 1958

Neobatrachia Reig, 1958: 115. (See nomenclatural comment in appendix 6.)

IMMEDIATELY MORE INCLUSIVE TAXON: [91] Acosmanura Savage, 1973.

SISTER TAXON: [92] Anomocoela Nicholls, 1916.

RANGE: Coextensive with Anura, excluding New Zealand.

CONCEPT AND CONTENT: Neobatrachia Reig, 1958, is conceived here as it was originally intended by Reig (1958), a monophyletic group of all frogs excluding his Archaeobatrachia (Leiopelmatidae, Discoglossidae [sensu lato], Pipidae, Rhinophrynidae, and Pelobatidae [sensu lato]). In other words, it is a monophyletic group composed of our [106] Heleophrynidae Noble, 1931, and [107] Phthanobatrachia **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Neobatrachia includes approximately 96% of the diversity of frogs, most of which have completely ossified vertebrae. Only one character in our analysis (from Haas, 2003) optimizes on this branch: m. sartorius discrete from the m. semitendinosus (Haas 153.1). Although many authors (e.g., Ford and Cannatella, 1993; Trueb, 1993) have reported the presence of palatine bones as a synapomorphy of Neobatrachia, it is reasonably clear (Haas, 2003; see also Acosmanura account) that this characteristic is a synapomorphy of Acosmanura. Nevertheless, one could argue that

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the developmentally distinct palatine of neobatrachians is a synapomorphy of this group, although polarization between the anomocoelan condition and the neobatrachian condition has to be made on the basis of considerations other than outgroup comparison.

Ford and Cannatella (1993) suggested these additional characters as synapomorphies of the Neobatrachia: (1) third distal carpal fused to other carpals (convergent in *Pelodytes*); (2) accessory head of m. adductor longus present; and (3) parahyoid ossification present. In addition, there are substantial numbers of molecular synapomorphies (appendix 5) that support recognition of this taxon.

COMMENT: Neobatrachia in our sense is equivalent to the Recent content of epifamily Ranoidia Rafinesque, 1814, of Dubois (2005).

[106] FAMILY: HELEOPHRYNIDAE NOBLE, 1931

Heleophryninae Noble, 1931: 498. Type genus: *Heleophryne* Sclater, 1898.

Heleophrynidae Hoffman, 1935: 2. Type genus: *Heleophryne* Sclater, 1898. Coined as new family apparently in ignorance of Noble, 1931.

IMMEDIATELY MORE INCLUSIVE TAXON: [105] Neobatrachia Reig, 1958.

SISTER TAXON: [107] Phthanobatrachia **new taxon.**

RANGE: Mountainous areas of the Cape and Transvaal regions of South Africa, from sea level to about 3,000 meters elevation.

CONTENT: ***Heleophryne*** Sclater, 1898.

CHARACTERIZATION AND DIAGNOSIS: Heleophrynidae is composed of moderately small treefrog-like anurans with expanded triangular digit tips, a typically biphasic life history, prolonged larval development, Type IV larvae, and inguinal amplexus, that live in rocky, high-gradient habitats (J.D. Lynch, 1973; Passmore and Carruthers, 1979). Considerable numbers of morphological characters (from Haas, 2003) in our analysis optimized on this branch: (1) m. transversus ventralis IV present (Haas 22.1); (2) interbranchial septum IV musculature invaded by lateral fibers of m. subarcualis rectus II–IV (Haas 29.1); (3) m. subarcualis rectus accessorius present (Haas 32.1); (4) processus ascendens thin (Haas 72.1); (5) processus muscularis absent (Haas 79.0); (6) partes corpores forming medial body (Haas 87.2); (7) adrostral cartilage very large and elongate (Haas 90.2); (8) admandibular cartilage present (Haas 95.1); (9) free basihyal absent (Haas 105.0); and (10) processus branchialis closed (Haas 114.1). In addition, Ford and Cannatella (1993) suggested that the loss of keratinous jaw sheaths in the larvae is a synapomorphy of this group. Channing (2003) corrected this, noting that larvae lack keratinized jaw sheaths, except for *Heleophryne rosei*, which retains the lower jaw sheath. Channing also noted that during the reproductive aquatic period, males develop folds of loose skin that increase the respiratory surface. Both of these characteristics are likely apomorphic.

[107] PHTHANOBATRACHIA **NEW TAXON**

ETYMOLOGY: Phthano- (Greek: anticipate, do first) + batrachos (Greek: frog). We propose this name to honor Arnold G. Kluge and James S. Farris's contribution to phylogenetics generally and to amphibian systematics specifically, especially with reference to the paper that started modern quantitative phyletics—Kluge and Farris, 1969).

IMMEDIATELY MORE INCLUSIVE TAXON: [105] Neobatrachia Reig, 1958.

SISTER TAXON: [106] Heleophrynidae Noble, 1931.

RANGE: Coextensive with Anura, excluding New Zealand.

CONCEPT AND CONTENT: Phthanobatrachia is a monophyletic group composed of all neobatrachians, excluding Heleophrynidae Noble, 1931. In other words, it is composed of our [314] Hyloides **new taxon** and [108] Ranoides **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Morphological characters (from Haas, 2003) that optimize on this branch are (1) upper marginal papillae with a broad diastema (Haas 8.1; reversed in several subsidiary lineages); (2) m. interhyoideus posterior present (Haas 23.1); (3) m. diaphragmatopraecordialis present (Haas 25.1); (4) m. constrictor branchialis I absent (Haas 27.0); and (5) secretory ridges present (Haas 136.1).

COMMENTS ON CHARACTER DISTRIBUTIONS: Another likely synapomorphy at this level is

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widely-separated atlantal cotyles (= Type I of J.D. Lynch, 1971, 1973), although apparently reversed in some taxa (e.g., Limnodynastidae, Bufonidae, part of Cycloramphidae [*Rhinoderma*, *Hylorina*, *Alsodes*, *Eupsophus*, *Proceratophrys*, *Odontophrynus*], and part of Ceratophryidae [*Ceratophrys*, *Lepidobatrachus*]).

Presence of an outer metatarsal tubercle (J.D. Lynch, 1971, 1973) is coherent on our tree and also *may* be a synapomorphy at the level of Phthanobatrachia, because outer metatarsal tubercles are never found outside of this clade, although clearly this character has been lost and regained several times within Phthanobatrachia. Optimization of this character requires more work, but we suggest that it will provide additional evidence of relationship. Our current understanding is that it is absent in Batrachophrynidae, except for *Batrachophrynus*; absent in Limnodynastidae, except for *Limnodynastes tasmaniensis* and *Adelotus*; and present in Myobatrachidae, except for six species of *Crinia* and *Taudactylus*, and, presumably, *Mixophyes* and *Rheobatrachus*. Within Meridianura they are present, with the exclusion of some Hylidae, Centrolenidae, *Rhinoderma* (Cycloramphidae), and *Lepidobatrachus* (Ceratophryidae). Interestingly, within Ranoides the trends are much less clear and much less well documented, the tubercle being absent in most Arthroleptidae (including Astylosternidae), most Hyperoliidae, Hemisotidae, and Rhacophoridae, some Microhylinae, Cophylinae, *Phrynomerus*, and some Ranidae (J.D. Lynch, 1973).

[314] HYLOIDES **NEW TAXON**

ETYMOLOGY: Hyloides is, for the most part, Hyloidea of traditional usage, excluding Heleophrynidae (as suggested by Haas, 2003), removed from regulated nomenclature, and with the ending changed so as to not imply family-group regulation.

IMMEDIATELY MORE INCLUSIVE TAXON: [107] Phthanobatrachia **new taxon.**

SISTER TAXON: [108] Ranoides **new taxon.**

RANGE: Coextensive with Anura, excluding New Zealand.

CONCEPT AND CONTENT: Hyloides as conceived here is the monophyletic group composed of arciferal (at least plesiomorphically within any of the groups) phthanobatrachian frogs. In other words, it is composed of [315] Sooglossidae Noble, 1931, and [318] Notogaeanura **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Only one morphological character in our analysis optimizes on this branch: m. diaphragmatopraecordialis meeting m. interhyoideus posterior in a smooth arch (Haas 26.0). Procoely may also be a synapomorphy, but with reversals to an anomocoelous condition in at least some taxa (e.g., Myobatrachidae). Nevertheless, substantial numbers of molecular synapomorphies support this clade (appendix 5).

COMMENT: Hyloides in our sense is not coextensive with the Recent content of Hyloidea of Dubois (1983), which included Heleophrynidae; of Dubois (2005), which excluded Heleophrynidae and Sooglossidae; or of Hyloidea (sensu stricto) of Biju and Bossuyt (2003) and Darst and Cannatella (2004), which excluded Batrachophrynidae (by implication), Limnodynastidae, Myobatrachidae, and Sooglossidae, rendering Hyloidea (sensu stricto) of these authors coextensive with our [348] Nobleobatrachia.

[315] FAMILY: SOOGLOSSIDAE NOBLE, 1931

Sooglossinae Noble, 1931: 494. Type genus: *Sooglossus* Boulenger, 1906.

Nasikabatrachidae Biju and Bossuyt, 2003: 711. Type genus: *Nasikabatrachus* Biju and Bossuyt, 2003. **New synonym.**

IMMEDIATELY MORE INCLUSIVE TAXON: [314] Hyloides **new taxon.**

SISTER TAXON: [318] Notogaeanura **new taxon.**

RANGE: Granitic islands of the Seychelles and the Western Ghats of South India.

CONTENT: ***Nasikabatrachus*** Biju and Bossuyt, 2003; ***Sooglossus*** Boulenger, 1906 (including ***Nesomantis*** Boulenger, 1909; see Systematic Comments and appendix 7).

CHARACTERIZATION AND DIAGNOSIS: Sooglossids are tiny to moderate-size frogs with weakly expanded digits in *Sooglossus* and unexpanded digits in *Nasikabatrachus*. The species of *Sooglossus* and *Nesomantis*, that are known, have inguinal amplexus and have either endotrophic larvae or direct develop-

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ment (Nussbaum, 1980; Thibaudeau and Altig, 1999), whereas *Nasikabatrachus* has free-living exotrophic larvae (Dutta et al., 2004). *Sooglossus sechellensis* is biphasic with presumably endotrophic larvae; *Nesomantis* life history is unknown, but presumably has direct development as no larvae have ever been found; and *Sooglossus gardineri* has direct development (Nussbaum, 1980).

This taxon was not studied by Haas (2003), so none of our morphological characters could optimize on this branch. Nevertheless, substantial numbers of molecular synapomorphies exist (appendix 5). Ford and Cannatella (1993) suggested the following to be synapomorphies of Sooglossidae, but because these characters have not been reported for *Nasikabatrachus*, they may only be synapomorphies of *Sooglossus* + *Nesomantis* and should be verified for *Nasikabatrachus*, as well: (1) tarsal sesamoid bones present (see Nussbaum, 1982, for description and discussion of differences among sesamoids among several taxa); (2) ventral gap in cricoid ring present (the universality of this characteristic is highly speculative); (3) m. semitendinosus passing dorsal to m. gracilis (level of universality highly speculative); (4) alary (= anterolateral) process of hyoid winglike (the level of universality speculative); and (5) sphenethmoid divided. In addition, J.D. Lynch (1973) reported the columella as absent in sooglossids, although he did not examine *Nasikabatrachus* (not discovered for another 30 years). Biju and Bossuyt (2003) reported the tympanum in *Nasikabatrachus sahyadrensis* as ''inconspicuous'', and Dutta et al. (2004) reported it to be absent in their unnamed species of *Nasikabatrachus*. The condition of the columella in *Nasikabatrachus* remains unreported. J.D. Lynch (1973) also reported Sooglossidae as exhibiting an ossified omosternum, which would be a synapomorphy at this level of universality.

SYSTEMATIC COMMENTS: Nussbaum et al. (1982) and Green et al. (1989) discussed the phylogeny of the Seychellean taxa (i.e., not including *Nasikabatrachus*) and suggested that *Sooglossus* is paraphyletic with respect to *Nesomantis*, although outgroup comparison for this suggestion was lacking and the evidence supporting this view rests on the assumption that a complex call (shared by *Sooglossus sechellensis* and *Nesomantis thomasseti*) is apomorphic (Nussbaum et al., 1982), as well as on the basis of allozymic distance measures (Green et al., 1988). Nevertheless, there has never been *any* evidence suggested to support the monophyly of the three species of *Sooglossus* with respect to *Nesomantis*, so the current taxonomy suggests a level of knowledge that is not warranted. For this reason we place *Nesomantis* into the synonymy of *Sooglossus*. We could have placed quotation marks around ''*Sooglossus*'' to note the lack of phylogenetic evidence, but this seems to us to be an extreme step to preserve a monotypic genus (i.e., *Nesomantis*). (This synonymy affects only one species name, *Nesomantis thomasseti* Boulenger, 1909, which becomes *Sooglossus thomasseti* [Boulenger, 1909].)

Because preservation of Nasikabatrachidae as a family would require us to have two sister families, each composed of monotypic genera, we consider it beneficial for taxonomic efficiency to place Nasikabatrachidae into the synonymy of Sooglossidae. Our enlarged Sooglossidae is identical to Sooglossoidea of Dubois (2005).

[318] NOTOGAEANURA **NEW TAXON**

ETYMOLOGY: Noto- (Greek: southern) + Gaea (Greek: earth) + anoura (Greek: tailless, i.e., frog), denoting the Gondwanaland origin of this taxon.

IMMEDIATELY MORE INCLUSIVE TAXON: [314] Hyloides **new taxon.**

SISTER TAXON: [315] Sooglossidae Noble, 1931.

RANGE: Coextensive with Anura, excluding New Zealand and the Seychelles.

CONCEPT AND CONTENT: Notogaeanura is a monophyletic taxon composed of all hyloid taxa except Sooglossidae Noble, 1931. In other words, it is composed of our [319] Australobatrachia **new taxon** and [348] Nobleobatrachia **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: None of our morphological characters optimize at this level of universality, so its diagnosis is based completely on molecular data, which

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are decisive. Unambiguous molecular transformations are listed in appendix 5.

[319] AUSTRALOBATRACHIA **NEW TAXON**

ETYMOLOGY: Australo- (Greek: southern) + batrachos (Greek: frog), denoting the southern continental distribution of these frogs, primarily in Australia and New Guinea, with outliers in South America, in Chile and Peru.

IMMEDIATELY MORE INCLUSIVE TAXON: [318] Notogaeanura **new taxon.**

SISTER TAXON: [348] Nobleobatrachia **new taxon.**

RANGE: New Guinea and Australia; southern Chile and north into southern Andean Peru and Bolivia.

CONCEPT AND CONTENT: Australobatrachia **new taxon** is a monophyletic taxon composed of [320] Batrachophrynidae Cope, 1875, and [321] Myobatrachoidea Schlegel, 1850.

CHARACTERIZATION AND DIAGNOSIS: None of the morphological characters in our analysis optimize unambiguously to this branch because the only exemplar of this group for which we have morphological data is *Limnodynastes peronii*. Therefore, any of the following characters could be synapomorphies of Australobatrachia, Myobatrachoidea, Limnodynastidae, *Limnodynastes*, or some subset of *Limnodynastes*: (1) m. transversus ventralis IV present (Haas 22.1); (2) lateral fibers of m. subarcualis rectus II–IV invade interbranchial septum IV (Haas 29.1); (3) two clearly separate heads of m. subarcualis obliquus originate from ceratobranchialia II and III (Haas 32.1); (4) processus ascendens thin (Haas 72.1); (5) processus muscularis present (Haas 79.0); (6) partes corpores forming medial body (Haas 87.2); (7) adrostral cartilage very large and elongate (Haas 90.2); (8) admandibular cartilage present (Haas 95.1); (9) free basihyal absent (Haas 105.0); (10) commissura proximalis II absent (Haas 110.0); (11) commissura proximalis III absent (Haas 111.0); and (12) processus branchialis closed (Haas 114.1). Unambiguous molecular transformations are listed in appendix 5.

[320] FAMILY: BATRACHOPHRYNIDAE COPE, 1875

Batrachophrynidae Cope, 1875: 9. Type genus: *Batrachophrynus* Peters, 1873.

Calyptocephalellinae Reig, 1960: 113. Type genus: *Calyptocephalella* Strand, 1928. **New synonym.** (See nomenclatural comment in appendix 6.)

IMMEDIATELY MORE INCLUSIVE TAXON: [319] Australobatrachia **new taxon.**

SISTER TAXON: [321] Myobatrachoidea Schlegel, 1850.

RANGE: Southern Chile and north into southern Andean Peru and Bolivia.

CONTENT: *Batrachophrynus* Peters, 1873; ***Caudiverbera*** Laurenti, 1768; ***Telmatobufo*** Schmidt, 1952.

CHARACTERIZATION AND DIAGNOSIS: None of the morphological characters in our analysis optimize on this branch because no part of it was studied by Haas (2003). Nevertheless, Burton (1998a) suggested that the presence of the m. lumbricalis longus digiti III is a synapomorphy (although convergently found in *Heleophryne* and *Petropedetes*). In addition, *Batrachophrynus*, *Caudiverbera*, and *Telmatobufo* share the presence of two origins of the m. lumbricalis brevis digiti III, otherwise unknown outside of Ranoides (e.g., *Cardioglossa*, *Discodeles*, most of Hyperoliidae, Mantellidae [excluding *Aglyptodactylus*], *Petropedetes*, *Phrynomantis*, *Platypelis*, *Plethodonthyla*, Rhacophoridae, *Scotobleps*, and *Trichobatrachus*). See appendix 5 for molecular synapomorphies of *Telmatobufo* + *Caudiverbera*, which we hypothesize are synapomorphies of Batrachophrynidae.

SYSTEMATIC COMMENTS: The association of *Batrachophrynus* with Calyptocephalellini is arguable, *Batrachophrynus* more traditionally having been allied with *Telmatobius* (Laurent, 1983; Sinsch and Juraske, 1995; Sinsch et al., 1995), although this association seems to have been assumed because of overall similarity. (Of course, both *Caudiverbera* and *Telmatobufo* had also been associated with *Telmatobius* [J.D. Lynch, 1971].) J.D. Lynch (1971: 26) noted that *Caudiverbera* and *Batrachophrynus* (as well as *Odontophrynus* and *Telmatobius*) have dextral larval vent tubes, possibly an apomorphy. Another character is pupil shape, vertical in *Caudiverbera* and *Telmatobufo* (presumably the apomorphic condition at this level of universality) and horizontal in *Batrachophrynus*.

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Telmatobufo and *Caudiverbera* exhibit the condition of the trigeminal nerve passing medial to the m. adductor mandibulae (the ''E'' condition); the condition is unknown in *Batrachophrynus*. This characteristic is otherwise known sporadically in *Ceratophrys* and *Lepidobatrachus*, some bufonids, *Craugastor*, *Mixophyes*, some hyperoliids, most microhylids, a few ranids, rhacophorids, *Rhinophrynus*, and in *Sooglossus thomasseti* (J.D. Lynch, 1986). We regard this condition as a likely synapomorphy of Batrachophrynidae (or minimally *Caudiverbera* + *Telmatobufo*), although the distribution of this feature across the anuran tree requires further study.

[321] SUPERFAMILY: MYOBATRACHOIDEA SCHLEGEL, 1850

IMMEDIATELY MORE INCLUSIVE TAXON: [319] Australobatrachia **new taxon.**

SISTER TAXON: [320] Batrachophrynidae Cope, 1875.

RANGE: Australia and New Guinea.

CONTENT: [322] Limnodynastidae Lynch, 1971, and [334] Myobatrachidae Schlegel, 1850.

CHARACTERIZATION AND DIAGNOSIS: See the characterization and diagnosis of Australobatrachia for morphological characters that may optimize on this branch with further study. At present, there are no morphological characters that can be documented to optimize on this branch so justification for recognizing this taxon is based entirely on molecular evidence (listed in appendix 5).

SYSTEMATIC COMMENTS: We recognize two families within Myobatrachoidea, corresponding substantially to Limnodynastidae and Myobatrachidae of previous usage (Zug et al., 2001; Davies, 2003a, 2003b), differing mildly only in the transfer of *Mixophyes* from Limnodynastidae to Myobatrachidae and the firm attachment of *Rheobatrachus* (formerly Rheobatrachidae) to Myobatrachidae. See those accounts for further discussion. Haas (2003) suggested a number of morphological characters that optimize on his terminal taxon, *Limnodynastes peronii*. Because this was the only myobatrachoid in that study, all of these characters might be synapomorphies of various monophyletic groups within this taxon. Hypothesized molecular synapomorphies are summarized in appendix 5. Further study is needed.

[322] FAMILY: LIMNODYNASTIDAE LYNCH, 1971

Limnodynastini J.D. Lynch, 1971: 83. Type genus: *Limnodynastes* Fitzinger, 1843.

IMMEDIATELY MORE INCLUSIVE TAXON: [321] Myobatrachoidea Schlegel, 1850.

SISTER TAXON: [334] Myobatrachidae Schlegel, 1850.

RANGE: Australia and New Guinea, including the Aru Islands.

CONTENT: ***Adelotus*** Ogilby, 1907; ***Heleioporus*** Gray, 1841; ***Lechriodus*** Boulenger, 1882; ***Limnodynastes*** Fitzinger, 1843; ***Neobatrachus*** Peters, 1863; ***Notaden*** Günther, 1873; ***Opisthodon*** Steindachner, 1867 (see Systematic Comments and appendix 7); *Philoria* Spencer, 1901 (including ***Kyarranus*** Moore, 1958).

CHARACTERIZATION AND DIAGNOSIS: Limnodynastids are predominantly small to moderately-sized toad-like terrestrial frogs. Amplexus is inguinal, and with the exception of *Neobatrachus* and *Notaden*, all species are foam-nesters (Martin, 1967).

See ''Characterization and diagnosis'' of Australobatrachia for morphological characters that may optimize on this branch. Ford and Cannatella (1993) suggested the following to be a morphological synapomorphy of Limnodynastidae: connection between the m. submentalis and m. intermandibularis. But, with the transfer of *Mixophyes* to Myobatrachidae on the basis of molecular evidence, this morphological character requires verification. Davies (2003a) noted that Limnodynastidae are united by the character of fusion of the first two vertebrae. Molecular evidence is decisive in support of this taxon; see appendix 5 for diagnostic transformations.

SYSTEMATIC COMMENTS: Our results suggest strongly that *Limnodynastes* as currently formulated is polyphyletic. Schäuble et al. (2000) provided a tree of species of *Limnodynastes* which corresponds in some ways with our results, but which differs in others. Their maximum-likelihood results, based on 450 bp of 16S mtDNA and 370 bp of ND4, suggest that *Adelotus* sits within the *Limnodynastes ornatus* group (*L. ornatus* and *L.*

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spenceri), and that this overall group forms the sister taxon of the remaing *Limnodynastes* in the arrangement *Limnodynastes dorsalis* group + (*L. peronii* group + *L. salmini* group). Our results, based on denser taxon sampling and substantially more data, place *Adelotus* outside of *Limnodynastes* (sensu lato), but place *Neobatrachus*, *Notaden*, *Lechriodus*, and *Heleioporus* within a paraphyletic *Limnodynastes*, or, alternatively, place *Limnodynastes ornatus* as the sister taxon of *Lechriodus fletcheri*, and far away from *Limnodynastes* (including *Megistolotis* as a synonym as suggested by Schäuble et al., 2000), which is the sister taxon of *Heleioporus*. In order to alleviate the polyphyly of *Limnodynastes*, we resurrect the name *Opisthodon* Steindachner, 1867 (type species: *Opisthodon frauenfeldi* Steindachner, 1867, by monotypy [= *Discoglossus ornatus Gray, 1842*]) for the former *Limnodynastes ornatus* group (i.e., *Opisthodon ornatus* [Gray, 1842] and *O. spenceri* [Parker, 1940]). This renders *Opisthodon* as the sister taxon of *Lechriodus*, and *Limnodynastes* as the sister taxon of *Heleioporus*, assuming that both *Opisthodon* and *Lechriodus* are monophyletic. We suggest that the molecular characters that optimize on the branch labeled *Limnodynastes ornatus* are synapomorphies of *Opisthodon* (appendix 5). See appendix 7 for new combinations produced by this generic change.

J.D. Lynch (1971: 76) distinguished two tribes within his Cycloraninae (equivalent to our Limnodynastinae with the removal of *Cyclorana* to Pelodryadinae): Cycloranini (*Cyclorana*, *Heleioporus*, *Mixophyes*, *Neobatrachus*, and *Notaden*), characterized by laying eggs in dry burrows in a foam nest, and Limnodynastini (*Adelotus*, *Lechriodus*, *Limnodynastes*, and *Philoria*), which lay their eggs in water or in moist terrestrial sites. When these characteristics are optimized on our cladogram, they provide a rather confusing picture of life history evolution in limnodynastine frogs, and our data do not support recognition of these taxa.

[334] FAMILY: MYOBATRACHIDAE SCHLEGEL, 1850

Myobatrachinae Schlegel *In* Gray, 1850b: 10. Type genus: *Myobatrachus* Schlegel, 1850.

Uperoliidae Günther, 1858b: 346. Type genus: *Uperoleia* Gray, 1841.

Criniae Cope, 1866: 89. Type genus: *Crinia* Tschudi, 1838.

Rheobatrachinae Heyer and Liem, 1976: 11. Type genus: *Rheobatrachus* Liem, 1973.

IMMEDIATELY MORE INCLUSIVE TAXON: [321] Myobatrachoidea Schlegel, 1850.

SISTER TAXON: [322] Limnodynastidae Lynch, 1971.

RANGE: Australia and New Guinea.

CONTENT: ***Arenophryne*** Tyler, 1976; ***Assa*** Tyler, 1972; ***Crinia*** Tschudi, 1838; ***Geocrinia*** Blake, 1973; ***Metacrinia*** Parker, 1940; ***Mixophyes*** Günther, 1864; ***Myobatrachus*** Schlegel, 1850; ***Paracrinia*** Heyer and Liem, 1976; ***Pseudophryne*** Fitzinger, 1843; ***Rheobatrachus*** Liem, 1973; ***Spicospina*** Roberts, Horwitz, Wardell-Johnson, Maxson, and Mahony, 1997; ***Taudactylus*** Straughan and Lee, 1966; ***Uperoleia*** Gray, 1841.

CHARACTERIZATION AND DIAGNOSIS: Myobatrachids are predominantly small frogs of heterogeneous appearance. All are assumed to have inguinal amplexus, except *Mixophyes* (which has axillary amplexus). Davies (2003b) noted that although *Mixophyes* had traditionally been associated with Limnodynastidae, its placement there was always problematic due to its lack of most limnodynastinae characteristics. All myobatrachids are assumed to have a typical biphasic life history (Martin, 1967). None of our morphological characters optimize on this branch because no member of this taxon was studied by Haas (2003), although Ford and Cannatella (1993) suggested the following to be a likely synapomorphy: (1) broad alary process of premaxilla (absent in *Mixophyes*, but also present in the leptodactylids *Adenomera*, *Pseudopaludicola*, and *Physalaemus* [in the sense of including *Engystomops* and *Eupemphix*]). In our topology, this character could be reversed in *Mixophyes* or convergent in *Rheobatrachus* and the clade bracketed by *Taudactylus* and *Arenophryne*. Regardless, the molecular evidence appears to be decisive (see appendix 5 for molecular synapomorphies for branch 334).

SYSTEMATIC COMMENT: We expected *Myobatrachus* and *Arenophryne* to obtain as sister taxa because they both are head-first burrowers in sandy soil (Tyler, 1989), with

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all of the concomitant morphological features that are associated with this behavior.

[348] NOBLEOBATRACHIA **NEW TAXON**

ETYMOLOGY: Noble (Gladwyn K. Noble) + batrachos (Greek: frog), to note one of the most influential herpetologists of the twentieth century and the father of modern integrative herpetology. Although Noble died relatively young, at age 47 (Adler, 1989), his contributions to amphibian systematics, life history, comparative anatomy, and experimental biology remain important milestones.

IMMEDIATELY MORE INCLUSIVE TAXON: [318] Notogaeanura **new taxon.**

SISTER TAXON: [319] Australobatrachia **new taxon.**

RANGE: Coextensive with Anura, excluding New Zealand and the Seychelles.

CONCEPT AND CONTENT: Nobleobatrachia is a monophyletic group containing Hemiphractidae Peters, 1862, and [349] Meridianura **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Optimization of claw-shaped terminal phalanges and intercalary elements is ambiguous, placed on this branch only under accelerated optimization. Under delayed optimization, however, the characters appear convergently in Hemiphractidae and in Cladophrynia. The character of bell-shaped gills optimizes on Meridianura, with a reversal at Athesphatanura. Nevertheless, the bulk of evidence for the existence of this clade is molecular; see appendix 5 for molecular synapomorphies. The length of the 28S fragment likely becomes much longer (greater than 740 bp) at this branch than found below this point (see appendix 3), although this must be confirmed by examining the 28S fragment in *Hemiphractus*.

FAMILY: HEMIPHRACTIDAE PETERS, 1862

Hemiphractidae Peters, 1862: 146. Type genus: *Hemiphractus* Wagler, 1828.

IMMEDIATELY MORE INCLUSIVE TAXON: [348] Nobleobatrachia **new taxon.**

SISTER TAXON: [349] Meridianura **new taxon.**

RANGE: Panama; Pacific slopes of Colombia and northwestern Ecuador; Brazil, Colombia, Ecuador, Peru, and Bolivia in the upper Amazon Basin to the Amazonian slopes of the Andes.

CONTENT: ***Hemiphractus*** Wagler, 1828.

CHARACTERIZATION AND DIAGNOSIS: None of the morphological characters in our analysis optimize on this branch because, as these species are direct-developers and therefore were not studied by Haas (2003). Nevertheless, *Hemiphractus*/Hemiphractidae is easily diagnosed by its wild appearance and triangular skull. Like most basal species of Meridianura, *Hemiphractus* exhibits direct development and bears the developing embryos on the back until hatching, but unlike species of Amphignathodontidae and Cryptobatrachidae, it does not have a dorsal pouch in which to carry developing embryos (Noble, 1931).

SYSTEMATIC COMMENT: *Hemiphractus* has two pairs of bell-shaped gills in embryos, derived from branchial arches I and II (del Pino and Escobar, 1981; Mendelson et al., 2000), as do members of Cryptobatrachidae and Amphignathodontidae (except for *Flectonotus pygmaeus*). This suggests that the character of bell-shaped gills optimizes on Meridianura, with a reversal in Athesphatanura.

[349] MERIDIANURA **NEW TAXON**

ETYMOLOGY: Meridianus (Greek: southern) + anoura (Greek: tailless, i.e., frog), referencing the South American center of distribution of this worldwide group.

IMMEDIATELY MORE INCLUSIVE TAXON: [348] Nobleobatrachia **new taxon.**

SISTER TAXON: Hemiphractidae Peters, 1862.

RANGE: Coextensive with Anura, excluding New Zealand and the Seychelles.

CONCEPT AND CONTENT: Meridianura is a monophyletic group containing [350] Brachycephalidae Günther, 1858, and [366] Cladophrynia **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: No morphological characters in our analysis optimize on this branch, and no authors have suggested morphological characters that would optimize here. Nevertheless, it is well-corroborated by molecular characters (see appendix 5 for molecular synapomorphies). Meridianura is characterized by a length of the 28S DNA fragment in excess of 740 bp

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(appendix 3). This may be plesiomorphic, shared with Sooglossidae and reversed in Australobatrachia, but long 28S molecules are characteristic nonetheless.

[350] FAMILY: BRACHYCEPHALIDAE GÜNTHER, 1858

Brachycephalina Günther, 1858a: 321. Type genus: *Brachycephalus* Fitzinger, 1826.

Cornuferinae Noble, 1931: 521. Type genus: *Cornufer* Tschudi, 1838.

Eleutherodactylinae Lutz, 1954: 157. Type genus: *Eleutherodactylus* Duméril and Bibron, 1841.

IMMEDIATELY MORE INCLUSIVE TAXON: [349] Meridianura **new taxon.**

SISTER TAXON: [366] Cladophrynia **new taxon.**

RANGE: Tropical North and South America; Antilles.

CONTENT: *Adelophryne* Hoogmoed and Lescure, 1984; *Atopophrynus* Lynch and Ruiz-Carranza, 1982; ***Barycholos*** Heyer, 1969; ***Brachycephalus*** Fitzinger, 1826; *Dischidodactylus* Lynch, 1979; ***Craugastor*** Cope, 1862 (see Systematic Comments and appendix 7); ''***Eleutherodactylus***'' Duméril and Bibron, 1841 (see Systematic Comments and appendix 7); ''***Euhyas***'' Fitzinger, 1843 (see Systematic Comments and appendix 7); *Euparkerella* Griffiths, 1959; *Geobatrachus* Ruthven, 1915; *Holoaden* Miranda-Ribeiro, 1920; ***Ischnocnema*** Reinhardt and Lütken, 1862 ''1861''; ''***Pelorius***'' Hedges, 1989 (see Systematic Comments and appendix 7); ***Phrynopus*** Peters, 1873; *Phyllonastes* Heyer, 1977; *Phyzelaphryne* Heyer, 1977; ***Syrrhophus*** Cope, 1878 (including ***Tomodactylus*** Günther, 1900; see Systematic Comments and appendix 7).

CHARACTERIZATION AND DIAGNOSIS: Brachycephalids are predominantly leaf-litter frogs with axillary amplexus and direct development (J.D. Lynch, 1971, 1973). None of the morphological characters in our analysis optimized on this branch due to incomplete taxon sampling in our morphological data set (from Haas, 2003, who restricted his study to groups with larvae). Nevertheless, Brachycephalidae is characterized by possessing very large terrestrial eggs and exhibiting direct development in all species so far examined (J.D. Lynch, 1971), with the exception of *Eleutherodactylus jasperi*, which exhibits the further derived character of ovoviviparity (Drewery and Jones, 1976). In addition, embryonic egg teeth have been reported for *Brachycephalus* and *Eleutherodactylus* (Duellman and Trueb, 1986; Pombal, 1999). Additional survey may find that this characteristic is synapomorphic for some larger group; is likely coextensive with direct development in this group; and therefore is possibly synapomorphic for the entire Brachycephalidae. For molecular transformations associated with this taxon see appendix 5.

SYSTEMATIC COMMENTS: We find nominal *Eleutherodactylus* (sensu lato—subtended by branch 350) to be in the same situation as nominal ''*Hyla*'' prior to its partition by Faivovich et al. (2005) into several tribes and many new genera—that of a gigantic and ill-defined group where the enormity of the taxon and lack of understanding of its species diversity has largely restricted taxonomic work for the past 45 years to two individuals (John D. Lynch and Jay M. Savage)[28]. Nevertheless, the current taxonomy of *Eleutherodactylus* (sensu lato, subdivided into the taxa *Craugastor*, *Euhyas*, *Eleutherodactylus* [sensu stricto], *Pelorius*, and *Syrrhophus*) extends from the work of Hedges (1989) in which he named *Pelorius* for the *Eleutherodactylus inoptatus* group and placed *Tomodactylus* as a synonym of *Syrrhophus* and his enlarged *Syrrhophus* as a subgenus of *Eleutherodactylus*.

Hedges' (1989) systematic arrangement was based on an allozymic study of six loci (223 alleles) focused on West Indian species, with a narrative discussion of evidence supporting recognition of non-West Indian taxa. In his UPGMA tree, Hedges' Group I (native Jamaican species, except *E. nubicola*) appears monophyletic. His Group II (*E. ricordii* group) obtained as polyphyletic, with two groups placed far from each other, one group (paraphyletic to group I) and another group much more basal. Group III (*E. auriculatus* group) obtained as polyphyletic, with both a basal and a ''central'' monophyletic group. Group IV (*E. inoptatus* group) obtained as a

[28] G.A. Boulenger (1882), in his extraordinarily influential ''Catalogue of the Batrachia Salientia'', had to deal with only about 50 species of what is now *Eleutherodactylus* (sensu lato). Life was *much* simpler then.

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monophyletic group. In the same paper a Distance Wagner tree also obtained Group I as monophyletic, Group II as polyphyletic, Group III as polyphyletic, and IV as monophyletic.

After performing these analyses, Hedges rejected the idea that any significant evolutionary meaning attached to these results, and suggested that Groups I–IV are each monophyletic on the basis of possessing unique alleles (no overall analysis of presence–absence provided): Group I (Icd^{q2}), Group II (Pgm^{jB}), Group III (Icd^{f1}), Group IV (Icd^{p5}, Lgl^{a1}, Pgm^{0}). (This survey of loci was based solely on Antillean taxa, without any sampling of the nominal subgenera *Craugastor* or *Syrrhophus*, and with very limited sampling of mainland species of subgenus *Eleutherodactylus*.) Hedges then considered Group I and Group II together to form his subgenus *Euhyas*; the rationale for this unification was not provided. His Group III he regarded as the *E. auriculatus* section of a presumed paraphyletic subgenus *Eleutherodactylus* (referred to later as *Eleutherodactylus* [sensu stricto]), and Group IV he considered to be his monophyletic subgenus *Pelorius*. In subsequent discussion, he noted that J.D. Lynch (1986) had provided a morphological synapomorphy for a group that Hedges had not examined, *Craugastor* (the mandibular ramus of the trigeminal nerve lying medial [deep] to the m. adductor mandibulae externus superficialis, the ''E'' condition of Starrett in J.D. Lynch, 1986), which Hedges also accepted as a subgenus. Hedges briefly discussed why he rejected Savage's (1987) contention that *Tomodactylus* and *Syrrhophus* are distantly related, and then regarded them as synonymous (as *Syrrhophus*) and considered *Syrrhophus* to be a subgenus of *Eleutherodactylus*. As with other authors before and since, Hedges provided no evidence for the monophyly of *Eleutherodactylus* (sensu lato) with respect to other eleutherodactyline genera. J.D. Lynch and Duellman (1997) disputed some assignments to *Euhyas*, but otherwise accepted Hedges' arrangement.

Our results showed *Eleutherodactylus* (sensu lato) to be rampantly nonmonophyletic (indicated below by quotation marks surrounding the name), and there is no reason to believe this will not worsen as sampling density increases. In addition to the paraphyly of ''*Eleutherodactylus*'' (sensu lato) with respect to *Brachycephalus*, discussed in ''Results'', we found *Ischnocnema*, *Barycholos*, and *Phrynopus* to be imbedded within it, as was anticipated by Ardila-Robayo (1979).

As regards *Ischnocnema*, J.D. Lynch (1972b: 9) noted its extreme resemblance to species of the *E. binotatus* group and could not eliminate the possibility that *Ischnocnema* represents ''a single morphological divergence of the *binotatus* group of *Eleutherodactylus*''. Our placement of *E. binotatus* and *Ischnocnema quixensis* as sister taxa supports that hypothesis (see below).

The sole basis for recognizing *Phrynopus* as distinct from ''*Eleutherodactylus*'' (sensu lato or sensu stricto) is the absence of expanded digital discs (J.D. Lynch, 1975). Expanded discs are also absent in several species of ''*Eleutherodactylus*'' (sensu stricto), which J.D. Lynch (1994: 201) considered to be evidence that ''*Phrynopus* are simply *Eleutherodactylus* having greatly reduced digital tips''. Our taxon sampling was inadequate to address the relationships among all brachycephalids (i.e., eleutherodactylines) with unexpanded discs and provided only a minimal test of *Phrynopus* monophyly, but our results leave little doubt that *Phrynopus* is nested within ''*Eleutherodactylus*'' (sensu lato).

J.D. Lynch (1980) considered *Barycholos* to be most closely related to *Eleutherodactylus nigrovittatus* (then placed in the *E. discoidalis* group but subsequently transferred to the new *E. nigrovittatus* group by J.D. Lynch, 1989). We did not sample any species of the *E. nigrovittatus* group in this study and therefore did not test the assertion of a *Barycholos–E. nigrovittatus* relationship directly. However, our finding (following Caramaschi and Pombal, 2001) that *Barycholos ternetzi* is nested within ''*Eleutherodactylus*'' (sensu lato) is consistent with J.D. Lynch's hypothesis. We also did not test the monophyly of *Barycholos*, which is characterized by sternal architecture (primarily the occurrence of a calcified sternal style; J.D. Lynch, 1980), but the 3,200 km separation between

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the only known species is strongly suggestive that it may not be monophyletic.

Adelophryne, *Brachycephalus*, and *Euparkerella* share the characteristic of reduction of phalanges in the fourth finger, a presumed synapomorphy, but this does not prevent this group from being imbedded within ''*Eleutherodactylus*'' (sensu lato or sensu stricto)[29], nor are we aware of any other characters that would exclude any of the other nominal genera of Brachycephalidae (including former Eleutherodactylinae) from ''*Eleutherodactylus*'' (sensu lato or sensu stricto).

Given the extent of the demonstrated nonmonophyly and lack of any evidence to distinguish even a phenetic ''*Eleutherodactylus*'' assemblage from other brachycephalid genera, the only immediately available remedy, and the most scientifically conservative action in that it enforces monophyly as *the* organizing principle of taxonomy, would be to place all species of the former Eleutherodactylinae in a single genus (coextensive with our Brachycephalidae), for which the oldest available name is *Brachycephalus* Fitzinger, 1826. But, as much as this appeals to us in principle, we believe that, in this particular case—where knowledge is so limited and species diversity is so great, and where we have sampled so few of the nominal genera of Brachycephalidae (i.e., we have not sampled *Adelophryne*, *Atopophrynus*, *Dischidodactylus*, *Euparkerella*, *Geobatrachus*, *Holoaden*, *Phyllonastes*, or *Phyzelaphryne*)—the scientific payoff from enforcing monophyly is not worth the practical cost of obscuring so much diversity under a single generic name and thereby concealing a considerable number of phylogenetic hypotheses that we would rather advertise in order to attract more work. Moreover, we strongly believe that progress in the scientific understanding of these frogs will be achieved by partitioning ''*Eleutherodactylus*'' into multiple monophyletic genera. Indeed, although evidence for the monophyly of the nominal subgenera is meager or lacking, several less inclusive species groups are delimited by synapomorphy, and we anticipate that several of these will be recognized formally as knowledge increases.

As a preliminary step in this direction, we take the action of treating all of the nominal subgenera of ''*Eleutherodactylus*'' (sensu lato) as genera. (As noted in the ''Review of Current Taxonomy'', Crawford and Smith, 2005, on the basis of molecular data, recently considered *Craugaster* a genus.) As discussed later, this is only partially successful inasmuch as it leaves ''*Eleutherodactylus*'', ''*Euhyas*'', and ''*Pelorius*'' of dubious monophyly or even demonstrated polyphyly (denoted by the quotation marks). Nevertheless, this illuminates the attendant problems of brachycephalid relationships and leaves us in an operationally healthier place than where we had been. That is, the extent of our knowledge of monophyly is represented by the recognition of Brachycephalidae and the demonstrably monophyletic units within it, and other genera are merely provisional units of convenience. (See appendix 7 for new combinations produced by these generic changes.)

Among the previous subgenera of ''*Eleutherodactylus*'' (sensu lato) we found [358] *Syrrhophus* to be monophyletic (tested by inclusion of *S. marnocki* of the *S. marnocki* group of J.D. Lynch and Duellman, 1997, and *S. nitidus* of the *S. nitidus* group of J.D. Lynch and Duellman, 1997; see appendix 5 for molecular synapomorphies). Our sole representative of the Antillean *Euhyas* (represented by *E. planirostris* of the *E. ricordii* group of J.D. Lynch and Duellman, 1997) did not allow us to test the monophyly of this taxon.

In an admittedly weak test of monophyly, we included two species of *Eleutherodactylus* (sensu stricto), both of the *E. binotatus* group: *E. binotatus* and *E. juipoca*. Nevertheless, we refuted the monophyly of ''*Eleutherodactylus*'' (sensu stricto) (and the *E. binotatus* group), showing *E. binotatus* and *E. juipoca* to be more closely related to *Ischnocnema* and *Brachycephalus*, respectively. Although this finding was unanticipated (but see above regarding *Ischnocnema*), no synapomorphy has yet been identi-

[29] Complicating this, *Adelophryne* and *Phyzelaphryne* (Hoogmoed and Lescure, 1984) and at least some members of the *Eleutherodactylus diastema* group (T. Grant, personal obs.) possess conspicuously pointed tips on the toe discs. This suggests that, beyond reformulation of genera within former ''*Eleutherodactylus*'' (sensu lato), some of the other genera will have to be redemarcated.

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fied to unite the species of ''*Eleutherodactylus*'' (sensu stricto) (J.D. Lynch and Duellman, 1997; but see below), and the *E. binotatus* group in particular was delimited only by overall similarity and biogeographic proximity (J.D. Lynch, 1976).

It should be noted that, although no synapomorphy is known for ''*Eleutherodactylus*'' (sensu stricto), J.D. Lynch and Duellman (1997) argued that a large number of its species form a clade delimited by the fifth toe being much longer than the third. Insofar as neither of the species of ''*Eleutherodactylus*'' (sensu stricto) in our sample exhibits this state, this hypothesis remains to be tested critically.

Our results also indicate that *Craugastor*, the so-called Middle American clade delimited by the synapomorphic ''E'' pattern of the m. adductor mandibulae (J.D. Lynch, 1986), was polyphyletic. However, the Middle American species we sampled, representing 5 of the 11 Middle American groups recognized by J.D. Lynch (2000)—*C. bufoniformis*, *C. bufoniformis* group; *C. alfredi*, *C. alfredi* group; *C. augusti*, *C. augusti* group; *C. punctariolus* and *C.* cf. *ranoides*, *C. rugulosus* group; and *C. rhodopis*, *C. rhodopis* group—were monophyletic, and the sole outlier was the Bolivian species ''*Eleuthorodactylus*'' *pluvicanorus*. De la Riva and Lynch (1997) placed this species and ''*E.*'' *fraudator* (grouped subsequently with ''*E.*'' *ashkapara* as the ''*E.*'' *fraudator* group by Köhler, 2000) in *Craugastor* on the basis of its jaw musculature, although they noted that no other species of *Craugastor* is known to extend farther south than northwestern Colombia (e.g., *C. bufoniformis*; J.D. Lynch, 1986; J.D. Lynch and Duellman, 1997), a possible but certainly unexpected biogeographic scenario.

Dissection of the jaw muscles of two specimens of ''*E.*'' *pluvicanorus* (both sides of AMNH A165194, right side of AMNH A165211) showed it to differ from the ''E'' pattern of other species (T. Grant, personal obs.). A single muscle (the m. adductor mandibulae externus) originates on the zygomatic ramus of the squamosal, and the mandibular ramus of the trigeminal nerve (V_3) does not lie lateral (superficial) to it (so it is not the ''S'' pattern), but it does not extend posteroventrad between that muscle and the deeper m. adductor mandibulae posterior (''E'' musculature), either. Instead, V_3 lies entirely posterior to both muscles and runs ventrolaterad toward the jaw—that is, it does not run around the anterior face of the m. adductor mandibulae posterior. J.D. Lynch (1986) reported a similar pattern for one of three specimens of ''*E.*'' *angelicus* and one of two specimens of ''*E.*'' *maussi* (now ''*E.*'' *biporcatus*—Savage and Myers, 2002; the other specimens exhibited the ''E'' condition), and further sampling could show the present observations to be individual anomalies as well. It should also be noted that we have not examined the m. adductor mandibulae of the other species of the ''*E.*'' *fraudator* group. Nevertheless, these observations are reason enough to question the placement of this Bolivian group in *Craugastor*, which is further validated by the strongly supported placement of ''*E.*'' *pluvicanorus* well outside of the *Craugastor* clade. Consequently, we remove the ''*E.*'' *fraudator* group from *Craugastor* and return it to the already demonstrably polyphyletic ''*Eleutherodactylus*'', where J.D. Lynch and McDiarmid (1987) placed ''*E.*'' *fraudator* originally. Another option would be to name the ''*E.*'' *fraudator* group as a new genus. However, the relationship of this group to ''*E.*'' *mercedesae* (which shares with this group the occurrence of a frontoparietal fontanelle; J.D. Lynch and McDiarmid, 1987) and the hundreds of other unsampled brachycephalids is unknown, and given that its placement in ''*Eleutherodactylus*'' (sensu stricto) simply inflicts additional damage on an already polyphyletic genus, we consider it to be premature to name this group at present.

With the exclusion from nominal *Craugastor* of the ''*E.*'' *fraudator* group, which J.D. Lynch (2000) considered to be outside the scope of his paper, *Craugastor* corresponds to the clade subtended (appendix 5) our topology to branch 351, and generally corroborates the topology of *Craugastor* suggested by J.D. Lynch (2000). Within *Craugastor*, J.D. Lynch (2000: 151, his fig. 9) proposed a clade delimited by extreme sexual dimorphism in tympanum size. In our tree *C. alfredi*, *C. augusti*, and *C. bufoniformis*, all with nondimorphic tympana, form a

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basal grade, while *C. punctariolus*, *C. rhodopis*, and *C.* cf. *ranoides*, with strongly sexually dimorphic tympana, are monophyletic.

''*Pelorius*'' has had four allozymic features suggested to be synapomorphies (Hedges, 1989), but as noted earlier, this is based on sparse taxon sampling. J.D. Lynch (1996) suggested not only that are there no morphological synapomorphies of this group, but that there is a lot less than meets the eye in Hedges' (1989) study, particularly with respect to how the allozymic data were interpreted. Alternatively, J.D. Lynch (1996: 153) suggested that ''*Pelorius*'' is united with at least some ''*Euhyas*'' by the possession of an epiotic flange. So, the evidence for ''*Pelorius*'' and ''*Euhyas*'' monophyly seems to be equivocal as well.

In summary, we recognize 16 genera within Brachycephalidae. Based on our limited sampling, we recognize as monophyletic *Craugastor*, *Syrrhophus*, *Phrynopus*, as dubiously monophyletic ''*Euhyas*'' and ''*Pelorius*''; and as demonstrably nonmonophyletic ''*Eleutherodactylus*'' (sensu stricto). We included in our analysis, but did not test the monophyly of *Barycholos*, *Brachycephalus*, and *Ischnocnema*, all of which fall within ''*Eleutherodactylus*'' (sensu stricto). We did not include any representative of *Adelophryne*, *Atopophrynus*, *Dischidodactylus*, *Euparkerella*, *Geobatrachus*, *Phyllonastes*, and *Phyzelaphryne*. (See appendix 7 for new combinations produced by these generic changes.)

[366] CLADOPHRYNIA **NEW TAXON**

ETYMOLOGY: Clados (Greek: branch) + phrynos (Greek: toad), referring to the observation that this taxon is a clade but not obviously united by any morphological synapomorphies.

IMMEDIATELY MORE INCLUSIVE TAXON: [349] Meridianura **new taxon.**

SISTER TAXON: [350] Brachycephalidae Günther, 1858.

RANGE: Coextensive with Anura, excluding New Zealand, Madagascar, and the Seychelles.

CONCEPT AND CONTENT: Cladophrynia is a monophyletic taxon composed of [367] Cryptobatrachidae **new family** and [368] Tinctanura **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: None of the morphological characters in our analysis (from Haas, 2003) optimize on this branch, so its recognition depends entirely on molecular evidence, which is decisive. (See appendix 5 for molecular synapomorphies associated with this taxon.)

[367] FAMILY: CRYPTOBATRACHIDAE **NEW FAMILY**

IMMEDIATELY MORE INCLUSIVE TAXON: [366] Cladophrynia **new taxon.**

SISTER TAXON: [368] Tinctanura **new taxon.**

RANGE: Northern Andes and Sierra Santa Marta of Colombia; moderate to high elevations of the Guayana Shield in Guyana, Venezuela, and adjacent Brazil.

CONTENT: ***Cryptobatrachus*** Ruthven, 1916 (type genus of the family); ***Stefania*** Rivero, 1968 ''1966''.

CHARACTERIZATION AND DIAGNOSIS: Cryptobatrachidae is characterized by claw-shaped terminal phalanges and intercalary elements (like Hylidae, Hemiphractidae, and Amphignathodontidae) and endotrophic larvae that develop on the back of the adult (like Hemiphractidae and Amphignathodontidae). Unlike Amphignathodontidae, but like Hemiphractidae, Cryptobatrachidae does not develop a dorsal pouch but differs from *Hemiphractus* in lacking fang-like teeth. None of the morphological characters in our analysis (from Haas, 2003) optimize on this branch, because no member of Cryptobatrachidae was studied by Haas (2003). (Molecular transformations associated with this taxon are listed in appendix 5.)

[368] TINCTANURA **NEW TAXON**

ETYMOLOGY: Tincta (Greek: colored, tinted) + anoura (Greek: frog), denoting the fact that many of the frogs in this clade are spectacularly colored (although some groups within it—notably, most species in Bufonidae—certainly lack this characteristic).

IMMEDIATELY MORE INCLUSIVE TAXON: [366] Cladophrynia **new taxon.**

SISTER TAXON: [367] Cryptobatrachidae **new family.**

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RANGE: Cosmopolitan in temperate and tropical areas of the continents, Madagascar, Seychelles, and New Zealand.

CONCEPT AND CONTENT: Tinctanura is a monophyletic taxon containing [369] Amphignathodontidae Boulenger, 1882, and [371] Athesphatanura **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: None of the morphological characters in our analysis optimized on this branch, so its recognition depends entirely on molecular data. (See appendix 5 for molecular synapomorphies associated with this taxon.)

[369] FAMILY: AMPHIGNATHODONTIDAE BOULENGER, 1882

Amphignathodontidae Boulenger, 1882: 449. Type genus: *Amphignathodon* Boulenger, 1882.
Gastrothecinae Noble, 1927: 93. Type genus: *Gastrotheca* Fitzinger, 1843.
Opisthodelphyinae Lutz, 1968: 13. Type genus *Opisthodelphys* Günther, 1859 ''1858''.

IMMEDIATELY MORE INCLUSIVE TAXON: [368] Tinctanura **new taxon.**

SISTER TAXON: [371] Athesphatanura **new taxon.**

RANGE: Costa Rica and Panama, northern and western South America southward to northwestern Argentina; eastern and southeastern Brazil; Trinidad and Tobago.

CONTENT: ***Flectonotus*** Miranda-Ribeiro, 1920; ***Gastrotheca*** Fitzinger, 1843.

CHARACTERIZATION AND DIAGNOSIS: Haas (2003) suggested the following characters that optimize on his exemplar *Gastrotheca riobambae* of amphignathodontids and may be synapomorphies of Amphignathodontidae: (1) m. subarcualis rectus I portion with origin from ceratobranchial III absent (Haas 35.0); (2) functional larval m. levator mandibulae lateralis present (Haas 56.0); (3) ramus mandibularis (cranial nerve V_3) posterior runs through the m. levator mandibulae externus group (Haas 65.1); (4) posterior palatoquadrate clearly concave with bulging and pronounced margin (Haas 68.1); (5) processus pseudopterygoideus long (Haas 77.2); and (6) dorsal connection from processus muscularis to commissura quadrato-orbitalis (Haas 78.2). All of these have the potential to be synapomorphies of Amphignathodontidae, although some or all may be located as less inclusive levels of universality within the group. Amphignathodontidae can be differentiated from other frog taxa by its possession of a dorsal pouch for brooding eggs, a likely synapomorphy. Molecular synapomorphies are presented in appendix 5.

[371] ATHESPHATANURA **NEW TAXON**

ETYMOLOGY: Athesphatos (Greek: inexpressible, marvelous) + anoura (Greek: tailless, i.e., frog), denoting the fact that even though much research has been done on these frogs, they continue to surprise.

IMMEDIATELY MORE INCLUSIVE TAXON: [368] Tinctanura **new taxon.**

SISTER TAXON: [369] Amphignathodontidae Boulenger, 1882.

RANGE: Coextensive with Anura, excluding Madagascar, Seychelles, and New Zealand.

CONCEPT AND CONTENT: As here conceived, Athesphatanura is a monophyletic group composed of [372] Hylidae Rafinesque, 1815, and [424] Leptodactyliformes **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Athesphatanura is a monophyletic group composed of Hylidae and the bulk of the former non-brachycephalid, non-batrachophrynid leptodactylids. The following characters suggested by Haas (2003) on the basis of a relatively small number of exemplars are potential synapomorphies of this group: (1) pars alaris and pars corporis separated by deep distal notch (Haas 86.1); (2) commissura proximalis II absent (Haas 110.0); and (3) commissura proximalis III absent (Haas 111.0). In addition, molecular synapomorphies are summarized in appendix 5.

[372] FAMILY: HYLIDAE RAFINESQUE, 1815

IMMEDIATELY MORE INCLUSIVE TAXON: [371] Athesphatanura **new taxon.**

SISTER TAXON: [424] Leptodactyliformes **new taxon.**

RANGE: North and South America, the West Indies, and the Australo-Papuan Region; temperate Eurasia, including extreme northern Africa and the Japanese Archipelago.

CONTENT: [386] Hylinae Rafinesque, 1815 + [373] ([374] Phyllomedusinae Günther, 1858 + [377] Pelodryadinae Günther, 1858).

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CHARACTERIZATION AND DIAGNOSIS: Morphological characters in our analysis (from Haas, 2003) that optimize on this branch are (1) m. mandibulolabialis superior present (Haas 50.1); and (2) shape of arcus subocularis in cross-section with margin sloping ventrally and laterally (Haas 82.1). As noted by Haas (2003), traditional characters of Hylidae, such as claw-shaped terminal phalanges and intercalary phalangeal elements, do not optimize as synapomorphies of this group because they are shared with Cryptobatrachidae, Hemiphractidae, and Amphignathodontidae.

COMMENT: Because Hylidae is so large, we deviate from our practice of providing accounts only for families and higher taxa and here provide accounts for the three nominal subfamilies of Hylidae, which have been very recently revised (Faivovich et al., 2005).

[386] SUBFAMILY: HYLINAE RAFINESQUE, 1815

Hylarinia Rafinesque, 1815: 78. Type genus: *Hylaria* Rafinesque, 1814.
Hylina Gray, 1825: 213. Type genus: *Hyla* Laurenti, 1768.
Dryophytae Fitzinger, 1843: 31. Type genus: *Dryophytes* Fitzinger, 1843.
Dendropsophi Fitzinger, 1843: 31. Type genus: *Dendropsophus* Fitzinger, 1843.
Pseudae Fitzinger, 1843: 33. Type genus: *Pseudis* Wagler, 1830.
Acridina Mivart, 1869: 292. Type genus: *Acris* Duméril and Bibron, 1841.
Cophomantina Hoffmann, 1878: 614. Type genus: *Cophomantis* Peters, 1870.
Lophiohylinae Miranda-Ribeiro, 1926: 64. Type genus: *Lophyohyla* Miranda-Ribeiro, 1926.
Triprioninae Miranda-Ribeiro, 1926: 64. Type genus: *Triprion* Cope, 1866.
Trachycephalinae Lutz, 1969: 275. Type genus: *Trachycephalus* Tschudi, 1838.

IMMEDIATELY MORE INCLUSIVE TAXON: [372] Hylidae Rafinesque, 1815.

SISTER TAXON: [373] unnamed taxon ([374] Phyllomedusinae Günther, 1858 + [377] Pelodryadinae Günther, 1858).

RANGE: North and South America, the West Indies; temperate Eurasia, including extreme northern Africa and the Japanese Archipelago.

CONTENT: ***Acris*** Duméril and Bibron, 1841; ***Anotheca*** Smith, 1939; *Aparaspheno*don Miranda-Ribeiro, 1920; ***Aplastodiscus*** Lutz *In* Lutz, 1950; ***Argenteohyla*** Trueb, 1970; *Bokermannohyla* Faivovich et al., 2005; *Bromeliohyla* Faivovich et al., 2005; ***Charadrahyla*** Faivovich et al., 2005; *Corythomantis* Boulenger, 1896; ***Dendropsophus*** Fitzinger, 1843; ***Duellmanohyla*** Campbell and Smith, 1992; ***Ecnomiohyla*** Faivovich et al., 2005; ***Exerodonta*** Brocchi, 1879; ***Hyla*** Laurenti, 1768; ***Hyloscirtus*** Peters, 1882; ***Hypsiboas*** Wagler, 1830; ***Isthmohyla*** Faivovich, et al., 2005; *Itapotihyla* Faivovich et al., 2005; ***Lysapsus*** Cope, 1862; *Megastomatohyla* Faivovich et al., 2005; *Myersiohyla* Faivovich et al., 2005; *Nyctimantis* Boulenger, 1882; *Osteocephalus* Steindachner, 1862; ***Osteopilus*** Fitzinger, 1843; ***Phyllodytes*** Wagler, 1830; ***Plectrohyla*** Brocchi, 1877; ***Pseudacris*** Fitzinger, 1843; ***Pseudis*** Wagler, 1830; ***Ptychohyla*** Taylor, 1944; ***Scarthyla*** Duellman and de Sá, 1988; ***Scinax*** Wagler, 1830; ***Smilisca*** Cope, 1865 (including *Pternohyla* Boulenger, 1882); ***Sphaenorhynchus*** Tschudi, 1838; *Tepuihyla* Ayarzagüena, Señaris, and Gorzula, 1993 ''1992''; ***Tlalocohyla*** Faivovich et al., 2005; ***Trachycephalus*** Tschudi, 1838 (including *Phrynohyas* Fitzinger, 1843); ***Triprion*** Cope, 1866; *Xenohyla* Izecksohn, 1998 ''1996''.

CHARACTERIZATION AND DIAGNOSIS: Only one morphological character in our analysis optimizes on this taxon: two clearly separate heads of m. subarcualis obliquus originate from ceratobranchialia II and III (character 31.1 of Haas, 2003). Faivovich et al. (2005) noted another morphological synapomorphy: tendo superficialis digiti V (manus) with an additional tendon that arises ventrally from the m. palmaris longus (da Silva *In* Duellman, 2001) and, likely, the 24 chromosome condition. Nevertheless, substantial numbers of molecular synapomorphies exist (appendix 5).

SYSTEMATIC COMMENTS: The latest revision of this taxon was by Faivovich et al. (2005), who provided a much larger analysis, denser taxonomic sampling, and more molecular data per terminal than we do. Our results, therefore, do not constitute a sufficient test of those results. Nevertheless, differences were noted. We did not find either *Hypsiboas* or *Hyla* to be monophyletic. We presume that these differences are due to our less-dense

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taxon sampling and application of fewer data than in the earlier study (Faivovich et al., 2005).

Faivovich et al. (2005) recognized four tribes within Hylinae: (1) Cophomantini Hoffmann, 1878 (*Aplastodiscus*, *Bokermannohyla*, *Hyloscirtus*, *Hypsiboas*, and *Myersiohyla*); (2) Dendropsophini Fitzinger, 1843 (*Dendropsophus*, *Lysapsus*, *Pseudis*, *Scarthyla*, *Scinax*, *Sphaenorhynchus*, and *Xenohyla*); (3) Hylini Rafinesque, 1815 (*Acris*, *Anotheca*, *Bromeliohyla*, *Charadrahyla*, *Duellmanohyla*, *Ecnomiohyla*, *Exerodonta*, *Hyla*, *Isthmohyla*, *Megastomatohyla*, *Plectrohyla*, *Pseudacris*, *Ptychohyla*, *Smilisca*, *Tlalocohyla*, *Triprion*); and (4) Lophiohylini Miranda-Ribeiro, 1926 (*Aparasphenodon*, *Argenteohyla*, *Corythomantis*, *Itapotihyla*, *Nyctimantis*, *Osteocephalus*, *Osteopilus*, *Phyllodytes*, *Tepuihyla*, and *Trachycephalus*). We refer the reader to that revision for a detailed discussion of the phylogenetics of the group.

[377] SUBFAMILY: PELODRYADINAE GÜNTHER, 1858

Pelodryadidae Günther, 1858b: 346. Type genus: *Pelodryas* Günther, 1858.

Chiroleptina Mivart, 1869: 294. Type genus: *Chiroleptes* Günther, 1858.

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

Nyctimystinae Laurent, 1975: 183. Type genus: *Nyctimystes* Stejneger, 1916.

IMMEDIATELY MORE INCLUSIVE TAXON: [373] unnamed taxon composed of [374] Phyllomedusinae Günther, 1858 + [377] Pelodryadinae Günther, 1858).

SISTER TAXON: [374] Phyllomedusinae Günther, 1858.

RANGE: Australia and New Guinea; introduced into New Zealand.

CONTENT: ***Litoria*** Tschudi, 1838 (including ***Cyclorana*** Steindachner, 1867, and ***Nyctimystes*** Stejneger, 1916; see Systematic Comments and appendix 7).

CHARACTERIZATION AND DIAGNOSIS: No morphological character optimizes unambiguously as a synapomorphy of Pelodryadinae. The molecular data, however, are decisive (see Systematic Comments below and appendix 5).

SYSTEMATIC COMMENTS: Evidence of monophyly of Pelodryadinae remains unsettled. One character suggested by Haas (2003) that may optimize on this branch is larval upper labial papillation complete (Haas 8.0), which is a reversal from the Phthanobatrachian condition. However, the number of pelodryadines with complete papillation is small, and because *Cruziohyla* and *Phrynomedusa* (basal taxa in Phyllomedusinae) also have complete papillation it may be that this characteristic is a synapomorphy of Phyllomedusinae + Pelodryadinae. Alternatively, more dense sampling may show convergence between the phyllomedusinae condition and that found in pelodryadines, with this condition in pelodryadines, a character of some subset of ''*Litoria*'' + *Nyctimystes* + *Cyclorana*.

Haas (2003) recovered the subfamily as paraphyletic with respect to phyllomedusines on the basis of six exemplars. Tyler (1971c) noted the presence of supplementary elements of the m. intermandibularis in both Pelodryadinae (apical) and Phyllomedusinae (posterolateral). These characters were interpreted by Duellman (2001) as nonhomologous and therefore synapomorphies of their respective groups. If these conditions are homologues, however, the polarity between the two states is ambiguous because either, the pelodryadine or the phyllomedusinae condition, might be ancestral at the Phyllomedusinae + Pelodryadinae level of generality (Faivovich et al., 2005).

One character in our analysis (originally from Haas, 2003) optimizes on an [373] unnamed taxon joining Pelodryadinae and Phyllomedusinae: ramus mandibularis (cranial nerve V_3) posterior runs through m. levator mandibulae externus group (Haas 65.1). As noted by Faivovich (2005), however, another morphological synapomorphy of Phyllomedusinae + Pelodryadinae is the presence of a tendon of the m. flexor ossis metatarsi II arising only from distal tarsi 2–3. See also appendix 5 for molecular synapomorphies of Phyllomedusinae + Pelodryadinae.

The extensive paraphyly of ''*Litoria*'' with respect to *Cyclorana* and ''*Nyctimystes*'' remains the elephant in the room for Australian herpetology, and for reasons that escape us this spectacular problem has largely been ig-

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nored until recently; S. Donnellan and collaborators are currently addressing pelodryadine relationships. A further dimension of this problem is that our results not only reject *Litoria* monophyly; they also show *Nyctimystes* nonmonophyly, even though morphological evidence would suggest that *Nyctimystes* is monophyletic. Our resolution at this time is to consider *Nyctimystes* as a synonym of *Litoria* and *Cyclorana* as a subgenus within *Litoria*. It is unfortunate to have to embrace such an uninformative taxonomy, but the generic taxonomy as it exists is seriously misleading and no good alternatives present themselves pending the resolution of this problem by S. Donnellan and collaborators. (See appendix 7 for new combinations produced by these generic changes.)

[374] SUBFAMILY: PHYLLOMEDUSINAE GÜNTHER, 1858

Phyllomedusidae Günther, 1858b: 346. Type genus: *Phyllomedusa* Wagler, 1830.
Pithecopinae Lutz, 1969: 274. Type genus: *Pithecopus* Cope, 1866.

IMMEDIATELY MORE INCLUSIVE TAXON: [373] unnamed taxon composed of [374] Phyllomedusinae Günther, 1858 and [377] Pelodryadinae Günther, 1858.

SISTER TAXON: [377] Pelodryadinae Günther, 1858.

RANGE: Tropical Mexico to Argentina.

CONTENT: ***Agalychnis*** Cope, 1864; ***Cruziohyla*** Faivovich et al., 2005; *Hylomantis* Peters, 1873 ''1872''; *Pachymedusa* Duellman, 1968; ***Phasmahyla*** Cruz, 1991 ''1990''; *Phrynomedusa* Miranda-Ribeiro, 1923; ***Phyllomedusa*** Wagler, 1830.

CHARACTERIZATION AND DIAGNOSIS: Phyllomedusinae is a group of bizarre hylids characterized by vertical pupils and a loris-like movement. Haas (2003) suggested several larval characters that are good candidates for being synapomorphies of Phyllomedusinae, although they could also be synapomorphies of less inclusive groups: (1) suspensorium ultralow (Haas 71.3); (2) processus pseudopterygoideus short (Haas 77.1); (3) arcus subocularis with three distinct processes (Haas 81.2); (4) cartilaginous roofing of the cavum cranii with taeniae transversalis et medialis (fenestrae parietales) present (Haas 96.2); (5) cleft between hyal arch and branchial arch I closed (Haas 123.0); and (6) pupil shape vertically elliptical (Haas 143.0). Additionally, Faivovich (2005) noted that ventrolateral position of the spiracle is a likely synapomorphy.

[424] LEPTODACTYLIFORMES **NEW TAXON**

ETYMOLOGY: Leptodactyli- (with reference to the former leptodactylids [Greek: leptos = narrow + dactylos = toe]) + formes [Greek: shaped]).

IMMEDIATELY MORE INCLUSIVE TAXON: [371] Athesphatanura **new taxon.**

SISTER TAXON: [372] Hylidae Rafinesque, 1815.

RANGE: Coextensive with Anura, excluding Australo-Papuan region, Madagascar, Seychelles, and New Zealand.

CONCEPT AND CONTENT: Leptodactyliformes is a monophyletic taxon composed of [425] Diphyabatrachia **new taxon** and [440] Chthonobatrachia **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Beyond our molecular data, no characters in our analysis (originally from Haas, 2003) optimize on this branch. (See appendix 5 for molecular synapomorphies of this taxon.) J.D. Lynch (1973) reported most of the taxa outside of Leptodactyliformes to have moderately to broadly dilated sacral diapophyses, so round sacral diapophyses may be a synapomorphy of this taxon, although reversed in Centrolenidae and Bufonidae.

[425] DIPHYABATRACHIA **NEW TAXON**

ETYMOLOGY: Diphya- (Greek: two-nature) + batrachos (Greek: frog), referencing the fact that the two components of this taxon (Centrolenidae and Leptodactylidae) have very different morphologies and life-histories.

IMMEDIATELY MORE INCLUSIVE TAXON: [424] Leptodactyliformes **new taxon.**

SISTER TAXON: [440] Chthonobatrachia **new taxon.**

RANGE: Neotropics of North, Central, and South America.

CONCEPT AND CONTENT: Diphyabatrachia is a monophyletic taxon containing [426] Centrolenidae Taylor, 1951, and [430] Leptodactylidae Werner, 1896 (1838).

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CHARACTERIZATION AND DIAGNOSIS: No morphological characters suggested by Haas (2003) optimize on this branch, although substantial amounts of molecular evidence are synapomorphic (see appendix 5).

[426] FAMILY: CENTROLENIDAE TAYLOR, 1951

Centrolenidae Taylor, 1951: 36. Type genus: *Centrolene* Jiménez de la Espada, 1872.
Allophrynidae Goin et al., 1978: 240. Type genus: *Allophryne* Gaige, 1926. **New synonym.**

IMMEDIATELY MORE INCLUSIVE TAXON: [425] Diphyabatrachia **new taxon.**

SISTER TAXON: [430] Leptodactylidae Werner, 1896 (1838).

RANGE: Tropical southern Mexico to Bolivia, northeastern Argentina, and southeastern Brazil.

CONTENT: ***Allophryne*** Gaige, 1926; ''***Centrolene***'' Jiménez de la Espada, 1872 (see Systematic Comments); ''***Cochranella***'' Taylor, 1951; ***Hyalinobatrachium*** Ruiz-Carranza and Lynch, 1991.

CHARACTERIZATION AND DIAGNOSIS: Haas (2003) suggested several characters for his exemplar, *Cochranella granulosa*, that are candidates for being synapomorphies of Centrolenidae (including *Allophryne*, which Haas did not examine): (1) anterior insertion of m. subarcualis rectus II–IV on ceratobranchial III (Haas 37.2); (2) larval m. levator mandibulae externus present as one muscle body (Haas 54.0); (3) processus anterolateralis of crista parotica absent (Haas 66.0); (4) partes corpores medially separate (Haas 87.0); (5) cleft between hyal arch and branchial arch I closed (Haas 123.0); and (6) terminal phalanges T-shaped (Haas 156.2). *Cochranella granulosa*, Haas' examplar species, lacks larval labial keratodonts (Haas 3.0) but this is unlikely to be a synapomorphy of the group (Altig and McDiarmid, 1999). Burton (1998a) provided evidence suggesting that the ventral origin of the m. flexor teretes III relative to the corresponding m. transversi metacarporum I is a synapomorphy. Regardless of whether all of these only apply to Centroleninae, there are substantial numbers of molecular synapomorphies (see appendix 5).

SYSTEMATIC COMMENTS: The association of *Allophryne* with centrolenids was first made on the basis of anatomical and external similarity (Noble, 1931), but subsequent molecular work (Austin et al., 2002; Faivovich et al., 2005) has substantiated this relationship. We recognize within Centrolenidae the subfamilies Allophryninae for *Allophryne*, and [427] Centroleninae, for *Centrolene*, *Cochranella*, and *Hyalinobatrachium*. Centroleninae is united by the possession of intercalary elements between the ultimate and penultimate phalanges, fusion of the fibula and tibia (Taylor, 1951; but see Sanchíz and de la Riva, 1993), and the presence of a medial projection on the third metacarpal (Hayes and Starrett, 1981 ''1980'').

Our results showed ''*Centrolene*'' to be paraphyletic with respect to ''*Cochranella*''. Morphological evidence for the monophyly of *Centrolene* consists of a single synapomorphy, the presence of a humeral spine in adult males (Ruiz-Carranza and Lynch, 1991a), which is conspicuously present (albeit morphologically different) in both ''*Centrolene*'' *geckoideum* and ''*Centrolene*'' *prosoblepon* (Ruiz-Carranza and Lynch, 1991b: 3, their fig. 1). Nevertheless, the humerus of some species of *Cochranella* exhibits a conspicuously developed ventral crest (e.g., *C. armata*, *C. balionota*, and *C. griffithsi*; J.D. Lynch and Ruiz-Carranza, 1997 ''1996''; see also Ruiz-Carranza and Lynch, 1991a), which at least suggests that coding this character as the presence or absence of a humeral spine may be simplistic. Indeed, the basis is unclear for coding the bladelike ''spine'' of *Centrolene grandisonae* as the same condition as the smooth, rounded, and protruding spine of *C. geckoideum* and as distinct from the strongly developed bladelike crest of *C. armata*. We urge centrolenid workers to examine the different ''spines'' in greater detail and to evaluate hypothesized homologies carefully. (Note that our findings do not rule out homology of the humeral spines. It is equally parsimonious for it to have been gained independently in the two lineages of ''*Centrolene*'' or gained once and lost in *Cochranella*.)

We did not test the monophyly of *Cochranella* or *Hyalinobatrachium*. No synapomorphy has been identified for *Cochranella* (Ruiz-Carranza and Lynch, 1991a) and Darst and Cannatella (2004; fig. 22) have presented

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molecular evidence for its nonmonophyly, whereas *Hyalinobatrachium* is delimited by the occurrence of a bulbous liver (Ruiz-Carranza and Lynch, 1991a, 1998).

Given our topology, the questions surrounding the homology of the humeral spines, and the lack of evidence for the monophyly of *Cochranella*, we were tempted to place *Cochranella* in the synonymy of *Centrolene*. A behavioral synapomorphy for the inclusive clade is male–male physical combat undertaken by hanging upside down by the feet and grappling venter-to-venter (Bolívar-G. et al., 1999), a behavior otherwise known only in phyllomedusines (Pyburn, 1970; Lescure et al., 1995; Wogel et al., 2004) and some species of *Hypsiboas* and *Dendropsophus* (Hylidae; J. Faivovich and C.F.B. Haddad, personal obs.). However, the resulting genus, though monophyletic, would be unwieldy (with 100 species). In light of the poverty of our taxon sampling, and our anticipation of more thorough phylogenetic studies of this charismatic group, we retain the current taxonomy and place quotation marks around ''*Centrolene*'' to denote its apparent paraphyly and around ''*Cochranella*'' to denote its nonmonophyly as well.

[430] FAMILY: LEPTODACTYLIDAE WERNER, 1896 (1838)

Cystignathi Tschudi, 1838: 26, 78. Type genus: *Cystignathus* Wagler, 1830.

Leiuperina Bonaparte, 1850: 1 p. Type genus: *Leiuperus* Duméril and Bibron, 1841.

Plectromantidae Mivart, 1869: 291. Type genus: *Plectromantis* Peters, 1862.

Adenomeridae Hoffmann, 1878: 613. Type genus: *Adenomera* Steindachner, 1867.

Leptodactylidae Werner, 1896: 357. Type genus: *Leptodactylus* Fitzinger, 1826.

Pseudopaludicolinae Gallardo, 1965: 84. Type genus: *Pseudopaludicola* Miranda-Ribeiro, 1926.

IMMEDIATELY MORE INCLUSIVE TAXON: [425] Diphyabatrachia **new taxon.**

SISTER TAXON: [426] Centrolenidae Taylor, 1951.

RANGE: Extreme southern USA and tropical Mexico throughout Central America and South America.

CONTENT: ***Edalorhina*** Jiménez de la Espada, 1871 ''1870''; *Engystomops* Jiménez de la Espada, 1872; *Eupemphix* Steindachner, 1863; *Hydrolaetare* Gallardo, 1963; ***Leptodactylus*** Fitzinger, 1826 (see Systematic Comments and appendix 7 for treatment of subsidiary taxa and synonyms ***Adenomera*** Steindachner, 1867, ***Lithodytes*** Fitzinger, 1843, and ***Vanzolinius*** Heyer, 1974); ***Paratelmatobius*** Lutz and Carvalho, 1958; ***Physalaemus*** Fitzinger, 1826; ***Pleurodema*** Tschudi, 1838; ***Pseudopaludicola*** Miranda-Ribeiro, 1926; ***Scythrophrys*** Lynch, 1971; *Somuncuria* Lynch, 1978.

CHARACTERIZATION AND DIAGNOSIS: This taxon corresponds reasonably closely to the former Leptodactylinae, excluding *Limnomedusa* (to Cycloramphidae) and adding *Paratelmatobius* and *Scythrophrys* (from the former Cycloramphinae). Most species are found on the forest floor, although a diversity of tropical biomes are inhabited. Many species are foam-nest builders (excluding *Paratelmatobius*, some *Pleurodema*, *Pseudopaludicola*, *Scythrophrys*, and *Somuncuria*; Barrio, 1977; Pombal and Haddad, 1999; C. Haddad, personal obs.), and this may be synapomorphic of the group. Several of the characters in our analysis (from Haas, 2003) optimize on our topology on the [431] branch subtending *Physalaemus* and *Pleurodema*. Because Haas did not study other members of our Leptodactylidae, these characters are candidates for being synapomorphies of our Leptodactylidae: (1) m. subarcualis rectus I portion with origin from ceratobranchial III absent (Haas 35.0); and (2) dorsal connection from processus muscularis to neurocranium and pointed (Haas 78.1).

We also suggest that the bony sternum of the former Leptodactylinae (J.D. Lynch, 1971) is a synapomorphy of this taxon, but reversed to the cartilaginous condition in the [435] branch subtending *Paratelmatobius* + *Scythrophrys*. The bony sternum occurs independently in *Limnomedusa* (J.D. Lynch, 1971) in Cycloramphidae, and a calcified sternum occurs in *Barycholos* (Brachycephalidae; J.D. Lynch, 1980).

SYSTEMATIC COMMENTS: *Hydrolaetare* Gallardo, 1963, is associated with this group because of its presumed association with *Leptodactylus* (Heyer, 1970), although we suggest that this proposition needs to be evaluated carefully. We place *Somuncuria* provisionally in this group on the basis of the

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evidence (though not the conclusions) suggested by J.D. Lynch (1978b), who placed *Somuncuria* as the sister taxon of *Pleurodema*. On the basis of our evidence, *Leptodactylus* is paraphyletic with respect to *Vanzolinius*; this agrees with the results of Heyer (1998) who presented evidence to place *Vanzolinius* deeply within a paraphyletic *Leptodactylus*, and likely the sister taxon of *Leptodactylus diedrus*. De Sá et al. (2005) also came to this conclusion and placed *Vanzolinus* in the synonymy of *Leptodactylus*. We regard *Vanzolinius* as a subjective junior synonym of *Leptodactylus*. Although our data are agnostic on the subject, Heyer (1998) and Kokubum and Giaretta (2005) also presented evidence that recognizing *Adenomera* renders *Leptodactylus* paraphyletic and that *Lithodytes* is the sister taxon of *Adenomera*. On the basis of this evidence, as well as Heyer's (1998) and Kokubum and Giaretta's (2005) evidence, we place *Adenomera* Steindachner, 1867, as a synonym of *Lithodytes* Fitzinger, 1843, and *Lithodytes* as a subgenus of *Leptodactylus*, without delimiting any other subgenera so as not to construct or imply any paraphyletic groups (see appendix 7 for new combinations). *Leptodactylus*, therefore is equivalent to the taxon subtended by branch 436 in our tree.

J.D. Lynch (1971: 26) noted that *Pseudopaludicola* and *Physalaemus* (including *Engystomops* and *Eupemphix* in his sense) share the feature of dextral vents in larvae, as do *Edalorhina* and some *Paratelmatobius* (Altig and McDiarmid, 1999).

[440] CHTHONOBATRACHIA **NEW TAXON**

ETYMOLOGY: Chthonos- (Greek: ground) + batrachos (Greek: frog), referencing the fact that most of the included species are ground-dwelling.

IMMEDIATELY MORE INCLUSIVE TAXON: [424] Leptodactyliformes **new taxon.**

SISTER TAXON: [425] Diphyabatrachia **new taxon.**

RANGE: Coextensive with Anura, excluding Australo-Papuan region, Madagascar, Seychelles, and New Zealand.

CONCEPT AND CONTENT: Chthonobatrachia is a monophyletic group composed of [441] Ceratophryidae Tschudi, 1838, and [448] Hesticobatrachia **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: None of the larval characters studied by Haas (2003) optimize on this branch, so the diagnosis of this taxon rests entirely on molecular evidence. See appendix 5 for molecular synapomorphies.

[441] FAMILY: CERATOPHRYIDAE TSCHUDI, 1838

Ceratophrydes Tschudi, 1838: 26. Type genus: *Ceratophrys* Wied-Neuwied, 1824.

Telmatobii Fitzinger, 1843: 31. Type genus: *Telmatobius* Wiegmann, 1834. **New synonym.**

Stombinae Gallardo, 1965: 82. Type genus: *Stombus* Gravenhorst, 1825.

Batrachylinae Gallardo, 1965: 83. Type genus: *Batrachylus* Bell, 1843. **New synonym.**

IMMEDIATELY MORE INCLUSIVE TAXON: [440] Chthonobatrachia **new taxon.**

SISTER TAXON: [448] Hesticobatrachia **new taxon.**

RANGE: Southern Andean and tropical lowland South America from Colombia and Venezuela south to extreme southern Argentina and Chile.

CONTENT: ***Atelognathus*** Lynch, 1978; ***Batrachyla*** Bell, 1843; ***Ceratophrys*** Wied-Neuwied, 1824; ***Chacophrys*** Reig and Limeses, 1963; *Insuetophrynus* Barrio, 1970 (see Systematic Comments); ***Lepidobatrachus*** Budgett, 1899; ***Telmatobius*** Wiegmann, 1834.

CHARACTERIZATION AND DIAGNOSIS: Morphological characters for this group were derived solely from *Ceratophrys* and *Lepidobatrachus*. Inasmuch as these are very derived taxa, the characters in our analysis that optimize on them are likely characters of *Lepidobatrachus* + *Ceratophrys*, although some of them may optimize at other hierarchic levels (including Ceratophryidae in our sense) once relevant specimens have been examined. Relevant morphological characters (from Haas, 2003) are (1) m. diaphragmatopraecordialis absent (Haas 25.0; a reversal from the phthanobatrachian condition, also in bufonids, microhylids, and some ranoids); (3) mm. levatores arcuum branchialium I and II narrow with a wide gap between them (Haas 40.0; a reversal from the phthanobatrachian condition, also in some *Litoria* and *Atelopus*); (4) m. suspensoriohyoideus absent

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(Haas 45.0; a reversal of the acosmanuran condition, also in some hylines and *Atelopus*); (5) ramus mandibularis (cranial nerve V_3) runs through the m. levator mandibulae externus group (Haas 65.1; one of many reversals on the overall tree); (6) anterolateral base of processus muscularis without conspicuous projection (Haas 86.0); (7) tectum of cavum cranii almost completely chondrified (Haas 96.4); (8) spicula short or absent (Haas 112.0); and (9) branchial food traps absent (Haas 134.0). Molecular synapomorphies for Ceratophryidae appear in appendix 5.

SYSTEMATIC COMMENTS: Within Ceratophryidae, the association of the genera is relatively weak, with the exception of *Lepidobatrachus* + *Ceratophrys* + *Chacophrys* and *Batrachyla* + *Atelognathus*.

We recognize two subfamilies within Ceratophryidae: [442] Telmatobiinae (for *Telmatobius*) and [444] Ceratophryinae. Within Ceratophryinae we recognize two tribes: [445] Batrachylini (for *Atelognathus*, *Batrachyla*, and, presumably *Insuetophrynus*), and [446] Ceratophryini (for *Lepidobatrachus*, *Ceratophrys*, and *Chacophrys*). Ceratophryinae has a continuous row of papilla on the upper lip in larvae (Haas 8.0), a synapomorphy. Batrachylini is also diagnosed on the basis of molecular evidence (appendix 5), and Ceratophryini is diagnosed on the basis of molecular evidence as well as on traditional morphological characters associated with this cluster of genera (J.D. Lynch, 1971, 1982b): (1) transverse processes of anterior presacral vertebrae widely expanded; (2) cranial bones dermosed; (3) teeth fang-like, nonpedicellate; and (4) absence of *pars palatina* of maxilla and premaxilla. Another character, presence of a vertebral shield, may be a synapomorphy of Ceratophryini although the optimization of this feature is ambiguous, requires detailed study, and was not considered a synapomorphy by Lynch (1982b). The shield is present in *Ceratophrys aurita*, *C. cranwelli*, *C. ornata*, *C. joazeirensis*, and in *Lepidobatrachus asper* and *L. llanensis* (in these two the morphology of the shield is quite different from that of *Ceratophrys*; J. Faivovich, personal obs.), and absent in *C. calcarata*, *C. cornuta*, *C. testudo*, *C. stolzmanni*, *Chacophrys pierottii*, and *Lepidobatrachus laevis*.

We did not study *Insuetophrynus* and it is therefore only provisionally allocated to this family. Lynch (1978bb), on the basis of a phylogenetic analysis of morphology, consistently recovered *Insuetophrynus* as the sister taxon of *Atelognathus*, while Diaz et al. (1983) considered the relationships of *Insuetophrynus* to lie with *Alsodes* (Cycloramphidae) or *Telmatobius* (Ceratophryidae). The characters suggested by Diaz et al. (1983) in support of their arrangement all are likely plesiomorphies, however, so we retain the hypothesis of Lynch (1978bb) pending additional evidence.

[448] HESTICOBATRACHIA **NEW TAXON**

ETYMOLOGY: Hestico- (Greek: agreeable, pleasing) + batrachos (Greek: frog), denoting the agreeable nature of these frogs, particularly with respect to the nature of the type genus of their sister taxon, Ceratophryidae.

IMMEDIATELY MORE INCLUSIVE TAXON: [440] Chthonobatrachia **new taxon.**

SISTER TAXON: [441] Ceratophryidae Tschudi, 1838.

RANGE: Coextensive with Anura, excluding Australo-Papuan region, Madagascar, Seychelles, and New Zealand.

CONCEPT AND CONTENT: Hesticobatrachia is a monophyletic group composed of [449] Cycloramphidae Bonaparte, 1858, and [460] Agastorophrynia **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Characters proposed by Haas (2003) that optimize on this branch are (1) posterior palatoquadrate curvature clearly concave with bulging and pronounced margin (Haas 68.1); and (2) presence of a dorsal connection from processus muscularis to neurocranium ligament (Haas 78.1). Molecular synapomorphies are summarized in appendix 5.

SYSTEMATIC COMMENTS: We did not study *Rupirana* Heyer, 1999, and cannot allocate it, even provisionally, although Heyer (1999) thought that it might have some kind of relationship, not close, with either *Batrachyla* (Cycloramphidae) or *Thoropa* (Thoropidae). The data to support either contention are ambiguous at best. The position of *Rupirana* remains to be elucidated.

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[449] FAMILY: CYCLORAMPHIDAE BONAPARTE, 1850

Cyclorhamphina Bonaparte, 1850: 1 p. Type genus: *Cycloramphus* Tschudi, 1838.

Rhinodermina Bonaparte, 1850: 1 p. Type genus: *Rhinoderma* Duméril and Bibron, 1841. **New synonym,** considered a junior synonym of Cyclorhamphina Bonaparte, 1850, under Article 24.2.1 (Rule of First Revisor) of the International Code of Zoological Nomenclature (ICZN, 1999).

Hylodinae Günther, 1858b: 346. Type genus: *Hylodes* Fitzinger, 1826. **New synonym.**

Alsodina Mivart, 1869: 290. Type genus: *Alsodes* Bell, 1843. **New synonym.**

Grypiscina Mivart, 1869: 295. Type genus: *Grypiscus* Cope, 1867 ''1866''.

Elosiidae Miranda-Ribeiro, 1923: 827. Type genus: *Elosia* Tschudi, 1838.

Odontophrynini J.D. Lynch, 1969: 3. Type genus: *Odontophrynus* Reinhardt and Lütken, 1862 ''1861''. (Odontophrynini subsequently named more formally by J.D. Lynch, 1971: 142.)

IMMEDIATELY MORE INCLUSIVE TAXON: [448] Hesticobatrachia **new taxon.**

SISTER TAXON: [460] Agastorophrynia **new taxon.**

RANGE: Southern tropical and temperate South America.

CONTENT: ***Alsodes*** Bell, 1843; *Crossodactylodes* Cochran, 1938; ***Crossodactylus*** Duméril and Bibron, 1841; ***Cycloramphus*** Tschudi, 1838; ***Eupsophus*** Fitzinger, 1843; ***Hylodes*** Fitzinger, 1826; ***Hylorina*** Bell, 1843; ***Limnomedusa*** Fitzinger, 1843; *Macrogenioglottus* Carvalho, 1946; ***Megaelosia*** Miranda-Ribeiro, 1923; ***Odontophrynus*** Reinhardt and Lütken, 1862 ''1861''; ***Proceratophrys*** Miranda-Ribeiro, 1920; ***Rhinoderma*** Duméril and Bibron, 1841; *Zachaenus* Cope, 1866.

CHARACTERIZATION AND DIAGNOSIS: One of the morphological characters suggested by Haas (2003) optimizes as a synapomorphy of this group: anterior insertion of m. subarcualis rectus II–IV on ceratobranchial I (Haas 37.0). All decisive evidence for the existence of this clade is molecular (see appendix 5).

SYSTEMATIC COMMENTS: Within Cycloramphidae we recognize two sister subfamilies, [450] Hylodinae Günther, 1858 (containing *Crossodactylus*, *Megaelosia*, and *Hylodes*) and [452] Cycloramphinae Bonaparte, 1850 (for the remaining genera). Other than molecular synapomorphies (see appendix 5), Hylodinae is diagnosed by the synapomorphy of having a lateral vector to the alary processes (J.D. Lynch, 1971: 39), T-shaped terminal phalanges, and dermal scutes on the top of the digital discs (J.D. Lynch, 1971, 1973). This latter character is also found in Petropedetidae (Ranoides) and Dendrobatidae.

Cycloramphinae is not readily diagnosed on the basis of morphology, but it is composed of two tribes. The first of these is [453] Cycloramphini Bonaparte, 1850 (*Cycloramphus*, *Crossodactylodes*, and *Zachaenus*), corresponding to Grypiscini Mivart, 1869, of J.D. Lynch (1971) with the addition of *Rhinoderma*. The second is [454] Alsodini Mivart, 1869 (composed of the remaining genera). Alsodini is diagnosed by its possession of Type II cotylar arrangement (cervical cotyles narrowly separated with two distinct articular surfaces; J.D. Lynch, 1971). This occurs otherwise in Hyloides only in Batrachophrynidae, Limnodynastidae, *Megaelosia*, and *Telmatobius* (J.D. Lynch, 1971), so is likely synapomorphic at this level. (See appendix 5 for relevant molecular synapomorphies.)

[460] AGASTOROPHRYNIA **NEW TAXON**

ETYMOLOGY: Agastoro- (Greek: near kinsman) + phrynia (Greek: having the nature of a toad), noting the surprisingly close relationship of Dendrobatoidea and Bufonidae.

IMMEDIATELY MORE INCLUSIVE TAXON: [448] Hesticobatrachia **new taxon.**

SISTER TAXON: [449] Cycloramphidae Bonaparte, 1850.

RANGE: Coextensive with Anura, excluding Australo-Papuan region, Madagascar, Seychelles, and New Zealand.

CONCEPT: Agastorophrynia is a monophyletic taxon composed of [461] Dendrobatoidea Cope, 1865, and [469] Bufonidae Gray, 1825.

CHARACTERIZATION AND DIAGNOSIS: None of the morphological characters suggested by Haas (2003) optimize in a way that would suggest their possible candidacy as synapomorphies of Agastorophrynia. All decisive evidence for the recognition of this taxa is

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molecular. These molecular synapomorphies are summarized in appendix 5.

[461] SUPERFAMILY: DENDROBATOIDEA COPE, 1865

IMMEDIATELY MORE INCLUSIVE TAXON: [460] Agastorophrynia **new taxon.**

SISTER TAXON: [469] Bufonidae Gray, 1825.

RANGE: Central America (Nicaragua to Panama) and South America (Guianas, Amazon drainage, south to Bolivia and southeastern Brazil).

CONTENT: Thoropidae **new family** and [462] Dendrobatidae Cope, 1865.

CHARACTERIZATION AND DIAGNOSIS: Evidence for Dendrobatoidea is derived entirely from DNA sequence data, as summarized in appendix 5.

SYSTEMATIC COMMENT: The sister group relationship of Dendrobatidae and *Thoropa*, to our knowledge, has never been proposed, and this is one of the most heterodox of our results. No morphological synapomorphies are apparent, and a large number of characters differ between the two taxa. Nevertheless, evidence for alternative placement of *Thoropa* appears to be lacking (although the larvae of *Thoropa* and *Cycloramphus* are very similar and semiterrestrial; Haddad and Prado, 2005), and most of the characters that differ between Dendrobatidae and *Thoropa* are either of unclear polarity or unique to Dendrobatidae among hyloids (e.g., thigh musculature, epicoracoid fusion and nonoverlap). Furthermore, it does not appear that this result is due to inadequate algorithmic searching. At numerous points in the analysis we placed Dendrobatidae, *Thoropa*, the hylodine genera, and various other cycloramphines and bufonids in alternative arrangements and submitted those topologies either as starting points or as constraint files for further searching, but our analysis invariably led away from those solutions. The Bremer values and jackknife frequencies are both strong for this clade (39% and 100%, respectively). The arrangement *Thoropa* (Hylodinae + Dendrobatidae) requires 56 extra steps, and placing *Thoropa* in the more conventional arrangement *Thoropa* + (*Hylorina* + (*Alsodes* + *Eupsophus*) and (Hylodinae + Dendrobatidae) requires 87 extra steps. The occurrence of paired dermal scutes atop the digits has been claimed as a synapomorphy of Dendrobatidae + Hylodinae (e.g, Noble, 1926), but its optimization on our optimal topology requires only a single extra step, versus the 39 steps required to disrupt the relationship between *Thoropa* and Dendrobatidae. Insofar as there is no compelling evidence against our optimal solution, and despite our astonishment at the result, we recognize these sister taxa as Dendrobatoidea and leave it to future tests based on greater character (including morphology) and taxon sampling to assess the reality of this clade. Alternatively, we could have left *Thoropa* insertae sedis—an obviously deficient solution—or have placed it inside Dendrobatidae.

FAMILY: THOROPIDAE **NEW FAMILY**

IMMEDIATELY MORE INCLUSIVE TAXON: [461] Dendrobatoidea.

SISTER TAXON: [462] Dendrobatidae Cope, 1865.

RANGE: Eastern, southeastern, and southern Brazil.

CONTENT: ***Thoropa*** Cope, 1865.

CHARACTERIZATION AND DIAGNOSIS: Because this taxon was not studied by Haas (2003) none of the morphological characters in our analysis could optimize on this branch. All evidence for the phylogenetic placement of this taxon as distinct from Cycloramphinae is molecular, although *Thoropa* larvae can be distinguished from all near relatives by being very attenuate and flattened (J.D. Lynch, 1971: 124). For additional differentia see J.D. Lynch (1972a).

SYSTEMATIC COMMENTS: See comment under Hesticobatrachia regarding *Rupirana*. J.D. Lynch (1971) considered *Thoropa* to be closely related to *Batrachyla*, sharing a Type I cotylar arrangement, although the polarity of the character was unclear in his study, and dendrobatids have the Type I condition as well, rendering this character uninformative.

[462] FAMILY: DENDROBATIDAE COPE, 1865 (1850)

Phyllobatae Fitzinger, 1843: 32. Type genus: *Phyllobates* Duméril and Bibron, 1841.

Eubaphidae Bonaparte, 1850: 1 p. Type genus: *Eubaphus* Bonaparte, 1831.

Hylaplesidae Günther, 1858b: 345. Type genus:

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Hylaplesia Boie, 1827 (= *Hysaplesia* Boie, 1826).

Dendrobatidae Cope, 1865: 100. Type genus: *Dendrobates* Wagler, 1830.

Colostethidae Cope, 1867: 191. Type genus: *Colostethus* Cope, 1866.

Calostethina Mivart, 1869: 293. Type genus: *Calostethus* Mivart, 1869.

IMMEDIATELY MORE INCLUSIVE TAXON: [461] Dendrobatoidea Cope, 1865.

SISTER TAXON: Thoropidae **new family.**

RANGE: Central America (Nicaragua to Panama) and South America (Guianas, Amazon drainage, south to Bolivia and central, southern, and southeastern Brazil).

CONTENT: ***Allobates*** Zimmermann and Zimmermann, 1988; ***Ameerega*** Bauer, 1986 (including ***Epipedobates*** Myers, 1987); *Aromobates* Myers, Paolillo O., and Daly, 1991; ***Colostethus*** Cope, 1866; *Cryptophyllobates* Lötters, Jungfer, and Widmer, 2000; ***Dendrobates*** Wagler, 1830 (including *Oophaga* Bauer, 1988, and *Ranitomeya* Bauer, 1986); ***Mannophryne*** La Marca, 1992; ***Minyobates*** Myers, 1987; *Nephelobates* La Marca, 1994; ***Phobobates*** Zimmermann and Zimmermann, 1988; ***Phyllobates*** Duméril and Bibron, 1841.

CHARACTERIZATION AND DIAGNOSIS: Dendrobatids are well-known, mostly diurnal, terrestrial, and frequently brightly colored frogs that have the exotic parental behavior of carrying tadpoles on their back to water. Likely synapomorphies of Dendrobatidae (as optimized on our topology) from those morphological characters reported by Haas (2003) are (1) insertion of m. rectus cervicis on proximal ceratobranchialia III and IV (Haas 39.2); (2) adrostral cartilage present but small (Haas 90.1); (3) cartilaginous roofing of the cavum cranii formed by taeniae tecti medialis only (Haas 96.5); (4) larvae picked up at oviposition site and transported to body of water adhering to dorsum of adult (Haas 137.1); (5) amplectic position cephalic (Haas 139.2); (6) guiding behavior (Haas 142.1); (7) firmisterny (Haas 144.1); and (8) terminal phalanges T-shaped (Haas 156.2).

Some of these characters may ultimately be found to be synapomorphies of Dendrobatoidea, because *Thoropa* has not been evaluated for these characters.

The systematics of dendrobatids is currently in a state of flux. Dendrobatid monophyly has been upheld consistently (e.g., Myers and Ford, 1986; Ford, 1993; Haas, 2003; Vences et al., 2003b) since first proposed by Noble (1926; see Grant et al., 1997), but the relationships among dendrobatids remain largely unresolved.

The most generally accepted view of dendrobatid systematics, as summarized by Myers et al. (1991; see also Kaplan, 1997), allocates approximately two-thirds of the species to a ''basal'' grade of usually dully colored, nontoxic frogs (including *Aromobates*, *Colostethus*, *Mannophryne*, and *Nephelobates*), while the remaining one-third is hypothesized to form a clade of putatively aposematic frogs (including *Allobates*, *Ameerega*[30], *Dendrobates*, *Minyobates*, *Phobobates*, and *Phyllobates*).

Compelling evidence for the monophyly of most genera is lacking. This is especially the case for the ''basal'' taxa. The nonmonophyly of *Colostethus* has been recognized for decades (J.D. Lynch, 1982a; J.D. Lynch and Ruiz-Carranza, 1982), and the naming of *Aromobates*, *Epipedobates*, *Mannophryne*, and *Nephelobates* has merely exacerbated the problem (Kaiser et al., 1994; Coloma, 1995; Meinhardt and Parmalee, 1996; Grant et al., 1997; Grant, 1998; Grant and Castro-Herrera, 1998). Molecular evidence for the monophyly of *Mannophryne* and *Nephelobates* was presented by La Marca et al. (2002) and Vences et al. (2003b), but the relationships of those genera to other dendrobatids are unclear. *Aromobates* has been hypothesized to be the monotypic sister group of all other dendrobatids (Myers et al., 1991), but synapomorphies shared with *Mannophryne* and *Nephelobates*, also from the northern Andes, cast doubt on that claim. No molecular evidence has been presented for this taxon.

Among the ''aposematic'' taxa, only *Phyllobates* is strongly corroborated as monophyletic (Myers et al., 1978; Myers, 1987;

[30] As noted earlier, our recognition of *Ameerega* Bauer, 1986, as a senior synonym of *Epipedobates* Myers, 1987, follows the recommendation of Walls (1994). *Ranitomeya* Bauer, 1988, and *Oophaga* Bauer, 1994, are nomenclaturally valid names, but insofar as they have not achieved common usage, and our sampling did not address their monophyly or placement, we exclude them from this discussion.

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Clough and Summers, 2000; Vences et al., 2000b; Widmer et al., 2000). No synapomorphy is known for *Ameerega*, and it is likely paraphyletic or polyphyletic with respect to *Allobates*, *Colostethus*, *Cryptophyllobates*, and *Phobobates*. Schulte (1989) and Myers et al. (1991) rejected *Allobates* and *Phobobates* on the basis of errors in the analysis of behavior, lack of evidence, unaccounted character conflict, incorrect character coding, and creation of paraphyly in *Ameerega* (as also found by Clough and Summers, 2000; Vences et al., 2000b; Santos et al., 2003; Vences et al., 2003b), but many authors continue to recognize them. In addition, *Phobobates* was found to be monophyletic by Vences et al. (2000b) but paraphyletic by Clough and Summers (2000). Similarly, *Minyobates* may or may not be nested within *Dendrobates* (Silverstone, 1975; Myers, 1982, 1987; Myers and Burrowes, 1987; Jungfer et al., 1996; Clough and Summers, 2000; Jungfer et al., 2000). Likewise, although neither study recognized *Minyobates*, it was found to be monophyletic by Santos et al. (2003) but polyphyletic by Vences et al. (2003b). *Cryptophyllobates* is the most recently named genus, but it is monotypic, and its relationship to other dendrobatids is unclear.

Difficulties in understanding the phylogeny of dendrobatid frogs are compounded by the taxonomic problems that surround many nominal species and under appreciation of species diversity (Grant and Rodriguez, 2001). Sixty-nine valid species were named over the past decade (more species than were known in 1960), 55 of which were referred to *Colostethus*. Many nominal species throughout Dendrobatidae are likely composed of multiple cryptic species awaiting diagnosis (e.g., Caldwell and Myers, 1990; Grant and Rodriguez, 2001; Grant, 2002), but the rapid increase in recognized diversity is not unaccompanied by error, and critical evaluation of the limits of nominal taxa will undoubtedly result in some number of these being placed in synonymy (e.g., Coloma, 1995; Grant, 2004).

[469] FAMILY: BUFONIDAE GRAY, 1825

Bufonina Gray, 1825: 214. Type genus: *Bufo* Laurenti, 1768.

Atelopoda Fitzinger, 1843: 32. Type genus: *Atelopus* Duméril and Bibron, 1841.

Phryniscidae Günther, 1858b: 346. Type genus: *Phryniscus* Wiegmann, 1834.

Adenomidae Cope, 1861 ''1860'': 371. Type genus: *Adenomus* Cope, 1861.

Dendrophryniscina Jiménez de la Espada, 1871 ''1870'': 65. Type genus: *Dendrophryniscus* Jiménez de la Espada, 1871 ''1870''.

Platosphinae Fejérváry, 1917: 147. Type genus: *Platosphus* d'Isle, 1877 (fossil taxon considered to be in this synonymy because *Platosophus* = *Bufo* [sensu lato]).

Bufavidae Fejérváry, 1920: 30. Type genus: *Bufavus* Portis, 1885 (fossil taxon considered to be in this synonymy because *Bufavus* = *Bufo* [sensu lato]).

Tornierobatidae Miranda-Ribeiro, 1926: 19. Type genus: *Tornierobates* Miranda-Ribeiro, 1926.

Nectophrynidae Laurent, 1942: 6. Type genus: *Nectophryne* Buchholz and Peters, 1875.

Stephopaedini Dubois, 1987 ''1985'': 27. Type genus: *Stephopaedes* Channing, 1978.

IMMEDIATELY MORE INCLUSIVE TAXON: [460] Agastorophrynia **new taxon.**

SISTER TAXON: [461] Dendrobatoidea Cope, 1865.

RANGE: Cosmopolitan in temperate and tropical areas except for the Australo-Papuan region, Madagascan, Seychelles, and New Zealand.

CONTENT: *Adenomus* Cope, 1861 ''1860''; *Altiphrynoides* Dubois, 1987 ''1986'' (including *Spinophrynoides* Dubois, 1987 ''1986''; see Systematic Comments); ***Amietophrynus*** new genus (see Systematic Comments and appendix 7); ***Anaxyrus*** Tschudi, 1845 (see Systematic Comments and appendix 7); *Andinophryne* Hoogmoed, 1985; ***Ansonia*** Stoliczka, 1870; *Atelophryniscus* McCranie, Wilson, and Williams, 1989; ***Atelopus*** Duméril and Bibron, 1841; ***Bufo*** Laurenti, 1768 (see Systematic Comments and appendix 7); *Bufoides* Pillai and Yazdani, 1973; ***Capensibufo*** Grandison, 1980; ***Chaunus*** Wagler, 1828 (see Systematic Comments and appendix 7); *Churamiti* Channing and Stanley, 2002; ***Cranopsis*** Cope, 1875 ''1876'' (see Systematic Comments and appendix 7); *Crepidophryne* Cope, 1889; ***Dendrophryniscus*** Jiménez de la Espada, 1871 ''1870''; ***Didynamipus*** Andersson, 1903; ***Duttaphrynus*** new genus (see appendix 7); *Epidalea* Cope, 1865 (see Sys-

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tematic Comments and appendix 7); *Frostius* Cannatella, 1986; ***Ingerophrynus*** new genus; *Laurentophryne* Tihen, 1960; *Leptophryne* Fitzinger, 1843; ***Melanophryniscus*** Gallardo, 1961; ***Mertensophryne*** Tihen, 1960 (including ***Stephopaedes*** Channing, 1979 ''1978''; see Systematic Comments and appendix 7); *Metaphryniscus* Señaris, Ayarzagüena, and Gorzula, 1994; *Nannophryne* Günther, 1870 (see Systematic Comments and appendix 7); ***Nectophryne*** Buchholz and Peters, 1875; ''***Nectophrynoides***'' Noble, 1926 (see Systematic Comment); *Nimbaphrynoides* Dubois, 1987 ''1986''; *Oreophrynella* Boulenger, 1895; ***Osornophryne*** Ruiz-Carranza and Hernández-Camacho, 1976; *Parapelophryne* Fei, Ye, and Jiang, 2003; ***Pedostibes*** Günther, 1876 ''1875''; ***Pelophryne*** Barbour, 1938; ***Peltophryne*** Fitzinger, 1843; ***Phrynoidis*** Fitzinger, 1843 (see Systematic Comments and appendix 7); *Poyntonophrynus* new genus (see Systematic Comments and appendix 7); *Pseudobufo* Tschudi, 1838; ***Pseudepidalea*** new genus (see appendix 7); ***Rhaebo*** Cope, 1862 (see Systematic Comments and appendix 7); ***Rhamphophryne*** Trueb, 1971; ***Rhinella*** Fitzinger, 1826 (see Systematic Comments and appendix 7); ***Schismaderma*** Smith, 1849; *Truebella* Graybeal and Cannatella, 1995; ***Vandijkophrynus*** new genus (see Systematic Comments and appendix 7); ***Werneria*** Poche, 1903; ''***Wolterstorffina***'' Mertens, 1939 (see Systematic Comments).

CHARACTERIZATION AND DIAGNOSIS: Several of the larval characters in our analysis (from Haas, 2003) optimize as synapomorphies of Bufonidae: (1) diastema in larval lower lip papillation (Haas 9.1); (2) m. diaphragmatopraecordialis absent (Haas 25.0); (3) lateral fibers of m. subarcualis rectus II–IV invade interbranchial septum IV (Haas 29.1); (4) processus anterolateralis of crista parotica absent (Haas 66.0); (5) larval lungs rudimentary or absent (Haas 133.0, also in *Ascaphus* and some *Litoria*). Graybeal and Cannatella (1995) noted the fusion of the basal process of the palatoquadrate with the squamosal (Baldauf, 1959), although they noted that not enough taxa had been evaluated to ensure that this is the appropriate level of optimization of this character.

Because *Melanophyniscus* (and *Truebella*, unexamined by us; Graybeal and Cannatella, 1995) lacks a Bidder's organ and because our molecular data place *Melanophryniscus* firmly as the sister taxon of remaining bufonids, the presence of a Bidder's organ is a synapomorphy not of Bufonidae, but of branch 470, Bufonidae excluding *Melanophryniscus* (and presumably *Truebella*). Larval characters (from Haas, 2003) that are synapomorphies of bufonids excluding *Melanophryniscus* (and possibly *Truebella*) are (1) ramus mandibularis (cranial nerve V_3) runs through the m. levator mandibulae externus group (Haas 65.1); (2) dorsal connection from processus muscularis to commissura quadratoorbitalis (Haas 78.2); (3) eggs deposited in strings (Haas 141.1, diversely modified higher up in the bufonid tree). Atlantal cotyles juxtaposed (J.D. Lynch, 1971, 1973) is also a likely synapomorphy of this taxon.

SYSTEMATIC COMMENTS: As evidenced by our results *Bufo* is wildly paraphyletic with a number of other nominal genera (as documented by Graybeal, 1997). Our sampling has likely hardly scratched the surface of this problem, and we hope that subsequent work will continue to add to the evidence so far presented so that a more universal resolution may be reached. A complete remedy of the polyphyly/paraphyly of *Bufo* is beyond the scope of this study, although we take limited actions to start this inevitable process. We could place all of the names that are demonstrably derived from ''*Bufo*'' into the synonymy of *Bufo*, thereby providing a monophyletic taxonomy. However, because much of this paraphyly was understood in 1972 (various papers in Blair, 1972a), it is clear that social inertia is standing in the way of progress. We judge that progress will require the partition of ''*Bufo*'' into more informative natural units.

A recent study on New World *Bufo* by Pauly et al. (2004) had not appeared when we were designing our sampling strategy. That work provides additional guidance in our development of an improved taxonomy, although the study differs from ours in analytical methods and assumptions, taxon sampling, and amount of data involved (2.5 kb of mtDNA in the study by Pauly et al., 2004, and ca. 3.7 kb/terminal of mtDNA and nuDNA in our study). Our results are shown

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in figure 50 and 60; the results of Pauly et al. (2004) are shown in figure 68, and a comparison of the taxa held in common by the two studies is shown in figure 69. Both studies found the position of *Bufo margaritifer* to be remarkable. The difference is that we think further resolution should come from additional data and denser sampling rather than from invoking one from among a restricted set of published models of molecular evolution to explain the issue away.

On the basis of our data analysis, as well as other information (e.g., Pauly et al., 2004), we can partition the following hypothesized monophyletic units out of ''*Bufo*'' (fig. 70):

(1) [476] *Rhaebo* Cope, 1862 (type species: *Bufo haematiticus* Cope, 1862). We recognize the species of the *Bufo guttatus* group, the sister group of all bufonids except *Melanophryniscus*, *Atelopus*, *Osorphophryne*, and *Dendrophryniscus* (see figs. 50, 60), as *Rhaebo* (see appendix 5 for molecular synapomorphies, appendix 6 for nomenclatural comment, and appendix 7 for content) on the basis of their lack of cephalic crests, their yellowish-orange skin secretions (white in other nominal *Bufo*; R.W. McDiarmid, personal commun.), presence of an omosternum (otherwise found, among bufonids, only in *Nectophrynoides* and *Werneria* [J.D. Lynch, 1973: 146], *Capensibufo* [Grandison, 1981], and the *Cranopsis valliceps* group [J. R. Mendelson, III, personal commun.]), and hypertrophied testes (Blair, 1972c, 1972d), which in combination differentiate *Rhaebo* from all other bufonids. (See appendix 6 for note under Bufonidae on this name.)

(2) *Phrynoidis* Fitzinger, 1843: 32 (type species: *Bufo asper* Gravenhorst, 1829). Because it is more closely related to *Pedostibes* than to other ''*Bufo*'', we recognize the *Bufo asper* group (see appendix 7 for content) as *Phrynoidis*. Inger (1972) provided morphological differentia that serve to distinguish *Phrynoidis* from other bufonid taxa. Which of the suggested characters is synapomorphic is not obvious, and additional morphological work is needed. Further, the monophyly of this taxon with respect to *Pedostibes*, and possibly to other unsampled genera, is an open question. The relationship of *Bufo galeatus* to this taxon is arguable. Dubois and Ohler (1999) provisionally allocated it to the *Bufo asper* group on the basis of morphology, while Liu et al. (2000) allied it with the *B. melanostictus* group on the basis of molecular evidence. For the present we accept its assignment to *Duttaphrynus* (the *Bufo melanostictus* group). Fei et al. (2005) regarded *Torrentophryne* to be part of this clade, a conclusion not supported either by the study of Liu et al. (2000) or by our analysis, which place *Torrentophryne* in *Bufo* (sensu stricto). We restrict *Phrynoidis* to the *Bufo asper* group. We also suggest that some of the characters that optimize to this branch in our tree (appendix 5) are synapomorphies of *Phrynoidis*.

(3) *Rhinella* Fitzinger, 1826: 39 (type species by monotypy: *Bufo* [*Oxyrhynchus*] *proboscideus* Spix, 1824). We apply this name to the *Bufo margaritifer* group (see appendix 6 for nomenclatural comment and appendix 7 for content). The most recent morphological characterization of the group (as the *Bufo typhonius* group) was by Duellman and Schulte (1992), although their diagnoses explicitly refer to overall similarity, not synapomorphy. Hass et al.'s (1995) study of immunological distances found the group to be monophyletic, but their outgroup samples were limited to *Bufo marinus* and *B. spinulosus*. Baldissera et al. (1999) provided evidence (restricted to *R. margaritifer*) from the nucleolar organizer region (NOR) that *Rhinella* may be distantly related to *Chaunus*. Most species of *Rhinella* have distinctive and extremely expanded postorbital crests in older adult females, although this does not appear to be the rule, so the diagnosis of the group needs refinement. Should *Rhinella* Fitzinger, 1826, be found to be nested within *Chaunus* Wagler, 1828, the name *Rhinella* will take precedence for the inclusive group.

Given our taxon sampling, we cannot rule out the possibility that *Rhinella* and *Rhamphophryne* are not reciprocally monophyletic. However, although placing all the involved species in a single genus would minimize the risk that we are wrong, we believe such caution to be counter-productive. Also, from a more pragmatic position, this would require all species currently placed in *Rhamphophryne* to be transferred to *Rhinella* based only on the possibility of nonmonophyly, not evidence. The genera may be di-

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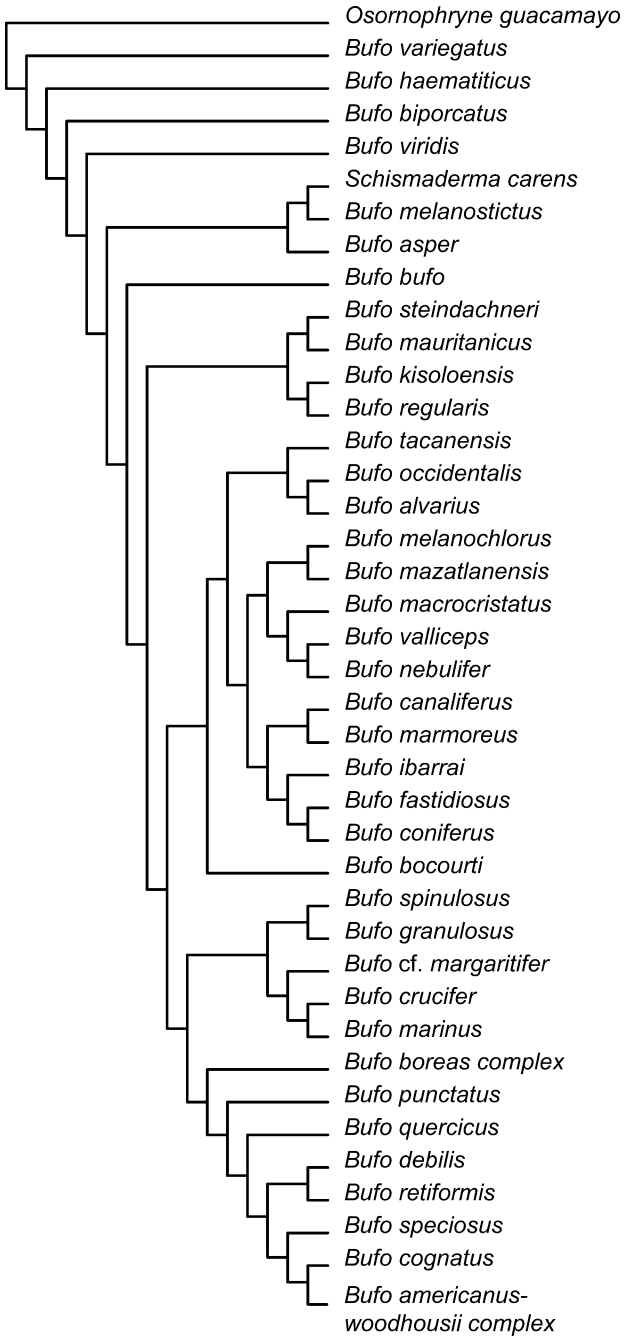

Fig. 68. Maximum-likelihood tree of predominantly New World Bufonidae suggested by Pauly et al. (2004) on the basis of 2,370 bp (730 informative sites) of mitochondrial DNA (12S, $tRNA^{Val}$, and 16S). Alignment was done under Clustal (Thompson et al., 1997; cost functions not disclosed) then modified manually. Gaps were considered to be missing data and the substitution model assumed for the maximum-likelihood analysis was GTR + Γ+ I.

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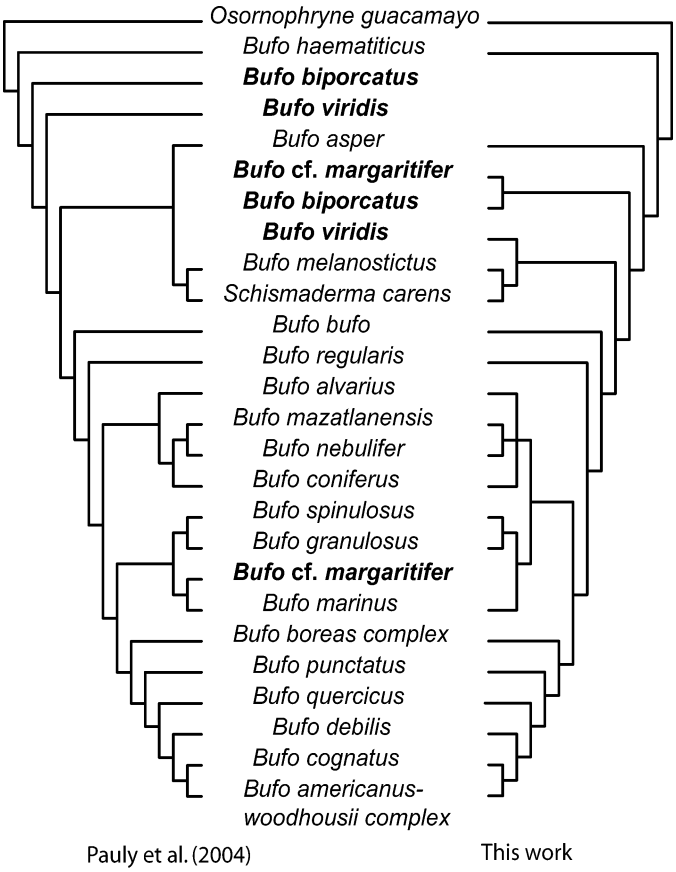

Fig. 69. Comparison of our bufonid parsimony results, via terminals held in common (see fig. 50, 60) with those of Pauly et al. (2004) (fig. 68). Taxa whose relative placement differs substantially between the two studies are in boldface.

agnosed by the number and size of eggs (many and small in *Rhinella*; few and large in *Rhamphophryne*); by the adductor mandibulae musculature (both the m. adductor mandibulae posterior subexternus and m. adductor mandibulae externus superficialis [''S + E'' of Starrett in J.D. Lynch, 1986] present in *Rhinella*; only m. adductor mandibulae subexternus [''E'' of Starrett in J.D. Lynch, 1986] present in *Rhamphophryne*); by the thigh musculature (m. adductor longus present in *Rhinella*, absent in *Rhamphophryne*); by liver morphology (trilobed with left side larger than right side in *Rhinella*, bilobed with right side massive, conspicuously larger than left side in *Rhamphophryne*); and by extensively webbed hands and feet in *Rhamphophryne* (T. Grant, personal obs.). Most (but not all) species of *Rhamphophryne* differ from all species of *Rhinella* in possessing a conspicuously elongate snout, reduced number of vertebrae, and vocal sacs with slit-like openings. Likewise, most (but not all) species of *Rhinella* differ from all species of *Rhamphophryne* in possessing protuberant vertebral spines, greatly expanded alate postorbital crests, and a leaf-like dorsal pattern.

Many questions remain regarding the relationships between these and other New World bufonids. For example, *Crepidophryne epiotica* possesses the same jaw musculature and liver morphology as *Rhamphophryne* and shares large, unpigmented eggs, similar hand and foot morphology, and absence of the ear, suggesting it may be closely related to *Rhamophophryne*. However, the morphological results of Graybeal (1997; data undisclosed) suggest that *Crepidophry-*

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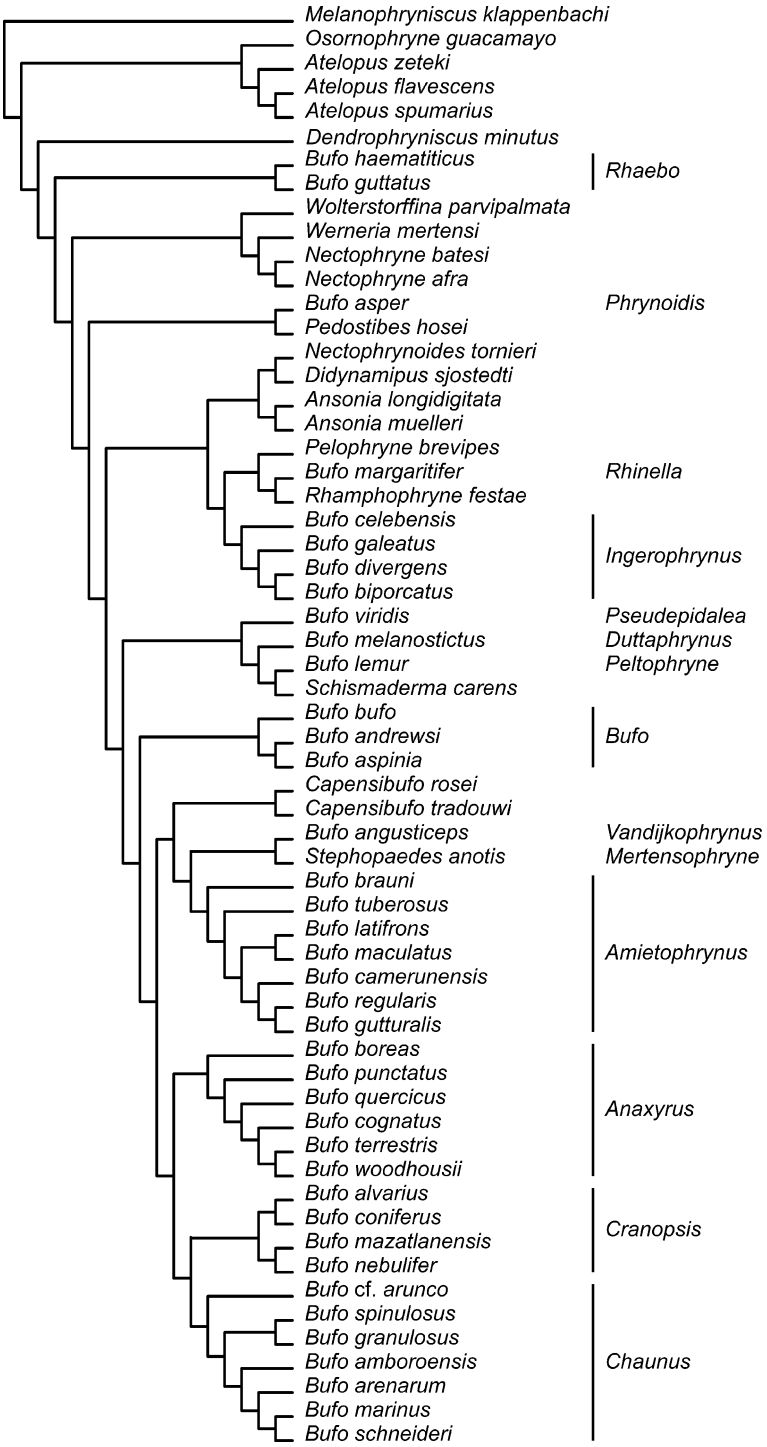

Fig. 70. Generic changes suggested for bufonid taxa that we studied. This figure shows our terminals and the new genera, but the text should be consulted for additional generic changes that involve species not addressed in our phylogenetic analysis.

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ne is imbedded within *Cranopsis*. Similarly, *Andinophryne* is characterized as possessing an omosternum, anteriorly ''firmisternal'' and posteriorly ''arciferal'' pectoral girdle (for pectoral girdle morphology see Kaplan, 2004), a complete ear, partially webbed hands, elongate paratoid glands, and lacking the m. adductor longus of the thigh (Hoogmoed, 1989b). However, none of these characters is unique or clearly derived relative to likely relatives (e.g., *Rhamophryne* or *Rhinella*), and their relationships require further investigation.

(4) [491] *Ingerophrynus* **new genus** (type species: *Bufo biporcatus* Gravenhorst, 1829; etymology: Robert F. Inger + Greek: phrynos [toad]). This name commemorates the extensive contributions of Robert F. Inger to the herpetology of tropical Asia and the Sundas, as well as to the systematics of Asian bufonids. The topology described by our exemplars *Bufo celebensis*, *B. galeatus*, *B. divergens*, and *B. biporcatus* suggests a major clade of tropical Asian bufonids. We presume that this clade contains all species of the *Bufo biporcatus* group (see appendix 7 for content) in addition to *B. celebensis* Günther, 1859 ''1858'', and *B. galeatus* Günther, 1864. Inger (1972) provided differentia that distinguish the *Bufo biporcatus* group from the remaining *Bufo*, although it is not obvious which of these characters are synapomorphies. We also suggest that our branch 491 (see appendix 5) contains several molecular synapomorphies that distinguish this clade from all others.

Association of *Bufo celebensis* and *B. galeatus* with the *Bufo biporcatus* group as parts of *Ingerophrynus* rests entirely on molecular evidence (summarized in appendix 5), although we expect that some of the characters that differentiate the *B. biporcatus* group from other ''*Bufo*'' also apply to these two species. *Bufo celebensis* had not previously been associated with any other species of *Bufo*, so our hypothesis of relationship is novel and suggests that *Ingerophrynus* sits astride Wallace's Line.

Dubois and Ohler (1999) provisionally allocated *B. galeatus* to the *B. asper* group (= *Phrynoidis*), but this allocation is not consistent with our molecular evidence. Liu et al. (2000) placed *B. galeatus* as the sister taxon of the *B. melanostictus* group, although this, too, is not consistent with our molecular evidence.

(5) *Epidalea* Cope, 1864 (type species: *Bufo calamita* Laurenti, 1768) is available for *Bufo calamita* (see appendix 6 for nomenclatural comment and appendix 7 for content). We had hoped to associate the name *Epidalea* Cope, 1864, through its type (*Bufo calamita* Laurenti, 1768), to the *Bufo viridis* group. However, association of *Bufo calamita* with the *Bufo viridis* group is seemingly based solely on overall similarity (Inger, 1972). The results based on DNA sequences presented by Graybeal (1997; fig. 25) do not place *B. calamita* and *B. viridis* as closest relatives. Because the phylogenetic evidence so far published (Graybeal, 1997) does not suggest that *B. calamita* is a member of the *B. viridis* group (but see caveat regarding Graybeal's data in ''Review of Current Taxonomy''), we place them in separate genera as an interim measure. We expect that, as bufonid phylogenetics become better understood, the name *Epidalea* will be attached to a larger group than just this one species.

(6) *Pseudepidalea* **new genus** (type species: *Bufo viridis* Laurenti, 1768; etymology: in reference to the overall morphological similarity of members of the ''*Bufo*'' *viridis* group to *Epidalea calamita*; see appendix 7 for content). Liu et al. (2000) presented weak evidence that *Bufo raddei* is not part of the *Bufo viridis* complex (their exemplars being *Bufo oblongus danatensis* and *B. viridis*). For this reason we regard *B. raddei* as being only provisionally assigned to this genus. A set of differentia provided by Martin (1972) will serve to distinguish this group from other bufonid taxa, although, as in many such diagnostic summaries, we cannot identify which characters are apomorphies and which are plesiomorphic. We do, however, suggest that the molecular synapomorphies provided in appendix 5 will serve to diagnose this taxon.

(7) *Duttaphrynus* **new genus** (type species: *Bufo melanostictus* Schneider, 1799; etymology: S.K. Dutta + Greek: phrynos [toad]) reflects the contributions to herpetology by Sushil Kumar Dutta, noted Indian herpetologist). We erect this generic name for the *Bufo melanostictus* group as defined by Inger (1972) and subsequent authors. Al-

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though decisive evidence for the monophyly of *Duttaphrynus* is currently lacking, we hypothesize that the group is monophyletic and suggest that detailed analysis of this group and close relatives will document this. Morphological differentia provided by Inger (1972) serve to distinguish this group from other ''*Bufo*'', although which characters are apomorphies and which are plesiomorphies remains unknown. We also suggest that at least some of the molecular synapomorphies for ''*Bufo*'' *melanostictus* in our tree are synapomorphies for *Duttaphrynus* (see appendix 5, for *Bufo melanostictus*).

(8) *Peltophryne* Fitzinger, 1843 (type species: *Bufo peltocephalus* Tschudi, 1838, by original designation) is a monophyletic radiation within nominal ''*Bufo*'' and was most recently synonymized with *Bufo* by Pramuk (2000). In the most recent study of the relationships of this group, Pramuk (2000) analyzed morphological characters and mtDNA sequence data and found *Peltophryne* (as the *Bufo peltocephalus* group) to be most closely related to the American *Bufo granulosus* group (see also Pregill, 1981; Pramuk, 2000; Pramuk et al., 2001). Nevertheless, Pramuk (2000) rooted her cladogram on the *Bufo regularis* group and otherwise had relatively sparse outgroup taxon sampling. Our data indicate strongly that the *Bufo peltocephalus* group is not closely related to the *Bufo granulosus* group or any other American toad, but is, instead, the sister taxon of the African taxon *Schismaderma*, which was not included in previous studies of *Peltophryne*. The biogeographic track suggested by this finding invites further work. We therefore resurrect *Peltophryne* (see appendix 7 for content) for the *Bufo peltocephalus* group, as distantly related to other Neotropical toads. (See the nomenclatural comment in appendix 6.)

(9) [499] *Bufo* Laurenti, 1768 (type species: *Rana vulgaris* Laurenti, 1768, by subsequent designation of Tschudi, 1838: 50). We restrict the generic name *Bufo* (sensu stricto) to the monophyletic *Bufo bufo* group of Inger (1972) and subsequent authors (see appendix 7 for content). Inger (1972) suggested morphological differentia for this taxon that separate it from other bufonid taxa, although their polarity remains to be documented. Liu et al. (2000) found a paraphyletic *Torrentophryne* to be nested within the otherwise monophyletic *Bufo bufo* group, which is consistent with our results. We therefore follow Liu et al. (2000) in placing *Torrentophryne* in the synonymy of *Bufo* (sensu stricto). Clearly, our taxon sampling is insufficient to allocate all species of remaining ''*Bufo*'' to identified clades and, as we suggest later, we think that ''*Bufo*'' species not allocated to this or other nominal clades should be associated with this generic name in quotation marks pending resolution of their phylogeny.

(10) *Vandijkophrynus* **new genus** (type species: *Bufo angusticeps* Smith, 1848; etymology: E. Van Dijk + Greek: phrynos [toad], commemorating Eddie Van Dijk, noted South African herpetologist and indefatigable tadpole specialist). (See appendix 7 for content and new combinations.) We erect this genus for the *Bufo angusticeps* group as differentiated by Tandy and Keith (1972; excluding *Bufo*/*Capensibufo tradouwi* and *C. rosei*, which do not have the distinctive reticulate dorsal pattern of the core group and are placed phylogenetically far away in our analysis) and by Cunningham and Cherry (2004). Our discovery of the exemplar of this group, *B. angusticeps*, as the sister taxon of *Stephopaedes* is consistent with the results of Cunningham and Cherry (2004). Should *Vandijkophrynus* be found to be synonymous with *Poyntonophrynus* (see below), we select *Vandijkophrynus* to have priority under the provisions of Article 24.2.1 (Rule of First Revisor) of the International Code of Zoological Nomenclature (ICZN, 1999).

(11) *Mertensophryne* Tihen, 1960 (type species: *Bufo micranotis rondoensis* Loveridge, 1942). We suggest that at least some of the molecular synapomorphies (appendix 5) that optimize to our *Stephopaedes anotis* are synapomorphies for a larger *Mertensophryne*. Complicating discussion of phylogeny in the vicinity of *Stephopaedes* is *Mertensophryne* and the *Bufo taitanus* group (see appendix 7 for content), which is a group of African toads that lack tympani and columellae; that frequently show digit reduction (Tandy and Keith, 1972); and that have been been suggested to be related to *Capensibufo* (Tandy and Keith, 1972). Graybeal and Cannatella (1995) and Graybeal (1997) suggest-

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ed that *Stephopaedes* and *Mertensophryne* are nested within at least some component of the *B. taitanus* group; Cunningham and Cherry (2004) arrived at similar conclusions. Müller et al. (2005) described the tadpole of *B. taitanus* and reported that it has a crown that encircles the eyes as in *Stephopaedes* but is not so well developed. In no studies have the relationships of *Mertensophryne*, *Stephopaedes*, and the *Bufo taitanus* group been evaluated with adequate taxon sampling, and the questions of relationship have remained recognized (e.g., Tandy and Keith, 1972) but unresolved for more than 30 years. What is known is that the *Bufo taitanus* group, *Mertensophryne*, and *Stephopaedes* lack columellae (convergently in the clades composed of [1] *Wolterstorffina*, *Werneria*, *Nectophryne*, and likely *Laurentophryne* [Tihen, 1960; Grandison, 1981]; [2] *Didynamipus*; and [3] *Capensibufo rosei*), and likely form a monophyletic group. Furthermore, *Stephopaedes*, *Mertensophryne*, and at least one member of the *Bufo taitanus* group (*B. taitanus*; H. Müller et al., 2005) have accessory respiratory structures on the head of the larva. (Nevertheless, differences among these structures suggest the possibility of nonhomology; Dubois, 1987 ''1985''; Poynton and Broadley, 1988.) *Mertensophryne* is currently monotypic, and *Stephopaedes* contains three species. Our action to promote further research is to place the *Bufo taitanus* group, *Mertensophryne*, and *Stephopaedes* into an enlarged *Mertensophryne*, retaining *Stephopaedes* as a subgenus, in order not to lose recognition of this monophyletic group. (See appendix 7 for new combinations.) Loss of the middle ear is synapomorphic at this level and, although larvae are unknown for several members of the *Bufo taitanus* group, we suspect that the accessory repiratory structures on the head of larvae is a synapomorphy as well. Ongoing work by Channing and collaborators will address this further.

(12) *Poyntonophrynus* **new genus** (type species: *Bufo vertebralis* Smith, 1848; etymology: J.C. Poyton [commemorating John C. Poynton, noted South African herpetologist] + phrynos [Greek: toad]). We recognize *Poyntonophrynus* for the *Bufo vertebralis* group of Tandy and Keith (1972; cf. Poynton, 1964) and Cunningham and Cherry (2004). *Poytonophrynus* is characterized by lacking a tarsal fold (a presumed apomorphy), having parotoid glands indistinct and flattened (Poynton, 1964a), and the tympanum being small but distinct (Tandy and Keith, 1972). We did not study any member of this group, but on the basis of the DNA sequence results presented by Cunningham and Cherry (2004), it is a monophyletic group, closely related to *Mertensophryne* (sensu lato) and *Vandijkophrynus*. See appendix 7 for content and new combinations. See appendix 7 for content and new combinations.

(13) [506] *Amietophrynus* **new genus** (type species: *Bufo regularis* Reuss, 1833; etymology: Jean-Louis Amiet, an influential herpetologist of West Africa, + Greek: phrynos [toad]). We erect this taxon for all African 20-chromosome ''*Bufo*'' discussed by Cunningham and Cherry (2004; the clade subtended by our branch 506), as well as the 22-chromosome ''*Bufo*'' imbedded within this clade (the *Bufo pardalis* group of Cunningham and Cherry, 2004). This includes toads previously included by various authors in the *Bufo blanfordi* group, *B. funereus* group, *B. kerinyagae* group, *B. latifrons* group, *B. lemairii* group, *B. maculatus* group, *B. pardalis* group, *B. perreti* group, *B. regularis* group, *B. superciliaris* group, and *B. tuberosus* group. Although at least some of these groups are monophyletic, we do not recognize species groups within *Amietophrynus* at this time, because several of the existing groups are monotypic (e.g., *B. lemairii*) or clearly nonmonophyletic (e.g., *B. regularis* group). We think that recognition of species groups should follow a more densely sampled study of the *Amietophrynus* and near relatives. Although not previously suggested to be a member of the 20-chromosome group, our phylogenetic results allow us to predict that *Bufo tuberosus* is a 20-chromosome frog.

Beyond the 20-chromosome condition that is apomorphic for group (Bogart, 1968; Cunningham and Cherry, 2004), molecular transformations diagnose the taxon unambiguously (see appendix 5). Moreover, the monophyly of this taxon is a testable proposition.

Other than the *Bufo pardalis* group (see above), we have no unambiguous evidence

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tying the African 22-chromosome toad groups (*B. gracilipes* and *B. mauritanicus* groups) or such African species of unknown karyotype such as the *B. pentoni* group and *B. arabicus* group to any of the African (or other) bufonid groups. Additional evidence and study will be needed to resolve their placement, which very clearly is not within *Bufo* (sensu stricto). For the moment, we merely place the generic name ''*Bufo*'' in quotation marks in combination with these species to denote their formal exclusion from *Bufo* (sensu stricto).

(14) *Nannophryne* Günther, 1870 (type species: *Nannophryne variegata* Günther, 1870, by monotypy). We resurrect the name *Nannophryne* for *Bufo variegatus* (Günther, 1870). Although we did not include this taxon in our analysis, the molecular evidence provided by Pauly et al. (2004) suggests strongly that this taxon, like *Rhinella* (the *Bufo margaritifer* group), is only distantly related to other New World ''*Bufo*''. Martin (1972) provided osteological differentia that serve to diagnose the taxon among ''*Bufo*'', but its exact phylogenetic position among bufonids remains to be determined. Prior to Pauly et al. (2004), some authors placed *B. variegatus* near the *B. spinulosus* group (e.g., Blair, 1972c), whereas others (e.g., Cei, 1980) have declined to place it in any species group. Pauly et al. (2004) placed it far from the *B. spinulosus* group, and attaching near the base of the bufonid exemplars that they studied. It remains possible that *Nannophryne* will be found to be most closely related to *Rhaebo*, in which case *Rhaebo* will take nomenclatural precedence for the larger group.

(15) [513] *Anaxyrus* Tschudi, 1845 (type species: *Anaxyrus melancholicus* Tschudi, 1845 [= *Bufo compactilis* Wiegmann, 1833]). We recognize the North American clade of ''*Bufo*'' subtended by branch 513 (see appendix 5) as the genus *Anaxyrus* Tschudi, 1845. We are unaware of any morphological synapomorphy for this group, although, with exceptions, they do have a different look and feel than the predominantly Middle-American (*Cranopsis*) and South-American (*Chaunus*) taxa. Recognition of this taxon is consistent with our results and those of Pauly et al. (2004). Formerly, this taxon was considered to comprise a number of casually-defined species groups, most of which require reevaluation. Although Tschudi (1845) provided an erroneous South American type locality for the type species, it was recognized as early as 1882 (Boulenger, 1882) that *Anaxyrus melancholicus* Tschudi, 1845, is a junior synonym of the Mexican *Bufo compactilis* Wiegmann, 1834. This was most recently detailed by Pramuk and Mendelson (2003). (See appendix 7 for content and new and revived combinations.)

A partial junior synonym of *Anaxyrus* is *Incilius* Cope (1863: 50). Under the provisions of the ''Principle of First Revisor'' (Art. 24; ICZN, 1999) we designate *Bufo cognatus* Say, 1823, as the type species of *Incilius* to solidify this synonymy, which otherwise could have been assigned through one of the originally included species to threaten the priority of *Cranopsis*.

(16) [519] *Cranopsis* Cope, 1875 ''1876'' (type species: *Bufo fastiodosus* Cope, 1875 ''1876''). We apply the name *Cranopsis* to the predominantly Middle American taxon subtended by branch 519. Although we know of no morphological synapomorphy for this taxon, species within it generally exhibit a distinctive appearance. Nevertheless, see appendix 5 for molecular synapomorphies. This group is composed of the former *Bufo valliceps* group and allies. See appendix 7 for content and new and revived combinations.

(17) [522] *Chaunus* Wagler, 1828 (type species: *Chaunus marmoratus* Wagler, 1828 [= *Bufo granulosus* Spix, 1824]). We recognize the predominantly South American taxon subtended by branch 522 as *Chaunus*. No morphological characters are known to diagnose this group, which is diagnosed completely on the basis of molecular data (see appendix 5, branch 522). *Rhamphophryne* and *Rhinella* may well be found to be nested within *Chaunus* (see Graybeal, 1997: her fig. 13; Pauly et al., 2004), in which case, *Rhinella* Fitzinger, 1826, will take precedence, but evidence has yet to be produced to support this synonymy without recourse to accepting a specific model of molecular evolution (Pauly et al., 2004).

Pauly et al. (2004) suggested on the basis of fewer data, more analytical assumptions, but denser sampling that the *Bufo margari-*

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tifer group (see below) is imbedded within this group. This remains an open question, but we suggest that decisive resolution will require denser taxon sampling and more data, not additional analytical assumptions.

There are several other groups of ''*Bufo*'' and various individual species we have not addressed because we did not include any of them in our analysis and because there is no substantial published evidence on their phylogenetic placement. All of these we simply treat as incertae sedis within Bufonidae, tacked to the generic label ''*Bufo*'' (see appendix 7 for a list). The reader will note that the bulk are Asian taxa, residing in geographic areas suggesting that they will be found to be related to a number of non-*Bufo* genera. Only additional work will elucidate this.

We think that our proposed breakup of ''*Bufo*'' will promote more rapid progress in the field, because the sociological principle that drives much of systematics is to show that other workers are wrong (Hull, 1988), and many graduate students will certainly take aim at our hypotheses. Most systematists recognize that, traditionally, the first species to receive novel generic names have been those that are highly autapomorphic, and subsequent authors are usually hesitant to apply these names to more generalized forms. Having taken the controversial first step, we hope that other workers will step in and address the rather large number of problems that we have identified. There is much work to be done in bufonids, and we intend our taxonomic proposal to serve as a framework that will guide additional studies.

We do not find any compelling reason to maintain the sister monotypic genera *Altiphrynoides* Dubois, 1987 ''1986'' and *Spinophrynoides* Dubois, 1987 ''1986''. Grandison (1981) and Graybeal and Cannatella (1995) showed these African toads to be each other's closest relatives. Acting as First Revisor, we consider *Altiphrynoides* Dubois, 1987 ''1986'', to be a senior synonym of *Spinophrynoides* Dubois, 1987 ''1986''. (See appendix 7 for the single new combination.) ''*Nectophrynoides*'' *cryptus* in their tree (fig. 26) is not part of a monophyletic group with other *Nectophrynoides*. We were tempted to name a new genus for *Nectophrynoides cryptus*. But, because we did not study that species, and because its sole reason for being placed outside of *Nectophrynoides* is its loss of columella, a character strongly contingent on immediate outgroups, we refrain from this action until the appropriate phylogenetic comparisons can be made.

In addition, the following monotypic genera have been named since the publication of Graybeal and Cannatella (1995) and Graybeal (1997): *Churamiti* Channing and Stanley, 2002, and *Parapelophryne* Fei, Ye, and Jiang, 2003. Neither obviously renders any other taxon paraphyletic. Clearly, a detailed revision of Bufonidae without reference to geographic boundaries is badly needed.

[108] RANOIDES **NEW TAXON**

ETYMOLOGY: Rana (Latin: frog) + oides (Greek: having the form of). The taxon is identical in content to the regulated superfamily name Ranoidea, but with an ending change made to remove the implication that it is regulated by the International Code of Zoological Nomenclature (ICZN, 1999). (See nomenclatural comment under Ranoides in appendix 6.)

IMMEDIATELY MORE INCLUSIVE TAXON: [107] Phthanobatrachia **new taxon.**

SISTER TAXON: [314] Hyloides **new taxon.**

RANGE: Worldwide temperate and tropical regions, except New Zealand, most of Australia, and southern South America.

CONCEPT AND CONTENT: Ranoides **new taxon** is a monophyletic group composed of [109] Allodapanura **new taxon** and [180] Natatanura **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Haas (2003) suggested the following characters that we regard as synapomorphies of our Ranoides: (1) insertion of m. rectus cervicis on proximal ceratobranchialia III and IV (Haas 39.2); (2) ramus mandibularis (cranial nerve V_3) is either posterior (ventral) to m. levator mandibulae externus group or runs through it—a change from being anterior (dorsal) to the externus group (Haas 65.0/1); and (3) firmisternal shoulder girdle (epicoracoids are fully fused along their length; Haas 144.2; convergent in Dendrobatidae). J.D. Lynch (1973: 146) suggested that an ossified omosternum is a synapomorphy of

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''Ranoidea'' (our Ranoides, excluding Microhylidae and Brevicipitidae). This may be, but there are alternative optimizations. Among others, the ossified omosternum may have been gained at the level of Ranoides and lost independently in Microhylidae and Brevicipitidae; gained at the level of Ranoides, lost at Allodapanura, and regained at Laurentobatrachia; or gained independently in Laurentobatrachia, Natatanura, and Hemisotidae. (See also appendix 5, branch 108, for molecular synapomorphies.)

SYSTEMATIC COMMENTS: Ranoides in our sense is coextensive with the Recent content of the superfamily Ranoidea Rafinesque, 1814, of Dubois (2005).

A preliminary survey of literature (Liem, 1970; Tyler, 1972, 1982; Burton, 1986, 1998b) as well as examination of a few exemplars of selected genera of several families suggests another likely synapomorphy of Ranoides, worthy of additional investigation. Anteromedially differentiated elements of the m. intermandibularis are present in Arthroleptidae, Brevicipitidae, Cacosterninae (Pyxicephalidae), Ceratobatrachidae, Hemisotidae, Hyperoliidae, Microhylidae, Ptychadenidae (however, absent in *Hildebrandtia*), Petropedetidae, Phrynobatrachidae, and are absent in Alytidae, Batrachophrynidae (although present in *Batrachophrynus brachydactylus*), Bombinatoridae, Heleophrynidae, Limnodynastidae, Myobatrachidae, Pelobatidae, Sooglossidae, and Hemiphractidae (Beddard, 1908 ''1907'', 1911; Tyler, 1972; Tyler and Duellman, 1995; Burton, 1998b). This taxonomic distribution suggest that the presence of differentiated elements of the m. intermandibularis is a synapomorphy of Ranoides. Many details about the morphological diversity and taxonomic distribution of this character remain unknown and several instances of homoplasy are known within Hyloides (see Tyler, 1971b, 1971c, 1972; Burton, 1998b, and Tyler and Duellman, 1995, for examples within Noblebatrachia), and there are possibly multiple subsequent transformations within Natatanura. (This character does not seem to occur in at least some Dicroglossidae [exemplars of *Occidozyga*, *Euphlyctis*, *Nannophrys*] or Nyctibatrachidae [*Lankanectes*, *Nyctibatrachus*], but is present in Mantellidae and Rhacophoridae; Liem, 1970). In addition, Tyler (1971a) suggested that the presence of the m. cutaneous pectoris could be a synapomorphy of Ranoides, although with several reversals.

[109] ALLODAPANURA **NEW TAXON**

ETYMOLOGY: Allodapos- (Greek: strange, foreign, or belonging to another kind) + anoura (Greek: without a tail, i.e., frog), referencing the exotic diversity of morphotypes in this taxon.

IMMEDIATELY MORE INCLUSIVE TAXON: [108] Ranoides **new taxon.**

SISTER TAXON: [180] Natatanura **new taxon.**

RANGE: North and South America; sub-Saharan Africa; India and Korea to northern Australia.

CONCEPT AND CONTENT: Allodapanura **new taxon** is a monophyletic group composed of [110] Microhylidae Günther, 1858 (1843), and [143] Afrobatrachia **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Morphological characters in our analysis (from Haas, 2003) that are synapomorphies are (1) m. tympanopharyngeus present (Haas 20.1); and (2) arcus subocularis round in cross section (Haas 82.2). In addition, absence of the palatine bone in adults (Haas 146.0; a reversal from the acosmanuran condition), may optimize on this branch (to reappear on the branch subtending Afrobatrachia), or, alternatively, the palatine may be lost in Microhylidae and independently in Xenosyneunitanura. Similarly, the presence of palatal folds may optimize on this branch and be reversed in Laurentobatrachia, or may appear twice, once on the branch subtending Microhylidae as well as on the branch subtending Xenosyneunitanura. Regardless, the primary evidence for the recognition of this taxon is molecular (see appendix 5).

[110] FAMILY: MICROHYLIDAE GÜNTHER, 1858 (1843)

Hylaedactyli Fitzinger, 1843: 33. Type genus: *Hylaedactylus* Duméril anbd Bibron, 1841.

Gastrophrynae Fitzinger, 1843: 33. Type genus: *Gastrophryne* Fitzinger, 1843.

Micrhylidae Günther, 1858b: 346. Type genus: *Micrhyla* Duméril and Bibron, 1841 (an incorrect subsequent spelling of *Microhyla* Tschudi, 1838).

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Asterophrydidae Günther, 1858b: 346. Type genus: *Asterophrys* Tschudi, 1838.
Kalophrynina Mivart, 1869: 289. Type genus: *Kalophrynus* Tschudi, 1838.
Xenorhinidae Mivart, 1869: 286. Type genus: *Xenorhina* Peters, 1863.
Dyscophidae Boulenger, 1882: 179. Type genus: *Dyscophus* Grandidier, 1872.
Cophylidae Cope, 1889: 248. Type genus: *Cophyla* Boettger, 1880.
Genyophrynidae Boulenger, 1890: 326. Type genus: *Genyophryne* Boulenger, 1890.
Rhombophryninae Noble, 1931: 529. Type genus: *Rhombophryne* Boettger, 1880.
Sphenophryninae Noble, 1931: 531. Type genus: *Sphenophryne* Peters and Doria, 1878, by monotypy.
Melanobatrachinae Noble, 1931: 538. Type genus: *Melanobatrachus* Beddome, 1878.
Kaloulinae Noble, 1931: 538. Type genus: *Kaloula* Gray, 1831.
Hoplophryninae Noble, 1931: 538–539. Type genus: *Hoplophryne* Barbour and Loveridge, 1928.
Scaphiophryninae Laurent, 1946: 337. Type genus: *Scaphiophryne* Boulenger, 1882.
Pseudohemisiinae Tamarunov, 1964a: 132. Type genus: *Pseudohemisus* Mocquard, 1895.
Otophryninae Wassersug and Pyburn, 1987: 166. Type genus: *Otophryne* Boulenger, 1900.
Phrynomantini Burton, 1986: 405–450. Type genus: ''*Phrynomantis* Peters, 1867''.
Barygenini Burton, 1986: 405–450. Type genus: *Barygenys* Parker, 1936.
Callulopini Dubois, 1988a: 3. Type genus: *Callulops* Boulenger, 1888.

IMMEDIATELY MORE INCLUSIVE TAXON: [109] Allodapanura **new taxon.**

SISTER TAXON: [143] Afrobatrachia **new taxon.**

RANGE: North and South America; East and South Africa; India and Korea to northern Australia.

CONTENT: [135] Asterophryninae Günther, 1858 (including Genyophryninae Boulenger, 1890), [118] Cophylinae Cope, 1889, Dyscophinae Boulenger, 1882, [121] Gastrophryninae Fitzinger, 1843, [130] Microhylinae Günther, 1858 (1843), Scaphiophryninae Laurent, 1946, as well as several nominal genera unassigned to subfamily either because we did not study them and assignment to subfamily based on published evidence is not possible, or because they fall outside of existing subfamilies: *Adelastes* Zweifel, 1986; *Altigius* Wild, 1995; *Arcovomer* Carvalho, 1954; *Chiasmocleis* Méhely, 1904; *Gastrophrynoides* Noble, 1926; *Glyphoglossus* Günther, 1869 ''1868''; *Hyophryne* Carvalho, 1954; *Hypopachus* Keferstein, 1867; ***Kalophrynus*** Tschudi, 1838; *Metaphrynella* Parker, 1934; ***Micryletta*** Dubois, 1987; *Myersiella* Carvalho, 1954; *Otophryne* Boulenger, 1900; *Paradoxophyla* Blommers-Schlösser and Blanc, 1991; *Phrynella* Boulenger, 1887; ***Phrynomantis*** Peters, 1867[31]; ***Ramanella*** Rao and Ramanna, 1925; *Relictivomer* Carvalho, 1954; *Stereocyclops* Cope, 1870 ''1869''; ***Synapturanus*** Carvalho, 1954; *Syncope* Walker, 1973; *Uperodon* Duméril and Bibron, 1841. (See Systematic Comments.)

CHARACTERIZATION AND DIAGNOSIS: A large number of morphological characters in our analysis (from Haas, 2003) are synapomorphies of Microhylidae: (1) keratodonts absent in larvae (Haas 3.0); (2) keratinized jaw sheaths absent in larvae (Haas 6.0); (3) vena caudalis dorsalis present in larvae (Haas 14.1); (4) spiracle position median posterior (Haas 18.2); (5) m. geniohyoideus origin in larvae from connective tissue lateral to glandula thyroidea (Haas 19.4); (6) m. interhyoideus posterior in larvae extensive and strongly developed (Haas 24.2); (7) m. diaphragmatopraecordialis absent in larvae (Haas 25.0); (8) lateral fibers of m. subarcualis rectus II–IV invade interbranchial septum IV musculature in larvae (Haas 29.1); (9) m. subarcualis rectus II–IV split into medial and lateral separate muscles (Haas 30.1); (10) m. subarcualis rectus I portion with origin from ceratobranchial III absent (Haas 35.0); (11) ventral portion of the m. subarcualis rectus I inserts laterally on ceratohyal (Haas 36.1); (12) origin of m. suspensoriohyoideus from posterior palatoquadrate (Haas 46.1); (13) m. interhyoideus and m. intermandibularis in close proximity (Haas 47.0); (14) m. mandibulolabialis inserting exclusively on cartilago labialis inferior (Haas 49.1); (15) m. levator mandibulae internus anterior (Haas

[31] We realize, of course, that *Phrynomantis* Peters, 1867, is the sole member of Phrynomerinae Noble, 1931. But, beyond the autapomorphic intercalary phalangeal elements, we have only weak evidence for its placement. In this case, recognition of a monotypic subfamily serves no purpose.

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58.2); (16) m. levator mandibulae longus originates exclusively from arcus subocularis (Haas 60.2); (17) profundus and superficialis portions of m. levator mandibulae longus not overlapping and parallel (Haas 62.1); (18) ramus mandibularis (cranial nerve V_3) between portions of m. levator mandibulae longus muscle (Haas 64.1); (19) processus suboticus quadrati present (Haas 76.1); (20) partes corpores forming medial body (Haas 87.2); (21) distal end of cartilago meckeli expanded and flattened with no fossa (Haas 94.2); (22) hypobranchial plates fused (Haas 107.1); (23) commissura proximalis I present (Haas 109.1); (24) processus branchialis closed (Haas 114.1); (25) accessory longitudinal bars of cartilage dorsal to ceratobranchialia II and III present (Haas 120.1); (26) posterior margin of ventral velum discontinuous (Haas 129.1); (27) glottis position posterior (Haas 130.1); (28) nostrils closed in larval stages (Haas 131.1); (29) branchial food traps divided and crescentic (Haas 135.1); and (30) eggs floating (Haas 141.2). Although most of these characters will survive denser taxon sampling, the placement of some of them is currently ambiguous inasmuch as some of the characters listed could actually be sitting on branches from which *Synapturanus* and *Kalophrynus* are derived.

Presence of palatal folds is optimization-dependent. Presence of palatal folds may be convergent in Microhylidae and Xenosyneunitanura, or a synapomorphy of Allodapanura and lost in Laurentobatrachia.

SYSTEMATIC COMMENTS: The obtained phylogenetic structure of Microhylidae surprised us as we expected Scaphiophryninae to form the sister taxon of the remaining microhylids, because the scaphiophrynine tadpole morphology (Blommers-Schlösser, 1975; Haas, 2003), is annectant in many ways between the ranid and more typical microhylid condition. As in several other parts of the tree, the density of our taxon sampling was inadequate to address all problems in microhylid systematics, and we intend our results to guide more thorough studies. Rafael de Sá and collaborators have begun such a study, and we anticipate further revision of microhylid systematics as a result. For this reason we leave several taxa unnamed and unaddressed. As an initial step toward an entirely monophyletic taxonomy we propose the following taxonomic changes: (1) place Asterophryinae and Genyophryninae in one subfamily, Asterophryinae (following Savage, 1973); (2) restrict Dyscophinae to *Dyscophus* (also following Savage, 1973) and transfer *Calluella* from Dyscophinae to Microhylinae; (3) retain Cophylinae, but note that it appears to be imbedded within a cluster of ''microhyline'' genera that, once their phylogeny is better resolved, may require some reconstitution of Cophylinae; and (4) partition Microhylinae into a New World group, Gastrophryninae, and an Old World group, Microhylinae, with several genera left incertae sedis until they can be adequately studied or placed in a more densely sampled framework. Another group of genera (i.e., *Kalophrynus*, *Synapturanus*, *Phrynomantis*, *Micryletta*) is left incertae sedis, as well, although the phylogenetic structure we obtained among these taxa is instructive and points to new questions for systematists to address. Nevertheless, our obtained structure suggests that the biogeography of Microhylidae is complex and old.

Our data show that the former ''Microhylinae'' (sensu lato) is heterogenous mixture of basal taxa (e.g., *Synapturanus*, *Micryletta*) and two distantly related clades with which we have associated the names Microhylinae (Asia) and Gastrophryninae (Americas). There is no published evidence that would allow us to allocate any of the unstudied Asian taxa to Microhylinae or to any other position in our cladogram beyond their being microhylids. Similarly, although we assume that such taxa as *Hypopachus* are in Gastrophryninae, our molecular results are so incongruent with results from morphology (e.g., Zweifel, 1986; Donnelly et al., 1990; Wild, 1995) that we hesitate to conjecture.

Morphological characters that are candidates as synapomorphies of [134] Dyscophinae + Asterophryninae + Scaphiophryninae + Microhylinae clade are (1) double-layered dermis (Haas 13.1, also in *Hemisus* and *Kassina*); (2) anterior insertion of m. subarcualis rectus II–IV on ceratobranchial I (Haas 37.0); and (3) partes corpores forming medial body (Haas 87.2).

Because the nominal subfamilies of Microhylidae are large and morphologically dis-

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parate, we include separate accounts for the nominal subfamilies.

[135] SUBFAMILY: ASTEROPHRYINAE GÜNTHER, 1858

Asterophrydidae Günther, 1858b: 346. Type genus: *Asterophrys* Tschudi, 1838.

Xenorhinidae Mivart, 1869: 286. Type genus: *Xenorhina* Peters, 1863.

Genyophrynidae Boulenger, 1890: 326. Type genus: *Genyophryne* Boulenger, 1890. **New synonym.**

Sphenophryninae Noble, 1931: 531. Type genus: *Sphenophryne* Peters and Doria, 1878, by monotypy. **New synonym.**

Phrynomantini Burton, 1986: 405–450. Type genus: ''*Phrynomantis* Peters, 1867''.

Barygenini Burton, 1986: 405–450. Type genus: *Barygenys* Parker, 1936.

Callulopini Dubois, 1988a: 3. Type genus: *Callulops* Boulenger, 1888.

IMMEDIATELY MORE INCLUSIVE TAXON: [134] unnamed taxon.

SISTER TAXON: Dyscophinae Boulenger, 1882.

RANGE: Southern Philippines, Sulawesi, and Lesser Sunda Islands and Moluccas eastwards through New Guinea and satellite islands to Australia.

CONTENT: *Albericus* Burton and Zweifel, 1995; ***Aphantophryne*** Fry, 1917 ''1916''; *Asterophrys* Tschudi, 1838; *Austrochaperina* Fry, 1912; *Barygenys* Parker, 1936; ***Callulops*** Boulenger, 1888; ***Choerophryne*** Kampen, 1914; ***Cophixalus*** Boettger, 1892; ***Copiula*** Méhely, 1901; ***Genyophryne*** Boulenger, 1890; *Hylophorbus* Macleay, 1878; ***Liophryne*** Boulenger, 1897; *Mantophryne* Boulenger, 1897; ***Oreophryne*** Boettger, 1895; *Oxydactyla* Kampen, 1913; *Pherohapsis* Zweifel, 1972; ***Sphenophryne*** Peters and Doria, 1878; *Xenorhina* Peters, 1863 (including *Xenobatrachus* Peters and Doria, 1878; see appendix 7 for new combinations).

CHARACTERIZATION AND DIAGNOSIS: None of the morphological characters in our analysis apply to this taxon because as direct developers they were not part of the tadpole study by Haas (2003). Among microhylids, only Asterophryinae and *Myersiella* (Microhylinae; Izecksohn et al., 1971; Zweifel, 1972; Thibaudeau and Altig, 1999) exhibit direct development, the development taking place completely within the egg capsule, although others (e.g., Cophylinae, some Gastrophryninae) are endotrophic and nidicolous (Blommers-Schlösser, 1975). (See appendix 5 for molecular synapomorphies.)

SYSTEMATIC COMMENTS: Former Genyophryninae is paraphyletic with respect to the old Asterophryinae, and for this reason the two nominal taxa were synonymized in ''Results''. Parker (1934) noted Genyophryninae (as Sphenophryninae) to be procoelous and Asterophryinae as diplasiocoelous, and this clearly influenced later authors (e.g., Zweifel, 1972) in retaining a distinction between the nominal subfamilies. The placement in our tree of Australo-Papuan Asterophryinae (sensu lato) as the sister taxon of the Madagascan Dyscophinae is a remarkable biogeographic signature.

Burton (1986: 443) provided evidence that *Xenorhina* is paraphyletic with respect to *Xenobatrachus*, the latter differing only in lacking large odontoids on the vomeropalatine. Zweifel (1972) provided no evidence for the monophyly of *Xenorhina*. On the basis of these works we consider them to be synonyms, with *Xenorhina* being the older name (see appendix 7 for new combinations). Burton (1986: 443) also noted that ''*Mantophryne*'' and ''*Hylophorbus*'' are dubiously monophyletic, so we place these names in quotation marks until their monophyly can be substantiated. Although Burton (1986) provided a number of morphological characters and a character matrix, no one so far has analyzed these data phylogenetically.

[118] SUBFAMILY: COPHYLINAE COPE, 1889

Cophylidae Cope, 1889: 248. Type genus: *Cophyla* Boettger, 1880.

Rhombophryninae Noble, 1931: 529. Type genus: *Rhombophryne* Boettger, 1880.

IMMEDIATELY MORE INCLUSIVE TAXON: [116] unnamed taxon.

SISTER TAXON: [117] An unnamed taxon in our analysis composed of our exemplars *Hoplophryne* Barbour and Loveridge, 1928 (Melanobatrachinae Noble, 1931) and *Ramanella* Rao and Ramanna, 1925 (formerly of ''Microhylinae''). Together these are the sister taxon of [121] Gastrophryninae Fitzinger, 1843.

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RANGE: Madagascar.

CONTENT: ***Anodonthyla*** Müller, 1892; *Cophyla* Boettger, 1880; *Madecassophryne* Guibé, 1974; ***Platypelis*** Boulenger, 1882; ***Plethodontohyla*** Boulenger, 1882 (see Systematic Comments); ***Rhombophryne*** Boettger, 1880 (see Systematic Comments and appendix 7); ***Stumpffia*** Boettger, 1881.

CHARACTERIZATION AND DIAGNOSIS: None of the morphological characters in our analysis optimizes on this branch; because our morphological characters were largely derived from larvae, and cophylines (as traditionally defined) are endotrophic and nidicolous. Nevertheless, endotrophy is a synapomorphy at this level. Also, cophylines have unfused sphenethmoids, which appear as paired elements (Parker, 1934), otherwise found convergently in *Dyscophus* (Dyscophinae) and *Calluella* (Microhylinae). (See appendix 5 for molecular synapomorphies on this branch [118].)

SYSTEMATIC COMMENTS: The association by our molecular data of Cophylinae (Madagascar) with our exemplars *Hoplophryne* (East Africa) and *Ramanella* (India) is suggestive. Madagascar–India is a repeated pattern in biogeography, as is an apparently later connection of India–Africa (e.g., *Chiromantis* in Africa + *Chirixalus* in Asia [Rhacophoridae]; *Petropedetes* + *Arthroleptides* in Africa and *Indirana* in India [Petropedetidae]). The association of Gastrophryninae with this overall clade also speaks to a standard biogeographic pattern, that of South America–Madagascar.

Andreone et al. (2004 ''2005'') provided considerable DNA sequence evidence that *Plethodontohyla* is polyphyletic (not paraphyletic as suggested in the original publication; see fig. 33). As noted by Andreone et al. (2004 ''2005'') the name *Plethodontohyla* Boulenger, 1882 (type species: *Callula notosticta* Gunther, 1877) adheres to his *Plethodontohyla* Group 1. Their second group of ''*Plethodontohyla*'' falls into a monophyletic group with *Rhombophryne testudo*. *Rhombophryne* Boettger, 1880, is substantially older than the next older name for this taxon, *Mantiphrys* Mocquard, 1901 (type species: *Mantiphrys laevipes* Mocquard, 1895), and to provide a monophyletic taxonomy, this inclusive taxon should be known as *Rhombophryne* (see appendix 7 for the species name changes that this causes). Andreone et al. (2004 ''2005'') hesitated to take this step because they did not feel there was sufficient statistical support for their maximum-likelihood conclusion. They did, however, note that their parsimony tree arrived at the same conclusion. We therefore think that it is better to recognize two clades that *might* be found to be each other's closest relatives when more data are added to the analysis, than to retain a taxon, ''*Plethodontohyla*'' (sensu lato) for which the preponderance of data does not support its monophyly. There are a number of species, nominally in *Plethodontohyla*, but not treated by Andreone et al. (2004 ''2005''). We retain those in *Plethodontohyla*, although some of may be found to be members of *Rhombophryne*.

SUBFAMILY: DYSCOPHINAE BOULENGER, 1882

Dyscophidae Boulenger, 1882: 179. Type genus: *Dyscophus* Grandidier, 1872.

IMMEDIATELY MORE INCLUSIVE TAXON: [134] unnamed taxon.

SISTER TAXON: [135] Asterophryinae Günther, 1858.

RANGE: Madagascar.

CONTENT: ***Dyscophus*** Grandidier, 1872.

CHARACTERIZATION AND DIAGNOSIS: Haas (2003) suggested the following larval characters that are presumed synapomorphies of the taxon: (1) ramus mandibularis (cranial nerve V_3) runs through the m. levator mandibulae externus group (Haas 65.1); and (2) free basihyal absent (Haas 105.0).

SYSTEMATIC COMMENT: Our data reject the association of *Calluella* with Dyscophinae (Blommers-Schlösser, 1976), which instead place *Calluella* deeply within Microhylinae. This is not surprising, inasmuch as the only characteristics suggested to ally *Calluella* with Dyscophinae are apparent plesiomorphies (e.g., presence of teeth, diplasiocoelous vertebral column, large vomer). The molecular synapomorphies supporting a relationship of this taxon to Asterophryinae (branch 134, appendix 5) is novel.

[121] SUBFAMILY: GASTROPHRYNINAE FITZINGER, 1843

Gastrophrynae Fitzinger, 1843: 33. Type genus: *Gastrophryne* Fitzinger, 1843.

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IMMEDIATELY MORE INCLUSIVE TAXON: [115] unnamed taxon.

SISTER TAXON: [116] unnamed taxon.

RANGE: Southern United States south to Argentina.

CONTENT: ***Ctenophryne*** Mocquard, 1904; ***Dasypops*** Miranda-Ribeiro, 1924; ***Dermatonotus*** Méhely, 1904; ***Elachistocleis*** Parker, 1927; ***Gastrophryne*** Fitzinger, 1843; ***Hamptophryne*** Carvalho, 1954; ***Nelsonophryne*** Frost, 1987.

CHARACTERIZATION AND DIAGNOSIS: Optimization is problematic because none of the direct-developing microhylids were sampled in our morphological data set. Nevertheless the following are candidates for being synapomorphies of Gastrophryninae, although they could be synapomorphies of Gastrophryninae + Cophylinae or some subset of Gastrophryninae inasmuch as the exemplars on which this supposition is built are *Gastrophryne carolinensis*, *Hamptophryne boliviana*, and *Elachistocleis ovalis*): (1) m. levator arcuum branchialium III split into two crossing bundles (Haas 41.1); (2) origin of m. suspensoriohyoideus from otic capsule (Haas 46.2); (3) posterolateral projections of the crista parotica processus otobranchialis (Haas 67.2); (4) processus muscularis absent (Haas 79.0); (5) anterolateral base of processus muscularis bearing ventrolateral process (Haas 80.1); and (6) ligamentum mandibulosuprarostrale absent (Haas 127.0).

Molecular evidence (branch 121, appendix 5) is strong that the New World microhylids (with the exception of *Synapturanus*, and possibly several others for which we had no tissues) form a clade that is most closely related to the Madagascan Cophylinae.

SYSTEMATIC COMMENTS: The exclusion of *Synapturanus* from this taxon comes as something of a surprise, inasmuch as both Zweifel (1986) and Wild (1995) provided evidence for its placement within a New World clade. Nevertheless, neither Zweifel (1986) nor Wild (1995) presented morphological evidence for the monophyly of the New World microhylids (of which our Gastrophryninae is a part). We expect that further research will show the New World microhylids to be a composite of gastrophrynines, some basal taxa (e.g., *Synapturanus*), and possibly some with relations in Asia.

SUBFAMILY: MELANOBATRACHINAE NOBLE, 1931

Melanobatrachinae Noble, 1931: 538. Type genus: *Melanobatrachus* Beddome, 1878.

Hoplophryninae Noble, 1931: 538–539. Type genus: *Hoplophryne* Barbour and Loveridge, 1928.

IMMEDIATELY MORE INCLUSIVE TAXON: [117] unnamed taxon.

SISTER TAXON: *Ramanella* Rao and Ramanna, 1925.

RANGE: Montane Tanzania and southern India.

CONTENT: ***Hoplophryne*** Barbour and Loveridge, 1928; *Melanobatrachus* Beddome, 1878; *Parhoplophryne* Barbour and Loveridge, 1928.

CHARACTERIZATION AND DIAGNOSIS: Melanobatrachinae shares two synapomorphies (Parker, 1934): (1) middle and outer ear absent; (2) parasphenoid and sphenethmoid fused.

SYSTEMATIC COMMENTS: Although we provisionally retain Melanobatrachinae as an untested taxon, the placement of *Hoplophryne* (our exemplar) in the general tree (see figs. 50 and 61) suggests that a more densely sampled analysis will provide results that render a Melanobatrachinae containing several more genera (such as *Ramanella*) than as currently composed. *Hoplophryne* and *Parhoplophryne* were placed in Hoplophrynine by Noble (1931) on the basis of sharing the apomorphy of a greatly reduced first finger. (Noble also allied these genera with Brevicipitidae on the basis of retaining a complete clavicle, but this alliance is not supported by our data.) Parker (1934) placed Hoplophryninae in the synonymy of Melanobatrachinae (India) because they share the absence of the auditory apparatus and fusion of the parasphenoid to the sphenenthmoid. We could not sample *Melanobatrachus*, but it remains possible that it is the sister taxon of Hoplophryninae and that *Hoplophryne* and *Parhoplophryne* are African outliers of a predominantly Indian group. This is conjecture, however, and only more data and denser sampling will resolve the issue.

[130] SUBFAMILY: MICROHYLINAE GÜNTHER, 1858 (1843)

Hylaedactyli Fitzinger, 1843: 33. Type genus: *Hylaedactylus* Duméril anbd Bibron, 1841.

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Micrhylidae Günther, 1858b: 346. Type genus: *Micrhyla* Duméril and Bibron, 1841 (an incorrect subsequent spelling of *Microhyla* Tschudi, 1838).

Kaloulinae Noble, 1931: 538. Type genus: *Kaloula* Gray, 1831.

IMMEDIATELY MORE INCLUSIVE TAXON: [129] unnamed taxon.

SISTER TAXON: Scaphiophryninae Laurent, 1946.

RANGE: India, China, Japan, and Korea to the Philippines and Greater Sunda Islands.

CONTENT: ***Calluella*** Stoliczka, 1872; ***Chaperina*** Mocquard, 1892; ***Kaloula*** Gray, 1831; ***Microhyla*** Tschudi, 1838.

CHARACTERIZATION AND DIAGNOSIS: Haas (2003) examined only *Kaloula* within this clade, so this is our only morphological exemplar for this subfamily, but the following are candidates for being synapomorphies of the Microhylinae: (1) vena caudalis dorsalis absent (Haas 14.0); (2) origin of m. suspensoriohyoideus from otic capsule (Haas 46.2); and (3) posterolateral projections of the crista parotica expansive flat chondrifications (Haas 67.2). Nevertheless, the molecular evidence is decisive for the recognition of this taxon (see appendix 5).

COMMENT: See Microhylidae account for comment on East Asian ''microhylines'' excluded from this taxon because of lack of evidence to place them.

SUBFAMILY: SCAPHIOPHRYNINAE LAURENT, 1946

Scaphiophryninae Laurent, 1946: 337. Type genus: *Scaphiophryne* Boulenger, 1882.

Pseudohemisiinae Tamarunov, 1964a: 132. Type genus: *Pseudohemisus* Mocquard, 1895.

IMMEDIATELY MORE INCLUSIVE TAXON: [129] unnamed taxon.

SISTER TAXON: [130] Microhylinae Günther, 1858 (1843).

RANGE: Madagascar.

CONTENT: ***Scaphiophryne*** Boulenger, 1882.

CHARACTERIZATION AND DIAGNOSIS: In our topology *Scaphiophryne* is deeply imbedded within Microhylidae, requiring a remarkable number of reversals. Nevertheless, we suggest these reversals are likely synapomorphies of the taxon, while noting that most of these are highly contingent on topological position of *Scaphiophryne*: (1) keratinized jaw sheaths present (Haas 6.1; reversal from the microhylid condition); (2) eye position dorsolateral (Haas 11.0; reversal from the microhylid condition); (3) spiracle position sinistral (Haas 18.1; reversal from the microhylid condition); (4) m. interhyoideus posterior absent (Haas 23.0; reversal from the phthanobatrachian condition); (5) m. subarcualis rectus II–IV represented by a single flat tract of fibers (Haas 30.0; reversal from the microhylid condition); (6) insertion of m. rectus cervicis on proximal ceratobranchialia III and IV (Haas 39.2; reversal from microhylid condition); (7) m. interhyoideus and m. intermandibularis well separated by a gap (Haas 47.1; reversal from the microhylid condition); (8) m. mandibulolabialis inserting in soft tissue of lip (Haas 49.0; reversal from microhylid condition); (9) m. levator mandibulae internus low (Haas 58.1; reversal from microhylid condition); (10) m. levator mandibulae longus originates from posterior palatoquadrate (Haas 60.1; reversal from microhylid condition); (11) ramus mandibularis (cranial nerve V_3) anterior (dorsal) to the m. levator mandibulae longus (Haas 64.2); (12) processus suboticus quadrati absent (Haas 76.0; reversal from microhylid condition); (13) arcus subocularis with irregular margin (Haas 81.1; reversal of microhylid condition); (14) cartilaginous roofing of the cavum cranii absent (Haas 96.0; reversal of predominant microhylid condition); and (15) glottis position posterior (Haas 130.0; reversal of microhylid condition).

SYSTEMATIC COMMENTS: Ford and Cannatella (1993: 94–117), found no evidence for the monophyly of this taxon. Haas (2003: 50) suggested on the basis of tadpole morphology that *Paradoxophyla* is more closely related to *Phrynomantis* than to the remaining Scaphiophryninae, rendering the latter nonmonophyletic. On that basis alone, because we did not have tissues of *Paradoxophyla*, we transfer *Paradoxophyla* from Scaphiophryninae to incertae sedis under Microhylidae. The association (branch 129, appendix 5) of Madagascan Scaphiophryninae with Microhylinae may suggest an Indian origin of Microhylinae. (See Systematic Comment under Cophylinae.)

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[143] AFROBATRACHIA **NEW TAXON**

ETYMOLOGY: Afro- (Latin: of Africa) + batrachos (Greek: frog), in reference to the predominantly African range of this taxon.

IMMEDIATELY MORE INCLUSIVE TAXON: [109] Allodapanura **new taxon.**

SISTER TAXON: [110] Microhylidae Günther, 1858 (1843).

RANGE: Sub-Saharan Africa, Madagascar, and the Seychelles.

CONCEPT AND CONTENT: Afrobatrachia is a monophyletic taxon composed of [144] Xenosyneunitanura **new taxon** and [148] Laurentobatrachia **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Likely candidates for being synapomorphies are the larval characters: (1) m. transversus ventralis IV present (Haas 22.1); (2) posterolateral projections of the crista parotica forming processus otobranchialis (Haas 67.3); (3) processus ascendens thin (Haas 72.1); (4) dorsal connection from processus muscularis to ''high'' commissura quadrato-orbitalis (Haas 78.3); and (5) anterolateral base of processus muscularis bearing ventrolateral process (Haas 80.1). See characterisation of Allodapanura for additional discussion of possible synapomorphies.

COMMENT: Our Afrobatrachia is identical in content to the enlarged Brevicipitidae of Dubois (2005).

[144] XENOSYNEUNITANURA **NEW TAXON**

ETYMOLOGY: Xeno- (Greek: strange) + syneunitos (Greek: bed sharer) + anoura (Greek: frog). In other words, the name means ''strange bedfellows'' inasmuch as Hemisotidae and Brevicipitidae, although cladistic nearest relatives, are dissimilar animals.

IMMEDIATELY MORE INCLUSIVE TAXON: [143] Afrobatrachia **new taxon.**

SISTER TAXON: [148] Laurentobatrachia **new taxon.**

RANGE: Sub-Ssaharan Africa.

CONCEPT AND CONTENT: Xenosyneunitanura **new taxon** is a monophyletic taxon containing Hemisotidae Cope, 1867, and [145] Brevicipitidae Bonaparte, 1850.

CHARACTERIZATION AND DIAGNOSIS: Hemisotidae and Brevicipitidae share the absence of the palatine bones (De Villiers, 1931), which at this position in the general cladogram is a synapomorphy. *Breviceps* and *Hemisus* also share a single median thyroid gland (Blommers-Schlösser, 1993), so we presume that this, too, is a synapomorphy joining the two taxa. *Breviceps* and *Hemisus* also exhibit nasal plugs (De Villiers, 1931) which may be homologous. (See also ''Characterization and Diagnosis'' under Hemisotidae for other characters that may optimize on this taxon.) Molecular synapomorphies are provided in appendix 5.

[145] FAMILY: BREVICIPITIDAE BONAPARTE, 1850

Brevicipitina Bonaparte, 1850: 1 p. Type genus: *Breviceps* Merrem, 1820.

Engystomidae Bonaparte, 1850: 1 p. Type genus: *Engystoma* Fitzinger, 1826.

IMMEDIATELY MORE INCLUSIVE TAXON: [144] Xenosyneunitanura **new taxon.**

SISTER TAXON: Hemisotidae Cope, 1867.

RANGE: Sub-Saharan East Africa and southern Africa, from Ethiopia south to Angola and South Africa.

CONTENT: *Balebreviceps* Largen and Drewes, 1989; ***Breviceps*** Merrem, 1820; ***Callulina*** Nieden, 1911 ''1910''; ***Probreviceps*** Parker, 1931; *Spelaeophryne* Ahl, 1924.

CHARACTERIZATION AND DIAGNOSIS: Parker (1934) noted that brevicipitids lack ossified sphenethmoids, which is clearly a synapomorphy at this level. In addition, the loss of the pterygoid, palatoquadrate, and m. opercularis (De Villiers, 1931) are likely synapomorphies for this group. The extremely short head and direct development exhibited by this taxon (Parker, 1934) are also synapomorphies.

SYSTEMATIC COMMENT: Loader et al. (2004) suggested a phylogeny of *Breviceps* (*Spelaeophryne* + (*Callulina* + *Probreviceps*)); they, like us, did not include *Balebreviceps* in their analysis. On the basis of our larger amount of evidence but less dense sampling, we placed *Probreviceps* nearer to *Breviceps* in our tree. Nevertheless, both arrangements conflict with the character of fusion of the urostyle and sacrum found in *Probreviceps* and *Breviceps* but not in *Spelaeophryne* and *Callulina* (Parker, 1934), suggesting that additional testing is warranted.

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FAMILY: HEMISOTIDAE COPE, 1867

Hemisidae Cope, 1867: 198. Type genus: *Hemisus* Günther, 1859 ''1858''. Emended to Hemisotina by Günther, 1870: 119.

IMMEDIATELY MORE INCLUSIVE TAXON: [144] Xenosyneunitanura **new taxon.**

SISTER TAXON: [145] Brevicipitidae Bonaparte, 1850.

RANGE: Sub-Saharan Africa.

CONTENT: ***Hemisus*** Günther, 1859 ''1858''.

CHARACTERIZATION AND DIAGNOSIS: All of the characters in our analysis (from Haas, 2003) that optimize on *Hemisus* (our only morphological exemplar in this clade) may be synapomorphies of this clade, the Hemisotidae, or some subset of *Hemisus*: (1) double-layered dermis in larvae (Haas 13.1); (2) posterior dorsal process of pars alaris expanded terminally, almost rectangular in lateral view (Haas 89.1); (3) larvae are guided by the female from the nest to pond (Haas 137.1); and (4) amplexus absent (Haas 139.0). Some of these may be synapomorphies at the level of Xenosyneunitanura inasmuch as Brevicipitidae was not studied by Haas (2003) because they lack exotrophic larvae, which were the focus of Haas' study.

Hemisus lacks vomers, middle ear, and ductus lacrimosus, and exhibits fusion of vertebrae 8 and 9 (De Villiers, 1931). Further, *Hemisus* burrows head-first (Channing, 1995). All of these characters can safely be considered synapomorphies of Hemisotidae.

[148] LAURENTOBATRACHIA **NEW TAXON**

ETYMOLOGY: R.L. Laurent + batrachia (Greek: batrachos, frog). This name celebrates the enormous contributions to amphibian systematics by the father of central African herpetology and a prominent figure in Argentinian herpetology, Raymond L. Laurent.

IMMEDIATELY MORE INCLUSIVE TAXON: [143] Afrobatrachia **new taxon.**

SISTER TAXON: [144] Xenosyneunitanura **new taxon.**

RANGE: Sub-Saharan Africa, Madagascar, and the Seychelles.

CONTENT AND CONCEPT: Laurentobatrachia is a monophyletic group composed of [149] Hyperoliidae Laurent, 1943, and [164] Arthroleptidae Mivart, 1869.

CHARACTERIZATION AND DIAGNOSIS: The characters (from Haas, 2003) 54.1 (larval m. levator manidbulae externus in two portion), 111.0 (commissura proximalis III absent), and 151.0 (intercalary elements absent) are likely synapomorphies of this group, although because of the low density of taxon sampling this requires additional specimen examination. In addition, claw-shaped terminal phalanges appear to optimize on this branch, appearing convergently in *Ptychadena* and several of the hyloids (Liem, 1970), although the distribution of this character is complicated, and further work may show that this optimization is mistaken. Drewes (1984) suggested that thyrohyals borne on cartilaginous stalks (his character 10.1) might be a synapomorphy, although this is optimization-dependent inasmuch as this character is not in *Leptopelis* (Laurent, 1978). The external metatarsal tubercle is absent or poorly developed throughout Laurentobatrachia (Laurent, 1986), but the exact distribution of this requires verification. Molecular synapomorphies for this taxon are summarized in appendix 5.

SYSTEMATIC COMMENT: Vences and Glaw (2001) and Van der Meijden et al. (2005) recognized this taxon as the epifamily Arthroleptoidae, and originally Laurent (1951) considered this clade (with the possible inclusion of Scaphiophryninae) to be a single family, and Dubois (2005) considered our Laurentobatrachia to be 4 of the 6 subfamilies of his Brevicipitidae. We attempted to retain familiar usage, with the exception of moving Leptopelinae from Hyperoliidae to Arthroleptidae. Because we think that the diversity of this taxon has been greatly underestimated, our approach leaves considerable room for more informative taxonomies as evidence becomes available.

[149] FAMILY: HYPEROLIIDAE LAURENT, 1943

Hyperoliinae Laurent, 1943: 16. Type genus: *Hyperolius* Rapp, 1842.

Kassinini Laurent, 1972: 201. Type genus: *Kassina* Girard, 1853.

Tachycneminae Channing, 1989: 127. Type genus: *Tachycnemis* Fitzinger, 1843.

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IMMEDIATELY MORE INCLUSIVE TAXON: [143] Afrobatrachia **new taxon.**

SISTER TAXON: [164] Arthroleptidae Mivart, 1869.

RANGE: Sub-Saharan Africa and Madagascar; Seychelles.

CONTENT: ***Acanthixalus*** Laurent, 1944; ***Afrixalus*** Laurent, 1944; ***Alexteroon*** Perret, 1988; *Arlequinus* Perret, 1988; *Callixalus* Laurent, 1950; *Chlorolius* Perret, 1988; *Chrysobatrachus* Laurent, 1951; ***Cryptothylax*** Laurent and Combaz, 1950; ***Heterixalus*** Laurent, 1944; ***Hyperolius*** Rapp, 1842 (including ***Nesionixalus*** Perret, 1976); ***Kassina*** Girard, 1853; *Kassinula* Laurent, 1940; ***Opisthothylax*** Perret, 1966; *Paracassina* Peracca, 1907; ***Phlyctimantis*** Laurent and Combaz, 1950; *Semnodactylus* Hoffman, 1939; ***Tachycnemis*** Fitzinger, 1843.

CHARACTERIZATION AND DIAGNOSIS: One larval character in our analysis that may be synapomorphy of this group is (from Haas, 2003): commissura proximalis II absent. Beyond that, hyperoliids are unique among frogs in having a distinctive gular gland (Drewes, 1984). Drewes (1984) summarized a character distribution suggesting that lacking sphincter control of the vocal slits may also be a synapomorphy of Hyperoliidae.

The presence of intercalary phalangeal elements *per se* is not a synapomorphy of this group (or at least not without making assumptions of character optimization), being found also in the Leptopelinae of Arthroleptidae. Nevertheless, Drewes (1984) noted that hyperoliid and leptopeline intercalary elements are histologically quite different from each other. The latter does not accept either Alizarin or Alcian Blue stain, suggesting that these elements may not be homologous.

SYSTEMATIC COMMENTS: The position in our tree of *Acanthixalus* is heterodox compared with previous studies (e.g., Drewes, 1984) and implies a number of reversals and convergences in the morphology of hyperoliid frogs. We considered recognizing subfamilies within Hyperoliidae, corresponding to the two major clades of exemplars, for which the name Kassininae Laurent, 1972, is available for the *Kassina–Phlyctimantis–Acanthixalus* clade and Hyperoliinae Laurent, 1943, for the remainder of our exemplar taxa. We did not sample *Chrysobatrachus* or *Callixalus* and cannot guess into which group they would fall. Their association with *Acanthixalus* in the tree of Drewes (1984) suggests that they might follow *Acanthixalus* into Kassininae, but this is merely conjecture and a combined study of morphology and molecules is ongoing by Drewes and collaborators. Our results differ substantially from the results of Vences et al. (2003d; figs. 28, 29) with respect to the relative placement of several genera. This is presumably due to our application of much denser sampling and more evidence.

The association by the molecular data of *Tachycnemis* (Seychelles) and *Heterixalus* (Madagascar) is of some biogeographic interest. We expected *Alexteroon* to be imbedded within *Hyperolius*, but our sampling of *Hyperolius* was insufficient to test this proposition adequately. On the basis of our limited exemplar selection, *Alexteroon* may be the sister taxon of *Hyperolius* (sensu lato). However, we found, as did Drewes and Wilkinson (2004), that *Nesionixalus* is clearly deeply imbedded in *Hyperolius*, but also represents a monophyletic group. We suggest that *Nesionixalus* be treated as a subgenus of *Hyperolius* with no coordinate taxon to imply that the remaining species of *Hyperolius* are a monophyletic group (see appendix 7 for new combinations). We expect that *Chlorolius* and *Arlequinus* will also be found to be imbedded within *Hyperolius*, although at this time no data can be brought to bear to test this proposition.

[164] FAMILY: ARTHROLEPTIDAE MIVART, 1869

Arthroleptina Mivart, 1869: 294. Type genus: *Arthroleptis* Smith, 1849.

Astylosterninae Noble, 1927: 110. Type genus: *Astylosternus* Werner, 1898.

Leptopelini Laurent, 1972: 201. Type genus: *Leptopelis* Günther, 1859. **New synonym.**

IMMEDIATELY MORE INCLUSIVE TAXON: [147] Laurentobatrachia **new taxon.**

SISTER TAXON: [149] Hyperoliidae Laurent, 1943.

RANGE: Sub-Saharan Africa.

CONTENT: ***Arthroleptis*** Smith, 1849 (including ***Schoutedenella*** De Witte, 1921; see

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Systematic Comments); ***Astylosternus*** Werner, 1898; ***Cardioglossa*** Boulenger, 1900; ***Leptodactylodon*** Andersson, 1903; ***Leptopelis*** Günther, 1859; ***Nyctibates*** Boulenger, 1904; ***Scotobleps*** Boulenger, 1900; ***Trichobatrachus*** Boulenger, 1900.

CHARACTERIZATION AND DIAGNOSIS: Arthroleptids are small frogs exhibiting forked omosterna that, with the exception of *Arthroleptis*, have a typically biphasic life history. Like many of the taxa within Afrobatrachia, many of the arthroleptids have vertical pupils, with the exceptions of *Leptodactylodon* (quadrangular) and Arthroleptini (horizontal, except for *Scotobleps*). None of the morphological characters in our analysis optimize unambiguously to this branch [164]. Regardless, the molecular data are decisive in support of recognition of this group (see appendix 5).

Larval characters of Haas' (2003) exemplar *Leptopelis*—a distinct medial ossification center of vertebral centra ventral to notochord present (Haas 100.1)—may be synapomorphies of Arthroleptidae, of Leptopelinae, or of some subset of *Leptopelis*. The direct development of *Arthroleptis* is subsequently derived.

SYSTEMATIC COMMENTS: We recognize two subfamilies within Arthroleptidae, [165] Leptopelinae Laurent, 1972, for *Leptopelis*, formerly associated with Hyperoliidae (although shown to be phylogenetically distant from them by Vences et al., 2003c), and [168] Arthroleptinae Mivart, 1869, containing two tribes, [169] Astylosternini Noble, 1931 (*Leptodactylodon*, *Nyctibates*, *Trichobatrachus*, and *Leptodactylodon*) and [172] Arthroleptini Mivart, 1869 (*Arthroleptis* [including *Schoutedenella*], *Cardioglossa*, and *Scotobleps*). *Scotobleps* formerly was associated with Astylosterninae, so its transfer to Arthroleptini is something of a surprise (on the basis of evidence shown in appendix 5).

[165] Leptopelinae Laurent, 1972, is distinguished morphologically from its near neighbors by the possession of an entire, rather than forked, omosternum and by histologically distinct intercalary phalangeal elements (Drewes, 1984).

[168] Arthroleptinae Mivart, 1869, is not diagnosable via morphology, although the absence of intercalary elements may be synapomorphic should one be willing to make assumptions about character optimization and that the phalangeal elements of leptopelines and hyperoliids are homologous.

Arthroleptis renders *Schoutedenella* paraphyletic, and we therefore consider them to be synonyms. Laurent and Fabrezi's (1986 ''1985'') contention that *Schoutedenella* and *Arthroleptis* are not each other's closest relatives is rejected, although the position of Poynton (1964a) and Poynton and Broadley (1967), that *Schoutedenella* are merely small *Arthroleptis* is also rejected. (Our tree suggests that if size were characteristic, we would have to say that *Arthroleptis* are big *Schoutedenella*.) Our molecular data support the notion that nominal *Arthroleptis* is imbedded within *Schoutedenella* and we place them in synonymy. (See appendix 7 for new and revived combinations.)

Perret (1966) suggested that *Nyctibates* is a synonym of *Astylosternus*, but Amiet (1971 ''1970'', 1973 ''1972'') resurrected *Nyctibates* on the basis of tadpole morphology being more similar to *Leptodactylodon* and *Trichobatrachus*. Our molecular data support recognition of *Nyctibates*.

[180] NATATANURA **NEW TAXON**

ETYMOLOGY: Natata- (Greek: swim) + anoura (Greek: tailless, i.e., frog), referencing that many of the frogs in this clade are semiaquatic.

IMMEDIATELY MORE INCLUSIVE TAXON: [108] Ranoides **new taxon.**

SISTER TAXON: [109] Allodapanura **new taxon.**

RANGE: Worldwide temperate and tropical habitats on all continents and major islands, except most of Australia and New Zealand.

CONCEPT AND CONTENT: Natatanura is a monophyletic group composed of [181] Ptychadenidae Dubois, 1987 ''1986'', and [183] Victoranura **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Natatanura is identical to the epifamily Ranoidae of Dubois (1992) and Ranidae (sensu lato) of Laurent (1986). Characters in our analysis (from Haas, 2003) that are likely synapomorphies of this taxon are (1) anterior insertion of m. subarcualis rectus II–IV on ceratobranchial III (Haas 37.2); (2) commissura

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proximalis II absent (Haas 110.0); and (3) commissura proximalis III absent (Haas 111.0).

J.D. Lynch (1973) and Laurent (1986) suggested that an ossified metasternal style is a synapomorphy at this level of universality, but this requires corroboration inasmuch as several groups within Natatanura have cartilaginous metasterna (Laurent, 1986).

SYSTEMATIC COMMENT: Burton (1998a) noted that several genera of Natatanura share the presence of an extra slip of the m. flexor teres digiti IV, which is ventral to the m. transversus metacarpus II: *Altirana*, *Aubria*, *Ceratobatrachus*, *Conraua*, *Hildebrandtia*, *Mantella*, *Mantidactylus*, *Petropedetes*, *Ptychadena*, *Pyxicephalus*, and *Rana*, but not in *Batrachylodes*, *Cacosternum*, *Discodeles*, *Laliostoma*, *Meristogenys*, *Micrixalus*, *Nannophrys*, *Nanorana*, *Natalobatrachus*, *Nyctibatrachus*, *Occidozyga*, *Palmatorappia*, *Platymantis*, or *Strongylopus* (with many taxa not examined). If this character is optimized on our most parsimonious tree, the implication is that this character arose at least six times, of which the following is one of several equally parsimonious arrangements: (1) *Ceratobatrachus*; (2) in the branch subtending *Conraua* + *Petropedetes*, and therefore likely to be in *Indirana* and *Arthroleptides*); (3) Ptychadenidae (*Hildebrantia*, *Ptychadena*, and presumably in *Lanzarana*); (4) Pyxicephalini (*Pyxicephalus* and *Aubria*); (5) *Altirana* (= part of *Nanorana*); (6) Aglaioanura (Rhacophoroidea + Ranidae). Nevertheless, considerably more specimens of more taxa need to be examined before the optimization of this feature can confidently be considered settled.

[181] FAMILY: PTYCHADENIDAE DUBOIS, 1987 ''1986''

Ptychadenini Dubois, 1987 ''1985'': 55. Type genus: *Ptychadena* Boulenger, 1917.

IMMEDIATELY MORE INCLUSIVE TAXON: [180] Natatanura **new taxon.**

SISTER TAXON: [183] Victoranura **new taxon.**

RANGE: Sub-Saharan tropical and subtropical Africa; Seychelles and Madagascar.

CONTENT: *Hildebrandtia* Nieden, 1907; *Lanzarana* Clarke, 1982; ***Ptychadena*** Boulenger, 1917.

CHARACTERIZATION AND DIAGNOSIS: In our analysis, the morphological (larval) characters that attach to the only exemplar of this taxon, *Ptychadena*, are (1) m. subarcualis rectus I portion with origin from ceratobranchial III absent (Haas 35.0); (2) partes corpores medially separate (Haas 87.0); and (3) eggs float as a surface film (Haas 141.2). Because of our limited sampling for morphology, it is possible that these characters do not apply to *Hildebrandtia* or *Lanazarana*; it is also possible that they apply only to a subset of *Ptychadena*. Only denser sampling will tell.

Other features that are likely synapomorphies, although originally suggested in a somewhat different outgroup structure (Clarke, 1981), are (1) otic plate absent or rudimentary; (2) (neo)palatines absent; (3) point overlap of the medial ramus of the pterygoid and the anterior lateral border of the parasphenoid ala in an anterior–posterior plane; (4) clavicles reduced and well-separated at midline; (5) sternal style a short compact bony element; (6) eight presacral and sacral vertebrae fused (also in some *Lithobates*); and (7) dorsal protuberance on ilium not or only slightly differentiated from dorsal prominence, which is smooth surfaced and confluent with a well-developed ilial crest.

SYSTEMATIC COMMENT: See Systematic Comments under Natatanura. Our association of *Hildebrandtia* and *Lanzarana* with this taxon rests on the morphological data analysis of Clarke (1981), who suggested a number of synapomorphies for the group (see above).

[183] VICTORANURA **NEW TAXON**

ETYMOLOGY: Victor (Latin: conqueror) + anoura (Greek: tailless; i.e., frog), alluding to the remarkable success of this taxon worldwide.

IMMEDIATELY MORE INCLUSIVE TAXON: [180] Natatanura **new taxon.**

SISTER TAXON: [181] Ptychadenidae Dubois, 1987 ''1986''.

RANGE: Worldwide continents and major islands in temperate and tropical regions, ex-

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cept southern Australia, the Seychelles, and New Zealand.

CONCEPT AND CONTENT: Victoranura is a monophyletic group composed of [184] Ceratobatrachidae Boulenger, 1884, and [189] Telmatobatrachia **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: None of the morphological characters in our analysis diagnose on this taxon, although the molecular data are decisive (see appendix 5 for summary of molecular synapomorphies).

[184] FAMILY: CERATOBATRACHIDAE BOULENGER, 1884

Ceratobatrachidae Boulenger, 1884: 212. Type genus: *Ceratobatrachus* Boulenger, 1884.

Platymantinae Savage, 1973: 354. Type genus: *Platymantis* Günther, 1859.

IMMEDIATELY MORE INCLUSIVE TAXON: [183] Victoranura **new taxon.**

SISTER TAXON: [189] Telmatobatrachia **new taxon.**

RANGE: Western China (Xizang and Yunnan); Myanmar, adjacent Thailand and peninsular Malaysia; Philippines, Borneo; New Guinea; Admiralty, Bismarck, and Solomon Islands; Fiji; Palau.

CONTENT: ***Batrachylodes*** Boulenger, 1887; ***Ceratobatrachus*** Boulenger, 1884; ***Discodeles*** Boulenger, 1918; ***Ingerana*** Dubois, 1987 ''1986''; *Palmatorappia* Ahl, 1927 ''1926''; ***Platymantis*** Günther, 1858.

CHARACTERIZATION AND DIAGNOSIS: None of the morphological characters in our analysis optimize as synapomorphies of this taxon, although all ceratobatrachids are characterized by large eggs and direct development (Noble, 1931). Many of the species have expanded toe tips, but this is likely plesiomorphic at this level of universality. Molecular synapomorphies for the clade are summarized in appendix 5.

SYSTEMATIC COMMENT: Dubois (1987 ''1985'', 1992) placed his Ceratobatrachiini Boulenger, 1884, within a larger Dicroglossinae Anderson, 1871. The subsequent implication of Dubois et al. (2001) that Ceratobatrachidae (his Ceratobatrachinae) is of uncertain relationship to Dicroglossinae was justified inasmuch as an inclusive Dicroglossinae (including Ceratobatrachiini Boulenger, 1884, Conrauini Dubois, 1992, and Dicroglossini Anderson, 1871) is rejected by our evidence.

Dubois (1992) placed *Batrachylodes* outside of his Ceratobatrachini, because, unlike the more typical members of Ceratobatrachinae, it lacks a forked omosternum. Nevertheless, *Batrachylodes* does have endotrophic larvae (Thibaudeau and Altig, 1999), and our molecular evidence places *Batrachylodes* firmly within the ceratobatrachine clade.

Roelants et al. (2004) provided molecular evidence suggesting that *Ingerana* is in Occidozyginae rather than Ceratobatrachinae, but this is not corroborated by our denser taxonomic sampling and larger amount of data, which place *Ingerana* in the more conventional location in Ceratobatrachidae and as the sister taxon of the remaining genera within Ceratobatrachinae. Like Roelants et al. (2004), we did not evaluate species of the nominal subgenus *Liurana*, a taxon that Dubois (1987 ''1985'') erected as a subgenus of *Ingerana*, but subsequently was recognized by some workers as a genus (Fei et al., 1997) and later (Dubois, 2005, without discussion) as a synonym of *Taylorana* (= *Limnonectes*). *Liurana* is reported to be differentiated from *Ingerana* by condition of the finger disc (absent in *Liurana*, present in *Ingerana*) and median lingual papilla (present in *Liurana*, absent in *Ingerana*; Dubois, 1987 ''1985''), but some species of *Liurana* possess small finger discs (Zhao and Li, 1984; Fei et al., 2005), and the condition of the tongue is known for only two of the five species of *Ingerana* (Smith, 1930; Inger, 1954, 1966). We treat *Liurana* as a synonym of *Ingerana*, pending evidence being published to substantiate Dubois' (2005) assertion of its placement in Limnonectini (Dicroglossidae).

[189] TELMATOBATRACHIA **NEW TAXON**

ETYMOLOGY: Telmato- (Greek: of a marsh) + batrachos (Greek: frog), referencing the preference of these frogs for wet microhabitats.

IMMEDIATELY MORE INCLUSIVE TAXON: [183] Victoranura **new taxon.**

SISTER TAXON: [184] Ceratobatrachidae Boulenger, 1884.

RANGE: Worldwide continents and major islands in temperate and tropical environ-

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ments, except for southern South America, Madagascar, New Zealand, and most of Australia.

CONCEPT AND CONTENT: Telmatobatrachia is a monophyletic taxon composed of [190] Micrixalidae Dubois, Ohler, and Biju, 2001, and [191] Ametrobatrachia **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: None of the morphological characters in our analysis optimize on the branch subtending this taxon although our molecular data decisively support its recognition. (See appendix 5 for listing of molecular synapomorphies.)

[190] FAMILY: MICRIXALIDAE DUBOIS, OHLER, AND BIJU, 2001

Micrixalinae Dubois et al., 2001: 54. Type genus: *Micrixalus* Boulenger, 1888.

IMMEDIATELY MORE INCLUSIVE TAXON: [189] Telmatobatrachia **new taxon.**

SISTER TAXON: [191] Ametrobatrachia **new taxon.**

RANGE: India.

CONTENT: ***Micrixalus*** Boulenger, 1888.

CHARACTERIZATION AND DIAGNOSIS: None of the morphological characters in our analysis optimize on this taxon and the decisive evidence for its recognition is entirely molecular (see appendix 5 for summary). Unlike Ptychadenidae, Ceratobatrachidae, and basally in Ametrobatrachia, the omosternum is unforked in Micrixalidae (Dubois et al., 2001), which at this level of universality is a synapomorphy of the group as is the low keratodont formula 1/0 (Dubois et al., 2001). The presence of digital discs in Micrixalinae is likely a plesiomorphy at this level of universality.

[191] AMETROBATRACHIA **NEW TAXON**

ETYMOLOGY: Ametros (Greek: beyond measure) + batrachos (Greek: frog), denoting the enormity of this taxon in terms of species and with respect to the enormous numbers of questions that remain about its internal phylogenetic structure.

IMMEDIATELY MORE INCLUSIVE TAXON: [189] Telmatobatrachia **new taxon.**

SISTER TAXON: [190] Micrixalidae Dubois, Ohler, and Biju, 2001.

RANGE: Worldwide in temperate and tropical continental areas and major islands, excluding Madagascar, New Zealand, Seychelles, and Australia except for the far north.

CONCEPT AND CONTENT: Ametrobatrachia is a monophyletic taxon composed of [192] Africanura **new taxon** and [220] Saukrobatrachia **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: None of the morphological characters in our analysis optimize as synapmorphies of this taxon. Nevertheless, the molecular data are decisive. (See appendix 5 for summary of molecular synapomorphies for this taxon.)

[192] AFRICANURA **NEW TAXON**

ETYMOLOGY: Afric- (Latin: of Africa) + anoura (Greek: tailless, i.e., frog).

IMMEDIATELY MORE INCLUSIVE TAXON: [191] Ametrobatrachia **new taxon.**

SISTER TAXON: [220] Saukrobatrachia **new taxon.**

RANGE: Sub-Saharan Africa.

CONTENT: [193] Phrynobatrachidae Laurent, 1941 ''1940'', and [200] Pyxicephaloidea Bonaparte, 1850.

CHARACTERIZATION AND DIAGNOSIS: None of the morphological characters in our analysis optimize on this taxon. Nevertheless, molecular data are decisive. (See appendix 5 for summary of molecular transformation associated with this taxon.)

SYSTEMATIC COMMENT: The existence of this taxon had not been suspected prior to the publication of Van der Meijden et al. (2005), although it certainly meets biogeographic expectations.

[193] FAMILY: PHRYNOBATRACHIDAE LAURENT, 1941 ''1940''

Hemimantidae Hoffmann, 1878: 613. Type genus: *Hemimantis* Peters, 1863.

Phrynobatrachinae Laurent, 1941 ''1940'': 79. Type species: *Phrynobatrachus* Günther, 1862.

IMMEDIATELY MORE INCLUSIVE TAXON: [192] Africanura **new taxon.**

SISTER TAXON: [200] Pyxicephaloidea Bonaparte, 1850.

RANGE: Sub-Saharan Africa.

CONTENT: *Ericabatrachus* Largen, 1991 (see Systematic Comments); ***Phrynobatrachus*** Günther, 1862 (including ***Dimorphog-***

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nathus Boulenger, 1906, and ***Phrynodon*** Parker, 1935; see Systematic Comments).

CHARACTERIZATION AND DIAGNOSIS: Phrynobatrachids are small terrestrial and semiaquatic frogs with poorly understood species boundaries and with a typically biphasic life history, with eggs laid in water. Like many members of Ranoides, phrynobatrachids frequently have T-shaped terminal phalanges, although they lack digital discs. They usually retain an outer metatarsal tubercle (Laurent, 1986) and are characterized by a tarsal tubercle (Channing, 2001) that is distinctive and may be synapomorphic. *Phrynobatrachus* species exhibit a median lingual tubercle (Grant et al., 1997), which may be synapomorphic, although this needs to be carefully surveyed. Its presence also in *Indirana*, *Arthroleptides*, and *Petropedetes* suggests that it may be synapomorphic at a more general level.

Nevertheless, none of the morphological characters in our analysis optimize on this taxon, although the molecular data are decisive in recognition of this taxon. (See appendix 5 for listing of molecular synapomorphies for this taxon.)

SYSTEMATIC COMMENTS: Our data show that *Phrynobatrachus* is paraphyletic with respect to *Phrynodon* and *Dimorphognathus*. Surprisingly, Amiet (1981) suggested a close relationship of *Phrynodon* with *Petropedetes* (Petropedetidae) to the exclusion of *Phrynobatrachus*. Our data do not support this relationship and because this nominal genus and *Dimorphognathus* are both monotypic and imbedded within *Phrynobatrachus*, we place *Phrynodon* and *Dimorphognathus* into the synonymy of *Phrynobatrachus*, which after this action is monophyletic. Nevertheless, *Phrynobatrachus* remains one of the larger taxonomic problems in Africa in terms of species boundaries and infrageneric clades. It will yield its secrets only with a considerable amount of morphological, behavioral, and molecular work. (See appendix 7 for new and revivied combinations caused by these synonymies.) Our inclusion in Phrynobatrachidae of *Ericabatrachus* Largen, 1991 (not studied by us) rests on the original publication, which suggests that *Ericabatrachus* is ''*Phrynobatrachus*-like''. Likely, it will be found to be imbedded within *Phrynobatrachus* as currently arrayed, but at present we cannot reject the possibility that it is the sister taxon of *Phrynobatrachus*. We presume that Dubois' (2005) association of *Ericabatrachus* with his Phrynobatrachinae is based on similar reasoning although he provided no justification for this inclusion.

[200] SUPERFAMILY: PYXICEPHALOIDEA BONAPARTE, 1850

IMMEDIATELY MORE INCLUSIVE TAXON: [192] Africanura **new taxon.**

SISTER TAXON: [193] Phrynobatrachidae Laurent, 1941 ''1940''.

RANGE: Sub-Saharan Africa.

CONTENT: [201] Petropedetidae Noble, 1931, and [209] Pyxicephalidae Bonaparte, 1850.

CHARACTERIZATION AND DIAGNOSIS: Although no morphological characters in our study optimize to this branch, our molecular data are decisive. See appendix 5 for summary of molecular synapomorphies.

COMMENT: This taxon is highy heterogenous morphologically, at least with respect to overall appearance. Nevertheless, the molecular evidence is strong, and the taxon should survive additional testing.

[201] LFAMILY: PETROPEDETIDAE NOBLE, 1931

Petropedetinae Noble, 1931: 520. Type genus: *Petropedetes* Reichenow, 1874.

Ranixalini Dubois, 1987 ''1985'': 66. Type genus: *Ranixalus* Dubois, 1986. **New synonym.**

Conrauini Dubois, 1992: 314. Type genus: *Conraua* Nieden, 1908. **New synonym.**

Indiraninae Blommers-Schlösser, 1993: 211. Type genus: *Indirana* Laurent, 1986. **New synonym.**

IMMEDIATELY MORE INCLUSIVE TAXON: [200] Pyxicephaloidea Bonaparte, 1850.

SISTER TAXON: [209] Pyxicephalidae Bonaparte, 1850.

RANGE: South India; tropical West and East Africa.

CONTENT: ***Arthroleptides*** Nieden, 1911 ''1910''; ***Conraua*** Nieden, 1908; ***Indirana*** Laurent, 1986; ***Petropedetes*** Reichenow, 1874.

CHARACTERIZATION AND DIAGNOSIS: Petropedetidae is heterogeneous morphologically, with forked omosterna. No morphological synapomorphies are evident to us, although the molecular data are decisive. (See appen-

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dix 5 for molecular synapomorphies for this taxon.)

SYSTEMATIC COMMENTS: The association of *Indirana* (India), *Conraua* (tropical West Africa; Ethiopia and Eritrea), and *Arthroleptides* + *Petropedetes* (tropical West Africa; Tanzania and Kenya) at first surprised us, even though we had expected the undiagnosable Petropedetidae (sensu lato, now distributed among Petropedetidae, Phrynobatrachidae, and Dicroglossidae) to be obliterated.

The stream-dwelling larvae of *Arthroleptides* and stream-dwelling and arboreal tadpoles of *Indirana* are amazingly similar (compare Altig and Johnston, 1989, and Channing et al., 2002b, with Annandale and Rao, 1918) in having elongate tails with very low caudal fins, large bulging eyes, a dorsoventrally flattened body, and a laterally compressed jaw sheath with prominent lateral processes (Annandale, 1918; Rao, 1920; Amiet and Perret, 1969; Inger et al., 1984; Dubois, 1986 ''1985''; Drewes et al., 1989; Channing et al., 2002b). Only larvae of *Petropedetes natator* and *P. palmipes* have been fully described (Lamotte and Zuber-Vogeli, 1954; Lamotte et al., 1959; Lamotte and Lescure, 1989), but some superficial references to morphology or behavior are available for the larvae of *P. cameronensis* (Boulenger, 1906 ''1905''; Lawson, 1993), *P. newtoni* (Perret, 1966; Amiet and Perret, 1969; Lawson, 1993), and *P. parkeri* and *P. johnstoni* (Amiet and Perret, 1969; Amiet, 1983; Lawson, 1993). Drewes et al. (1989) noted inconsistencies in the description of the larva of *P. palmipes*. Regardless, from the comments or illustrations presented by the authors mentioned above, larvae of *Petropedetes* seem to have the same morphological peculiarities as do those of *Arthroleptides* and *Indirana*. The only exception is the larva of *P. natator*, which has an abdominal disc and an oral disc that is proportionally larger, with conspicuous lateral folds, and jaw sheaths that are not compressed laterally (Lamotte and Zuber-Vogeli, 1954; Lamotte and Lescure, 1989).

In transforming larvae of *Arthroleptides*, *Indirana*, and *Petropedetes*, the hind legs are large and seem to develop precociously, on a different growth trajectory from the front legs (Annandale, 1918; Lamotte et al., 1959; Amiet and Perret, 1969; Inger et al., 1984; Drewes et al., 1989).

Adults of *Arthroleptides*, *Indirana*, and *Petropedetes* also share characters whose polarity is less clear. Males of most *Petropedetes* and *Arthroleptides*, and males of *Indirana* (where they are known) share the presence of femoral glands of variable size and the presence of spicules around the margins of jaw and/or chin in the pectoral area (Amiet, 1973; Inger et al., 1984; Perret, 1984; Dubois, 1986 ''1985''; Klemens, 1998; however spicules are absent in *Petropedetes parkeri* [Amiet, 1983], and femoral glands are absent in *A. yakusini* [Channing et al., 2002b]). Note that spicules around the margins of jaw and/or chin and pectoral area, occur also in *Conraua* and in at least several phrynobatrachids as redefined here (Perret, 1966). Until this character can be widely assessed its level of generality remains unknown.

Dubois (1987 ''1985'') proposed the recognition of the tribe Ranixalini (later treated as a subfamily by Dubois, 1992), for the genera *Nannophrys*, *Nyctibatrachus*, and *Indirana* on the basis of the presence of femoral glands in males of *Nyctibatrachus* and *Indirana* (unknown in *Nannophrys*), and the morphological proximity of *Nannophrys* and *Nyctibatrachus* was noted by Clarke (1981). *Nannophrys* and *Indirana* further share the modifications of larval morphology associated with semiterrestrial life that were mentioned earlier (Kirtisinghe, 1958). From a morphological perspective, the evidence supporting the monophyly of *Nannophrys* + *Indirana* is the same as that favoring a relationship among *Indirana*, *Arthroleptides*, and *Petropedetes*. As discussed earlier, other characters of still unclear polarity that could further support this hypothesis are the presence of femoral glands and spicules around the margins of jaw and/or chin and pectoral area.

Petropedetes and *Arthroleptides* have large digital discs, a long metasternal style, and T-shaped terminal phalanges. *Indirana* has Y-shaped terminal phalanges (Laurent, 1986), which may be synapomorphic with the T-shaped terminal phalanges of *Petropedetes* + *Arthroleptides* although in our topology the simple terminal phalanges of

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Conraua presumably represent the apomorphy. Roelants et al. (2004) suggested that *Indirana* would find its closest relatives in India. However, inasmuch as these authors did not include any African taxa in their analysis, it was impossible for them to detect a relationship with African taxa. Van der Meijden et al. (2005) placed *Indirana* as the sister taxon of our Dicroglossinae. They also placed *Conraua* outside of a clade composed of *Petropedetes* + Pyxicephalinae, in both cases on the basis of fewer data and more analytical assumptions. Additional data or denser taxon sampling may rearrange these taxa, but at present our molecular data are decisive and, as discussed earlier, they are consistent with the distribution of various larval and adult characteristics.

[209] FAMILY: PYXICEPHALIDAE BONAPARTE, 1850

Pyxicephalina Bonaparte, 1850: 1. Type genus: *Pyxicephalus* Tschudi, 1838.

Phrynopsinae Noble, 1931: 518. Type genus: *Phrynopsis* Pfeffer, 1893.

Cacosterninae Noble, 1931: 540. Type genus: *Cacosternum* Boulenger, 1887.

Tomopternini Dubois, 1987 ''1985'': 56. Type genus: *Tomopterna* Duméril and Bibron, 1841. **New synonym.**

IMMEDIATELY MORE INCLUSIVE TAXON: [200] Pyxicephaloidea Bonaparte, 1850.

SISTER TAXON: [201] Petropedetidae Noble, 1931.

RANGE: Sub-Saharan Africa.

CONTENT: ***Amietia*** Dubois, 1987 ''1986'' (including ***Afrana*** Dubois, 1992, see Systematic Comments); ***Anhydrophryne*** Hewitt, 1919; ***Arthroleptella*** Hewitt, 1926; ***Aubria*** Boulenger, 1917; ***Cacosternum*** Boulenger, 1887; *Microbatrachella* Hewitt, 1926; ***Natalobatrachus*** Hewitt and Methuen, 1912; *Nothophryne* Poynton, 1963; *Poyntonia* Channing and Boycott, 1989; ***Pyxicephalus*** Tschudi, 1838; ***Strongylopus*** Tschudi, 1838; ***Tomopterna*** Duméril and Bibron, 1841.

CHARACTERIZATION AND DIAGNOSIS: Although we know of no morphological synapomorphies for this group, the molecular evidence is decisive in support of this branch. (See appendix 5 for molecular synapomorphies of this taxon; also see Systematic Comments.)

SYSTEMATIC COMMENTS: This morphologically heterogeneous taxon is coherent geographically. Although the association of these genera was only noted recently (Van der Meijden et al., 2005), much of the earlier taxonomy was based on very general notions of overall similarity, which are significantly influenced by perceptions of body size. The association of *Afrana* and *Strongylopus* (formerly in Ranini of Dubois, 1992) with *Anhydrophryne*, *Arthroleptella*, *Cacosternum*, and *Natalobatrachus* (formerly of Phrynobatrachidae [Petropedetidae] of Dubois, 1992), and with *Pyxicephalus* and *Aubria* (in Pyxicephalinae of Dubois, 1992), was something of a surprise (at least for us, as this was before Van der Meijden et al., 2005, appeared), although no evidence beyond overall similarity ever supported the older taxonomy. We still have three ''flavors'' of frogs in this group: those that look like *Rana* (*Afrana* and *Strongylopus*); those that are stocky and big (*Pyxicephalus* and *Aubria*); and those that are generally small and have not attracted from systematists the attention they deserve (the remainder). The absence of a median lingual process may be synapomorphic, as this feature is present in Petropedetidae and Phrynobatrachidae (Grant et al., 1997). Dubois (2005), anticipating the publication of Van der Meijden et al. (2005), recognized this taxon as a subfamily of Ranidae, Pyxicephalinae, which we recognize as a family.

Within Pyxicephalidae, we recognize two subfamilies: [210] Pyxicephalinae Bonaparte, 1850 (*Pyxicephalus* and *Aubria*) and [212] Cacosterninae Noble, 1931 (for the remaining genera). Pyxicephalinae is united by the following synapomorphies: (1) skull exostosis; (2) occipital canal present; (3) zygomatic ramus much longer than otic ramus, articulating with the postorbital process of the pars facialis of the maxilla; and (4) strong overlap of the medial ramus of the pterygoid and the parasphenoid ala (Clarke, 1981). Cacosterninae in our sense is not united by any morphological feature that we can identify with any certainty, although the molecular data are decisive (see appendix 5).

We place *Afrana* Dubois, 1992, into the synonymy of [218] *Amietia* Dubois, 1987 ''1986'', to resolve the paraphyly of *Afrana*.

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No characteristics of ''*Afrana*'' or *Amietia* reject this placement.

Clearly, our data do not support the notion (Poynton, 1964a) that *Cacosternum* is closely related to *Phrynobatrachus*. Our association of *Microbatrachella*, *Nothophryne*, and *Poyntonia* with this clade is provisional, based on the assertion by Blommers-Schlösser (1993) that these genera are allied by reduced ossification of the omosternal style and procoracoid clavicular bar.

[220] SAUKROBATRACHIA **NEW TAXON**

ETYMOLOGY: Saukro- (Latin: graceful, pretty) + batrachos (Greek: frog), referencing the beauty of many of the species included in this clade.

IMMEDIATELY MORE INCLUSIVE TAXON: [191] Ametrobatrachia **new taxon.**

SISTER TAXON: [192] Africanura **new taxon.**

RANGE: Eurasia, Africa, and Madagascar, to northern Australia; North and Central-America to central South America.

CONCEPT AND CONTENT: Saukrobatrachia **new taxon** is a monophyletic taxon composed of [221] Dicroglossidae Anderson, 1871, and [244] Aglaioanura **new taxon.**

CHARACTERIZATION AND DIAGNOSIS: Although no morphological characters that we are aware of optimize on this branch, the molecular data are decisive in support of this taxon. (See appendix 5 for listing of molecular synapomorphies.)

[221] FAMILY: DICROGLOSSIDAE ANDERSON, 1871

IMMEDIATELY MORE INCLUSIVE TAXON: [220] Saukrobatrachia **new taxon.**

SISTER TAXON: [244] Aglaioanura **new taxon.**

RANGE: Northwestern and sub-Saharan Africa; southern Arabian Peninsula; Pakistan, Afghanistan, India, Sri Lanka, and Nepal, through southern China (including part of Xizang) and Indochina to Japan and the Philippines; islands of the Sunda Shelf as far as Flores.

CONTENT: [225] Dicroglossinae Anderson, 1871, and [222] Occidozyginae Fei, Ye, and Huang, 1991 ''1990''.

CHARACTERIZATION AND DIAGNOSIS: None of the morphological characters in our analysis optimize on this taxon although the molecular data decisively support recognition of this taxon. (See appendix 5 for molecular transformations.) We recognized two subfamilies within Dicroglossidae, which are discussed in separate accounts because of the size and complexity of discussion.

[225] SUBFAMILY: DICROGLOSSINAE ANDERSON, 1871

Dicroglossidae J. Anderson, 1871: 38. Type genus: *Dicroglossus* Günther, 1860.

Limnonectini Dubois, 1992: 315. Type genus: *Limnonectes* Fitzinger, 1843.

Paini Dubois, 1992: 317. Type genus: *Paa* Dubois, 1975.

IMMEDIATELY MORE INCLUSIVE TAXON: [221] Dicroglossidae Anderson, 1871.

SISTER TAXON: [222] Occidozyginae Fei, Ye, and Huang, 1991 ''1990''.

RANGE: Northwestern and sub-Saharan Africa; southern Arabian Peninsula; Pakistan, Afghanistan, India, Sri Lanka, and Nepal, through southern China (including part of Xizang) and Indochina to the islands of the Sunda Shelf; Japan.

CONTENT: *Annandia* Dubois, 1992 (see Systematic Comments); *Eripaa* Dubois, 1992 (see Systematic Comments); ***Euphlyctis*** Fitzinger, 1843; ''***Fejervarya***'' Bolkay, 1915 (see Systematic Comments); ***Hoplobatrachus*** Peters, 1863; ***Limnonectes*** Fitzinger, 1843 (including ***Taylorana*** Dubois, 1987 ''1986''); *Minervarya* Dubois, Ohler, and Biju, 2001; ***Nannophrys*** Günther, 1869 ''1868''; ***Nanorana*** Günther, 1896 (including *Altirana* Stejneger, 1927; *Chaparana* Bourret, 1939; and *Paa* Dubois, 1975; see Systematic Comments); *Ombrana* Dubois, 1992 (see Systematic Comments); ***Quasipaa*** Dubois, 1992; ***Sphaerotheca*** Günther, 1859 ''1858''.

CHARACTERIZATION AND DIAGNOSIS: Although the molecular evidence is decisive for the existence of Dicroglossinae, we are aware of no morphological synapomorphies that optimize to this branch. (See Systematic Comments.) Appendix 5 shows the molecular transformations associated with this taxon.

SYSTEMATIC COMMENTS: Within Dicroglossinae Anderson, 1871, we recognize two

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monophyletic tribes, [226] Limnonectini Dubois, 1992, for *Limnonectes* (including as synonyms *Elachyglossa* Anderson, 1916; *Taylorana* Dubois, 1987), and [232] Dicroglossini Anderson, 1871, for the remaining genera, *Annandia*, ''*Fejervarya*'' (see below), *Nanorana* (including *Chaparana* and *Paa*), *Quasipaa*, *Sphaerotheca*, *Nannophrys*, *Euphlyctis*, and *Hoplobatrachus*. (Evidence for both is listed in appendix 5.) This agrees with several other phylogenetic analyses that used DNA evidence (e.g., Bossuyt and Milinkovitch, 2000; Emerson et al., 2000b; Marmayou et al., 2000; Vences et al., 2000c; Kosuch et al., 2001; Grosjean et al., 2004; Roelants et al., 2004; Jiang et al., 2005; Jiang and Zhou, 2005), although our expanded taxon sampling and data altered some relationships within Dicroglossini.

As noted in ''Results'', our results are strongly congruent with those of Jiang et al. (2005), especially when the rooting point is corrected by our larger outgroup sampling (see fig. 64). Because their analysis provided DNA sequence evidence unrejected by morphological synapomorphies, we take their results at face value: *Nanorana* as they viewed it is imbedded within a paraphyletic ''*Paa*'', and ''*Chaparana*'' is polyphyletic with the two components both imbedded within ''*Paa*''. Nevertheless, they provided evidence that their Group 1 (composed of nominal *Paa*, *Nanorana*, and *Chaparana*, and excluding *Quasipaa*), is monophyletic. Group 1 is characterized by paired patches of spines on the chest (Jiang et al., 2005), which may not be synapomorphic but distinguishes this taxon morphologically from *Quasipaa*. The oldest name for Group 1 is *Nanorana* Günther, 1896. (See appendix 7 for the name changes that extend from the synonymy of *Chaparana* Bourret, 1939, and *Paa* Dubois, 1975, with *Nanorana* Günther, 1896.) *Annandia* Dubois, 1992, and *Ombrana* Dubois, 1992, were originally named as subgenera of *Chaparana*, and *Eripaa* Dubois, 1992, was originally named as a subgenus of *Paa*. None of these three taxa were included, discussed, or even mentioned in the study of Jiang et al. (2005). Without discussion, Dubois (2005) transferred *Annandia* into Limnonectini. The placement of these taxa in Dicroglossinae is presumably not controversial, so pending the publication of evidence, we regard these as monotypic genera of uncertain placement within Dicroglossidae (see appendix 7 for combinations).

Previous authors (Dubois and Ohler, 2000; Dubois et al., 2001; Grosjean et al., 2004) demonstrated that *Sphaerotheca* and *Fejervarya* are closely related. Our data permit us to go further and suggest strongly that recognition of *Sphaerotheca* (as well as *Euphlyctis*, *Hoplobatrachus*, and *Nannophrys*) renders *Fejervarya* sensu Dubois and Ohler (2000) paraphyletic, as does a group composed of *Nannophrys*, *Euphlyctis*, and *Hoplobatrachus*. J. M. Hoyos (in Dubois and Ohler, 2000) suggested that *Fejervarya* does have a morphological synapomorphy: ventrolateral edge of the m. pectoralis pars abdominalis slightly attached to muscles that are dorsal relative to it, which results in a dark ventrolateral line from axilla to groin, especially visible in live specimens. This needs to be verified with reference to the condition in *Sphaerotheca* and the other satellite genera as well as to assure that this is universal in *Fejervarya* and not just in some subset of the nominal genus. Serious systematic and nomenclatural issues impede resolution of this paraphyly. The most important is that there are many species of nominal *Fejervarya* that we did not study, and there may be several species of frogs masquerading under the name *Fejervarya limnocharis* (Dubois and Ohler, 2000). Because our exemplar of *Fejervarya limnocharis* is from Vietnam and the type locality of this same nominal taxon is Java, we are reluctant to assume too much about the phylogenetic placement of *F. limnocharis* sensu stricto. Ongoing research by Dubois and Ohler (cited in Dubois and Ohler, 2000) should provide some resolution in the near future to this problem. In the interim we recommend using quotation marks around the name ''*Fejervarya*'' to denote the paraphyly of this taxon.

We reaffirm that placement of *Limnonectes limborgi* in the monotypic genus *Taylorana* renders *Limnonectes* paraphyletic and therefore continue the synonymy of *Taylorana* with *Limnonectes*, following Inger (1996) and Emerson et al. (2000a). Emerson et al. (2000a) and Evans et al. (2004) provided considerable evidence that *Elachyglos-*

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sa (formerly *Bourretia*) renders *Limnonectes* paraphyletic as well. We therefore reject the use of subgenera—at least as currently formulated—within *Limnonectes*, even though some authors (e.g., Delorme et al., 2004) have retained their use even though they mislead about evolutionary relationship.

Although *Minervarya* exhibits the ''Fejervaryan line'' (of Dubois and Ohler, 2000; see Dubois et al., 2001), it was not included in our study, so we are unable to make any comments about its position in the tree. Our inclusion of *Minervarya* in Dicroglossinae is obviously provisional; additional study is needed.

[222] SUBFAMILY: OCCIDOZYGINAE FEI, YE, AND HUANG, 1991 ''1990''

Occydozyginae Fei et al., 1991 ''1990'': 123. Type genus: *Occidozyga* Kuhl and Van Hasselt, 1822.

IMMEDIATELY MORE INCLUSIVE TAXON: [221] Dicroglossidae Anderson, 1871.

SISTER TAXON: [225] Dicroglossinae Anderson, 1871.

RANGE: Southern China (Guangxi, Yunnan, and Hainan), Thailand, Indochina, Malaya, Greater and Lesser Sunda Islands as far as Flores, and Philippines.

CONTENT: ***Occidozyga*** Kuhl and Hasselt, 1822 (including ***Phrynoglossus*** Peters, 1867; see Systematic Comments).

CHARACTERIZATION AND DIAGNOSIS: Although the molecular data are decisive (see appendix 5), Occidozyginae has other synapomorphies: (1) aquatic larvae with a keratodont formula of 0/0; and (2) a lateral line system that persists into adulthood (absent in *Occidozyga lima*; Dubois et al., 2001; convergent in *Euphlyctis*: Dicroglossinae).

SYSTEMATIC COMMENTS: Our data demonstrate that *Phrynoglossus* (which retains the lateral line system into adulthood) is paraphyletic with respect to *Occidozyga* (which does not). We therefore agree with Inger (1996) that *Phrynoglossus* is a synonym of *Occidozyga* (the senior name), providing a monophyletic *Occidozyga*. (See appendix 7 for new and revived combinations resulting from this synonymy.)

[244] AGLAIOANURA **NEW TAXON**

ETYMOLOGY: Aglaio- [Greek: splendid or noble] + anoura [Greek: tailless, i.e., frog].

IMMEDIATELY MORE INCLUSIVE TAXON: [220] Saukrobatrachia **new taxon.**

SISTER TAXON: [221] Dicroglossidae Anderson, 1871.

RANGE: Eurasia, Africa, and Madagascar, to northern Australia; the Americas excluding southern South America.

CONCEPT AND CONTENT: Aglaioanura is a monophyletic group composed of [245] Rhacophoroidea Hoffman, 1932 (1858), and [269] Ranoidea Rafinesque, 1814.

CHARACTERIZATION AND DIAGNOSIS: On the basis of our few exemplars for morphology (*Chiromantis xerampelina*, *Rhacophorus pardalis*, *Rana nigrovittata*, and *Rana temporaria*) the following characters are suggested as possibly synapomorphies of this group: (1) functional larval m. levator mandibulae lateralis absent (Haas 56.0); and (2) terminal phalanges bifurcated T-shape or Y-shaped (Haas 156.2; reversed in several lineages of Ranidae). (Molecular synapomorphies are provided in appendix 5.)

[245] SUPERFAMILY: RHACOPHOROIDEA HOFFMAN, 1932 (1858)

IMMEDIATELY MORE INCLUSIVE TAXON: [244] Aglaioanura **new taxon.**

SISTER TAXON: [269] Ranoidea Rafinesque, 1814.

RANGE: Tropical sub-Saharan Africa; Madagascar; South India and Sri Lanka; Japan; northeastern India to eastern China south through the Philippines and Greater Sundas; Sulawesi.

CONTENT: [246] Mantellidae Laurent, 1946, and [253] Rhacophoridae Hoffman, 1932 (1858).

CHARACTERIZATION AND DIAGNOSIS: See Rhacophoridae. One character in our analysis definitely optimizes on this taxon: intercalary element present (Haas 151.1). Channing (1989) also suggested the following as synapomorphies: (1) only one slip of the m. extensor digitorum communis longus, inserting on distal portion of fourth metatarsal; and (2) outermost slip of the m. palmaris longus inserting on the proximolateral rim of the aponeurosis palmaris. Ford and Cannatella

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(1993) also suggested that bifurcate terminal phalanges are a synapomorphy of this taxon, although this character may optimize at a more general level inasmuch as expanded toe tips seem to optimize on or near Aglaioanura.

SYSTEMATIC COMMENTS: Our study puts to rest whether mantellids and rhacophorids are sister taxa (e.g., Emerson et al., 2000b) or mantellids are imbedded in some way within the rhacophorids (Liem, 1970). Whether they should be considered mutual subfamilies of a larger Rhacophoridae (= Rhacophoroidea in our use) is not a scientific proposition. We follow the usage of Glaw and Vences (e.g., Vences et al., 2002; Vallan et al., 2003; Vences et al., 2003a; Vences and Glaw, 2004).

[246] FAMILY: MANTELLIDAE LAURENT, 1946

Mantellinae Laurent, 1946: 336. Type genus: *Mantella* Boulenger, 1882.

Boophinae Vences and Glaw, 2001: 88. Type genus: *Boophis* Tschudi, 1838.

Laliostominae Vences and Glaw, 2001: 88. Type genus: *Laliostoma* Glaw, Vences, and Böhme, 1998.

IMMEDIATELY MORE INCLUSIVE TAXON: [245] Rhacophoroidea Hoffman, 1932 (1858).

SISTER TAXON: [253] Rhacophoridae Hoffman, 1932 (1858).

RANGE: Madagascar.

CONTENT: ***Aglyptodactylus*** Boulenger, 1919 ''1918''; ***Boophis*** Tschudi, 1838; ***Laliostoma*** Glaw, Vences, and Böhme, 1998; ***Mantella*** Boulenger, 1882; ''***Mantidactylus***'' Boulenger, 1895.

CHARACTERIZATION AND DIAGNOSIS: Mantellids are small to medium-size terrestrial or arboreal frogs, predominantly found in semiarid to wet forested habitats. Although most are drab or cryptically colored, species of Mantellini in particular are brightly colored. Life history is varied, from the usual biphasic life history with aquatic eggs and feeding tadpoles (*Boophis*) to nidicolous larvae (e.g., many *Mantidactylus*). At least some (e.g., *Mantidactylus eiselti*) have direct development. Most species lay eggs away from water, in some cases in a suspended nest from which the tadpoles drop into water (Glaw and Vences, 1994). They share with their sister taxon, Rhacophoridae, intercalary phalangeal elements.

Laurent (1986: 764) distinguished mantellids from rhacophorids solely on basis of the third carpal being fused with the fourth and fifth in rhacophorids, but being free in mantellids (this feature is likely synapomorphic at this level of universality). Nevertheless, this feature has not been adequately assayed, so at present the molecular evidence is particularly decisive in distinguishing this as a monophyletic group that forms the sister taxon of Rhacophoridae. None of the morphological characters in our analysis optimize on this taxon. (Molecular transformations are listed in appendix 5.)

SYSTEMATIC COMMENTS: Vences and Glaw (2001) recognized three subfamilies on the basis of molecular data arranged phylogenetically: Laliostominae (Boophinae + Mantellinae). We consider Mantellinae and Laliostominae of Vences and Glaw (2001) to be tribes within a larger subfamily [248] Mantellinae, this subfamily forming the sister taxon of [247] Boophinae. *Aglyptodactylus* and *Laliostoma* are in [249] Laliostomini, and within Boophini, only *Boophis*, and [252] *Mantella* and [251] ''*Mantidactylus*'' are in [250] Mantellini. Although ''*Mantidactylus*'' is clearly paraphyletic with respect to *Mantella* (e.g., Vences and Glaw, 2001), our limited taxon sampling did not reveal this. It should be noted that there are many nominal subgenera that require reformulation as well (Raxworthy, Grant, and Faivovich, in preparation). For instance, Vences et al. (2002) revised the species of the ''*Mantidactylus*'' subgenus *Laurentomantis* and presented evidence in their resulting tree of the paraphyly of ''*Mantidactylus*'' with respect to *Mantella*, the paraphyly of the subgenus *Brygoomantis*, and the polyphyly of *Guibemantis* and *Gephyromantis*, as well as a lack of evidence for either paraphyly or monophyly of *Pandanusicola*. Much remains to be done, and we cannot recommend the use of subgenera within ''*Mantidactylus*'' until the inconsistency of taxonomy with phylogeny is addressed within that group.

Pseudophilautus Laurent, 1943, was placed in the synonymy of *Philautus* by R.F. Inger (*In* Frost, 1985). This was accepted by

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Dubois (1999b: 5) although the assignment to Mantellidae by Laurent (1986) has not been directly challenged through discussion of evidence. A second look is warranted.

[253] FAMILY: RHACOPHORIDAE HOFFMAN, 1932 (1858)

Polypedatidae Günther, 1858b: 346. Type genus: *Polypedates* Tschudi, 1838.
Rhacophoridae Hoffman, 1932: 581. Type genus: *Rhacophorus* Kuhl and Van Hasselt, 1822.
Philautinae Dubois, 1981: 258. Type genus: *Philautus* Gistel, 1848.
Buergeriinae Channing, 1989. Type genus: *Buergeria* Tschudi, 1838.

IMMEDIATELY MORE INCLUSIVE TAXON: [244] Rhacophoroidea.

SISTER TAXON: [246] Mantellidae.

RANGE: Tropical sub-Saharan Africa; South India and Sri Lanka; Japan; northeastern India to eastern China south through the Philippines and Greater Sundas; Sulawesi.

CONTENT: ***Aquixalus*** Delorme, Dubois, Grosjean, and Ohler, 2005 (see Systematic Comments); ***Buergeria*** Tschudi, 1838; ***Chiromantis*** Peters, 1854 (including ***Chirixalus*** Boulenger, 1893; see Systematic Comments); *Feihyla* **new genus** (see Systematic Comments); ***Kurixalus*** Ye, Fei, and Dubois, 1999 (see Systematic Comments); ***Nyctixalus*** Boulenger, 1882; ***Philautus*** Gistel, 1848; ***Polypedates*** Tschudi, 1838; ***Rhacophorus*** Kuhl and Hasselt, 1822; ***Theloderma*** Tschudi, 1838.

CHARACTERIZATION AND DIAGNOSIS: Although a few groups are primarily terrestrial, rhacophorids are predominantly treefrogs, sharing with basal ranids expanded digital pads and with mantellids the characteristic of intercalary phalangeal elements. Most species have T-shaped terminal phalanges. Several larval characters that optimized on this branch may actually be synapomorphies of Rhacophoroidea, or some part of Rhacophoridae: (1) anterior insertion of m. subarcualis rectus II–IV on ceratobranchial II (Haas 37.1); (2) larval m. levator mandibulae externus present as two portions (profundus and superficialis; Haas 54.1); (3) posterior dorsal process of pars alaris expanded terminally, almost rectangular in lateral view (Haas 89.1); (4) cartilaginous roofing of the cavum cranii composed of taeniae tecti medialis only (Haas 96.5); (5) free basihyal absent (Haas 105.0); (6) commissura proximalis II present (Haas 110.1); and (7) commissura proximalis III present (Haas 111.1).

SYSTEMATIC COMMENTS: Taxonomic decisions taken here are guided by our results (figs. 50, 65), the DNA sequence study of J.A. Wilkinson et al. (2002; fig. 48) and the essentially data-free tree of Delorme et al. (2005; fig. 49), which was presented along with a system of morphological differentia that delimited a number of monophyletic and paraphyletic groups, seemingly without reference to the tree itself. Results of the three have basic agreements.

Buergeriinae Channing, 1989, may be recognized for *Buergeria* and Rhacophorinae Hoffman, 1932 (1858), for the remaining rhacophorines, as was suggested by Channing (1989) and as diagnosed by J.A. Wilkinson et al. (2002). We cannot subscribe to the tribal taxonomy of Delorme et al. (2005) because their Philautini is not monophyletic on their own figure (fig. 49), and because the evidence in support of their tree was largely undisclosed.

On the basis of our results, and the studies of J.A. Wilkinson et al. (2002) and Delorme et al. (2005), two problems of generic delimitation appear to persist in the taxonomy. The first of these, the paraphyly/polyphyly of ''*Rhacophorus*'' is beyond the scope of this paper; more taxa need to be analyzed before this problem can be addressed. The second problem is that nominal ''*Chirixalus*'' seemingly falls into four generic units. We can help correct the problems surrounding the polyphyly/paraphyly ''*Chirixalus*'', although the phylogenetic position of many species of both ''*Chirixalus*'' and nominal *Philautus* needs to be evaluated.

(1) *Kurixalus* Fei, Ye, and Dubois (*in* Fei, 1999). As noted in ''Results'', we apply this name to a taxon that includes *K. eiffingeri* and *K. idiootocus*, which is diagnosed by our molecular evidence (see appendix 5, branch 256). We provisionally include *K. verrucosus*, which Delorme et al. (2005), without evidence or discussion, figured as the sister taxon of *Kurixalus eiffingeri* + *K. idiootocus*. (These authors included *idiootocus* and *verrucosus* without discussion in their new polyphyletic/paraphyletic ''*Aquixalus*'', even as

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they illustrated these species as being in an exclusive monophyletic group with *Kurixalus eiffingeri*). Under this concept, there are currently no identified morphological synapomorphies of *Kurixalus*, because the purported synapomorphies associated with *Kurixalus eiffingeri* (well-developed prepollex and oophagus tadpoles) are not exhibited in *K. idiootocus* or *K. verrucosus* (Kuramoto and Wang, 1987; Ziegler and Vences, 2002; Matsui and Orlov, 2004). Excluding ''*Aquixalus*'' *idiootocus* and ''*A.*'' *verrucosus* from ''*Aquixalus*'', we suggest, renders *Aquixalus* (sensu stricto) monophyletic (see below), if we assume that the tree of Delorme et al. (2005) survives testing by evidence.

(2) *Feihyla* **new genus** (type species: *Philautus palpebralis* Smith, 1924. Etymology: Fei Liang + *hyla* [Greek: vocative form of Hylas, a traditional generic root for treefrogs] to commemorate the extensive contributions to Chinese herpetology by Fei Liang). J.A. Wilkinson et al. (2002) found his exemplar of the ''*Philautus*'' *palpebralis* group of Fei (1999), ''*Chirixalus*'' *palpebralis*, to be the sister taxon of a group composed of all rhacophorids except *Buergeria*. Delorme et al. (2005) placed ''*Chirixalus*'' *palpebralis* in their Rhacophorini, which otherwise corresponds to a monophyletic group recovered by us and by J.A. Wilkinson et al. (2002). In fact, this is the major point of disagreement between J.A. Wilkinson et al. (2002) and Delorme et al. (2005). What is clear is that ''*Chirixalus*'' *palpebralis* is not in a monophyletic group with *Chirixalus* (sensu stricto), nor obviously associated closely with any other generic grouping. For this reason we have named *Feihyla* to recognize its distinctiveness. We cannot construe *Feihyla* to the ''*Philautus*'' *palpebralis* group of Fei (1999) because the diagnosis of this group is insufficient to distinguish it from many other species outside of China (i.e., Fei, 1999, diagnosed his ''*Philautus*'' *palpebralis* group as ''*Philautus*'' from China, with an X or)(shape on the dorsum and lacking vomerine teeth), such as *Aquixalus gracilipes* and *A. supercornutus*; see discussion below). We therefore diagnose *Feihyla* by the characters for the species ''*Philautus*'' *palpebralis* provided by Fei (1999). Association of other species with this taxon will require considerable additional work.

Although ''*Chirixalus*'' *palpebralis* has been demonstrated to be phylogenetically distinct (J.A. Wilkinson et al., 2002; Delorme et al., 2005) and deserving a new generic name, the status of presumably closely related species ''*Chirixalus*'' *romeri* and ''*C.*'' *ocellatus* of the ''*Philautus*'' *palpebralis* group of Fei, 1999) remains an open question, although no evidence so far has suggested that these species form a monophyletic group. Morphological evidence provided by Delorme et al. (2005) differentiating their Rhacophorini (including ''*Chirixalus*'' *palpebralis* on their tree) and Philautini (a paraphyletic group that on their tree includes ''*Philautus*'' *gracilipes* [= *Aquixalus gracilipes*]), suggests that *Aquixalus* (including ''*Chirixalus*'' *gracilipes*) is not close to *Feihyla* (see discussion below under *Aquixalus*).

(3) *Chiromantis* Peters, 1854, and *Chirixalus* Boulenger, 1893. A third unit is the cluster of species paraphyletic with respect to *Chiromantis*. The paraphyly of *Chirixalus* (sensu stricto) with respect to *Chiromantis* was not a surprise to us. J.A. Wilkinson et al. (2002) had suggested that *Chirixalus doriae* is the sister taxon of *Chiromantis*, and that *Chirixalus vittatus* is close to *Polypedates* (compare their results with ours, which are based on substantially more data). We place *Chirixalus* Boulenger, 1893, into the synonymy of *Chiromantis* Peters, 1854, to correct this paraphyly. (See appendix 7 for new combinations that extend from this change and appendix 5 for molecular synapomorphies.)

(4) *Aquixalus* Delorme, Dubois, Grosjean, and Ohler, 2005. We recognize a monophyletic *Aquixalus* (i.e., *Aquixalus* sensu Delorme et al., 2005, but excluding ''*Aquixalus*'' *idiootocus* and ''*Aquixalus*'' *verrucosus*; that is, without the molecular synapomorphies of branch 256—see above). Delorme et al (2005) diagnosed this taxon (although we do not know which of the listed species they actually evaluated for these characters), but our exclusion of *Kurixalus idiootocus* (and provisionally *K. verrucosus*) from *Aquixalus* on the basis of the molecular synapomorphies that place *Kurixalus* distant from *Aquixalus* should render *Aquixalus* mono-

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phyletic if the tree provided by Delorme et al. (2005) is correct. We suggest, on the basis of the tree provided by Delorme et al (2005), that the morphological similarities shared by *Kurixalus* and *Aquixalus* are plesiomorphic.

We follow the recognition by Delorme et al. (2005) of a putatively monophyletic subgenus *Gracixalus* for ''*Philautus*'' *gracilipes* Bourret, 1937, and ''*Philautus*'' *supercornutus* Orlov, Ho, and Nguyen, 2004 (not studied by us). The morphological diagnosis of *Gracixalus* (spines on the upper eyelid, rictal gland connected to the mouth, foot very thin, two outer palmar tubercles, white spot on snout tip of tadpole, five pairs of prelingual papillae on the tadpole, crescent-shaped crest on the tadpole) purportedly separates it from the nominate subgenus *Aquixalus*, but the absence of adequate published tadpole descriptions suggest that this diagnosis should be treated as provisional (Bain and Nguyen, 2004; Matsui and Orlov, 2004; Delorme et al., 2005). Although *Gracixalus* can be separated from *Feihyla palpebralis* (the latter in parentheses): snout triangularly pointed (obtusely pointed); skin translucent (not translucent); small white tubercles along the head, anal region, and large conical tubercles on upper eyelid (all absent), these characters do not unambiguously separate *Gracixalus* from ''*P.*'' *romeri*, ''*P.*'' *ocellatus*, the other members of the ''*P.*'' *palpebralis* group of Fei (1999). The placement of these two species, as well as higher level relationships will be dependent upon a rigorous phylogenetic analysis.

Although we cannot reject the putative monophyly of the subgenus *Aquixalus* (including the type species *A. odontotarsus*, as well as *A. ananjevae*, *A. baliogaster*, *A. bisacculus*, *A. carinensis*, and *A. naso*; modified from Delorme et al., 2005), we do not see any reason to recognize it, either, until the relevant phylogenetic data are published by the original authors. According to Delorme et al. (2005), the morphological diagnosis of *Aquixalus* (webbing on feet not extending to toes, rictal gland not connected to mouth, foot very thick, one outer palmar tubercle, concavity on tadpole snout in lateral view, four pairs of prelingual papillae in tadpole, median crest in tadpole triangular shaped, 180–240 eggs per clutch) also applies to *Kurixalus verrucosus*, so this diagnosis must be largely or entirely based on plesiomorphies, with the nominal subgenus *Aquixalus* being those members of *Aquixalus* that do not share the apomorphies of *Gracixalus*. Detailed analysis of disclosed evidence is necessary.

[269] SUPERFAMILY: RANOIDEA RAFINESQUE, 1814

IMMEDIATELY MORE INCLUSIVE TAXON: [244] Aglaioanura **new taxon.**

SISTER TAXON: [245] Rhacophoroidea Hoffman, 1932 (1858).

RANGE: Worldwide temperate and tropical environments, except for southern Australia, New Zealand, Seychelles, and southern South America.

CONTENT: [270] Nyctibatrachidae Blommers-Schlösser, 1993, and [272] Ranidae Rafinesque, 1814.

CHARACTERIZATION AND DIAGNOSIS: Morphological synapomorphies for Ranidae (see below) may actually optimize at this level. Regardless, the molecular data are decisive in support of this taxon (appendix 5).

[270] FAMILY: NYCTIBATRACHIDAE BLOMMERS-SCHLÖSSER, 1993

Nyctibatrachinae Blommers-Schlösser, 1993: 211. Type genus: *Nyctibatrachus* Boulenger, 1882.

Lankanectinae Dubois and Ohler, 2001: 82. Type genus: *Lankanectes* Dubois and Ohler, 2001. **New synonym.**

IMMEDIATELY MORE INCLUSIVE TAXON: [269] Ranoidea Rafinesque, 1814.

SISTER TAXON: [272] Ranidae Rafinesque, 1814.

RANGE: Sri Lanka and India.

CONTENT: ***Nyctibatrachus*** Boulenger, 1882; ***Lankanectes*** Dubois and Ohler, 2001.

CHARACTERIZATION AND DIAGNOSIS: None of our analyzed morphology optimizes on this branch, although the molecular data are decisive. See appendix 5 for list of unambiguous molecular synapomorphies.

SYSTEMATIC COMMENTS: Nyctibatrachidae in our sense brings two genera together, *Nyctibatrachus*, with a median lingual process (unknown polarity), digital discs present (plesiomorphic), femoral glands present (unknown polarity), and lateral line system not persisting into adulthood (plesiomorphic),

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and *Lankanectes*, with no median lingual process, digital discs absent, femoral glands absent, and lateral line system persisting into adulthood (Dubois et al., 2001). They are arranged in a single family to avoid the taxonomic redundancy of having monotypic (and therefore uninformative) family-group names.

[272] FAMILY: RANIDAE RAFINESQUE, 1814

Ranaridia Rafinesque, 1814: 102. Type genus: *Ranaridia* Rafinesque, 1814
Limnodytae Fitzinger, 1843: 31. Type genus: *Limnodytes* Duméril and Bibron, 1841.
Amolopsinae Yang, 1991a: 172. Type genus: *Amolops* Cope, 1865.

IMMEDIATELY MORE INCLUSIVE TAXON: [269] Ranoidea Rafinesque, 1814.

SISTER TAXON: [270] Nyctibatrachidae Blommers-Schlösser, 1993.

RANGE: Temperate and tropical Africa and Eurasia through Indonesia to northern Australia, North America, Central America, and northern South America.

CONTENT: ***Amolops*** Cope, 1865 (including *Amo* Dubois, 1992); *Babina* Thompson, 1912 (including ***Nidirana*** Dubois, 1992); ***Clinotarsus*** Mivart, 1869; ***Glandirana*** Fei, Ye, and Huang, 1991 ''1990''[32] (including *Rugosa* Fei, Ye, and Huang, 1991 ''1990''); ***Hydrophylax*** Fitzinger, 1843 (including ***Amnirana*** Dubois, 1992, and ***Chalcorana*** Dubois, 1992); ***Hylarana*** Tschudi, 1838; ***Huia*** Yang, 1991 (including ***Eburana*** Dubois, 1992; *Bamburana* Fei, Ye, Jiang, Xie, and Huang, 2005; ***Odorrana*** Fei, Ye, and Huang, 1991 ''1990''); *Humerana* Dubois, 1992; ***Lithobates*** Fitzinger, 1843 (including ***Aquarana*** Dubois, 1992; ***Pantherana*** Dubois, 1992; ***Sierrana*** Dubois, 1992; ***Trypheropsis*** Cope, 1868; *Zweifelia* Dubois, 1992); ***Meristogenys*** Yang, 1991; *Nasirana* Dubois, 1992; ***Pelophylax*** Fitzinger, 1843; *Pterorana* Kiyasetuo and Khare, 1986; *Pulchrana* Dubois, 1992; ***Rana*** Linnaeus, 1758 (including ***Amerana*** Dubois, 1992; ***Aurorana*** Dubois, 1992; ***Pseudoamolops*** Jiang, Fei, Ye, Zeng, Zhen, Xie, and Chen, 1997; and ***Pseudorana*** Dubois, 1992); *Sanguirana* Dubois, 1992; ***Staurois*** Cope, 1865; ***Sylvirana*** Dubois, 1992 (including ***Papurana*** Dubois, 1992, and ***Tylerana*** Dubois, 1992[32]). (See Systematic Comments.)

CHARACTERIZATION AND DIAGNOSIS: Although Haas (2003) included only two ranids in his study, *Sylvirana nigrovittata* and *Rana temporaria*, characters that optimize on their subtending branch are candidates as synapomorphies for Ranidae: (1) posterolateral projections of the crista parotica absent (Haas 67.0); and (2) processus branchialis closed (Haas 114.1). Denser sampling should test this proposition. These characters may actually optimize on Ranoides. Regardless, the molecular data are decisive (see appendix 5).

SYSTEMATIC COMMENTS: As noted in ''Results'', *Batrachylodes* is transferred definitively to Ceratobatrachidae and *Amietia* (including *Afrana*) and *Strongylopus* are transferred to Pyxicephalidae. For discussion of these taxa see those familial accounts.

As noted in the ''Review of Current Taxonomy'', the sections and subsections of ''*Rana*'' (sensu lato) provided by Dubois (1992) do not inform about evolutionary relationships, so for this discussion and the taxonomic remedies we suggest, we will focus on genera and subgenera. The discussion that follows addresses the generic taxonomy that we recommend (moving from top to bottom of Ranidae [new taxonomy] in figure 71, although addressing other genera and problems in passing).

Staurois Cope, 1865: We accept *Staurois* as a genus, although we note that evidence for this taxon's monophyly is equivocal and requires testing. The traditional diagnosis of *Staurois*—digital discs broader than long; T-shaped terminal phalanges with horizontal arm longer than longitudinal arm; outer metatarsals separated to base but webbed; nasals small separated from each other and frontoparietal; omosternal style not forked (Boulenger, 1918); and lacking a raised abdominal sucker disc on larva (Inger, 1966)—are plesiomorphic for Ranidae. Although some larval characters are thought to be common among species of *Staurois* (tadpole

[32] Dubois (1999a: 91) considered *Glandirana* Fei, Ye, and Huang, 1991, to have priority over *Rugosa* Fei, Ye, and Huang, 1991, and *Sylvirana* Dubois, 1992, to have priority over *Papurana* Dubois, 1992, and *Tylerana* Dubois, 1992, under the provisions of Article 24.2 (''Principle of First Revisor'') of the International Code of Zoological Nomenclature (ICZN, 1999).

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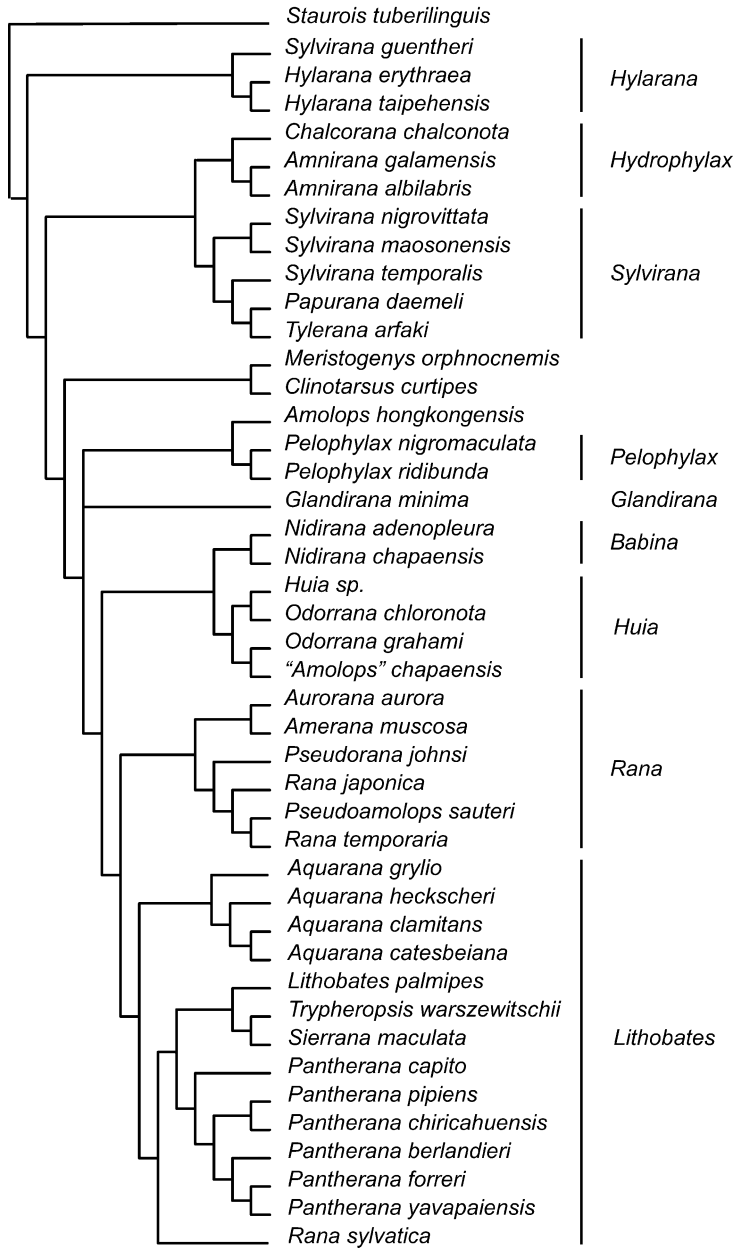

Fig. 71. Generic changes suggested for ranid taxa that we studied. This is not exhaustive and the Systematic Comments under Ranidae in ''A Taxonomy of Living Amphibians'' should be consulted for additional taxonomic changes.

with deep, cup-like labial parts; upper lip of oral disc with two continuous rows of papillae; lower lip with one broad continuous band of papillae; Inger, 1966), the diagnostic value of these characters is unknown due to the large number of ranid species whose adults are morphologically similar to those of *Staurois*, but whose larvae remain undescribed.

[274] *Hylarana* Tschudi, 1838: We asso-

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ciate our exemplars of *Hylarana* Tschudi, 1838 (*H. erythraea*, the type species, and *H. taipehensis*), as well as of ''*Sylvirana*'' *guentheri*, with the generic name *Hylarana*. Although these two units were assigned, respectively, to the no-humeral-gland (*Hylarana*) and humeral-gland subsections (*Hydrophylax*) of Dubois (1992), our data suggest strongly that the humeral gland is convergent in ''*S.*'' *guentheri* and *Sylvirana* (sensu strico) or that the presence of the structure has been missed in a widespread way because of the lack of detailed morphological study (including dissections). *Hylarana* (including ''*Sylvirana*'' *guentheri* and *H. macrodactyla*, the third species of *Hylarana* sensu Dubois, 1992) lacks dermal glands in the larvae, a character that appears to optimize on the sister branch of *Hylarana*. The vocal sac condition is variable among species of *Hylarana*, with ''*S.*'' *guentheri* possessing gular pouches and *H. taipehensis* and *H. erythraea* lacking gular pouches. This character is highly homoplastic throughout the ranid portion of our tree. We take the molecular apomorphies for branch 274 (appendix 5) to be synapomorphies of *Hylarana*.

We are unable to diagnose *Hylarana* on the basis of morphology. We did not study, and so cannot document, the phylogenetic position of *H. macrodactyla*. Thus, our association of this species with *Hylarana* requires testing. Similarly, we do not know which other species may be included in this historically ambiguously diagnosed genus.

[278] *Hydrophylax* Fitzinger, 1843 (including *Amnirana* Dubois, 1992, and *Chalcorana* Dubois, 1992): We associate our exemplars of humeral-gland-bearing genera (*Hydrophylax* and *Amnirana*), as well as the imbedded *Chalcorana*, with the generic name *Hydrophylax* Fitzinger, 1843. Channing (2001) had already considered the African member of *Hydrophylax* (*H. galamensis*) to be in *Amnirana*, along with other African *Hylarana*-like frogs. Our association of the type species of *Hydrophylax*, *H. malabarica* (unstudied by us), with the clade of studied terminals requires testing, of course, as does the association of the unstudied members of these nominal taxa. The association of unstudied members of *Amnirana*, *Hydrophylax*, and *Chalcorana* (some of which are reported to not bear humeral glands[33]) is done on the assumption that some of the molecular apomorphies of this taxon are synapomorphies of *Hydrophylax* in the sense of including the species that we did not study. On the basis of evidence presented by Matsui et al. (2005), we place *Chalcorana hosii* in our *Huia*. *Chalcorana* is likely broadly polyphyletic, but without evidence of the remainder's placement we provisionally regard them as close to *Chalcorana chalconota*, the type-species of *Chalcorana*. We could have retained *Chalcorana* as a genus, but it is clear that, as data emerge, the species in this nominal taxon will be assigned to *Hydrophylax*, *Sylvirana*, and likely others as well. This is not a satisfactory solution to the problem of trying to sort through this morass, but it is the only practical solution available to us at present.

We retain *Humerana* Dubois, 1992, and *Pulchrana* Dubois, 1992, as nominal genera only because we did not study these humeral-gland-bearing genera. Future work should test the hypothesis that the remaining species of the ''humeral-gland group'' constitute a monophyletic unit. The results of Matsui et al. (2005; fig. 46) suggest that *Humerana* ultimately will be assigned to *Hylarana*.

[280] *Sylvirana* Dubois, 1992: Our results demonstrate the polyphyly of nominal *Sylvirana* (see discussion of ''*S.*'' *guentheri* under discussion of *Hylarana*) and the paraphyly of the major group of nominal *Sylvirana* (including its type species, *S. nigrovittata*). To remedy the demonstrated polyphyly of *Sylvirana*, we transfer ''*S.*'' *guentheri* into *Hylarana* Tschudi, 1838 (see above). To relieve the paraphyly of remaining *Sylvirana*, we place *Papurana* Dubois, 1992, and *Tylerana* Dubois, 1992, into the synonymy of *Sylvirana* Dubois, 1992. Although it is clear on the basis of molecular data that ''*S.*'' *guentheri* is not in the clade containing *S. nigrovittata* (the type species of *Sylvirana*), it is also not clear how many species of nom-

[33] Possession of humeral glands can be a difficult characteristic to assess due to level of development, and their presence may be apparent only on dissection. Therefore, any statement that humeral glands are absent really requires that a dissection has been made. Dubois (1992) did not mention whether he had made such dissections.

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inal *Sylvirana* are associated with ''*S.*'' *guentheri*. We take the most falsifiable position—that only ''*S.*'' *guentheri* is far from *Sylvirana nigrovittata*—and suggest that careful study is needed.

Meristogenys Yang, 1991, *Clinotarsus* Mivart, 1869, and *Nasirana* Dubois, 1992: Our results place *Meristogenys* as the sister taxon of *Clinotarsus* (as found by Roelants et al., 2004; fig. 35), and far from both *Amolops* and *Huia*, to which it was considered to be closely related by Yang (1991b) and Dubois (1992). Besides the molecular evidence, *Clinotarsus* shares several larval characters with *Meristogenys*: (1) dermal glands on the flank; (2) increased numbers of rows of labial keratodonts (5–9/5–10 in *Meristogenys* and 6–8/6–8 in *Clinotarsus*; over 1–5/2–8 in *Amolops* and *Huia*; Boulenger, 1920: 132–133; Chari, 1962; Yang, 1991b; Hiragond et al., 2001); and (3) upper labial keratodont rows with a medial gap. Unlike *Clinotarsus*, but like *Amolops*, *Huia*, and (superficially) *Pseudoamolops*, *Meristogenys* have a raised abdominal sucker in the larvae (Kuramoto et al., 1984; Yang, 1991b; Jiang et al., 1997).

Clinotarsus lacks the obvious synapomorphies associated with *Meristogenys* (a raised, sharply defined abdominal sucker in the larvae, ribbed jaw sheaths, and upper or both jaw sheaths divided (Yang, 1991b). Because most of the species of *Meristogenys*, like most *Hylarana*-like species (sensu lato), have not been sampled and may be involved with this group, we retain both *Clinotarsus* and *Meristogenys* as genera.

Nasirana alticola (not studied by us) may be allied with *Clinotarsus*, as their larvae share two possible synapomorphies: (1) large size; and (2) supracaudal glands (Grosjean et al., 2003). Furthermore, *Nasirana* shares with *Meristogenys* and *Clinotarsus* other larval characters of uncertain polarity: multiple (3–7) medially divided upper labial keratodont rows; high numbers of labial keratodont rows (7–8: 7–8); and presence of dermal glands on the flanks of the body (Yang, 1991b; Hiragond et al., 2001; Grosjean et al., 2003). *Nasirana* can be distinguished from all other frogs by a fleshy prominence on the snout of the male. As with *Clinotarsus*, we provisionally retain *Nasirana* as a genus.

Sanguirana Dubois, 1992, and *Pterorana* Kiyasetuo and Khare, 1986: We provisionally retain *Sanguirana* Dubois, 1992, and *Pterorana* Kiyasetuo and Khare, 1986 (both unstudied by us) as genera, owing to the ambiguous nature of their putative synapomorphies (both genera are *Hylarana*-like forms). *Sanguirana sanguinea* (type species of *Sanguirana*) has a tadpole with characters shared with *Meristogenys*, *Clinotarsus*, and *Altirana*: a moderate to high number of labial keratodont rows (4–6/4–5); upper lip with divided keratodont rows; and dermal glands on the head and body; and ventral portions of the body and tail fins (Alcala and Brown, 1982). *Pterorana khare* (tadpole unknown) is distinguished from other ranid frogs by the large, fleshy folds on the flanks and thighs and over the vent that extend away from the body when the frog is under water (Kiyasetuo and Khare, 1986).

Amolops Cope, 1865, and *Amo* Dubois, 1992: The phylogenetic association of *Amolops*, *Meristogenys*, and *Huia* (Yang, 1991b; Dubois, 1992), as noted in ''Results'' and in the discussion above of *Meristogenys*, was rejected. Further, the association of *Pseudoamolops* Jiang et al., 1997, suggested by Kuramoto et al. (1984) and Fei et al. (2000) is also rejected, suggesting that in each case the ventral sucker on the larvae is nonhomologous and should be considered independently apomorphic in each lineage. Kuramoto et al. (1984) provided morphological evidence that the ventral sucker disc on the larvae of *Amolops* is not homologous with that of ''*Pseudorana*'' *sauteri*: the edge of the disc is sharply defined in *Amolops* (not so in *sauteri*); the m. diaphragmatobranchialis medialis engages the floor of the sucker to generate negative pressure in *Amolops* (muscle does not communicate with sucker in *sauteri*); and inframarginal U-shaped band of keratinized material on the sucker in *Amolops* (absent in *sauteri*). Regardless, Kuramoto et al. (1984) suggested a close relationship of *sauteri* to *Amolops*.

The status of *Amo* Dubois, 1992 (not studied by us), is arguable. Dubois (1992) suggested that *Amo* is unique among *Amolops* in having axillary glands in both sexes and an outer metatarsal tubercle (a character plesiomorphic at the base of the ranids), but the outer metatarsal tubercle is nevertheless pre-

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sent in *Amolops nepalicus*[34] and *A. torrentis* (after Yang, 1991b). *Amo* lacks the characteristics of both *Huia* and *Meristogenys* (tibia elongate; having lateral dermal glands on the larvae; high number of larval keratodont rows on the lower lip) but otherwise shares one apomorphy with *Amolops* (sensu stricto) in our topology: first metacarpal greater than half the length of the second. So, rather than suggest that a sucker developed on the venter of the larvae five times in ranids (rather than the four events currently required by our topology) we regard *Amo* as a synonym of *Amolops*.

We found nominal *Amolops* to be polyphyletic (figs. 50, 65). In this case, the larva of *Amolops chapaensis* is unknown (Yang, 1991b), and that species had been assigned to *Amolops* on the basis of having an adult morphology more similar to *Amolops* than to *Hylarana* (i.e., no humeral glands and presence of gular pouches in males; after Inger, 1966: 257), rather than its having the larval synapomorphies of *Amolops*. We transfer this species out of *Amolops* and into another genus below. (See discussion of *Huia*, *Odorrana*, and *Eburana*). Although we obtain *Amolops* as the sister taxon of *Pelophylax*, we are unaware of any morphological synapomorphy uniting these groups (see appendix 5, branch 287).

[288] *Pelophylax* Fitzinger, 1843: We restrict the generic name *Pelophylax* to the subgenus *Pelophylax* of Dubois (1992). We are unaware of any morphological synapomorphy for this group, although the molecular data are seemingly decisive (see appendix 5, branch 288).

Glandirana Fei, Ye, and Huang, 1991 ''1990'', and *Rugosa* Fei, Ye, and Huang, 1991 ''1990'': *Glandirana minima* is the sole species in its nominal genus (formerly a subgenus of the section *Hylarana*, subsection *Hylarana*: Dubois, 1992). It is diagnosed by having skin densely covered in granular yellow glands; axillary glands and distal femoral glands densely packed, forming a roll; and intermittent longitudinal ridges, densely covered with small tubercles on the dorsum (Fei et al., 1991 ''1990''). It shares with *Pelophylax* a very low number of labial keratodont rows in larvae (likely plesiomorphic on our topology). Jiang and Zhou (2005; their fig. 1), with different taxon sampling, found *Glandirana* to be the sister taxon of *Rugosa* (not studied by us, but placed by Dubois, 1992, in his section *Pelophylax*), and phylogenetically distant from their samples of *Pelophylax* (*P. hubeiensis* and *P. nigromaculata*).

Glandirana and *Rugosa* share the following characteristics that appear to be synapomorphic (on our tree and on that of Jiang and Zhou, 2005): entire body of tadpole covered in glands; digital discs absent in adults; and dorsum densely covered with longitudinal, tubercular skin ridges in adults (Stejneger, 1907: 123–126; Okada, 1966; Ting and T'sai, 1979; Fei et al., 1991 ''1990''; Fei et al., 2005: 132–138). There are morphological differences between the two genera (Okada, 1966; Fei et al., 1991 ''1990''; Fei et al., 2005: 132–138; Stejneger, 1907: 123–126; Ting and T'sai, 1979): sternal cartilage forked posteriorly in *Glandirana* [deeply notched in *Rugosa*]; toes half-webbed, reaching the second subarticular tubercle on toe IV in *Glandirana* [fully webbed to beyond second subarticular tubercle on toe IV in *Rugosa*]; skin densely covered in granular yellow glands, as well as axillary and distal femoral glands densely packed, forming a roll in *Glandirana* [prominent glands only behind tympanum in *Rugosa*]). However, none of these characters is obviously in conflict with *Glandirana* + *Rugosa* forming a monophyletic group. In light of this evidence, we recognize this clade as one genus, *Glandirana*, placing *Rugosa* into synonomy. *Rugosa rugosa*, the type species of *Rugosa*, should be included in subsequent phylogenetic analysis to test this hypothesis.

[291] *Babina* Thompson, 1912, and *Nidirana* Dubois, 1992: *Nidirana* Dubois, 1992, has been associated with *Babina* Thompson, 1912 (unstudied by us) on the basis of two characters: presence of a large suprabrachial gland in breeding-condition males, and egg

[34] Dubois (2000: 331; 2004a: 176) suggested, on the basis of examination of the holotype, this taxon is synonymous with *Amolops formosus* but did not provide any discussion regarding the differences itemized in the original description or the diagnostic differences noted by Yang (1991b). Dubois (2004a: 176) subsequently criticized Anders (2002) for retaining *Amolops nepalicus* without providing a detailed discussion of the issue.

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deposition in water-filled nests of terrestrial burrows or open puddles (Pope, 1931: 536–538; C.-C. Liu, 1950: 258–260; Kuramoto, 1985; Dubois, 1992: 154–156; Chou, 1999: 398–399). *Babina* is further diagnosable from *Nidirana* on the basis of the male having a spine on the prepollex (absent in *Nidirana*; Okada, 1966; Kuramoto, 1985; Chou, 1999). *Nidirana*, however, has no characters that suggest that it is monophyletic with respect to *Babina* (Dubois, 1992; Chou, 1999). For this reason, although a subgenus *Babina* (the group with the large prepollical spine) could be employed, the name *Nidirana* applies to no monophyletic group that can be identified at this time. We therefore transfer all members of Dubois' subgenus *Nidirana* to the genus *Babina*.

[292] *Huia* Yang, 1992, *Odorrana* Fei, Ye, and Huang, 1991 ''1990'', *Bamburana* Fei et al., 2005, ''*Amolops*'' *chapaensis*, and *Eburana* Dubois, 1992: Although our molecular evidence capturing this clade of Himalayan and Southeast Asian cascade-dwelling species is unambiguous (see appendix 5, branch 292), insufficient sampling, the lack of morphological data, and the concomitant taxonomic confusion surrounding these taxa presented us with a significant taxonomic challenge. ''*Amolops*'' *chapaensis* is embedded in our *Huia–Eburana–Odorrana* clade, but its assignment to *Amolops* was done on the basis of overall similarity (see discussion in *Amolops* section), and it is clearly not part of that genus. There is no known morphological synapomorphy linking species of *Odorrana*, as its purported synapomorphy, colorless spines on chest of the male, is also known in *Huia nasica* (B.L. Stuart and Chan-ard, 2005) and species of at least two other genera (i.e., some *Chalcorana* and at least *Babina caldwelli* [R. Bain, personal obs.]), and is absent in many species of *Odorrana* sensu Fei et al. (1991 ''1990''; see discussion in ''Review of Current Taxonomy''). Similarly, there is no evidence suggesting that *Eburana* is monophyletic, because its putative synapomorphy, unpigmented eggs, is shared by at least some species of three other genera (e.g., *Chalcorana*, *Odorrana*, *Amolops*; see discussion in ''Review of Current Taxonomy''). *Huia* (sensu stricto) represents a third example in our tree of convergence of a raised, sharply defined abdominal sucker in the tadpole (Yang, 1991b; see discussion of *Meristogenys* and *Amolops* above). Beyond this structure, the only characters uniting *Huia* with *Amolops* and *Meristogenys* are ventral and postorbital glands of the larvae. None of these characters is present in *Odorrana grahami*, the only other member of this clade whose tadpole is known.

We know of no morphological synapomorphy that unites this clade (branch 292), but our molecular data are decisive for its being a monophyletic group (see appendix 5). We therefore apply a single generic name. The oldest available name from this group of species is *Huia* Yang, 1991b (published 18 February, 1991; the publication containing *Odorrana* did not appear until at least March of 1991; Fei et al., 1991 ''1990''). We therefore place ''*Amolops*'' *chapaensis*; *Eburana* Dubois, 1992; and *Odorrana* Fei, Ye, and Huang, 1991 ''1990'', into the synonymy of *Huia* Yang, 1991.

We recognize that this taxonomy is problematic for two reasons. First, we did not include any of the types of the nominal genera in this study. Thus, the assigned name may be inappropriate. Indeed, *Huia nasica* may not be closely related to *Huia cavitympanum* Boulenger, 1893 (the type species of *Huia* and not studied by us). The association with *Huia nasica* of a tadpole with a raised, sharply defined abdominal sucker and ventral and postorbital glands of the larvae was based on one specimen (C.-C. Liu and Hu, 1961). Yang (1991b) cast doubt on this assignment when he reported that a ''tadpole from Menyang assigned to *H. nasica* by Liu and Hu (1961), is certainly *Huia* even if not larval *H. nasica*''. Our grouping of *H. nasica* within a clade of *Odorrana* and *Eburana* might be evidence that *nasica* is not a member of *Huia*. And second, our small sample size (4 species, only 2 of which have known tadpoles) from this large, undiagnosed group of species (minimum 36 species; Frost, 2004) may speak to an oversimplification of the relationships among these taxa.

Whereas both of these problems are real concerns, this decision, as with all of our taxonomic decisions, is a hypothesis based on the preponderance of the available evidence, which we prefer to taxonomic decisions

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based on similarity groupings. As this entire section of former *Rana* seems to have avoided detailed study, we suggest that a concerted effort to amass the necessary comparative morphological and molecular data is needed, and we interpret our results as identifying key areas for further study and not as a decisive resolution of these problems.

[296] *Rana* Linnaeus, 1758 (including *Aurorana* Dubois, 1992, *Amerana* Dubois, 1992, *Pseudoamolops* Jiang, Fei, Ye, Zeng, Zhen, Xie, and Chen, 1997, and *Pseudorana* Fei, Ye, and Huang, 1991 ''1990''): To render a monophyletic grouping, we place *Pseudorana* and *Pseudoamolops* as junior synonyms of *Rana*, because they are both embedded within the same clade as *Rana temporaria* (the type species of *Rana*). The abdominal sucker disc of the tadpole of *Pseudoamolops* is not homologous with those of *Amolops*, *Huia*, and *Meristogenys*, all of which are distant from each other in our tree.

Because *Amerana* + *Aurorana* form the sister taxon of our exemplars of a clade with *Rana temporaria*, we also place both of these genera as junior synonyms of *Rana* (sensu stricto) to render a monophyletic group. These frogs are unusual among American ''*Rana*'', but otherwise similar to members of *Rana* (sensu stricto) in retaining an outer metatarsal tubercle.

Dubois (1992) recognized *Pseudorana* as including *Rana sangzhiensis*, *Rana sauteri*, and *R. weiningensis*, characterized as lacking dermal glands in the larvae (likely a synapomorphy at this level of universality) and having a labial keratodont row formula of 4–7/5–8, an abdominal sucker in the larvae (although not as well-developed as in *Amolops*), digit I longer than digit II (likely plesiomorphy), toe pads present on digit I and toe IV; metatarsal tubercle present (plesiomorphy), dorsolateral folds present; no gular pouches in males; and a chevron-shaped mark on the anterior dorsum. Subsequently, Jiang et al. (1997) partitioned *Pseudorana*, with *P. weiningensis* staying in *Pseudorana* along with *johnsi* and *sangzhiensis*, but *sauteri* being transferred to *Pseudoamolops* on the basis of several features. The most distinctive feature is that *Pseudorana* (contra the diagnosis of Dubois, 1992) actually lacks the abdominal suction cup on the larvae. This structure is found in *sauteri* alone, although in a less-developed form than in *Amolops*, *Meristogenys*, and *Huia* (sensu stricto; Jiang et al., 1997). Tanaka-Ueno et al. (1998a) suggested on the basis of 587 bp of mtDNA that *sauteri* is imbedded within the brown frog clade (Dubois' subgenus *Rana*). Our results corroborate this. Unlike *Amolops*, *Meristogenys*, and *Huia*, both *Pseudorana* and *Pseudoamolops* lack dermal glands on the larvae, which might be a synapomorphy, although we do not know the condition of this feature in the *Rana temporaria* group. For our taxonomy, we relegate *Pseudoamolops* and *Pseudorana* to the synonymy of *Rana*, which is decisively diagnosable on the basis of molecular data (appendix 5, branch 296).

[301] *Lithobates* Fitzinger, 1843 (including *Aquarana* Dubois, 1992, *Pantherana* Dubois, 1992, *Sierrana* Dubois, 1992, *Trypheropsis* Cope, 1868, and ''*Rana*'' *sylvatica*): Because of the phylogenetic propinquity of *Aquarana* Dubois, 1992, *Lithobates* Fitzinger, 1843, *Pantherana* Dubois, 1992, *Sierrana* Dubois, 1992, *Trypheropsis* Cope, 1868, ''*Rana*'' *sylvatica*, and *Zweifelia* Dubois, 1992 (the latter not studied by us, but placed phylogenetically in this group by Hillis and Wilcox, 2005; fig. 44), we place these taxa into their own genus, for which the oldest available name is *Lithobates* Fitzinger, 1843. Therefore, we consider *Lithobates* to be a genus, within which we place *Aquarana*, *Trypheropsis*, *Sierrana*, *Zweifelia*, and *Pantherana* as junior synonyms. Absence of an outer metatarsal tubercle is a morphological synapomorphy. (For species affected by this nomenclatural change see Frost, 2004, and appendix 7).

We considered recognizing *Aquarana* for the former *R. clamitans/R. catesbeiana* group; *Lithobates* for the former *R. palmipes* group; *Pantherana* for the *R. pipiens* group; and *Zweifelia* for the former *R. pustulosa/R. tarahumarae* group. However, this would have necessitated naming a new monotypic genus for *Rana sylvatica*. Hillis and Wilcox (2005) also suggested, on the basis of a generally more limited study, but much more densely sampled within ''*Rana*'' than ours, that ''*Rana*'' *sylvatica* is the sister taxon of

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Aquarana. We found it to be the sister taxon of the (old) *Pantherana–Sierrana–Lithobates–Typheropsis* clade. However, this result is weakly corroborated (due to the variable placement of ''*R.*'' *sylvatica*; this branch has a Bremer value of 1 and jackknife frequency of 52%), and the results of Hillis and Wilcox (2005) therefore deserve further careful consideration. What does seem to be highly corroborated by both our data and those of Hillis and Wilcox (2005) is that, excluding the species formerly assigned to *Amerana* and *Aurorana*, all North American species currently assigned to *Rana* form a clade. To recognize this and to underscore the fact that the species on the West Coast are more closely related to Eurasian species than to other North American species, we recognize the completely American group as *Lithobates*. (See appendix 7 for new combinations and content.) Hillis and Wilcox (2005) provided several new names for various clades within *Lithobates*, but inasmuch as these were not associated with organismal characteristics that purport to delimit them, they are *nomina nuda*.

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REFERENCES

Abel, O. 1919. Die Stämme der Wirbeltiere. Klasse Amphibia. Berlin and Leipzig: Walter de Gruyter.

Abourachid, A., and D.M. Green. 1999. Origins of the frog kick? Alternate-leg swimming in primitive frogs, families Leiopelmatidae and Ascaphidae. Journal of Herpetology 33: 657–663.

Adler, K.A. 1989. Herpetologists of the past. *In* K.A. Adler (editor), Contributions to the history of herpetology. Contributions to Herpetology, no. 5. Ithaca, NY: Society for the Study of Amphibians and Reptiles: 5–143.

Ahl, E. 1930. Neuere Erkenntnisse über die systematische Einteilung der Amphibian. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1930: 78–85.

Alcala, A.C., and W.C. Brown. 1982. Reproductive biology of some species of *Philautus* (Rhacophoridae) and other Philippine anurans. Philippine Journal of Biology 11: 203–226.

Alford, R.A., and S.J. Richards. 1999. Global amphibian declines: a problem in applied ecology. Annual Review of Ecology and Systematics 30: 133–165.

Allard, M.W., M.M. Miyamoto, L. Jarecki, F. Kraus, and M.R. Tennant. 1992. DNA systematics and evolution of the artiodactyl family Bovidae. Proceedings of the National Academy of Sciences of the United States of America 89: 3972–3976.

Altig, R.I., and G.F. Johnston. 1989. Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. Herpetological Monographs 3: 81–109.

Altig, R.I., and R.W. McDiarmid. 1999. Diversity: familial and generic characterizations. *In* R.W. McDiarmid and R. Altig (editors), Tadpoles: the biology of anuran larvae: 295–337. Chicago: University of Chicago Press.

Amiet, J.-L. 1970. Morphologie et développement de la larve de *Leptodactylodon ventrimarmor-*

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atus (Boulenger) (amphibien, anoure). Annales de la Faculte des Sciences du Cameroun. Yaoundé 4: 53–71.

Amiet, J.-L. 1971 ''1970''. Les batraciens orophiles du Cameroun. Annales de la Faculte des Sciences du Cameroun. Yaoundé 5: 83–102.

Amiet, J.-L. 1973 ''1972''. Compte rendu d'une mission batachologique dans le Nord-Cameroun. Annales de la Faculte des Sciences du Cameroun. Yaoundé 12: 63–78.

Amiet, J.-L. 1973. Caracteres diagnostiques de *Petropedetes perreti*, nov. sp. et notes sur les autres espèces camerounaises du genre (amphibiens anoures). Bulletin de l'Institut Fondamental d'Afrique Noire, Série A, Sciences Naturelles 35: 462–474.

Amiet, J.-L. 1981. Ecologie, ethologie et developpement de *Phrynodon sandersoni* Parker, 1939 (Amphibia, Anura, Ranidae). Amphibia-Reptilia 2: 1–13.

Amiet, J.-L. 1983. Une espèce meconnue de *Petropedetes* du Cameroun: *Petropedetes parkeri* n. sp. (Amphibia, Anura, Ranidae, Phrynobatrachinae). Revue Suisse de Zoologie 90: 457–468.

Amiet, J.-L. 1989. Quelques aspects de la biologie des amphibiens anoures du Cameroun. Année Biologique. Paris 28: 73–116.

Amiet, J.-L., and J.-L. Perret. 1969. Contributions à la faune de la région de Yaoundé (Cameroun II. Amphibiens anoures. Annales de la Faculte des Sciences du Cameroun. Yaoundé 1969: 117–137.

Anders, C.C. 2002. Class Amphibia (amphibians). *In* H.H. Schleich and W. Kästle (editors), Amphibians and reptiles of Nepal: biology, systematics, field guide: 133–340. Ruggell: A.R.G. Gantner.

Anderson, J. 1871. A list of the reptilian accession to the Indian Museum, Calcutta from 1865 to 1870, with a description of some new species. Journal of the Asiatic Society of Bengal 40: 12–39.

Anderson, J.S. 2001. The phylogenetic trunk: maximal inclusion of taxa with missing data in an analysis of the Lepospondyli (Vertebrata, Tetrapoda). Systematic Biology 50: 170–193.

Andreone, F., M. Vences, D.R. Vieites, F. Glaw, and A. Meyer. 2004 ''2005''. Recurrent ecological adaptations revealed through a molecular analysis of the secretive cophyline frogs of Madagascar. Molecular Phylogenetics and Evolution 34: 315–322.

Annandale, N. 1918. Some undescribed tadpoles from the hills of southern India. Records of the Indian Museum 15: 17–23.

Annandale, N., and C.R.N. Rao. 1918. The tadpoles of the families Ranidae and Bufonidae found in the plains of India. Records of the Indian Museum 15: 24–40.

Anonymous. 1956. Opinion 417. Rejection for nomenclatorial purposes of volume 3 (Zoologie) of the work by Lorenz Oken entitled ''Okens Lehrbuch der Naturgeschichte'' published in 1815–1816. Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature 14: 1–42.

Anonymous. 1977. Opinion 1071. Emendation under the plenary powers of Liopelmatina to Leiopelmatidae (Amphibia, Salientia). Bulletin of Zoological Nomenclature 33: 167–169.

Anonymous. 1990. Opinion 1604. Ichthyophiidae Taylor, 1968 (Amphibia, Gymnophiona): conserved. Bulletin of Zoological Nomenclature 47: 166–167.

Anonymous. 1996. Opinion 1830. Caeciliidae Kolbe, 1880 (Insecta, Psocoptera): spelling emended to Caeciliusidae, so removing the homonymy with Caeciliidae Rafinesque, 1814 (Amphibia, Gymnophiona). Bulletin of Zoological Nomenclature 53: 68–69.

Aplin, K.P., and M. Archer. 1987. Recent advances in marsupial systematics with a new syncretic classification. *In* M. Archer (editor), vol. 1. Possums and opossums: studies in evolution: xv–lxxii. Chipping Norton, Australia: Surrey Beatty.

Archey, G. 1922. The habitat and life history of *Liopelma hochstetteri*. Records of the Canterbury Museum 2: 59–71.

Archibald, J.D. 1994. Metataxon concepts and assessing possible ancestry using phylogenetic systematics. Systematic Biology 43: 27–40.

Ardila-Robayo, M.C. 1979. Status sistematico del genero *Geobatrachus* Ruthven, 1915 (Amphibia: Anura). Caldasia 12: 383–495.

Austin, J.D., S.C. Lougheed, K. Tanner, A.A. Chek, J.P. Bogart, and P.T. Boag. 2002. A molecular perspective on the evolutionary affinities of an enigmatic Neotropical frog, *Allophryne ruthveni*. Zoological Journal of the Linnean Society. London 134: 335–346.

Báez, A.M., and N.G. Basso. 1996. The earliest known frogs of the Jurassic of South America: review and cladistic appraisal of their relationships. Münchner Geowissenschaftliche Abhandlungen. Reihe A. Geologie und Paläontologie 30: 131–158.

Báez, A.M., and L.A. Pugener. 2003. Ontogeny of a new Paleogene pipid frog from southern South America and xenopodinomorph evolution. Zoological Journal of the Linnean Society. London 139: 439–476.

Báez, A.M., and L. Trueb. 1997. Redescription of the Paleogene *Shelania pascuali* from Patagonia and its bearing on the relationships of fossil

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and Recent pipoid frogs. Scientific Papers. Natural History Museum, University of Kansas 4: 1–41.

Bain, R.H., A. Lathrop, R.W. Murphy, N.L. Orlov, and T.C. Ho. 2003. Cryptic species of a cascade frog from Southeast Asia: taxonomic revisions and descriptions of six new species. American Museum Novitates 3417: 1–60.

Bain, R.H., and Q.T. Nguyen. 2004. Herpetofauna diversity of Ha Giang Province in northeastern Vietnam, with descriptions of two new species. American Museum Novitates 3453: 1–42.

Baldauf, R.J. 1959. Morphological criteria and their use in showing bufonid phylogeny. Journal of Morphology 104: 527–560.

Baldissera, F.A., Jr., R.F. Batistic, and C.F.B. Haddad. 1999. Cytotaxonomic considerations with the description of two new NOR locations for South American toads, genus *Bufo* (Anura: Bufonidae). Amphibia-Reptilia 20: 413–420.

Barbour, T., and A. Loveridge. 1928. A comparative study of the herpetological faunae of the Uluguru and Usambara Mountains, Tanganyika Territory, with descriptions of new species. Memoires of the Museum of Comparative Zoology 50: 85–265.

Barrio, A. 1954. Sistemática, morfología y reproduccion de *Physalaemus henselii* (Peters) y *Pseudopaludicola falcipes* (Hensel). Physis. Buenos Aires 20: 379–389.

Barrio, A. 1963. Consideraciones sobre comportamiento y ''grito agresivo'' propio de algunas especies de Ceratophrynidae (Anura). Physis. Buenos Aires 24: 143–148.

Barrio, A. 1968. Revision del genero *Lepidobatrachus* Budgett (Anura, Ceratophrynidae). Physis. Buenos Aires 27: 445–454.

Barrio, A. 1977. Aportes para la elucidacion del ''status'' taxonomico de *Pleurodema bibroni* Tschudi y *Pleurodema kriegi* (Muller) (Amphibia, Anura, Leptodactylidae). Physis. Buenos Aires 37: 311–331.

Barrio, A., and P. Rinaldi de Chieri. 1971. Contribución al esclarecimiento de la posición taxofilética de algunos batracios argentinos mediante el análisis cariotípico. Physis. Buenos Aires 30: 673–685.

Barrio-Amorós, C.L. 2004. Amphibians of Venezuela. Systematic list, distribution and references. Revista de Ecología Latino-Americana 9: 1–48.

Bauer, L. 1986. A new genus and a new specific name in the dart poison frog family (Dendrobatidae, Anura, Amphibia). Ripa. Netherlands 1986(November): 1–12.

Beddard, F.E. 1908 ''1907''. Contributions to the knowledge of the anatomy of the batrachian family Pelobatidae. Proceedings of the Zoological Society of London 1907: 871–911.

Beddard, F.E. 1911. Contributions to the anatomy of the Anura. Proceedings of the Zoological Society of London 1911: 393–412.

Bell, B.D., and R.J. Wassersug. 2003. Anatomical features of *Leiopelma* embryos and larvae: implication for anuran evolution. Journal of Morphology 256: 160–170.

Benton, M.J. 2000. Stems, nodes, crown clades, and rank-free lists: is Linnaeus dead? Biological Reviews of the Cambridge Philosophical Society 75: 633–648.

Berthold, A.A. 1827. Latreille's natürliche Familien der Thierreichs aus dem Französischen mit Anmerkungen und Zusätzen von Dr. Arnold Adoph Berthold. Weimar: Landes-Industrie Comptoir.

Biju, S.D., and F. Bossuyt. 2003. New frog family from India reveals an ancient biogeographical link with the Seychelles. Nature. London 425: 711–714.

Bishop, S.C. 1943. Handbook of salamanders. Ithaca: Comstock Publishing Company.

Blair, W.F. (editor), 1972a. Evolution in the genus *Bufo*. Austin: University of Texas Press.

Blair, W.F. 1972b. *Bufo* of North and Central America. *In* W.F. Blair (editor), Evolution in the genus *Bufo*: 93–101. Austin: University of Texas Press.

Blair, W.F. 1972c. Evidence from hybridization. *In* W.F. Blair (editor), Evolution in the genus *Bufo*: 196–243. Austin: University of Texas Press.

Blair, W.F. 1972d. Characteristics of the testes. *In* W.F. Blair (editor), Evolution in the genus *Bufo*: 324–328. Austin: University of Texas Press.

Blaustein, A.R., and J.M. Kiesecker. 2002. Complexity in conservation: lessons from the global decline of amphibian populatons. Ecology Letters 5: 597–608.

Blommers-Schlösser, R.M.A. 1975. Observations on the larval development of some Malagasy frogs, with notes on their ecology and biology (Anura: Dyscophinae, Scaphiophryninae and Cophylinae). Beaufortia 24: 7–26.

Blommers-Schlösser, R.M.A. 1976. Chromosomal analysis of twelve species of Microhylidae (Anura) from Madagascar. Genetica 46: 199–210.

Blommers-Schlösser, R.M.A. 1993. Systematic relationships of the Mantellinae Laurent 1946 (Anura Ranoidea). Ethology Ecology & Evolution 5: 199–218.

Blommers-Schlösser, R.M.A., and C.P. Blanc. 1991. Amphibiens (premiere partie). Faune de Madagascar 75: 1–379.

Blommers-Schlösser, R.M.A., and C.P. Blanc. 1993. Amphibiens (deuxieme partie). Faune de Madagascar 75: 385–530.

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Bogart, J.P. 1968. Chromosome number difference in the amphibian genus *Bufo*: the *Bufo regularis* group. Evolution 22: 42–45.

Bogart, J.P. 2003. Genetics and systematics of hybrid species. *In* D.M. Sever (editor), Reproductive biology and phylogeny of Urodela (Amphibia): 109–134. Enfield, New Hampshire: Science Publishers, Inc.

Bogart, J.P., and M. Tandy. 1981. Chromosome lineages in African ranoid frogs. Monitore Zoologico Italiano. Nuova Serie, Supplemento 15: 55–91.

Boie, H. 1828. Bemerfungen über die Ubtheilungen im natürlichen Systeme und deren Characteristit. Isis von Oken 21: 351–363.

Bokermann, W.C.A. 1965. Notas sôbre as espécies de *Thoropa* Fitzinger (Amphibia, Leptodactylidae). Anais da Academia Brasileira de Ciências. Rio de Janeiro 37: 525–537.

Bolívar-G., W., T. Grant, and L.A. Osorio. 1999. Combat behavior in *Centrolene buckleyi* and other centrolenid frogs. Alytes 16: 77–83.

Bolkay, S.J. 1919. Osnove uporedne osteologije anurskih batrahija [Elements of the comparative osteology of the tailless batrachians]. Glasnika Zemaljskog Muzeja u Bosni i Hercegovini. Sarejevo 31: 275–357.

Bonacum, J., J. Stark, and E. Bonwich. 2001. PCR methods and approaches. *In* R. DeSalle, G. Giribet, and W.C. Wheeler (editors), Techniques in molecular systematics and evolution: 302–328. Boston: Birkhäuser.

Bonaparte, C.L.J.L. 1839. Iconographia della fauna italica per le quattro classi degli animali vertebrati. Tomo II. Amphibi. Fascicolo 26. Roma: Salviucci.

Bonaparte, C.L.J.L. 1840. Prodromus systematis herpetologiae. Nuovi Annali delle Scienze Naturali. Bologna 4: 90–101.

Bonaparte, C.L.J.L. 1845. Specchio generale dei sistemi erpetologico, anfibiologico ed ittiologico. Milano: Coi Tipi di Luigi di Giacomo Pirola.

Bonaparte, C.L.J.L. 1850. Conspectus systematum. Herpetologiae et amphibiologiae. Editio altera reformata. Leiden: Brill.

Bonett, R.M., and P.T. Chippindale. 2004. Speciation, phylogeography and evolution of life history and morphology in plethodontid salamanders of the *Eurycea multiplicata* complex. Molecular Ecology 13: 1189–1203.

Bossuyt, F., and M.C. Milinkovitch. 2000. Convergent adaptive radiations in Madagascan and Asian ranid frogs reveal covariation between larval and adult traits. Proceedings of the National Academy of Sciences of the United States of America 97: 6585–6590.

Bossuyt, F., and M.C. Milinkovitch. 2001. Amphibians as indicators of early Tertiary ''out-of-India'' dispersal of vertebrates. Science 292: 93–95.

Boulenger, G.A. 1882. Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum, 2nd ed. London: Taylor and Francis.

Boulenger, G.A. 1884. Diagnoses of new reptiles and batrachians from the Solomon Islands, collected and presented to the British Museum by H.B. Guppy, Esq., M.B., H.M.S. ''Lark''. Proceedings of the Zoological Society of London 1884: 210–213.

Boulenger, G.A. 1890. Second report on additions to the batrachian collection in the Natural-History Museum. Proceedings of the Zoological Society of London 1890: 323–328.

Boulenger, G.A. 1892 ''1891''. A synopsis of the tadpoles of the European batrachians. Proceedings of the Zoological Society of London 1891: 593–627.

Boulenger, G.A. 1906 ''1905''. Report on the batrachians collected by the late L. Fea in West Africa. Annali del Museo Civico di Storia Naturale di Genova. Serie 3, 2: 157–172.

Boulenger, G.A. 1918. Remarks on the batrachian genera *Cornufer*, Tschudi, *Platymantis*, Gthr., *Simomantis*, g.n., and *Staurois*, Cope. Annals and Magazine of Natural History, Series 9, 1: 372–375.

Boulenger, G.A. 1920. A monograph of the South Asian, Papuan, Melanesian and Australian frogs of the genus *Rana*. Records of the Indian Museum 20: 1–226.

Boycott, R.C. 1982. On the taxonomic status of *Heleophryne regis* Hewitt, 1909 (Anura: Leptodactylidae). Annals of the Cape Provincial Museums. Natural History 14: 89–108.

Bremer, K. 1994. Branch support and tree stability. Cladistics 10: 295–304.

Brongniart, A.T. 1800a. Essai d'une classification naturelle des reptiles. Iere Partie. Bulletin des Sciences, par La Société Philomathique 2: 81–82.

Brongniart, A.T. 1800b. Essai d'une classification naturelle des reptiles. II Partie. Bulletin des Sciences, par La Société Philomathique 2: 89–91.

Brown, W.C. 1952. The amphibians of the Solomon Islands. Bulletin of the Museum of Comparative Zoology 107: 3–64.

Brummitt, R.K. 2002. How to chop up a tree. Taxon 51: 31–41.

Burton, T.C. 1986. A reassessment of the Papuan subfamily Asterophryninae (Anura: Microhylidae). Records of the South Australian Museum 19: 405–450.

Burton, T.C. 1998a. Pointing the way: the distribution and evolution of some characters of the

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finger muscles of frogs. American Museum Novitates 3229: 1–13.

Burton, T.C. 1998b. Variation in the hand and superficial throat musculature of Neotropical leptodactylid frogs. Herpetologica 54: 53–72.

Burton, T.C. 2004. Muscles and pes of hylid frogs. Journal of Morphology 260: 209–233.

Caccone, A., M.C. Milinkovitch, V. Sbordoni, and J.R. Powell. 1994. Molecular biogeography: using the Corsica-Sardinia microplate disjunction to calibrate mitochondrial rDNA evolutionary rates in mountain newts (*Euproctus*). Journal of Evolutionary Biology 7: 227–245.

Caldwell, J.P., and C.W. Myers. 1990. A new poison frog from Amazonian Brazil, with further revision of the *quinquevittatus* group of *Dendrobates*. American Museum Novitates 2988: 1–21.

Cannatella, D.C. 1985. A phylogeny of primitive frogs (Archeobatrachia). Ph.D. dissertation. Department of Systematics and Ecology, University of Kansas, Lawrence.

Cannatella, D.C. 1989. On the monophyly of discoglossoid frogs. Fortschritte der Zoologie/Progress in Zoology 35: 230–231.

Cannatella, D.C., and D.M. Hillis. 1993. Amphibian relationships: phylogenetic analysis of morphology and molecules. Herpetological Monographs 7: 1–7.

Cannatella, D.C., and D.M. Hillis. 2004. Amphibians: leading a life of slime. *In* J. Cracraft and M.J. Donoghue (editors), Assembling the tree of life: 430–450. Oxford, U.K.: Oxford University Press.

Cannatella, D.C., D.M. Hillis, P.T. Chippindale, L.A. Weigt, A.S. Rand, and M.J. Ryan. 1998. Phylogeny of frogs of the *Physalaemus pustulosus* species group, with an examination of data incongruence. Systematic Biology 47: 311–335.

Cannatella, D.C., and L. Trueb. 1988. Evolution of pipoid frogs: intergeneric relationships of the aquatic frog family Pipidae (Anura). Zoological Journal of the Linnean Society. London 94: 1–38.

Cantino, P.D., H.N. Bryant, K. de Queiroz, M.J. Donoghue, T. Eriksson, D.M. Hillis, and M.S.Y. Lee. 1999. Species names in phylogenetic nomenclature. Systematic Biology 48: 790–807.

Cantino, P.D., R.G. Olmstead, and S.J. Wagstaff. 1997. A comparison of phylogenetic nomenclature with the current system: a botanical case study. Systematic Biology 46: 313–331.

Caramaschi, U., and J.P. Pombal, Jr. 2001. *Barycholos savagei*: a junior synonym of *Paludicola ternetzi*, with notes on development. Journal of Herpetology 35: 357–360.

Carpenter, J.M. 2003. Critique of pure folly. Botanical Review 69: 79–92.

Carroll, R.L. 2000a. The lissamphibian enigma. *In* H. Heatwole and R.L. Carroll (editors), Amphibian biology, vol. 4. Paleontology, the evolutionary history of amphibians: 1270–1273. Chipping Norton, Australia: Surrey Beatty.

Carroll, R.L. 2000b. *Eocaecilia* and the origin of caecilians. *In* H. Heatwole and R.L. Carroll (editors), Amphibian biology, vol. 4. Paleontology, the evolutionary history of amphibians: 1402–1411. Chipping Norton, Australia: Surrey Beatty & Sons.

Carroll, R.L., and P.J. Currie. 1975. Microsaurs as possible apodan ancestors. Zoological Journal of the Linnean Society. London 57: 229–247.

Carroll, R.L., A. Kunst, and K. Albright. 1999. Vertebral development and amphibian evolution. Evolution and Development 1: 36–48.

Case, S.M. 1978. Biochemical systematics of members of the genus *Rana* native to western North America. Systematic Zoology 27: 299–311.

Cei, J.M. 1970. La posición filetica de Telmatobiinae, su discusión reciente y significado critico de algunos imunotests. Acta Zoologica Lilloana 27: 181–192.

Cei, J.M. 1972. *Bufo* of South America. *In* W.F. Blair (editor), Evolution in the genus *Bufo*: 82–92. Austin: University of Texas Press.

Cei, J.M. 1980. Amphibians of Argentina. Monitore Zoologico Italiano. Nuova Serie, Monographia 2: 1–609.

Channing, A. 1989. A re-evaluation of the phylogeny of Old World treefrogs. South African Journal of Zoology 24: 116–131.

Channing, A. 1995. The relationship between *Breviceps* (Anura: Microhylidae) and *Hemisus* (Hemisotidae) remains equivocal. Journal of the Herpetological Association of Africa 44: 55–57.

Channing, A. 2001. Amphibians of central and southern Africa. Ithaca, NY: Cornell University Press.

Channing, A. 2003. Ghost frogs (Heleophrynidae). *In* W.E. Duellman (editor), Grzimek's animal life encyclopedia, 2nd ed. Vol. 6. Amphibians: 131–134. Detroit: Gale Group.

Channing, A., D. Moyer, and M. Burger. 2002. Cryptic species of sharp-nosed reed frogs in the *Hyperolius nasutus* complex: advertisement call differences. African Zoology 36: 91–99.

Channing, A., D.C. Moyer, and K.M. Howell. 2002. Description of a new torrent frog in the genus *Arthroleptides* from Tanzania (Amphibia, Anura, Ranidae). Alytes 20: 13–27.

Chari, V.K. 1962. A description of the hitherto undescribed tadpole of, and some field notes on

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the fungoid frog *Rana malabarica* (Bibr.). Journal of the Bombay Natural History Society 59: 71–76.

Chen, L.Q., R.W. Murphy, A. Lathrop, A. Ngo, N.L. Orlov, T.C. Ho, and I.L.M. Somorjai. 2005. Taxonomic chaos in Asian ranid frogs: an initial phylogenetic resolution. Herpetological Journal 15: 231–243. [Not seen prior to December, 2005.]

Chen, N., J.X. Ma, D.W. Corson, E.S. Hazard, and R.K. Crouch. 1996. Molecular cloning of a rhodopsin gene from salamander rods. Investigations in Ophthalmology and Vision Science 37: 1907–1913.

Chippindale, P.T., R.M. Bonett, A.S. Baldwin, and J.J. Wiens. 2004. Phylogenetic evidence for a major reversal of life-history evolution in plethodontid salamanders. Evolution 58: 2809–2822.

Chou, W.-H. 1999. A new frog of the genus *Rana* (Anura: Ranidae) from China. Herpetologica 55: 389–400.

Clarke, B.T. 1981. Comparative osteology and evolutionary relationships in the African Raninae (Anura: Ranidae). Monitore Zoologico Italiano. Nuova Serie, Supplemento 15: 285–331.

Clough, M.E., and K. Summers. 2000. Phylogenetic systematics and biogeography of the poison frogs: evidence from mitochondrial DNA sequences. Biological Journal of the Linnean Society 70: 515–540.

Cogger, H.G., E.E. Cameron, and H.M. Cogger. 1983. Zoological catalogue of Australia, vol. 1. Amphibia and Reptilia. Canberra: Australian Government Publishing Service.

Colgan, D.J., A. McLauchlan, G.D.F. Wilson, S.P. Livingston, G.D. Edgecombe, J. Macaranas, and G. Cassis. 1999. Histone H3 and U2 snRNA DNA sequences and arthropod molecular evolution. Australian Journal of Zoology 46: 419–437.

Collins, J.P., and A. Storfer. 2003. Global amphibian declines: sorting the hypotheses. Diversity and Distributions 9: 89–98.

Coloma, L.A. 1995. Ecuadorian frogs of the genus *Colostethus* (Anura: Dendrobatidae). University of Kansas Museum of Natural History, Miscellaneous Publications 87: 1–72.

Cope, E.D. 1859. On the primary divisions of the Salamandridae, with descriptions of two new species. Proceedings of the Academy of Natural Sciences of Philadelphia 11: 122–128.

Cope, E.D. 1861 ''1860''. Descriptions of reptiles from tropical America and Asia. Proceedings of the Academy of Natural Sciences of Philadelphia 12: 368–374.

Cope, E.D. 1862. Catalogues of the reptiles obtained during the explorations of the Parana, Paraguay, Vermejo and Uraguay [sic] Rivers, by Capt. Thos. J. Page, U.S.N.; and of those procured by Lieut. N. Michler, U.S. Top. Eng., Commander of the expedition conducting the survey of the Atrato River. Proceedings of the Academy of Natural Sciences of Philadelphia 14: 346–359.

Cope, E.D. 1863. On *Trachycephalus*, *Scaphiopus* and other Batrachia. Proceedings of the Academy of Natural Sciences of Philadelphia 15: 43–54.

Cope, E.D. 1865. Sketch of primary groups of Batrachia s. Salientia. Natural History Review. New Series 5: 97–120.

Cope, E.D. 1866. On the structure and distribution of the genera of the arciferous Anura. Journal of the Academy of Natural Sciences of Philadelphia. Series 2, 6: 67–112.

Cope, E.D. 1867. On the families of the raniform Anura. Journal of the Academy of Natural Sciences of Philadelphia. Series 3, 6: 189–206.

Cope, E.D. 1869. A review of the species of Plethodontidae and Desmognathidae. Proceedings of the Academy of Natural Sciences of Philadelphia 21: 93–118.

Cope, E.D. 1875. Check-list of North American Batrachia and Reptilia; with a systematic list of the higher groups, and an essay on geographical distribution based on specimens contained in the U.S. National Museum. Bulletin of the United States National Museum 1: 1–104.

Cope, E.D. 1880. Geology and paleontology. American Naturalist 14: 609–610.

Cope, E.D. 1887. The hyoid structure in the amblystomid salamanders. American Naturalist 21: 88.

Cope, E.D. 1889. Batrachia of North America. Bulletin of the United States National Museum 34: 5–525.

Couper, P. 1992. Hope for our missing frogs. Wildlife Australia. Brisbane 1992: 10–11.

Crawford, A.J. 2003. Huge populations and old species of Costa Rican and Panamanian dirt frogs inferred from mitochondrial and nuclear gene sequences. Molecular Ecology 12: 2525–2540.

Crawford, A.J., and E.N. Smith. 2005. Cenozoic biogeography and evolution in direct-developing frogs of Central America (Leptodactylidae: *Eleutherodactylus*) as inferred from a phylogenetic analysis of nuclear and mitochondrial genes. Molecular Phylogenetics and Evolution 35: 536–555.

Cunningham, M., and M.I. Cherry. 2000. Mitochondrial DNA divergence in southern African bufonids: are species equivalent entities? African Journal of Herpetology 49: 9–22.

Cunningham, M., and M.I. Cherry. 2004. Molec-

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ular systematics of African 20-chromosome toads (Anura: Bufonidae). Molecular Phylogenetics and Evolution 32: 671–685.

Cuvier, G.L.C.F.D. 1829. Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Nouvelle ed., revue et augmentée par P.A. Latreille, vol. 2. Paris: Deterville.

Daltry, J.C., and G.N. Martin. 1997. Rediscovery of the black narrow mouthed frog, *Melanobatrachus indicus* Beddome, 1878. Hamadryad 22: 57–58.

Darst, C.R., and D.C. Cannatella. 2004. Novel relationships among hyloid frogs inferred from 12S and 16S mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 31: 462–475.

da Silva, H.R. 1998. Phylogenetic relationships of the family Hylidae with emphasis on the relationships within the subfamily Hylinae (Amphibia: Anura). Ph.D. dissertation. Department of Sytematics and Ecology, University of Kansas, Lawrence.

da Silva, H.R., and J.R. Mendelson, III. 1999. A new organ and sternal morphology in toads (Anura: Bufonidae): descriptions, taxonomic distribution, and evolution. Herpetologica 55: 114–126.

Davies, M.M. 2003a. Australian ground frogs (Limnodynastidae). *In* W.E. Duellman (editor), Grzimek's animal life encyclopedia, 2nd ed. Vol. 6. Amphibians: 139–146. Detroit: Gale Group.

Davies, M.M. 2003b. Australian toadlets and water frogs (Myobatrachidae). *In* W.E. Duellman (editor), Grzimek's animal life encyclopedia, 2nd ed. Vol. 6. Amphibians: 147–154. Detroit: Gale Group.

Dawood, A., A. Channing, and J.P. Bogart. 2002. A molecular phylogeny of the frog genus *Tomopterna* in southern Africa: examining species boundaries with mitochondrial 12S rRNA sequence data. Molecular Phylogenetics and Evolution 22: 407–413.

De Bavay, J.M. 1993. The developmental stages of the sphagnum frog, *Kyarranus sphagnicolous* Moore (Anura, Myobatrachidae). Australian Journal of Zoology 41: 151–201.

de Blainville, H.M.D. 1816. Prodrome d'une nouvelle distribution systematique du regne animal. Bulletin de la Société Philomathique de Paris. Series 3, 3: 113–124.

de Blainville, H.M.D. 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'erpétologie et d'amphibiologie. Nouvelles Annales du Muséum d'Histoire Naturelle. Paris 4: 233–296, 4 pl.

de Carvalho, M.R., F.A. Bockman, D.S. Amorim, M. de Vivo, M. de Toledo-Piza, N.A. Menezes, J.L. De Figueiredo, R.M.C. Castro, A.C. Gill, J.D. McEachran, L.J.V. Compagno, R.C. Schelly, R. Britz, J.C. Lundberg, R.P. Vari, and G. Nelson. 2005. Revisiting the taxonomic impediment. Science 307: 353.

De la Riva, I., and J.D. Lynch. 1997. New species of *Eleutherodactylus* from Bolivia (Amphibia: Leptodactylidae). Copeia 1997: 151–157.

Delorme, M., and A. Dubois. 2001. Une nouvelle espèce de *Scutiger* du Bhutan, et quelques remarques sur la classification subgénérique du genre *Scutiger* (Megophryidae, Leptobrachiinae). Alytes 19: 141–153.

Delorme, M., A. Dubois, S. Grosjean, and A. Ohler. 2005. Une nouvelle classification generique et subgenerique de la tribu des Philautini (Amphibia, Anura, Ranidae, Rhacophorinae). Bulletin Mensuel de la Société Linnéenne de Lyon 74: 165–171.

Delorme, M., A. Dubois, J. Kosuch, and M. Vences. 2004. Molecular phylogenetic relationships of *Lankanectes corrugatus* from Sri Lanka: endemism of South Asian frogs and the concept of monophyly in phylogenetic studies. Alytes 22: 53–64.

del Pino, E.M., and B. Escobar. 1981. Embryonic stages of *Gastrotheca riobambae* (Fowler) during maternal incubation and comparison with development with other marsupial frogs. Journal of Morphology 167: 277–295.

de Queiroz, K. 1988. Systematics and the Darwinian Revolution. Philosophy of Science 55: 238–259.

de Queiroz, K., and J.A. Gauthier. 1992. Phylogenetic taxonomy. Annual Review of Ecology and Systematics 23: 449–480.

de Queiroz, K., and J.A. Gauthier. 1994. Toward a phylogenetic system of biological nomenclature. Trends in Ecology and Evolution 9: 27–31.

de Sá, R.O., W.R. Heyer, and A. Camargo. 2005. A phylogenetic analysis of *Vanzolinius* (Amphibia, Anura, Leptodactylidae): taxonomic and life history implications. Arquivos do Museu Nacional do Rio de Janeiro, In press.

de Sá, R.O., and D.M. Hillis. 1990. Phylogenetic relationships of the pipid frogs *Xenopus* and *Silurana*: an integration of ribosomal DNA and morphology. Molecular Biology and Evolution 7: 365–376.

de Sá, R.O., and C.C. Swart. 1999. Development of the suprarostral plate of pipoid frogs. Journal of Morphology 240: 143–153.

De Villiers, C.G.S. 1929. The development of a

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species of *Arthroleptella* from Jonkershoek, Stellenbosch. South African Journal of Science 26: 481–510.

De Villiers, C.G.S. 1931. Über den Schädelbau des *Breviceps fuscus*. Anatomischer Anzeiger 72: 164–178.

D'Haese, C.A. 2003. Morphological appraisal of Collembola phylogeny with special emphasis on Poduromorpha and a test of the aquatic origin hypothesis. Zoologica Scripta 32: 563–586.

Diaz, N.F., J. Valencia, and M. Sallaberry. 1983. Life history and phylogenetic relationships of *Insuetophrynus acarpicus* (Anura: Leptodactylidae). Copeia 1983: 30–37.

Donnelly, M.A., and M.L. Crump. 1998. Potential effects of climate change on two Neotropical amphibian assemblages. Climatic Change 39: 541–561.

Donnelly, M.A., R.O. de Sá, and C. Guyer. 1990. Description of the tadpoles of *Gastrophryne pictiventris* and *Nelsonophryne aterrima* (Anura: Microhylidae), with a review of morphological variation in free-swimming microhylid larvae. American Museum Novitates 2796: 1–19.

Donoghue, M.J. 1985. A critique of the biological species concept and recommendations for a phylogenetic alternative. Bryologist 88: 172–181.

Drewery, G.E., and K.L. Jones. 1976. A new ovoviviparous frog, *Eleutherodactylus jasperi* (Amphibia, Anura, Leptodactylidae) from Puerto Rico. Journal of Herpetology 10: 161–165.

Drewes, R.C. 1984. A phylogenetic analysis of the Hyperoliidae (Anura): treefrogs of Africa, Madagascar, and the Seychelles Islands. Occasional Papers of the California Academy of Sciences 139: 1–70.

Drewes, R.C., R.I. Altig, and K.M. Howell. 1989. Tadpoles of three frog species endemic to the forest of the Eastern Arc Mountains, Tanzania. Amphibia-Reptilia 10: 435–443.

Drewes, R.C., and J.A. Wilkinson. 2004. The California Academy of Sciences Gulf of Guinea Expedition (2001) I. The taxonomic status of the genus *Nesionixalus* Perret, 1976 (Anura: Hyperoliidae), treefrogs of São Tomé and Príncipe, with comments on the genus *Hyperolius*. Proceedings of the California Academy of Sciences 55: 395–407.

Dubois, A. 1980. Notes sur la systematique et la repartition des amphibiens anoures de Chine et des regions avoisinantes IV. Classification generique et subgenerique des Pelobatidae Megophryinae. Bulletin Mensuel de la Société Linnéenne de Lyon 49: 469–482.

Dubois, A. 1981. Liste des genres et sous-genres nominaux de Ranoidea (amphibiens anoures) du monde, avec identification de leurs espèces types; consequences nomenclaturales. Monitore Zoologico Italiano. Nuova Serie, Supplemento 15: 225–284.

Dubois, A. 1982. Les notions de genre, sous-genre et groupe d'espèces en zoologie à la lumière de la systématique évolutive. Monitore Zoologico Italiano. Nuova Serie, Supplemento 16: 9–65.

Dubois, A. 1983. Classification et nomenclature supragenerique des amphibiens anoures. Bulletin Mensuel de la Société Linnéenne de Lyon 52: 270–276.

Dubois, A. 1984a. Miscellanea nomenclatorica batrachologica (V). Alytes 3: 111–116.

Dubois, A. 1984b. La nomenclature supragénérique des amphibiens anoures. Mémoires du Muséum National d'Histoire Naturelle. Paris. Série A, Zoologie 131: 1–64.

Dubois, A. 1985. Miscellanea nomenclatorica batrachologica (VII). Alytes 4: 61–78.

Dubois, A. 1986 ''1985''. Diagnose préliminaire d'un nouveau genre de Ranoidea (amphibiens, anoures) du sud de l'Inde. Alytes 4: 113–118.

Dubois, A. 1987 ''1985''. Miscellanea taxinomica batrachologica (I). Alytes 5: 7–95.

Dubois, A. 1987 ''1986''. Living amphibians of the world: a first step towards a comprehensive checklist. Alytes 5: 99–149.

Dubois, A. 1987. Discoglossidae Günther, 1858 (Amphibia, Anura): proposed conservation. Alytes 6: 56–68.

Dubois, A. 1988a. Miscellanea nomenclatorica batrachologica (XVII). Alytes 7: 1–5.

Dubois, A. 1988b. The genus in zoology: a contribution to the theory of evolutionary systematics. Mémoires du Muséum National d'Histoire Naturelle. Paris. Série A, Zoologie 140: 1–122.

Dubois, A. 1992. Notes sur la classification des Ranidae (amphibiens anoures). Bulletin Mensuel de la Société Linnéenne de Lyon 61: 305–352.

Dubois, A. 1995. Keratodont formulae in anuran tadpoles: proposals for a standardization. Journal of Zoological Systematics and Evolutionary Research 33: 1–15.

Dubois, A. 1999a. Miscellanea nomenclatorica batrachologica. 19. Notes on the nomenclature of Ranidae and related groups. Alytes 17: 81–100.

Dubois, A. 1999b. South Asian Amphibia: a new frontier for taxonomists. Journal of South Asian Natural History 4: 1–11.

Dubois, A. 2000. The influence of man on the distribution of amphibians in the Himalayas of

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Nepal: an example of critical evaluation of biogeographical data. *In* G. Miehe and Y. Zhang (editors), Environmental changes in High Asia. Proceedings of an international symposium at the University of Marburg, Faculty of Geography, 29 May to 1 June 1997, under the auspices of the Unesco. Marburger Geographische Schriften 135: 326–345.

Dubois, A. 2003. True frogs (Ranidae). *In* W.E. Duellman (editor), Grzimek's animal life encyclopedia, 2nd ed. Vol. 6. Amphibians: 245–264. Detroit: Gale Group.

Dubois, A. 2004a. Amphibians of Nepal: a few words of caution. Alytes 21: 174–180.

Dubois, A. 2004b. The higher nomenclature of recent amphibians. Alytes 22: 1–14.

Dubois, A. 2005. Amphibia Mundi. 1.1. An ergotaxonomy of Recent amphibians. Alytes 23: 1–24.

Dubois, A., and R. Günther. 1982. Klepton and synklepton: two new evolutionary systematics categories in zoology. Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie. Jena 109: 290–305.

Dubois, A., and A. Ohler. 1998. A new species of *Leptobrachium* (*Vibrissaphora*) from northern Vietnam, with a review of the taxonomy of the genus *Leptobrachium* (Pelobatidae, Megophyinae). Dumerilia 4: 1–32.

Dubois, A., and A. Ohler. 1999. Asian and Oriental toads of the *Bufo melanostictus*, *Bufo scaber* and *Bufo stejnegeri* groups (Amphibia, Anura): a list of available and valid names and redescription of some name-bearing types. Journal of South Asian Natural History 4: 133–180.

Dubois, A., and A. Ohler. 2000. Systematics of *Fejervarya limnocharis* (Gravenhorst, 1829) (Amphibia, Anura, Ranidae) and related species. 1. Nomenclatural status and type-specimens of the nominal species *Rana limnocharis* Gravenhorst, 1829. Alytes 18: 15–50.

Dubois, A., and A. Ohler. 2001. A new genus for an aquatic ranid (Amphibia, Anura) from Sri Lanka. Alytes 19: 81–106.

Dubois, A., A. Ohler, and S.D. Biju. 2001. A new genus and species of Ranidae (Amphibia, Anura) from south-western India. Alytes 19: 53–79.

Duellman, W.E. 1975. On the classification of frogs. Occasional Papers of the Museum of Natural History, University of Kansas 42: 1–14.

Duellman, W.E. 2001. Hylid frogs of Middle America, 2nd ed. 2 vol. Contributions to Herpetology, no. 18. Ithaca, NY: Society for the Study of Amphibians and Reptiles.

Duellman, W.E. 2003. Leptodactylid frogs (Leptodactylidae). *In* W.E. Duellman (editor), Grzimek's animal life encyclopedia, 2nd ed. Vol. 6. Amphibians: 155–171. Detroit: Gale Group.

Duellman, W.E., and P. Gray. 1983. Developmental biology and systematics of the egg-brooding hylid frogs, genera *Flectonotus* and *Fritziana*. Herpetologica 39: 333–359.

Duellman, W.E., and M.S. Hoogmoed. 1984. The taxonomy and phylogenetic relationships of the hylid frog genus *Stefania*. University of Kansas Museum of Natural History, Miscellaneous Publications 75: 1–39.

Duellman, W.E., and R. Schulte. 1992. Description of a new species of *Bufo* from northern Peru with comments on phenetic groups of South American toads (Anura: Bufonidae). Copeia 1992: 162–172.

Duellman, W.E., and L. Trueb. 1986. Biology of amphibians. New York: McGraw-Hill.

Duellman, W.E., and A. Veloso M. 1977. Phylogeny of *Pleurodema* (Anura: Leptodactylidae): a biogeographic model. Occasional Papers of the Museum of Natural History, University of Kansas 64: 1–46.

Duméril, A.H.A. 1863. Catalogue méthodique de la collection des batraciens du Muséum d'Histoire Naturelle de Paris. Mémoires de la Société Impériale des Sciences Naturelles de Cherbourg 9: 295–321.

Duméril, A.M.C. 1806. Zoologie analytique, ou méthode naturelle de classification des animaux, rendue plus facile à l'dide de tableaux synoptiques. Paris: Allais.

Dunn, E.R. 1920. Notes on two Pacific coast Ambystomidae. Proceedings of the New England Zoological Club 7: 55–59.

Dunn, E.R. 1922. The sound-transmitting apparatus of salamanders and the phylogeny of the Caudata. American Naturalist 56: 418–487.

Dunn, E.R. 1939. *Bathysiredon*, a new genus of salamanders, from Mexico. Notulae Naturae of the Academy of Natural Sciences of Philadelphia 36: 1.

Dutta, S.K., K. Vasudevan, M.S. Chaitra, K. Shanker, and R.-K. Aggarwal. 2004. Jurassic frogs and the evolution of amphibian endemism in the western Ghats. Current Science. Bangalore 86: 211–216.

Echeverria, D.D. 1998. Aspectos de la reproduccion in-vitro del desarrollo larval de *Melanophryniscus stelzneri* (Weyenbergh, 1875) (Anura, Bufonidae), con comentarios acerca del organo de Bidder. Alytes 15: 158–170.

Edwards, J.L. 1976. Spinal nerves and their bearing on salamander phylogeny. Journal of Morphology 148: 305–328.

Elias, P., and D.B. Wake. 1983. *Nyctanolis pernix*, a new genus and species of plethodontid sala-

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mander from northwestern Guatemala and Chiapas, Mexico. *In* A. Rhodin and K. Miyata (editors), Advances in herpetology and evolutionary biology. Essays in honor of Ernest E. Williams: 1–12. Cambridge, MA: Museum of Comparative Zoology, Harvard University.

Emerson, S.B., and D. Berrigan. 1993. Systematics of Southeast Asian ranids: multiple origins of voicelessness in the subgenus *Limnonectes* (Fitzinger). Herpetologica 49: 22–31.

Emerson, S.B., R.F. Inger, and D.T. Iskandar. 2000a. Molecular systematics and biogeography of the fanged frogs of Southeast Asia. Molecular Phylogenetics and Evolution 16: 131–142.

Emerson, S.B., C.M. Richards, R.C. Drewes, and K.M. Kjer. 2000b. On the relationships among ranoid frogs: a review of the evidence. Herpetologica 56: 209–230.

Estes, R. 1965. Fossil salamanders and salamander origins. American Zoologist 5: 319–334.

Estes, R. 1970. New fossil pelobatid frogs and a review of the genus *Eopelobates*. Bulletin of the Museum of Comparative Zoology 139: 239–340.

Estes, R. 1981. Handbuch der Paläoherpetologie/Encyclopedia of paleoherpetology. Part 2. Gymnophiona, Caudata. Stuttgart: Gustav Fischer.

Estes, R., K. de Queiroz, and J.A. Gauthier. 1988. Phylogenetic relationships within Squamata. *In* R. Estes and G.K. Pregill (editors), Phylogenetic relationships of the lizard families, essays commemorating Charles L. Camp: 119–281. Stanford, CA: Stanford University Press.

Estes, R., and O.A. Reig. 1973. The early fossil record of frogs: a review of the evidence. *In* J. Vial (editor), Evolutionary biology of the anurans: contemporary research on major problems: 11–63. Columbia: University of Missouri Press.

Evans, B.J., R.M. Brown, J.A. McGuire, J. Supriatna, N. Andayani, A.C. Diesmos, D.T. Iskandar, D.J. Melnick, and D.C. Cannatella. 2004. Phylogenetics of fanged frogs: testing biogeographical hypotheses at the interface of the Asian and Australian fauna zones. Systematic Biology 52: 794–819.

Evans, B.J., D.J. Melnick, D.C. Cannatella, J. Supriatna, N. Andayani, and M.I. Setiadi. 2003. Monkeys and toads define areas of endemism on Sulawesi. Evolution 57: 1436–1443.

Evans, S.E., and D. Sigogneau-Russell. 2001. A stem-group caecilian (Lissamphibia: Gymnophiona) from the Lower Cretaceous of North Africa. Palaeontology 44: 259–274

Fabrezi, M., and J.A. Langone. 2000. Los caracteres morfológicos del controvertido Neobatrachia arborícola *Allophryne ruthveni* Gaige, 1926. Cuadernos de Herpetología 14: 47–59.

Faivovich, J. 2002. A cladistic analysis of *Scinax* (Anura: Hylidae). Cladistics 18: 367–393.

Faivovich, J., C.F.B. Haddad, P.C.A. Garcia, D.R. Frost, J.A. Campbell, and W.C. Wheeler. 2005. Systematic review of the frog family Hylidae, with special reference to Hylinae: a phylogenetic analysis and taxonomic revision. Bulletin of the American Museum of Natural History 294: 1–240.

Farris, J.S. 1973. On comparing the shapes of taxonomic trees. Systematic Zoology 22: 50–54.

Farris, J.S., A.G. Kluge, and M.F. Mickevich. 1979. Paraphyly of the *Rana boylii* species group. Systematic Zoology 28: 627–634.

Farris, J.S., A.G. Kluge, and M.F. Mickevich. 1982a. Phylogenetic analysis, the monothetic group method, and myobatrachid frogs. Systematic Zoology 31: 317–327.

Farris, J.S., A.G. Kluge, and M.F. Mickevich. 1982b. Immunological distance and the phylogenetic relationships of the *Rana boylii* species group. Systematic Zoology 31: 479–491.

Fatio, V. 1872. Faune des vertébrés de la Suisse, vol. III. Histoire naturelle des reptiles et des batraciens. Paris: J.-P. Bailliere.

Fei, L. 1999. [Atlas of amphibians of China.] Zhengzhou: Henan Press of Science and Technology. [In Chinese.]

Fei, L., and C. Ye. 2000. A new hynobiid subfamily with a new genus and new species of Hynobiidae from West China. Cultum Herpetologica Sinica 8: 64–70. [In Chinese with English abstract.]

Fei, L., and C. Ye. 2001. [The color handbook of the amphibians of Sichuan.] Chengdu, China: Sichuan Forestry Department, Sichuan Association of Wildlife Conservation, and Chengdu Institute of Biology. [In Chinese.]

Fei, L., C. Ye, and Y. Huang. 1991 ''1990''. [Key to Chinese amphibians.] Chongqing, China: Publishing House for Scientific and Technological Literature. [In Chinese.]

Fei, L., C. Ye, and Y. Huang. 1997. Taxonomic studies of the genus *Liurana* of China including descriptions of a new species (Amphibia: Ranidae). Cultum Herpetologica Sinica 6–7: 75–80.

Fei, L., C. Ye, and J. Jiang. 2000. A new genus of the subfamily Amolopinae—*Pseudoamolops*, and its relationship to related genera. Acta Zoologica Sinica 46: 19–26.

Fei, L., C. Ye, J. Jiang, X. Feng, and Y. Huang. 2005. [An illustrated key to Chinese amphibians.] Chongqing: Sichuan Publishing House of Science and Technology. [In Chinese.]

Fei, L., C. Ye, and C. Li. 2001. Descriptions of

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two new species of the genus *Odorrana* in China. Acta Zootaxonomica Sinica 26: 108–114.

Fejérváry, G.J. 1917. Anoures fossiles des couches préglaciares de Püspökfürdö en Hongrie. Földtani Közlöny 47: 141–172.

Fejérváry, G.J. 1920. Remarques sur la position systematique des genres *Bufavus* et *Ranavus*. Annales Historico-Naturales Musei Nationalis Hungarici 18: 28–30.

Fejérváry, G.J. 1921. Kritische Bemerkungen zur Osteologie, Phylogenie und Systematik der Anuren. Archiv für Naturgeschichte. Abteilung A 87: 1–30.

Fejérváry, G.J. 1923. Ascaphidae, a new family of the tailless batrachians. Annales Historico-Naturales Musei Nationalis Hungarici 20: 178–181.

Feller, A.E., and S.B. Hedges. 1998. Molecular evidence for the early history of living amphibians. Molecular Phylogenetics and Evolution 9: 509–516.

Fink, W.L. 1990. Review of: The genus in zoology: a contribution to the theory of evolutionary systematics, by Alain Dubois. Mem. du Museum national d'Histoire Naturelle, Serie A, Zoology, Tome 140. 1988. Quarterly Review of Biology 65: 79–80.

Fischer von Waldheim, G. 1813. Zoognosia tabulis synopticis illustrata, in usum prælectionum Academiæ Imperialis Medico-Chirurgicæ Mosquensis edita. 3rd ed. Vol. 1. Moscow: Nicolai Sergeidis Vsevolozsky.

Fitzinger, L.J.F.J. 1826. Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften nebst einer Verwandtschafts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des k.k. zoologisch Museum's zu Wien. Wien: J.G. Heubner.

Fitzinger, L.J.F.J. 1835. Entwurf einer systematischen Anordnung der Schildkröten nach den Grandsätzen der natürlichen Methode. Annalen des Naturhistorischen Museums in Wien 1: 105–128.

Fitzinger, L.J.F.J. 1843. Systema reptilium. Fasciculus primus. Wien: Braumüller et Seidel.

Ford, L.S. 1990. The phylogenetic position of poison-dart frogs (Dendrobatidae): reassessment of the neobatrachian phylogeny with commentary on complex character systems. Ph.D. dissertation. Department of Systematics and Ecology, University of Kansas, Lawrence.

Ford, L.S. 1993. The phylogenetic position of the dart-poison frogs (Dendrobatidae) among anurans: an examination of the competing hypotheses and their characters. Ethology Ecology & Evolution 5: 219–231.

Ford, L.S., and D.C. Cannatella. 1993. The major clades of frogs. Herpetological Monographs 7: 94–117.

Formas, J.R., and N.D. Espinoza. 1975. Karyological relatonships of frogs of the genus *Telmatobufo* (Anura: Leptodactylidae). Herpetologica 31: 429–432.

Formas, J.R., E. Pugin, and B. Jorquera. 1975. La identidad del batracio chileno *Heminectes rufus* Philippi, 1902. Physis. Buenos Aires 34: 147–157.

Frost, D.R. (editor), 1985. Amphibian species of the world. A taxonomic and geographical reference. Lawrence, KS: Association of Systematics Collections and Allen Press.

Frost, D.R. 2004. Amphibian species of the world: an online reference. Version 3.0. New York: American Museum of Natural History. [Electronic database available at http://research.amnh.org/herpetology/amphibia/index.html.]

Frost, D.R., and A.G. Kluge. 1994. A consideration of epistemology in systematic biology, with special reference to species. Cladistics 10: 259–294.

Frost, D.R., M.T. Rodrigues, T. Grant, and T.A. Titus. 2001. Phylogenetics of the lizard genus *Tropidurus* (Squamata: Tropiduridae: Tropidurinae): direct optimization, descriptive efficiency, and sensitivity analysis of congruence between molecular data and morphology. Molecular Phylogenetics and Evolution 21: 352–371.

Gadow, H. 1901. The Cambridge natural history, vol. 8. Amphibia and reptiles. London: Macmillan and Co.

Gallardo, J.M. 1965. A proposito de los Leptodactylidae (Amphibia, Anura). Papéis Avulsos de Zoologia. São Paulo 17: 77–87.

Gao, K., and N.H. Shubin. 2001. Late Jurassic salamanders from northern China. Nature. London 410: 574–577.

Gao, K., and N.H. Shubin. 2003. Earliest known crown group salamanders. Nature. London 422: 424–429.

Gao, K., and Y. Wang. 2001. Mesozoic anurans from Liaoning Province, China, and phylogenetic relationships of archaeobatrachian anuran clades. Journal of Vertebrate Paleontology 21: 460–476.

García-París, M., D.R. Buchholz, and G. Parra-Olea. 2003. Phylogenetic relationships of Pelobatoidea re-examined using mtDNA. Molecular Phylogenetics and Evolution 28: 12–23.

García-París, M., A. Monton, and M.A. Alonso-Zarazaga. 2004a. Apéndice 1. Nomenclatura: lista de sinónimos y combinaciones. *In* M. García-París, A. Montori, and P. Herrero (editors), Fauna Iberica, vol. 24. Amphibia. Lissamphibia: 589–602. Madrid: Museo Nacional

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de Ciencias Naturales and Consejo Superior de Investigaciones Científica.

García-París, M., A. Montori, and P. Herrero. 2004b. Fauna Iberica, vol. 24. Amphibia. Lissamphibia. Madrid: Museo Nacional de Ciencias Naturales and Consejo Superior de Investigaciones Científica.

García-París, M., and D.B. Wake. 2000. Molecular phylogenetic analysis of relationships of the tropical salamander genera *Oedipina* and *Nototriton*, with descriptions of a new genus and three new species. Copeia 2000: 42–70.

Gardiner, B.G. 1982. Tetrapod classification. Zoological Journal of the Linnean Society. London 74: 207–232.

Gardner, J.D. 2001. Monophyly and affinities of albanerpetontid amphibians (Temnospondyli; Lissamphibia). Zoological Journal of the Linnean Society. London 131: 309–352.

Gardner, J.D. 2002. Monophyly and intra-generic relationships of *Albanerpeton* (Lissamphibia; Albanerpetontidae). Journal of Vertebrate Paleontology 22: 12–22.

Gauthier, J.A., D.C. Cannatella, K. de Queiroz, A.G. Kluge, and T. Rowe. 1989. Tetrapod phylogeny. *In* B. Fernholm, K. Bremer, and H. Jornvall (editors), The hierarchy of life: 337–353. New York: Elsevier.

Gauthier, J.A., A.G. Kluge, and T. Rowe. 1988a. Amniote phylogeny and the importance of fossils. Cladistics 4: 105–209.

Gauthier, J.A., A.G. Kluge, and T. Rowe. 1988b. The early evolution of the Amniota. *In* M.J. Benton (editor), The phylogeny and classification of the tetrapods, vol. 1. Amphibians, reptiles, birds: 103–155. Systematics Association Special vol. 23. New York: Academic Press.

Ghiselin, M.T. 1966. On psychologism in the logic of taxonomic controversies. Systematic Zoology 15: 207–215.

Giaretta, A.A., and R.J. Sawaya. 1998. Second species of *Psyllophryne* (Anura: Brachycephalidae). Copeia 1998: 985–987.

Glaw, F., and M. Vences. 1994. A fieldguide to the amphibians and reptiles of Madagascar, 2nd ed., including mammals and freshwater fish. Köln: Moos Druck.

Glaw, F., and M. Vences. 2002. A new sibling species of the anuran subgenus *Blommersia* from Madagascar (Amphibia: Mantellidae: *Mantidactylus*) and its molecular phylogenetic relationships. Herpetological Journal. London 12: 11–20.

Goebel, A.M., J.M. Donnelly, and M.E. Atz. 1999. PCR primers and amplification methods for 12S ribosomal DNA, the control region, cytochrome oxidase I, and cytochrome *b* in bufonids and other frogs, and an overview of PCR primers which have amplified DNA in amphibians successfully. Molecular Phylogenetics and Evolution 11: 163–199.

Goin, C.J., O.B. Goin, and G.R. Zug. 1978. Introduction to herpetology, 3rd ed. San Francisco: W.H. Freeman and Co.

Goldfuss, G.A. 1820. Handbuch der Zoologie. Zweite Abtheilung. Nürnburg: Johann Leonhard Schrag.

Goloboff, P.A. 1993–1999. NONA. Version 2.9. Tucumán, Argentina: Computer software distributed by the author.

Goloboff, P.A. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. Cladistics 15: 415–428.

Goloboff, P.A., and J.S. Farris. 2001. Methods of quick consensus estimation. Cladistics 17: S26–S34.

Goloboff, P.A., J.S. Farris, and K.C. Nixon. 2003. T.N.T.: Tree analysis using new technology, version 1.0. Program and documentation available from the authors and at www.zmuc.dk/public/phylogeny.

Good, D.A., and D.B. Wake. 1992. Geographic variation and speciation in the torrent salamanders of the genus *Rhyacotriton* (Caudata: Rhyacotritonidae). University of California Publications in Zoology 126: 1–91.

Gower, D.J., A. Kupfer, O.V. Oommen, W. Himstedt, R.A. Nussbaum, S.P. Loader, B. Presswell, H. Müller, S.B. Krishna, R. Boistel, and M. Wilkinson. 2002. A molecular phylogeny of ichthyophiid caecilians (Amphibia: Gymnophiona: Ichthyophiidae): out of India or out of South East Asia? Proceedings of the Royal Society of London. Series B, Biological Sciences 269: 1563–1569.

Gower, D.J., and M. Wilkinson. 2002. Phallus morphology in caecilians (Amphibia, Gymnophiona) and its systematic utility. Bulletin of the Natural History Museum. London. Zoology Series 68: 143–154.

Grandison, A.G.C. 1981. Morphology and phylogenetic position of the West African *Didynamipus sjoestedti* Andersson, 1903 (Anura, Bufonidae). Monitore Zoologico Italiano. Nuova Serie, Supplemento 15: 187–215.

Grant, T. 1998. Una nueva especie de *Colostethus* del grupo *edwardsi* de Colombia. Revista de la Academia Colombiana de Ciencias Exactas, Fisicas y Naturales 22: 423–428.

Grant, T. 2002. Testing methods: the evaluation of discovery operations in evolutionary biology. Cladistics 18: 94–111.

Grant, T. 2004. On the identities of *Colostethus inguinalis* (Cope, 1868) and *C. panamensis* (Dunn, 1933), with comments on *C. latinasus*

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(Cope, 1863) (Anura: Dendrobatidae). American Museum Novitates 3444: 1–24.

Grant, T., and F. Castro-Herrera. 1998. The cloud forest *Colostethus* (Anura, Dendrobatidae) of a region of the Cordillera Occidental of Colombia. Journal of Herpetology 32: 378–392.

Grant, T., E.C. Humphrey, and C.W. Myers. 1997. The median lingual process of frogs: a bizarre character of Old World ranoids discovered in South American dendrobatids. American Museum Novitates 3212: 1–40.

Grant, T., and A.G. Kluge. 2004. Transformation series as an ideographic character concept. Cladistics 20: 23–31.

Grant, T., and L.O. Rodriguez. 2001. Two new species of frogs of the genus *Colostethus* (Dendrobatidae) from Peru and a redescription of *C. trilineatus* (Boulenger, 1883). American Museum Novitates 3355: 1–24.

Gray, J.E. 1825. A synopsis of the genera of reptiles and Amphibia, with a description of some new species. Annals of Philosophy. Series 2, 10 193–217.

Gray, J.E. 1850a. Catalogue of the specimens of Amphibia in the collection of the British Museum. Part. II. Batrachia Gradientia, etc. London: Spottiswoodes and Shaw.

Gray, J.E. 1850b. Description of a new genus of batrachians from Swan River. By Dr. H. Schlegel, Curator of the Royal Zoological Museum, Leyden. (Extracted from a letter to J.E. Gray, Esq.). Proceedings of the Zoological Society of London 1850: 9–10.

Graybeal, A. 1995. Phylogenetic relationships and evolution of bufonid frogs based on molecular and morphological characters. Ph.D. dissertation. Department of Integrative Biology, University of California, Berkeley.

Graybeal, A. 1997. Phylogenetic relationships of bufonid frogs and tests of alternate macroevolutionary hypotheses characterizing their radiation. Zoological Journal of the Linnean Society. London 119: 297–338.

Graybeal, A., and D.C. Cannatella. 1995. A new taxon of Bufonidae from Peru, with descriptions of two new species and a review of the phylogenetic status of supraspecific bufonid taxa. Herpetologica 51: 105–131.

Green, D.M. 2005. The ecology of extinction: population fluctuation and decline in amphibians. Biological Conservation 111: 331–343.

Green, D.M., and D.C. Cannatella. 1993. Phylogenetic significance of the amphicoelous frogs, Ascaphidae and Leiopelmatidae. Ethology Ecology & Evolution 5: 233–245.

Green, D.M., R.A. Nussbaum, and D. Yang. 1988. Genetic divergence and heterozygosity among frogs of the family Sooglossidae. Herpetologica 44: 113–119.

Green, D.M., T.F. Sharbel, R.A. Hitchmough, and C.H. Daugherty. 1989. Genetic variation in the genus *Leiopelma* and relationships to other primitive frogs. Zeitschrift für Zoologische Systematik und Evolutionsforschung 27: 65–79.

Griffiths, I. 1954. On the ''otic element'' in Amphibia Salientia. Proceedings of the Zoological Society of London 124: 3–50.

Griffiths, I. 1959a. The phylogenetic status of the Sooglossinae. Annals and Magazine of Natural History, Series 13, 2: 626–640.

Griffiths, I. 1959b. The phylogeny of *Sminthillus limbatus* and the status of the Brachycephalidae (Amphibia Salientia). Proceedings of the Zoological Society of London 132: 457–487.

Griffiths, I. 1963. The phylogeny of the Salientia. Biological Reviews of the Cambridge Philosophical Society 38: 241–292.

Grosjean, S., M. Perez, and A. Ohler. 2003. Morphology and buccopharyngeal anatomy of the tadpole of *Rana* (*Nasirana*) *alticola* (Anura: Ranidae). Raffles Bulletin of Zoology 51: 101–107.

Grosjean, S., M. Vences, and A. Dubois. 2004. Evolutionary significance of oral morphology in the carnivorous tadpoles of tiger frogs, genus *Hoplobatrachus* (Ranidae). Biological Journal of the Linnean Society 81: 171–181.

Günther, A. 1858a. Neue Batrachier in der Sammlung des britischen Museums. Archiv für Naturgeschichte 24: 319–328.

Günther, A. 1858b. On the systematic arrangement of the tailless batrachians and the structure of *Rhinophrynus dorsalis*. Proceedings of the Zoological Society of London 1858: 339–352.

Günther, A. 1859 ''1858''. Catalogue of the Batrachia Salientia in the collection of the British Museum. London: Taylor and Francis.

Günther, A. 1870. Reptilia (1869). Zoological Record 6: 105–122.

Haas, A. 1995. Cranial features of dendrobatid larvae (Amphibia: Anura: Dendrobatidae). Journal of Morphology 224: 241–264.

Haas, A. 2003. Phylogeny of frogs as inferred from primarily larval characters (Amphibia: Anura). Cladistics 19: 23–90.

Haas, A., and S.J. Richards. 1998. Correlations of cranial morphology, ecology, and evolution in Australian suctorial tadpoles of the genera *Litoria* and *Nyctimystes* (Amphibia: Anura: Hylidae: Pelodryadinae. Journal of Morphology 238: 109–141.

Haddad, C.F.B., and C.P.A. Prado. 2005. Reproductive modes in frogs and their unexpected di-

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versity in the Atlantic Forest of Brazil. BioScience 55: 207–217.

Haeckel, E.H.P.A. 1866. Generelle Morphologie der Organismen, vol. 2. Berlin: Georg Reimer.

Hall, J.A., and J.H. Larsen, Jr. 1998. Postembryonic ontogeny of the spadefoot toad, *Scaphiopus intermontanus* (Anura: Pelobatidae): skeletal morphology. Journal of Morphology 238: 179–244.

Halliday, T. 2005. Diverse factors influencing amphibian population declines. *In* M.J. Lannoo (editor), Amphibian declines: the conservation status of United States species: 3–9. Berkeley: University of California Press.

Hallowell, E. 1856. Description of several species of Urodela, with remarks on the geographical distribution of the Caducibranchiata division of these animals and their classification. Proceedings of the Academy of Natural Sciences of Philadelphia 8: 6–11.

Hanken, J., and D.B. Wake. 1982. Genetic differentiation among plethodontid salamanders (genus *Bolitoglossa*) in Central and South America: implications for the South American invasion. Herpetologica 38: 272–287.

Harris, D.J. 2001. Reevaluation of 16S ribosomal RNA variation in *Bufo* (Anura: Amphibia). Molecular Phylogenetics and Evolution 19: 326–329.

Hass, C.A., J.F. Dunski, L.R. Maxson, and M.S. Hoogmoed. 1995. Divergent lineages within the *Bufo margaritifera* complex (Amphibia: Anura; Bufonidae) revealed by albumin immunology. Biotropica 27: 238–249.

Hay, J.M., I. Ruvinsky, S.B. Hedges, and L.R. Maxson. 1995. Phylogenetic relationships of amphibian families inferred from DNA sequences of mitochondrial 12S and 16S ribosomal RNA genes. Molecular Biology and Evolution 12: 928–937.

Hayes, M.P., and P.H. Starrett. 1981 ''1980''. Notes on a collection of centrolenid frogs from the Colombia Choco. Bulletin of the Southern California Academy of Science 79: 89–96.

Hedges, S.B. 1989. Evolution and biogeography of West Indian frogs of the genus *Eleutherodactylus*: slow-evolving loci and the major groups. *In* C.A. Woods (editor), Biogeography of the West Indies: past, present, and future: 305–370. Gainesville, FL: Sandhill Crane Press.

Hedges, S.B. 1994. Molecular evidence for the origin of birds. Proceedings of the National Academy of Science of the United States of America 91: 2621–2624.

Hedges, S.B., and L.R. Maxson. 1993. A molecular perspective on lissamphibian phylogeny. Herpetological Monographs 7: 27–42.

Hedges, S.B., R.A. Nussbaum, and L.R. Maxson. 1993. Caecilian phylogeny and biogeography inferred from mitochondrial DNA sequences of the 12S rRNA and 16S rRNA genes (Amphibia: Gymnophiona). Herpetological Monographs 7: 64–76.

Hedges, S.B., and L.L. Poling. 1999. A molecular phylogeny of reptiles. Science 283: 998–1001.

Hennig, W. 1966. Phylogenetic systematics. Chicago: University of Illinois Press.

Henrici, A.C. 1991. *Chelomophrynus bayi* (Amphibia, Anura, Rhinophrynidae), a new genus and species from the Middle Eocene of Wyoming: ontogeny and relationships. Annals of the Carnegie Museum 60: 97–144.

Hertwig, S., R.O. de Sá, and A. Haas. 2004. Phylogenetic signal and the utility of 12S and 16S mtDNA in frog phylogeny. Journal of Zoological Systematics and Evolutionary Research 42: 2–18.

Hewitt, J. 1919. *Anhydrophryne rattrayi*, a remarkable new frog from Cape Colony. Record of the Albany Museum. Grahamstown 3: 182–189.

Heyer, W.R. 1970. Studies on the frogs of the genus *Leptodactylus* (Amphibia: Leptodactylidae). VI. Biosystematics of the *melanonotus* group. Natural History Museum of Los Angeles County Contributions in Science 191: 1–48.

Heyer, W.R. 1975. A preliminary analysis of the intergeneric relationships of the frog family Leptodactylidae. Smithsonian Contributions in Zoology 199: 1–55.

Heyer, W.R. 1998. The relationships of *Leptodactylus diedrus* (Anura, Leptodactylidae). Alytes 16: 1–24.

Heyer, W.R. 1999. A new genus and species of frog from Bahia, Brazil (Amphibia: Anura: Leptodactylidae) with comments on the zoogeography of the Brazilian campos rupestres. Proceedings of the Biological Society of Washington 112: 19–30.

Heyer, W.R. 2003. Viewpoint: ultraviolet-B and Amphibia. BioScience 53: 540–541.

Heyer, W.R., and R.I. Crombie. 1979. Natural history notes on *Craspedoglossa stejnegeri* and *Thoropa petropolitana* (Amphibia: Salientia, Leptdactylidae). Journal of the Washington Academy of Sciences 69: 17–20.

Heyer, W.R., and D.S.S. Liem. 1976. Analysis of the intergeneric relationships of the Australian frog family Myobatrachidae. Smithsonian Contributions in Zoology 233: 1–29.

Highton, R. 1997. Geographic protein variation and speciation in the *Plethodon dorsalis* complex. Herpetologica 53: 345–356.

Highton, R. 1998. Is *Ensatina eschscholtzii* a ring species? Herpetologica 54: 254–278.

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Highton, R. 1999. Geographic protein variation and speciation in the salamanders of the *Plethodon cinereus* group with the description of two new species. Herpetologica 55: 43–90.

Highton, R., and R.B. Peabody. 2000. Geographic protein variation and speciation in salamanders of the *Plethodon jordani* and *Plethodon glutinosus* complexes in the southern Appalachian Mountains with the description of four new species. *In* R.C. Bruce, R.G. Jaeger, and L.D. Houck (editors), The biology of plethodontid salamanders: 31–93. New York: Kluwer Academic/Plenum Publishers.

Hillis, D.M., and S.K. Davis. 1986. Evolution of ribosomal DNA: fifty million years of recorded history in the frog genus *Rana*. Evolution 40: 1275–1288.

Hillis, D.M., and M.T. Dixon. 1991. Ribosomal DNA: molecular evolution and phylogenetic inference. Quarterly Review of Biology 66: 411–453.

Hillis, D.M., and T.P. Wilcox. 2005. Phylogeny of the New World true frogs (*Rana*). Molecular Phylogenetics and Evolution 34: 299–314.

Hiragond, N.C., B.A. Shanbhag, and S.K. Saidapur. 2001. Description of the tadpole of a stream breeding frog, *Rana curtipes*. Journal of Herpetology 35 166–168.

Hoffman, A.C. 1932. Researches relating to the validity of the South African Polypedatidae (Rhacophoridae) as an autonomous family of the Anura. South African Journal of Science 29: 562–583.

Hoffman, A.C. 1935. Die sistematiese posiesie van *Heleophryne*. Soölogiese Navorsing van die Nasionale Museum. Bloemfontein 1: 1–2.

Hoffmann, C.K. 1878. Die Klassen und Ordnungen des Thier-Reichs wissenschaftlich dargestelldt in Wort und Bild, vol. 6 (part 2). Klassen und Ordnungen der Amphibien wissenschaftlich dargestelldt in Wort un Bild. Leipzig and Heidelberg: C.F. Winter.

Hogg, J. 1838. On the classification of the Amphibia. Annals of Natural History 1: 152.

Hogg, J. 1839a. On the classification of the Amphibia. Magazine of Natural History, New Series 3: 265–274.

Hogg, J. 1839b. On the classification of the Amphibia (continued from page 274). Magazine of Natural History, New Series 3: 367–378.

Hoogmoed, M.S. 1989a. South American bufonids (Amphibia: Anura: Bufonidae), an enigma for taxonomists. Treballs d'Ictiologia i Herpetologia 2: 167–180.

Hoogmoed, M.S. 1989b. On the identity of some toads of the genus *Bufo* from Ecuador, with additional remarks on *Andinophryne colomai* Hoogmoed, 1985 (Amphibia: Anura: Bufonidae). Zoologische Verhandelingen. Leiden 250: 1–32.

Hoogmoed, M.S., and J. Lescure. 1984. A new genus and two new species of minute leptodactylid frogs from northern South America, with comments upon *Phyzelaphryne* (Amphibia: Anura: Leptodactylidae). Zoologische Mededelingen. Leiden 58: 85–115.

Houlahan, J.E., C.S. Findlay, B.R. Schmidt, A.H. Meyer, and S.L. Kuzmin. 2000. Quantitative evidence for global amphibian population declines. Nature. London 404: 752–755.

Hu, S., E. Zhao, and C.-C. Liu. 1966. A herpetological survey of the Tsinling and Ta-Pa Shan region. Acta Zoologica Sinica 18: 57–89. [In Chinese with English abstract.]

Hu, S., E. Zhao, and C.-C. Liu. 1973. A survey of amphibians and reptiles in Kweichow province, including a herpetofaunal analysis. Acta Zoologica Sinica 19: 149–181.

Hull, D.L. 1988. Science as a process: an evolutionary account of the social and conceptual development of science. Chicago: University of Chicago Press.

Hutchinson, M.N., and L.R. Maxson. 1987. Phylogenetic relationships among Australian tree frogs (Anura: Hylidae: Pelodryadinae): an immunological approach. Australian Journal of Zoology 35: 61–74.

Huxley, T.H. 1863. Description of *Anthracosaurus russelli*, a new labyrinthodont from the Lanarkshire coal field. Quarterly Journal of the Geological Society of London 19: 56–68.

Inger, R.F. 1954. Systematics and zoogeography of Philippine Amphibia. Fieldiana. Zoology 33: 183–531.

Inger, R.F. 1966. The systematics and zoogeography of the Amphibia of Borneo. Fieldiana. Zoology 52: 1–402.

Inger, R.F. 1967. The development of a phylogeny of frogs. Evolution 21: 369–384.

Inger, R.F. 1972. *Bufo* of Eurasia. *In* W.F. Blair (editor), Evolution in the genus *Bufo*: 102–118. Austin: University of Texas Press.

Inger, R.F. 1996. Commentary on a proposed classification of the family Ranidae. Herpetologica 52: 241–246.

Inger, R.F., H.B. Shaffer, M. Koshy, and R. Bakde. 1984. A report on a collection of amphibians and reptiles from the Ponmudi, Kerala, South India. Journal of the Bombay Natural History Society 81: 406–427.

International Commission of Zoological Nomenclature. 1999. International code of zoological nomenclature, 4th ed. London: International Trust for Zoological Nomenclature.

Iordansky, N.N. 1996. Evolution of the musculature of the jaw apparatus in the Amphibia. Ad-

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vances in Amphibian Research in the Former Soviet Union 1: 3–26.

Iwabe, N., Y. Hara, Y. Kumazawa, K. Shibamoto, Y. Saito, T. Miyata, and K. Kazutaka. 2005. Sister-group relationship of turtles to the bird-crocodilian clade revealed by nuclear DNA-coded proteins. Molecular Biology and Evolution 22: 810–813.

Izecksohn, E. 1971. Nôvo gênero e nova espécie de Brachycephalidae do Estado do Rio de Janeiro, Brasil (Amphibia, Anura). Boletim do Museu Nacional, Rio de Janeiro. Nova Série, Zoologia 280: 1–12.

Izecksohn, E. 1988. Algumas considerações sôbre o gênero *Euparkerella*, coma descrição de três novas espécies (Amphibia, Anura, Leptodactylidae). Revista Brasileira de Biologia 48: 59–74.

Izecksohn, E., J.J. Jim, S.T. de Albuquerque, and W.F. de Mendonça. 1971. Observações sôbre o desenvolvimento e os hábitos de *Myersiella subnigra* (Miranda-Ribeiro). Arquivos do Museu Nacional. Rio de Janeiro 43: 69–73.

Jackman, T.R., G. Applebaum, and D.B. Wake. 1997. Phylogenetic relationships of bolitoglossine salamanders: a demonstration of the effects of combining morphological and molecular data sets. Molecular Biology and Evolution 14: 883–891.

Janies, D., and W.C. Wheeler. 2001. Efficiency of parallel direct optimization. Cladistics 17: S71–S82.

Janke, A., D. Erpenbeck, M. Nilsson, and U. Arnason. 2001. The mitochondrial genomes of the iguana (*Iguana iguana*) and the caiman (*Caiman crocodylus*): implications for amniote phylogeny. Proceedings of the Royal Society of London. Series B, Biological Sciences 268: 623–631.

Jenkins, F.A., and D.M. Walsh. 1993. An early Jurassic caecilian with limbs. Nature. London 365: 246–250.

Jiang, J., A. Dubois, A. Ohler, A. Tillier, X. Chen, F. Xie, and M. Stöck. 2005. Phylogenetic relationships of the tribe Paini (Amphibia, Anura, Ranidae) based on partial sequences of mitochondrial 12S and 16S rRNA genes. Zoological Science. Tokyo 22: 353–362.

Jiang, J., L. Fei, C. Ye, X. Zeng, M. Zhen, F. Xie, and Y. Chen. 1997. Studies on the taxonomics of species of *Pseudorana* and discussions of the phylogenetical relationships with its relative genera. Cultum Herpetologica Sinica 6–7: 67–74.

Jiang, J., and K. Zhou. 2001. Evolutionary relationships among Chinese ranid frogs inferred from mitochondrial DNA sequences of 12S rRNA gene. Acta Zoologica Sinica 47: 38–44.

Jiang, J., and K. Zhou. 2005. Phylogenetic relationships among Chinese ranids inferred from sequence data set of 12S and 16S rDNA. Herpetological Journal. London 15: 1–8.

Jiménez de la Espada, M. 1871 ''1870''. Fauna neotropicalis species quaedam nondum cognitae. Jornal de Sciências, Mathemáticas, Physicas e Naturaes. Lisbõa 3: 57–65.

Jockusch, E.L., and D.B. Wake. 2002. Falling apart and merging: diversification of slender salamanders (Plethodontidae: *Batrachoseps*) in the American West. Biological Journal of the Linnean Society 76: 361–391.

Jockusch, E.L., K.P. Yanev, and D.B. Wake. 2001. Molecular phylogenetic analysis of slender salamanders, genus *Batrachoseps* (Amphibia: Plethodontidae), from central coastal California with descriptions of four new species. Herpetological Monographs 15: 54–99.

Jungfer, K.-H., H. Birkhahn, V. Külpmann, and K. Wassmann. 1996. Haltung und Fortpflanzung von *Dendrobates fulguritus* Silverstone, 1975, mit Anmerkungen zur Gattung *Minyobates* Myers, 1987. Herpetofauna. Weinstadt 15: 19–27.

Jungfer, K.-H., S. Lötters, and D. Jörgens. 2000. Der kleinste Pfeilgiftfrosche—eine neue *Dendrobates*-Art aus West-Panama. Herpetofauna. Weinstadt 22: 11–18.

Jurgens, J.D. 1971. The morphology of the nasal region of the Amphibia and its bearing on the phylogeny of the group. Annals of the University of Stellenbosch 46: 1–146.

Kaiser, H., L.A. Coloma, and H.M. Gray. 1994. A new species of *Colostethus* (Anura: Dendrobatidae) from Martinique, French Antilles. Herpetologica 50: 23–32.

Kaplan, M. 1994. Analysis of some long-standing controversies concerning the pectoral girdle of *Atelopus* (Bufonidae) using ontogenetic studies. Journal of Herpetology 28: 128–131.

Kaplan, M. 1995. On the presence of overlap during the development of the pectoral girdle of *Colostethus subpunctatus* (Amphibia: Anura) and its relevance in the classification of Dendrobatidae. Journal of Herpetology 29: 300–304.

Kaplan, M. 1997. A new species of *Colostethus* from the Sierra Nevada de Santa Marta (Colombia) with comments on intergeneric relationships within the Dendrobatidae. Journal of Herpetology 31: 369–375.

Kaplan, M. 2000. The pectoral girdles of *Rana rugulosa* (Ranidae) and *Nesomantis thomasseti* (Sooglossidae). Herpetologica 56: 188–195.

Kaplan, M. 2001. On the relevance of the character ''absence of epicoracoid horns'' in the systematics of anurans. Alytes 19: 196–204.

Kaplan, M. 2002. Histology of the anteroventral part of the breast-shoulder apparatus of *Bra-*

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chycephalus ephippium (Brachycephalidae) with comments on the validity of the genus *Psyllophryne* (Brachycephalidae). Amphibia-Reptilia 23: 225–227.

Kaplan, M. 2004. Evaluation and redefinition of the states of anuran pectoral girdle architecture. Herpetologica 60: 84–97.

Keller, R.A., R.N. Boyd, and Q.D. Wheeler. 2003. The illogical basis of Phylogenetic Nomenclature. Botanical Review 69: 93–110.

King, M., M.J. Tyler, M.M. Davies, and D. King. 1979. Karyotypic studies on *Cyclorana* and associated genera of Australian frogs. Australian Journal of Zoology 27: 699–708.

Kirsch, J.A., A.W. Dickerman, O.A. Reig, and M.S. Springer. 1991. DNA hybridization evidence for the Australasian affinity of the American marsupial *Dromiciops australis*. Proceedings of the National Academy of Sciences of the United States of America 88: 10465–10469.

Kirtisinghe, P. 1958. Some hitherto undescribed anuran tadpoles. Ceylon Journal of Science 1: 171–176.

Kiyasetuo and M.K. Khare. 1986. A new genus of frog (Anura: Ranidae) from Nagaland at the northeastern hills of India. Asian Journal of Exploration and Science 1: 12.

Kjer, K.M. 1995. Use of rRNA secondary structure in phylogenetic studies to identify homologous positions: an example of alignment and data presentation from frogs. Molecular Phylogenetics and Evolution 4: 314–330.

Klein, S.L., R.L. Strausberg, L. Wagner, J. Pontius, S.W. Clifton, and P. Richardson. 2002. Genetic and genomic tools for *Xenopus* research: the NIH *Xenopus* initiative. Developmental Dynamics 225: 384–391.

Klemens, M.W. 1998. The male nuptial characteristics of *Arthroleptides martiensseni* Nieden, an endemic torrent frog from Tanzania's Eastern Arc Mountains. Herpetological Journal. London 8: 35–40.

Kluge, A.G. 1966. A new pelobatine frog from the lower Miocene of South Dakota with a discussion of the evolution of the *Scaphiopus-Spea* complex. Natural History Museum of Los Angeles County Contributions in Science 113: 1–26.

Kluge, A.G. 2005. Taxonomy in theory and practice, with arguments for a new phylogenetic system of taxonomy. *In* M.A. Donnelly, B.I. Crother, C. Guyer, M.H. Wake, and M.E. White (editors), Ecology and evolution in the tropics: a herpetological perspective: 7–47. Chicago: University of Chicago Press.

Kluge, A.G., and J.S. Farris. 1969. Quantitative phyletics and the evolution of anurans. Systematic Zoology 18: 1–32.

Knauer, F.K. 1883. Naturgeschichte der Lurche. (Amphibiologie.) Eine umfassendere Darlegung unserer Kenntnisse von dem anatomischen Bau, der Entwicklung und systematischen Eintheilung der Amphibien, & c. Zweite Ausgabe. Wien and Leipzig: A. Pilchler's Witwe & Sohn.

Köhler, J. 2000. New species of *Eleutherodactylus* (Anura: Leptodactylidae) from cloud forest of Bolivia. Copeia 2000: 516–520.

Kojima, J.-I. 2003. Apomorphy-based definition also pinpoints a node, and PhyloCode names prevent effective communication. Botanical Review 69: 44–58.

Kokubum, M.N., de Carvalho, and A.A. Giaretta. 2005. Reproductive ecology and behaviour of a species of *Adenomera* (Anura, Leptodactylinae) with endotrophic tadpoles: systematic implications. Journal of Natural History. London 39: 1745–1758.

Kosuch, J., M. Vences, A. Dubois, A. Ohler, and W. Böhme. 2001. Out of Asia: mitochondrial DNA evidence for an oriental origin of tiger frogs, genus *Hoplobatrachus*. Molecular Phylogenetics and Evolution 21: 398–407.

Kress, W.J., and P. DePriest. 2001. What's in a Phylocode name? Science 292: 6.

Kuramoto, M. 1985. A new frog (genus *Rana*) from the Yaeyama Group of the Ryukyu Islands. Herpetologica 41: 150–158.

Kuramoto, M. 1990. A list of chromosome numbers of anuran amphibians. Bulletin of Fukuoka University of Education 39: 83–127.

Kuramoto, M., and C.-S. Wang. 1987. A new rhacophorid treefrog from Taiwan, with comparisons to *Chirixalus eiffingeri* (Anura, Rhacophoridae). Copeia 1987: 931–942.

Kuramoto, M., C.-S. Wang, and H.-T. Yu. 1984. Breeding, larval morphology and experimental hybridization of Taiwanese brown frogs, *Rana longicrus* and *R. sauteri*. Journal of Herpetology 18: 387–395.

Kwon, A.S., and Y.H. Lee. 1995. Comparative spermatology of anurans with special references to phylogeny. *In* B.G.M. Jamieson, J. Ausio, and J.-L. Justine (editors), Advances in spermatozoal phylogeny and taxonomy. Mémoires du Muséum National d'Histoire Naturelle. Paris. Série A, Zoologie 166: 321–332.

La Marca, E., M. Vences, and S. Lötters. 2002. Rediscovery and mitochondrial relationships of the dendrobatid frog *Colostethus humilis* suggest parallel colonization of the Venezuelan Andes by poison frogs. Studies on Neotropical Fauna and Environment 37: 233–240.

Lamotte, M. 1961. Contribution à l'étude des batraciens de l'ouest africain XII. Les formes larvaires de *Cardioglossa leucomystax* Blgr. Bul-

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letin de l'Institut Fondamental d'Afrique Noire 23: 211–216.

Lamotte, M., and J. Lescure. 1989. Les têtards rhéophiles et hygropétriques de l'Ancien et du Noveau Monde. Annales des Sciences Naturelles. Zoologie. Paris. Serie 13, 10: 111–122.

Lamotte, M., J.-L. Perret, and S. Dzieduszycka. 1959. Contribution à l'étude des batraciens de l'ouest africain. IX. Les formes larvaires de *Petropedetes palmipes*, *Conraua goliath* et *Acanthixalus spinosus*. Bulletin de l'Institut Française d'Afrique Noire. Série A, Sciences Naturelles 21: 762–776.

Lamotte, M., and F. Xavier. 1972. Les amphibiens anoures a developpement direct d'Afrique. Observations sur la biologie de *Nectophrynoides tornieri* (Roux). Bulletin de la Société Zoologique de France 97: 413–428.

Lamotte, M., and M. Zuber-Vogeli. 1954. Contribution à l'étude des batraciens de l'ouest africain. III. Les formes larvaires de *Astylosternus diadematus* et *Petropedetes natator*. Bulletin de l'Institut Française d'Afrique Noire. Série A, Sciences Naturelles 16: 1222–1233.

Langone, J.A. 1994. Ranas y sapos del Uruguay (reconocimientos y aspectos biológicos). Museo Damaso Antonio Larrañaga, Serie de Divulgación 5: 1–123.

Largen, M.J. 1991. A new genus and species of petropedetine frog (Amphibia, Anura, Ranidae) from high altitude in the mountains of Ethiopia. Tropical Zoology. Firenze 4: 139–152.

Largen, M.J., and R.C. Drewes. 1989. A new genus and species of brevicipitine frog (Amphibia, Anura, Microhylidae) from high altitude in the mountains of Ethiopia. Tropical Zoology. Firenze 2: 13–30.

Larson, A. 1991. A molecular perspective on the evolutionary relationship of the salamander families. *In* M.K. Hecht, B. Wallace, and R.J. MacIntyre (editors), Evolutionary biology, vol. 25: 211–277. New York: Plenum Publishing Corporation.

Larson, A., and W. Dimmick. 1993. Phylogenetic relationships of the salamander families: an analysis of congruence among morphological and molecular characters. Herpetological Monographs 7: 77–93.

Larson, A., D.B. Wake, L.R. Maxson, and R. Highton. 1981. A molecular phylogenetic perspective on the origins of morphological novelties in the salamanders of the tribe Plethodontini (Amphibia, Plethodontidae). Evolution 35: 405–422.

Larson, A., D.W. Weisrock, and K.H. Kozak. 2003. Phylogenetic systematics of salamanders (Amphibia: Urodela), a review. *In* D.M. Sever (editor), Reproductive biology and phylogeny of Urodela (Amphibia): 31–108. Enfield, NH: Science Publishers.

Lataste, F. 1879. Étude sur le *Discoglossus pictus* Otth. Actes de la Société Linnéenne de Bordeaux, Série 4, 3: 275–342.

Lathrop, A. 1997. Taxonomic review of the megophryid frogs (Anura: Pelobatoidea). Asiatic Herpetological Research 7: 68–79.

Lathrop, A. 2003. Asian toadfrogs (Megophryidae). *In* W.E. Duellman (editor), Grzimek's animal life encyclopedia, 2nd ed. Vol. 6. Amphibians: 109–117. Detroit: Gale Group.

Latreille, P.A. 1800. Histoire naturelle des salamandres de France, précédée d'un tableau méthodique des autres reptiles indigènes. Paris: Imprimerie de Crapelet.

Latreille, P.A. 1825. Familles naturelles du règne animal, exposées succinctement et dans un ordre analytique, avec l'indication de leurs genres. Paris: J.B. Baillière.

Laurent, R.F. 1941 ''1940''. Contribution à l'ostéologie et à la systématique des ranides africains. Première note. Revue de Zoologie et de Botanique Africaines 34: 74–96.

Laurent, R.F. 1941. Contribution à l'ostéologie et à la systematique des ranides africains. Deuxième note. Revue de Zoologie et de Botanique Africaines 34: 192–234.

Laurent, R.F. 1942. Note sur les procoeliens firmisternes (Batrachia Anura). Bulletin du Musée Royal d'Histoire Naturelle de Belgique 18: 1–20.

Laurent, R.F. 1943. Contribution a l'osteologie et a la systematique des rhacophorides non africaines. Bulletin du Musée Royal d'Histoire Naturelle de Belgique 19: 1–16.

Laurent, R.F. 1946. Mises au point dans la taxonomie des ranides. Revue de Zoologie et de Botanique Africaines 39: 336–338.

Laurent, R.F. 1951. Sur la necessité de supprimer la famille des Rhacophoridae mais de créer celle des Hyperoliidae. Revue de Zoologie et de Botanique Africaines 45: 116–122.

Laurent, R.F. 1954. Remarques sur le genre *Schoutedenella*. Annales du Musée Royal du Congo Belge. Nouvelle Série in Quarto. Sciences Zoologiques. Tervuren 1: 34–40.

Laurent, R.F. 1961. Notes on some South African amphibians. Publications de l'Université de l'État à Elisabethville. Lubumbashi 1: 197–209.

Laurent, R.F. 1972. The morphology, systematics, and evolution of the Old World treefrogs (Rhacophoridae and Hyperoliidae) [Review]. Copeia 1972: 198–201.

Laurent, R.F. 1973. The natural classification of the Arthroleptinae (Amphibia, Hyperoliidae). Revue de Zoologie et de Botanique Africaines 87: 666–678.

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Laurent, R.F. 1975. Biogéographie et liaisons intercontinentales au course du Mésozoïque. Mémoires du Muséum National d'Histoire Naturelle. Paris. Série A, Zoologie 88: 176–191.

Laurent, R.F. 1978. L'appareil hyoidien des Astylosterninae et des Arthroleptinae (Amphibia). Revue Zoologique Africaine 92: 233–240.

Laurent, R.F. 1980 ''1979''. Esquisse d'une phylogenèse des anoures. Bulletin de la Société Zoologique de France 104: 397–422.

Laurent, R.F. 1983. Heterogeneidad del genero *Batrachophrynus* Peters (Leptodactylidae). Acta Zoologica Lilloana 37: 107–113.

Laurent, R.F. 1984a. Heterogeneidad de la familia Caeciliidae (Amphibia-Apoda). Acta Zoologica Lilloana 37: 199–200.

Laurent, R.F. 1984b. La phylogenese des Ranoidea et le cladisme. Alytes 3: 97–111.

Laurent, R.F. 1986. Sous classe des lissamphibiens (Lissamphibia). *In* P. Grassé and M. Delsol (editors), Traité de zoologie. Anatomie, systematique, biologie, vol. 14. Batraciens, fasc. 1-B: 594–797. Paris: Masson.

Laurent, R.F. 1986 ''1985''. Sur la classification et la nomenclature des amphibiens. Alytes 4: 119–120.

Laurent, R.F., and M. Fabrezi. 1986 ''1985''. Le carpe des Arthroleptinae. Alytes 4: 85–93.

Laurenti, J.N. 1768. Specimen medicum, exhibens synopsin reptilium emendatum cum experimentis circa venena et antidota Reptilium Austriacorum. Wien.

Laurin, M. 1998a. The importance of global parsimony and historical bias in understanding tetrapod evolution. Part I. Systematics, middle ear evolution and jaw suspension. Annales des Sciences Naturelles. Zoologie et Biologie Animale. Paris. Serie 13, 1998: 1–42.

Laurin, M. 1998b. The importance of global parsimony and historical bias in understanding tetrapod evolution. Part II. Vertebral centrum, costal ventilation, and paedomorphosis. Annales des Sciences Naturelles. Zoologie et Biologie Animale. Paris. Serie 13, 1998: 99–114.

Laurin, M. 1998c. A reevaluation of the origin of pentadactyly. Evolution 52: 1476–1482.

Laurin, M. 2002. Tetrapod phylogeny, amphibian origins, and the definition of the name Tetrapoda. Systematic Biology 51: 364–369.

Laurin, M., and R.R. Reisz. 1997. A new perspective on tetrapod phylogeny. *In* S.S. Sumida and K.L.M. Martin (editors), Amniote origins: completing the transition to land: 9–59. San Diego: Academic Press.

Laurin, M., R.R. Reisz, and M. Girondot. 2000. Caecilian viviparity and amniote origins: a reply to Wilkinson and Nussbaum. Journal of Natural History. London 34: 311–315.

Lavilla, E.O., and J.M. Cei. 2001. Amphibians of Argentina. A second update, 1987–2000. Museo Regionale di Scienze Naturali Monografie. Torino 28: 1–177.

Lawson, D.P. 1993. The reptiles and amphibians of Korup National Park Project, Cameroon. Herpetological Natural History 1: 27–90.

Lebedkina, N.S. 2004. Evolution of the amphibian skull. Advances in Amphibian Research in the Former Soviet Union 9: 1–265.

Lescure, J., V. Marty, C. Marty, F. Starace, M.A. Thomay, and F. Letellier. 1995. Contribution à l'étude des amphibiens de Guyane française. X. Les *Phyllomedusa* (Anura, Hylidae). Revue Française d'Aquariologie, Herpétologie 22 35–50.

Lescure, J., S. Renous, and J.-P. Gasc. 1986. Proposition d'une nouvelle classification des amphibiens gymnophiones. Mémoires de la Société Zoologique de France 43: 145–177.

Leuckart, F.S. 1821. Einiges über die fischartigen Amphibien. Isis von Oken 9: 257–265.

Li, W.-H., and Z.-Y. Wang. 1985. Karyotype of *Rana livida*. Acta Herpetologica Sinica 4: 56. [In Chinese with English abstract.]

Licht, L.E. 2003. Shedding light on ultraviolet radiation and amphibian embryos. BioScience 53: 551–561.

Liem, D.S.S. 1970. The morphology, systematics, and evolution of the Old World treefrogs (Rhacophoridae and Hyperoliidae). Fieldiana. Zoology 57: i–vii, 1–145.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 10th ed. Stockholm.

Lips, K.R., P.A. Burrowes, J.R. Mendelson III, and G. Parra-Olea. 2005. Amphibian declines in Latin America: a synthesis. Biotropica 37: 222–228.

Littlejohn, M.J. 1963. The breeding biology of the Baw Baw frog *Philoria frosti* Spencer. Proceedings of the Linnaean Society of New South Wales 88: 273–276.

Liu, C.-C. 1950. Amphibians of western China. Fieldiana. Zoology Memoires 2: 1–397 + 10 pl.

Liu, C.-C., and S. Hu. 1961. [Tailless amphibians of China.] Shanghai: Science Press. [In Chinese.]

Liu, C.-C., and S. Hu. 1962. A herpetological report of Kwangsi. Acta Zoologica Sinica 14: 73–104. [In Chinese with English abstract and translations of descriptions.]

Liu, W., A. Lathrop, J. Fu, D. Yang, and R.W. Murphy. 2000. Phylogeny of East Asian bufonids inferred from mitochondrial DNA sequenc-

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es (Anura: Amphibia). Molecular Phylogenetics and Evolution 14: 423–435.

Loader, S.P., D.J. Gower, K.M. Howell, N. Doggart, M.-O. Rödel, R.O. de Sá, B.L. Cohen, and M. Wilkinson. 2004. Phylogenetic relationships of African microhylid frogs inferred from DNA sequences of mitochondrial 12S and 16S rRNA genes. Organisms, Diversity & Evolution 4: 227–235.

Lombard, R.E., and S.S. Sumida. 1992. Recent progress in understanding early tetrapods. American Zoologist 32: 609–622.

Lombard, R.E., and D.B. Wake. 1986. Tongue evolution in the lungless salamanders, family Plethodontidae IV. Phylogeny of plethodontid salamanders and the evolution of feeding dynamics. Systematic Biology 35: 532–551.

Loveridge, A. 1957. Check list of the reptiles and amphibians of East Africa (Uganda; Kenya; Tanganyika; Zanzibar). Bulletin of the Museum of Comparative Zoology 117: 153–362.

Löytynoja, A., and M.C. Milinkovitch. 2000. SOAP, cleaning multiple alignments from unstable blocks, version 1.0. Bioinformatics 17: 573–574.

Löytynoja, A., and M.C. Milinkovitch. 2003. A hidden Markov model for progressive multiple alignments. Bioinformatics 19: 1505–1513.

Lutz, B. 1954. Anfíbios anuros do Distrito Federal/The frogs of the Federal District of Brazil. Memórias do Instituto Oswaldo Cruz. Rio de Janeiro 52: 155–197 (Portuguese), 219–238 (English).

Lutz, B. 1968. Taxonomy of the Neotropical Hylidae. Pearce-Sellards Series. Texas Memorial Museum 11: 3–26.

Lutz, B. 1969. Adaptações, especializações e linhagens nos anuros neotropicais. Acta Zoologica Lilloana 24: 267–292.

Lynch, J.D. 1969. Program. Final Ph.D. examination. Department of Zoology, University of Kansas, Lawrence.

Lynch, J.D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. University of Kansas Museum of Natural History, Miscellaneous Publications 53: 1–238.

Lynch, J.D. 1972a. Generic partitioning of the South American leptodactyloid frog genus *Eupsophus* Fitzinger, 1843 (*sensu lato*). Bulletin of the Southern California Academy of Science 71: 2–11.

Lynch, J.D. 1972b. Two new species of frogs (*Eleutherodactylus*: Leptodactylidae) from the páramos of northern Ecuador. Herpetologica 28: 141–147.

Lynch, J.D. 1973. The transition from archaic to advanced frogs. *In* J.L. Vial (editor), Evolutionary biology of the anurans: contemporary research on major problems: 133–182. Columbia: University of Missouri Press.

Lynch, J.D. 1975. A review of the Andean leptodactylid frog genus *Phrynopus*. Occasional Papers of the Museum of Natural History, University of Kansas 35: 1–51.

Lynch, J.D. 1976. The species groups of the South American frogs of the genus *Eleutherodactylus* (Leptodactylidae). Occasional Papers of the Museum of Natural History, University of Kansas 61: 1–24.

Lynch, J.D. 1978a. A new eleutherodactyline frog from the Andes of northern Colombia. Copeia 1978: 17–21.

Lynch, J.D. 1978b. A re-assessment of the telmatobiine leptodactylid frogs of Patagónia. Occasional Papers of the Museum of Natural History, University of Kansas 72: 1–57.

Lynch, J.D. 1980. A new species of *Barycholos* from Estado Goiás, Brasil (Amphibia, Anura, Leptodactylidae) with remarks on related genera. Bulletin du Museum National d'Histoire Naturelle. Paris. Section A, Zoologie, Biologie et Ecologie Animales 2: 289–302.

Lynch, J.D. 1982a. Two new species of poison-dart frogs (*Colostethus*) from Colombia. Herpetologica 38: 366–374.

Lynch, J.D. 1982b. Relationships of the frogs of the genus *Ceratophrys* (Leptodactylidae) and their bearing on hypotheses of Pleistocene forest refugia in South America and punctuated equilibrium. Systematic Zoology 31: 166–179.

Lynch, J.D. 1986. The definition of the Middle American clade of *Eleutherodactylus* based on jaw musculature (Amphibia: Leptodactylidae). Herpetologica 42: 248–258.

Lynch, J.D. 1989. Intrageneric relationships of mainland *Eleutherodactylus* (Leptodactylidae). I. A review of the frogs assigned to the *Eleutherodactylus discoidalis* species group. Milwaukee Public Museum Contributions in Biology and Geology 79: 1–25.

Lynch, J.D. 1994. A new species of high-altitude frog (*Eleutherodactylus*: Leptodactylidae) from the Cordillera Oriental of Colombia. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 19: 195–203.

Lynch, J.D. 1996. The relationships of the Hispaniolan frogs of the subgenus *Pelorius* (*Eleutherodactylus*: Leptodactylidae). *In* R. Powell and R.W. Henderson (editors), Contributions to West Indian herpetology: a tribute to Albert Schwartz: 141–155. Contribution to Herpetology, no. 12. Ithaca, NY: Society for the Study of Amphibians and Reptiles.

Lynch, J.D. 2000. The relationships of an ensemble of Guatemalan and Mexican frogs (*Eleutherodactylus*: Leptodactylidae: Amphibia). Re-

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vista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 24: 129–156.

Lynch, J.D., and W.E. Duellman. 1997. Frogs of the genus *Eleutherodactylus* in western Ecuador. Systematics, ecology, and biogeography. University of Kansas Natural History Museum, Special Publication 23: 1–236.

Lynch, J.D., and H.L. Freeman. 1966. Systematic status of a South American frog, *Allophryne ruthveni* Gaige. University of Kansas Publications, Museum of Natural History 17: 493–502.

Lynch, J.D., and R.W. McDiarmid. 1987. Two new species of *Eleutherodactylus* (Amphibia: Anura: Leptodactylidae) from Bolivia. Proceedings of the Biological Society of Washington 100: 337–346.

Lynch, J.D., and P.M. Ruiz-Carranza. 1982. A new genus and species of poison-dart frog (Amphibia: Dendrobatidae) from the Andes of northern Colombia. Proceedings of the Biological Society of Washington 95: 557–562.

Lynch, J.D., and P.M. Ruiz-Carranza. 1997 ''1996''. A remarkable new centrolenid frog from Colombia with a review of nuptial excrescences in the family. Herpetologica 52: 525–535.

Lynch, J.F., and D.B. Wake. 1978. A new species of *Chiropterotriton* (Amphibia: Caudata) from Baja Verapaz, Guatemala, with comments on relationships among Central American members of the genus. Natural History Museum of Los Angeles County Contributions in Science 294: 1–22.

Lynch, J.F., D.B. Wake, and S.-Y. Yang. 1983. Genic and morphological differentiation in Mexican *Pseudoeurycea* (Caudata: Plethodontidae). Copeia 1983: 884–894.

Macey, J.R., J.L. Strasburg, J.A. Brisson, V.T. Vredenburg, M. Jennings, and A. Larson. 2001. Molecular phylogenetics of western North American frogs of the *Rana boylii* species group. Molecular Phylogenetics and Evolution 19: 131–143.

Macey, J.R. 2005. Plethodontid salamander mitochondrial genomics: a parsimony evaluation of character conflict and implications for historical biogeography. Cladistics 21: 194–202.

Maglia, A.M. 1998. Phylogenetic relationships of extant pelobatoid frogs (Anura: Pelobatoidea): evidence from adult morphology. Scientific Papers. Natural History Museum, University of Kansas 10: 1–19.

Maglia, A.M., L.A. Pugener, and L. Trueb. 2001. Comparative development of anurans: using phylogeny to understand ontogeny. American Zoologist 41: 538–551.

Mahoney, M.J. 2001. Molecular systematics of *Plethodon* and *Aneides* (Caudata: Plethodontidae: Plethodontini): phylogenetic analysis of an old and rapid radiation. Molecular Phylogenetics and Evolution 18: 174–188.

Maienschein, J. 1994. Cutting edges cut both ways. Biology and Philosophy 9: 1–24.

Mannen, H., and S.S.-L. Li. 1999. Molecular evidence for a clade of turtles. Molecular Phylogenetics and Evolution 13: 144–148.

Manzano, A.S., and E.O. Lavilla. 1995. Myological peculiarities in *Rhinoderma darwini* (Anura: Rhinodermatidae). Journal of Morphology 224: 125–129.

Manzano, A.S., S.A. Moro, and V. Abdala. 2003. The depressor mandibulae muscle in Anura. Alytes 20: 93–131.

Marmayou, J., A. Dubois, A. Ohler, E. Pasquet, and A. Tillier. 2000. Phylogenetic relationships in the Ranidae (Amphibia, Anura). Independent origin of direct development in the genera *Philautus* and *Taylorana*. Comptes Rendus de l'Academie des Sciences. Series 3, Life Sciences Paris 323: 287–297.

Martin, A.A. 1967. Australian anuran life histories: some evolutionary and ecological aspects. *In* A.H. Weatherly (editor), Australian inland waters and their fauna: eleven studies: 175–191. Canberra: Australian National University Press.

Martin, R.F. 1972. Evidence from osteology. *In* W.F. Blair (editor), Evolution in the genus *Bufo*: 37–70. Austin: University of Texas Press.

Martin, W.F. 1972. Evolution of vocalization in the genus *Bufo*. *In* W.F. Blair (editor), Evolution in the genus *Bufo*: 279–309. Austin: University of Texas Press.

Matsui, M. 1994. A taxonomic study of the *Rana narina* complex, with description of three new species (Amphibia: Ranidae). Zoological Journal of the Linnean Society. London 111: 385–415.

Matsui, M., and N.L. Orlov. 2004. A new species of *Chirixalus* from Vietnam (Anura: Rhacophoridae). Zoological Science. Tokyo 21: 671–676.

Matsui, M., H. Ota, M.W.-N. Lau, and A. Bogadek. 1995. Cytotaxonomic studies of three ranid species (Amphibia: Anura) from Hong Kong. Japanese Journal of Herpetology/ Hachu-Ryoseiruigaku Zasshi 16: 12–17.

Matsui, M., T. Shimada, H. Ota, and T. Tanaka-Ueno. 2005. Multiple invasions of the Ryukyu Archipelago by Oriental frogs of the subgenus *Odorrana* with phylogenetic reassessment of the related subgenera of the genus *Rana*. Molecular Phylogenetics and Evolution 37: 733–742. [Seen as an electronic/pdf preprint available from the publisher.]

Maxson, L.R., R. Highton, and D.B. Wake. 1979.

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Albumin evolution and its phylogenetic implications in the plethodontid salamander genera *Plethodon* and *Ensatina*. Copeia 1979: 502–508.

Maxson, L.R., D.P. Ondrula, and M.J. Tyler. 1985. An immunological perspective on evolutionary relationships in Australian frogs of the hylid genus *Cyclorana*. Australian Journal of Zoology 33: 17–22.

Maxson, L.R., and D.B. Wake. 1981. Albumin evolution and its phylogenetic implications in the plethodontid salamander genera *Pseudoeurycea* and *Chiropterotriton*. Herpetologica 37: 109–117.

Mayer, A.F.J.K. 1849. System des Thier-Reiches oder Eintheilung der Thiere nach einem Princip, entworfen. Verhandlungen des Naturhistorischen Vereines der Preussischen Rheinlande 6: 177–210.

McDiarmid, R.W., and R.I. Altig. 1999. Research materials and techniques. *In* R.W. McDiarmid and R. Altig (editors), Tadpoles: the biology of anuran larvae: 7–23. Chicago: University of Chicago Press.

McDiarmid, R.W., and S.J. Gorzula. 1989. Aspects of the reproductive ecology and behavior of the tepui toads, genus *Oreophrynella* (Anura, Bufonidae). Copeia 1989: 445–451.

McGowan, G.J., and S.E. Evans. 1995. Albanerpetontid amphibians from the Cretaceous of Spain. Nature. London 373: 143–145.

Meegaskumbura, M., F. Bossuyt, R. Pethiyagoda, K. Manamendra-Arachchi, M. Bahir, M.C. Milinkovitch, and C.J. Schneider. 2002. Sri Lanka: an amphibian hot spot. Science 298: 379.

Meinhardt, D.J., and J.R. Parmalee. 1996. A new species of *Colostethus* (Anura: Dendrobatidae) from Venezuela. Herpetologica 52: 70–77.

Mendelson, J.R., III, H.R. da Silva, and A.M. Maglia. 2000. Phylogenetic relationships among marsupial frog genera (Anura: Hylidae: Hemiphractinae) based on evidence from morphology and natural history. Zoological Journal of the Linnean Society. London 128: 125–148.

Merrem, B. 1820. Versuch eines Systems der Amphibien/ Tentamen systematis amphibiorum. Marburg: Johann Christian Krieger.

Milner, A.R. 1988. The relationships and origin of the living amphibians. *In* M.J. Benton (editor), The phylogeny and classification of the tetrapods, vol. 1. Amphibians, reptiles, birds: 59–102. Systematics Association Special Volume 23. New York: Academic Press.

Milner, A.R. 1993. The Paleozoic relatives of lissamphibians. Herpetological Monographs 7: 8–27.

Milner, A.R. 1994. Late Triassic and Jurassic amphibians: fossil record and phylogeny. *In* N.C. Fraser and H.-D. Sues (editors), In the shadow of the dinosaurs: 5–23. New York: Cambridge University Press.

Milner, A.R. 2000. Mesozoic and Tertiary Caudata and Albanerpetontidae. *In* H. Heatwole and R.L. Carroll (editors), Amphibian biology, vol. 4. Paleontology, the evolutionary history of amphibians: 1412–1444. Chipping Norton, Australia: Surrey Beatty.

Min, M.-S., S.-Y. Yang, R.M. Bonett, D.R. Vieites, R.A. Brandon, and D.B. Wake. 2005. Discovery of the first Asian plethodontid salamander. Nature. London 435: 87–90.

Miranda-Ribeiro, A., de. 1923. Os hylodideos do Museu Paulista. Revista do Museu Paulista. São Paulo 13: 825–846 (reprint pages 3–24).

Miranda-Ribeiro, A., de. 1926. Notas para servirem ao estudo dos Gymnobatrachios (Anura) brasileiros. Arquivos do Museu Nacional do Rio de Janeiro 27: 1–227.

Mivart, S.G. 1869. On the classification of the anurous batrachians. Proceedings of the Zoological Society of London 1869: 280–295.

Mookerjee, H.K. 1931. On the development of the vertebral column of Anura. Philosophical Transactions of the Royal Society of London 219: 165–196.

Morrison, D.A., and J.T. Ellis. 1997. Effects of nucleotide sequence alignment on phylogeny estimation: a case study of 18S rDNAs of Apicomplexa. Molecular Biology and Evolution 14: 428–441.

Mueller, R.L., J.R. Macey, M. Jaekel, D.B. Wake, and J.L. Boore. 2004. Morphological homoplasy, life history evolution, and historical biogeography of plethodontid salamanders inferred from complete mitochondrial genomes. Proceedings of the National Academy of Sciences of the United States of America 101: 13820–13825.

Müller, H., G.J. Measey, and P.K. Malonza. 2005. Tadpole of *Bufo taitanus* (Anura: Bufonidae) with notes on its systematic significance and life history. Journal of Herpetology 39: 138–141.

Müller, J. 1831. An einer jungen *Coecilia hypocyanea* im Museum der Naturgeschichte. Isis von Oken 1831: 710–711.

Müller, J. 1832. Beiträge zur Anatomie und Naturgeschichte der Amphibien. I. Ueber die natürliche Eintheilung der Amphibien. Zeitschrift für Physiologie 4: 190–275, pl. 18–22.

Müller, K. 2004. PRAP—computation of Bremer support for large data sets. Molecular Phylogenetics and Evolution 31: 780–782.

Myers, C.W. 1982. Spotted poison frogs: descriptions of three new *Dendrobates* from western Amazonia, and resurrection of a lost species

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from ''Chiriqui''. American Museum Novitates 2721: 1–23.

Myers, C.W. 1987. New generic names for some Neotropical poison frogs (Dendrobatidae). Papéis Avulsos de Zoologia. São Paulo 36: 301–306.

Myers, C.W., and P.A. Burrowes. 1987. A new poison frog (*Dendrobates*) from Andean Colombia, with notes on a lowland relative. American Museum Novitates 2899: 1–17.

Myers, C.W., J.W. Daly, and B. Malkin. 1978. A dangerously toxic new frog (*Phyllobates*) used by Emberá indians of western Colombia, with discussion of blowgun fabrication and dart poisoning. Bulletin of the American Museum of Natural History 161: 307–366.

Myers, C.W., and L.S. Ford. 1986. On *Atopophrynus*, a recently described frog wrongly assigned to the Dendrobatidae. American Museum Novitates 2843: 1–15.

Myers, C.W., A. Paolillo O., and J.W. Daly. 1991. Discovery of a defensively malodorous and nocturnal frog in the family Dendrobatidae: phylogenetic significance of a new genus and species from the Venezuelan Andes. American Museum Novitates 3002: 1–33.

Nascimento, L.B., U. Caramaschi, and C.A.G. Cruz. 2005. Taxonomic review of the species group of the genus *Physalameus* Fitzinger, 1826 with revalidation of the genera *Engystomops* Jimenez de la Espada, 1872 and *Eupemphix* Steindachner, 1836 (Amphibia, Anura, Leptodactylidae). Arquivos do Museu Nacional do Rio de Janeiro 63: 297–320.

Nicholls, G.E. 1916. The structure of the vertebral column in the Anura Phaneroglossa and its importance as a basis of classification. Proceedings of the Linnaean Society of London 128: 80–92.

Niklas, K.J. 2001. Taxing debate for taxonomists. Science 292: 2249–2250.

Nixon, K.C. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. Cladistics 15: 407–414.

Nixon, K.C. 1999–2002. WinClada. Version 1.0. Ithaca, New York: Computer software distributed by the author.

Nixon, K.C., and J.M. Carpenter. 2000. On the other ''phylogenetic systematics''. Cladistics 16: 298–318.

Nixon, K.C., J.M. Carpenter, and D.W. Stevenson. 2003. The PhyloCode is fatally flawed and the ''Linnaean'' system can be easily fixed. Botanical Review 69: 111–120.

Noble, G.K. 1924. A new spadefoot toad from the Oligocene of Mongolia with a summary of the evolution of the Pelobatidae. American Museum Novitates 132: 1–15.

Noble, G.K. 1926. The pectoral girdle of the brachycephalid frogs. American Museum Novitates 230: 1–14.

Noble, G.K. 1927. The value of life history data in the study of the evolution of the Amphibia. Annals of the New York Academy of Sciences 30: 31–128.

Noble, G.K. 1929. The adaptive modifications of the arboreal tadpoles of *Hoplophryne* and the torrent tadpoles of *Staurois*. Bulletin of the American Museum of Natural History 58: 291–334.

Noble, G.K. 1931. The biology of the Amphibia. New York: McGraw-Hill.

Noble, G.K., and P.G. Putnam. 1931. Observations on the life history of *Ascaphus truei* Stejneger. Copeia 1931: 97–101.

Nussbaum, R.A. 1976. Geographic variation and systematics of salamanders of the genus *Dicamptodon* Strauch (Ambystomatidae). Miscellaneous Publications. Museum of Zoology, University of Michigan 149: 1–94.

Nussbaum, R.A. 1977. Rhinatrematidae: a new family of caecilians (Amphibia: Gymnophiona). Occasional Papers of the Museum of Zoology, University of Michigan 682: 1–30.

Nussbaum, R.A. 1979. The taxonomic status of the caecilian genus *Uraeotyphlus* Peters. Occasional Papers of the Museum of Zoology, University of Michigan 687: 1–20.

Nussbaum, R.A. 1980. Phylogenetic implications of amplectic behavior in sooglossid frogs. Herpetologica 36: 1–5.

Nussbaum, R.A. 1982. Heterotopic bones in the hindlimbs of frogs of the families Pipidae, Ranidae and Sooglossidae. Herpetologica 38: 312–320.

Nussbaum, R.A., A.P. Jaslow, and J. Watson. 1982. Vocalization in frogs of the family Sooglossidae. Journal of Herpetology 16: 198–203.

Nussbaum, R.A., and M. Wilkinson. 1989. On the classification and phylogeny of caecilians (Amphibia: Gymnophiona), a critical review. Herpetological Monographs 3: 1–42.

Nussbaum, R.A., and M. Wilkinson. 1995. A new genus of lungless tetrapod: a radically divergent caecilian (Amphibia: Gymnophiona). Proceedings of the Royal Society of London. Series B, Biological Sciences 261: 331–335.

Ohler, A., S.R. Swan, and J.C. Daltry. 2002. A recent survey of the amphibian fauna of the Cardamom Mountains, Southwest Cambodia with descriptions of three new species. Raffles Bulletin of Zoology. Singapore 50: 465–481.

Okada, Y. 1966. Fauna Japonica. Anura (Amphibia). Tokyo: Biogeographical Society of Japan.

Olsson, L., and J. Hanken. 1996. Cranial neural-crest migration and chondrogenic fate in the

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oriental fire-bellied toad *Bombina orientalis*: defining the ancestral pattern of head development in anuran amphibians. Journal of Morphology 299: 105–120.

Oppel, M. 1810. Second memoire sur las classification des reptiles. Annales du Muséum d'Histoire Naturelle 16: 394–418.

Orlov, N.L., L.N. Ngat, and T.C. Ho. 2003. A new species of cascade frog from North Vietnam (Ranidae, Anura). Russian Journal of Herpetology 10: 123–134.

Orton, G.L. 1949. Larval development of *Nectophrynoides tornieri* (Roux), with comments on direct development in frogs. Annals of the Carnegie Museum 31: 257–274.

Orton, G.L. 1953. The systematics of vertebrate larvae. Systematic Zoology 2: 63–75.

Orton, G.L. 1957. The bearing of larval evolution on some problems in frog classification. Systematic Zoology 6: 79–86.

Page, L.M, H.L. Bart, Jr., R. Beaman, L. Bohs, L.T. Deck, V.A. Funk, D. Lipscomb, M.A. Mares, L.A. Prather, J. Stevenson, Q.D. Wheeler, J.B. Wooley, and D.W. Stevenson. 2005. LINNE: legacy infrastructure network for natural environments. Champaign, IL: Illinois Natural History Survey.

Palma, R.E., and A.E. Spotorno. 1999. Molecular systematics of marsupials based on the rRNA 12S mitochondrial gene: the phylogeny of didelphimorphia and the living fossil microbiotheriid *Dromiciops gliroides* Thomas. Molecular Phylogenetics and Evolution 13: 525–535.

Palumbi, S.R., A. Martin, S. Romano, W.O. McMillan, L. Stice, and G. Grabawski. 1991. The simple fool's guide to PCR, version 2.0. University of Hawaii, Honolulu: Privately published, compiled by S. Palumbi.

Papavero, N., J. Llorente-Bousquets, and J.M. Abe. 2001. Proposal of a new system of nomenclature for phylogenetic systematics. Arquivos de Zoologia. São Paulo 36: 1–145.

Parker, H.W. 1934. A monograph of the frogs of the family Microhylidae. London: Trustees of the British Museum.

Parker, H.W. 1940. The Australasian frogs of the family Leptodactylidae. Novitates Zoologicae. Tring 42: 1–106.

Parra-Olea, G. 2002. Molecular phylogenetic relationships of Neotropical salamanders of the genus *Pseudoeurycea*. Molecular Phylogenetics and Evolution 22: 234–246.

Parra-Olea, G., M. García-París, and D.B. Wake. 2002. Phylogenetic relationships among the salamanders of the *Bolitoglossa macrinii* species group (Amphibia: Plethodontidae), with descriptions of two new species from Oaxaca (Mexico). Journal of Herpetology 36: 356–366.

Parra-Olea, G., M. García-París, and D.B. Wake. 2004. Molecular diversification of salamanders of the tropical American genus *Bolitoglossa* (Caudata: Plethodontidae) and its evolutionary and biogeographical implications. Biological Journal of the Linnean Society 81: 325–346.

Parra-Olea, G., and D.B. Wake. 2001. Extreme morphological and ecological homoplasy in tropical salamanders. Proceedings of the National Academy of Sciences of the United States of America 98: 7888–7891.

Parsons, T.S., and E.E. Williams. 1963. The relationships of the modern Amphibia: a re–examination. Quarterly Review of Biology 38: 26–53.

Passmore, N.I., and V.C. Carruthers. 1979. South African frogs. Johannesburg: Witwatersrand University Press.

Patterson, C., and D.E. Rosen. 1977. Review of the ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. Bulletin of the American Museum of Natural History 158: 85–172.

Pauly, G.B., D.M. Hillis, and D.C. Cannatella. 2004. The history of Nearctic colonization: molecular phylogenetics and biogeography of the Nearctic toads (*Bufo*). Evolution 58: 2517–2535.

Peixoto, O.L. 1995. Associação de anuros a bromeliáceas na mata Atlântica. Revista de Universidade Federal Rural do Rio de Janeiro. Série Ciências da Vida 17: 75–83.

Pennisi, E. 2001. Linnaeus's last stand? Science 291: 2304–2307.

Perret, J.-L. 1966. Les amphibiens du Cameroun. Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie. Jena 93: 289–464.

Perret, J.-L. 1977. Les *Hylarana* (amphibiens, ranidés) du Cameroun. Revue Suisse de Zoologie 84: 841–868.

Perret, J.-L. 1984. Identification des syntypes de *Petropedetes obscurus* Ahl, 1924 (Amphibia, Phrynobatrachinae), conservés au muséum de Berlin. Bulletin de la Société Neuchâteloise des Sciences Naturelles 107: 167–170.

Peters, W.C.H. 1862. Über die Batrachier-Gattung *Hemiphractus*. Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin 1862: 144–152.

Philippe, H. 1993. MUST: management utilities for sequences and trees. Nucleic Acids Research 21: 5264–5272.

Phillips, A., D. Janies, and W.C. Wheeler. 2000. Multiple sequence alignment in phylogenetic analysis. Molecular Phylogenetics and Evolution 16: 317–330.

Pickett, K.M. 2005. The new and improved

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PhyloCode, now with types, ranks, and even polyphyly: a conference report from the First International Phylogenetic Nomenclature Meeting. Cladistics 21: 79–82.

Platnick, N.I. 1977. Cladograms, phylogenetic trees, and hypothesis testing. Systematic Zoology 26: 438–443.

Pombal, J.P., Jr. 1999. Oviposição e desenvolvimento de *Brachycephalus ephippium* (Spix) (Anura, Brachycephalidae). Revista Brasileira de Zoologia 16: 967–976.

Pombal, J.P., Jr., and C.F.B. Haddad. 1999. Frogs of the genus *Paratelmatobius* (Anura: Leptodactylidae) with descriptions of two new species. Copeia 1999: 1014–1026.

Pope, C.H. 1931. Notes on amphibians from Fukien, Hainan and other parts of China. Bulletin of the American Museum of Natural History 61: 397–611.

Posada, D., and K.A. Crandall. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14: 817–818.

Post, T.J., and T. Uzzell. 1981. The relationships of *Rana sylvatica* and the monophyly of the *Rana boylii* group. Systematic Zoology 30: 170–180.

Poynton, J.C. 1964a. Amphibia of southern Africa: a faunal study. Annals of the Natal Museum 17: 1–334.

Poynton, J.C. 1964b. Amphibia of the Nyasa-Luangwa region of Africa. Senckenbergiana Biologica 45: 193–225.

Poynton, J.C. 1976. Classification and the Arthroleptinae. Revue Zoologique Africaine 90: 215–220.

Poynton, J.C. 2003. *Arthroleptis troglodytes* and the content of *Schoutedenella* (Amphibia: Anura: Arthroleptidae). African Journal of Herpetology 52: 49–51.

Poynton, J.C., and D.G. Broadley. 1967. A new species of *Probreviceps* (Amphibia) from Rhodesia. Arnoldia. Zimbabwe 3: 1–3.

Poynton, J.C., and D.G. Broadley. 1985. Amphibia Zambesiaca 2. Ranidae. Annals of the Natal Museum 27: 115–181.

Poynton, J.C., and D.G. Broadley. 1988. Amphibia Zambesiaca, 4. Bufonidae. Annals of the Natal Museum 29: 447–490.

Pramuk, J.B. 2000. Prenasal bones and snout morphology in West Indian bufonids and the *Bufo granulosus* species group. Journal of Herpetology 34: 334–340.

Pramuk, J.B. 2002. Combined evidence and cladistic relationships of West Indian toads (Anura: Bufonidae). Herpetological Monographs 16: 121–151.

Pramuk, J.B., C.A. Hass, and S.B. Hedges. 2001. Molecular phylogeny and biogeography of West Indian toads (Anura: Bufonidae). Molecular Phylogenetics and Evolution 20: 294–301.

Pramuk, J.B., and J.R. Mendelson, III. 2003. *Anaxyrus melanocholicus* Tschudi: synonym of the Mexican taxon *Bufo compactilis* Wiegmann (Anura: Bufonidae). Southwestern Naturalist 48: 676–680.

Pregill, G.K. 1981. Cranial morphology and the evolution of West Indian toads: resurrection of the genus *Peltophryne* (Fitzinger). Copeia 1981: 273–285.

Procter, J.B. 1925. Notes on the nests of some African frogs. Proceedings of the Zoological Society of London 1925: 909–910.

Pugener, L.A., A.M. Maglia, and L. Trueb. 2003. Revisiting the contribution of larval characters to an analysis of phylogenetic relationships of basal anurans. Zoological Journal of the Linnean Society. London 139: 129–155.

Pusey, H.K. 1943. On the head of the liopelmid frog, *Ascaphus truei* I. The chondrocranium, jaws, arches, and muscles of a partly grown larva. Quarterly Journal of Microscopical Science 84: 106–185.

Pyburn, W.F. 1970. Breeding behavior of the leaf-frogs *Phyllomedusa callidryas* and *Phyllomedusa dacnicolor* in Mexico. Copeia 1970: 209–218.

Pytel, B.A. 1986. Biochemical systematics of the eastern North American frogs of the genus *Rana*. Herpetologica 42: 273–282.

Rabb, G.B. 1960. On the unique sound production of the Surinam toad, *Pipa pipa*. Copeia 1960: 368–369.

Rafinesque, C.S. 1814. Fine del prodromo d'erpetologia siciliana. Specchio delle Scienze, o, Giornale Enciclopedico di Sicilia 2: 102–104.

Rafinesque, C.S. 1815. Analyse de nature, ou tableau de l'universe et des corps organisés. Palermo: Jean Barravecchia.

Rambaut, A. 1995. Se-Al. Sequence alignment editor, version 1.d1. University of Oxford, U.K.: Computer software distributed by the author.

Rao, C.R.N. 1920. Some South Indian batrachians. Journal of the Bombay Natural History Society 27: 119–127.

Read, K., J.S. Keogh, I.A. Scott, J.D. Roberts, and P. Doughty. 2001. Molecular phylogeny of the Australian frog genera *Crinia*, *Geocrinia*, and allied taxa (Anura: Myobatrachidae). Molecular Phylogenetics and Evolution 21: 294–308.

Regal, P.J. 1966. Feeding specializations and the classification of terrestrial salamanders. Evolution 20: 392–407.

Reig, O.A. 1958. Proposiciones para una nueva

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macrosistematica de los anuros (nota preliminar). Physis. Buenos Aires 21: 109–118.

Reig, O.A. 1960. Las relaciones genéricas del anuro chileno *Calyptocephalella gayi* (Dum. & Bibr.). *In* Actas y trabajos del Primer Congreso Sudamericano de Zoología (La Plata, 12–24 Octubre 1959), vol. 4: 113–147. La Plata: Comisión de Investigación Científica de la Provincia de Buenos Aires y Consejo Nacional de Investigaciones Científicas y Técnicas.

Reig, O.A. 1972. *Macrogenioglottus* and the South American bufonid toads. *In* W.F. Blair (editor), Evolution in the genus *Bufo*: 14–36. Austin: University of Texas Press.

Richards, C.M., and W.S. Moore. 1996. A phylogeny for the African treefrog family Hyperoliidae based on mitochondrial rDNA. Molecular Phylogenetics and Evolution 5: 522–532.

Richards, C.M., and W.S. Moore. 1998. A molecular phylogenetic study of the Old World treefrog family Rhacophoridae. Herpetological Journal. London 8: 41–46.

Richards, C.M., R.A. Nussbaum, and C.J. Raxworthy. 2000. Phylogenetic relationships within the Madagascan boophids and mantellids as elucidated by mitochondrial ribosomal genes. African Journal of Herpetology 49: 23–32.

Rieppel, O., and M. de Braga. 1996. Turtles as diapsid reptiles. Nature. London 384: 453–455.

Risch, J.-P. 1985. The Himalayan salamander and its relatives: a short review of the Pleurodelinae (Amphibia, Caudata, Salamandridae). Journal of the Bengal Natural History Society. New Series 4: 139–143.

Ritgen, F.A. 1828. Versuch einer naturlichen Eintheilung der Amphibien. Nova Acta Physico-medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum. Halle 14: 277, 278.

Ritland, R.M. 1955. Studies on the post-cranial morphology of *Ascaphus truei*. II. Journal of Morphology 97: 215–282.

Roček, Z. 1981 ''1980''. Cranial anatomy of frogs of the family Pelobatidae Stannius, 1856, with outlines of their phylogeny and systematics. Acta Universitatis Carolinae. Biologica. Prague 1980: 1–160.

Roček, Z. 1989. Developmental pattern of the ethmoidal region of the anuran skull. *In* H. Splechtna (editor), Trends in vertebrate morphology: 412–515. Stuttgart: G. Fischer.

Roček, Z. 1990. Ethmoidal endocranial structures in primitive tetrapods: their bearing on the search for anuran ancestry. Zoological Journal of the Linnean Society. London 99: 389–407.

Roček, Z., and M. Vesely. 1989. Development of the ethmoidal structures of the endocranum in the anuran *Pipa pipa*. Journal of Morphology 200: 300–319.

Rödel, M.-O., J. Kosuch, M. Veith, and R. Ernst. 2003. First record of the genus *Acanthixalus* Laurent, 1944 from the upper Guinean rain forest, West Africa, with the description of a new species. Journal of Herpetology 37: 43–52.

Rodman, J.E., and J.H. Cody. 2003. The taxonomic impediment overcome: NSF's Partnerships for Enhancing Expertise in Taxonomy (PEET) as a model. Systematic Biology 52: 428–435.

Roelants, K., and F. Bossuyt. 2005. Archaeobatrachian paraphyly and Pangaean diversification of crown-group frogs. Systematic Biology 54: 111–126.

Roelants, K., J. Jiang, and F. Bossuyt. 2004. Endemic ranid (Amphibia: Anura) genera in southern mountain ranges of the Indian subcontinent represent ancient frog lineages: evidence from the molecular data. Molecular Phylogenetics and Evolution 31: 730–740.

Romer, A.S. 1933. Vertebrate paleontology. Chicago: University of Chicago Press.

Romer, A.S. 1945. Vertebrate paleontology, 2nd ed. Chicago: University of Chicago Press.

Ruiz-Carranza, P.M., and J.D. Lynch. 1991a. Ranas Centrolenidae de Colombia I. Propuesta de una nueva clasificacion generica. Lozania 57: 1–30.

Ruiz-Carranza, P.M., and J.D. Lynch. 1991b. Ranas Centrolenidae de Colombia II. Nuevas especies de *Centrolene* de la Cordillera Oriental y Sierra Nevada de Santa Marta. Lozania 58: 1–26.

Ruiz-Carranza, P.M., and J.D. Lynch. 1998. Ranas Centrolenidae de Colombia XI. Nuevas especies de ranas cristal del genero *Hyalinobatrachium*. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 22: 571–586.

Ruta, M., M.I. Coates, and D.L.J. Quicke. 2003. Early tetrapod relationships revisited. Biological Reviews of the Cambridge Philosophical Society 78: 251–345.

Ruvinsky, I., and L.R. Maxson. 1996. Phylogenetic relationships among bufonoid frogs (Anura: Neobatrachia) inferred from mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 5: 533–547.

Saint-Aubain, M.L., de. 1981. Amphibian limb ontogeny and its bearing on the phylogeny of the group. Zeitschrift für Zoologische Systematik und Evolutionsforschung 19: 175–194.

Salthe, S.N. 1967. The courtship patterns and the phylogeny of the urodeles. Copeia 1967: 100–117.

Sanchíz, F.B. 1984. Análisis filogenético de la tribu Alytini (Anura, Discoglossidae) mediante el

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estudio de su morfoestructura ósea. *In* H. Hemmer and J.A. Alcover (editors), Història bioògica del ferreret (Life history of the Mallorcan midwife toad): 61–108. Mallorca, Spain: Editorial Moll.

Sanchíz, F.B. 1998. Encyclopedia of paleoherpetology, vol. 4. Salientia. München: Dr. Friedrich Pfeil.

Sanchíz, F.B., and I. de la Riva. 1993. Remarks on the tarsus of centrolenid frogs (Amphibia, Anura). Graellsia 49: 115–117.

Sankoff, D. 1975. Minimal mutation trees of sequences. SIAM Journal on Applied Mathematics 28: 35–42.

Sankoff, D., R.J. Cedergren, and G. Lapalme. 1976. Frequency of insertion-deletion, transversion, and transition in evolution of 5S ribosomal RNA. Journal of Molecular Evolution 7: 133–149.

San Mauro, D., D.J. Gower, O.V. Oommen, M. Wilkinson, and R. Zardoya. 2004. Phylogeny of caecilian amphibians (Gymnophiona) based on complete mitochondrial genomes and nuclear RAG1. Molecular Phylogenetics and Evolution 33: 413–427.

San Mauro, D., M. Vences, M. Alcobendas, R. Zardoya, and A. Meyer. 2005. Initial diversification of living amphibians predated the breakup of Pangaea. American Naturalist 165: 590–599.

Santos, J.C., L.A. Coloma, and D.C. Cannatella. 2003. Multiple, recurring origins of aposematism and diet specialization in poison frogs. Proceedings of the National Academy of Sciences of the United States of America 100: 12792–12797.

Sarasin, P., and F. Sarasin. 1890. Zur Entiwicklungsgeschichte und Anatomie der ceylonischen Blindwuehle, *Ichthyophis glutinosus* (*Epicrium glutinosum* Aut.). Ergebnisse naturwissenschaftlicher Forschungen auf Ceylon in den Jahren 1884–86. Vol. II. Heft 4. Wiesbaden: C.W. Kreidel.

Savage, J.M. 1973. The geographic distribution of frogs: patterns and predictions. *In* J.L. Vial (editor), Evolutionary biology of the anurans: contemporary research on major problems: 351–445. Columbia: University of Missouri Press.

Savage, J.M. 1987. Systematics and distribution of the Mexican and Central American rainfrogs of the *Eleutherodactylus gollmeri* group (Amphibia: Leptodactylidae). Fieldiana. Zoology. New Series 33: 1–57.

Savage, J.M., and C.W. Myers. 2002. Frogs of the *Eleutherodactylus biporcatus* group (Leptodactylidae) of Central America and northern South America, including rediscovered, resurrected, and new taxa. American Museum Novitates 3357: 1–48.

Schäuble, C.S., C. Moritz, and R.W. Slade. 2000. A molecular phylogeny for the frog genus *Limnodynastes* (Anura: Myobatrachidae). Molecular Phylogenetics and Evolution 16: 379–391.

Scheel, J.J. 1970. Notes on the biology of the African tree-toad, *Nectophryne afra* Buchholz & Peters, 1875 (Bufonidae, Anura) from Fernando Poo. Revue de Zoologie et de Botanique Africaines 81: 225–236.

Scheltinga, D.M., B.G.M. Jamieson, D.P. Bickford, A.A. Garda, S.N. Bao, and K.R. McDonald. 2002. Morphology of the spermatozoa of the Microhylidae (Anura, Amphibia). Acta Zoologica. Stockholm 83: 263–275.

Schmidt, K.P., and R.F. Inger. 1959. Amphibians exclusive of the genera *Afrixalus* and *Hyperolius*. Exploration du Parc National de l'Upemba. Mission G.F. de Witte, en Collaboration avec W. Adam, A. Janssens, L. van Meel et R. Verheyen (1946–1949) 56: 1–264.

Schoch, R.R., and A.R. Milner. 2004. Structure and implications of theories on the origins of lissamphibians. *In* G. Arratia, M.V. Wilson, and R. Cloutier (editors), Recent advances in the origin and early radiation of vertebrates: 345–377. München: Pfeil.

Scholz, K.P. 1995. Zur Stammesgeschichte der Salamandridae Gray, 1825. eine kladistische Analyse anhand von Merkmalen aus Morphologie und Balzverhalten. Acta Biologica Benrodis 7: 25–75.

Schuh, R.T. 2003. The Linnaean system and its 250-year persistence. Botanical Review 69: 59–79.

Schulte, R. 1989. Nueva especie de rana venenosa del genero *Epipedobates* registrada en la Cordillera Oriental, Departamento de San Martin. Boletín de Lima 11: 41–46.

Schwenk, K., and D.B. Wake. 1993. Prey processing in *Leurognathus marmoratus* and the evolution of form and function in desmognathine salamanders (Plethodontidae). Biological Journal of the Linnean Society 49: 141–162.

Scopoli, G.A. 1777. Introductio ad historiam naturalem, sistens genera lapidium, planatarum, et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae. Prague: Gerle.

Scott, E. 2002. Phylogenetic relationships of the subfamily Petropedetinae Noble, 1931 (Anura: Ranidae): a simultaneous analysis of morphological and molecular data. Ph.D. dissertation. Department of Zoology, University of the Western Cape, Bellville, South Africa.

Sever, D.M. 1990. Cloacal anatomy of female salamanders of the plethodontid subfamily Des-

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mognathinae (Amphibia: Urodela). Transactions of the American Microscopical Society 109: 193–204.

Sever, D.M. 1991a. Comparative anatomy and phylogeny of the cloacae of salamanders (Amphibia: Caudata). 1. Evolution at the family level. Herpetologica 47: 165–193.

Sever, D.M. 1991b. Comparative anatomy and phylogeny of the cloacae of salamanders (Amphibia: Caudata). 2. Cryptobranchidae, Hynobiidae, and Sirenidae. Journal of Morphology 207: 283–301.

Sever, D.M. 1992. Comparative anatomy and phylogeny of the cloacae of salamanders (Amphibia: Caudata). VI. Ambystomatidae and Dicamptodontidae. Journal of Morphology 212: 305–322.

Sever, D.M. 1994. Comparative anatomy and phylogeny of the cloacae of salamanders (Amphibia: Caudata). VII. Plethodontidae. Herpetological Monographs 7: 276–337.

Sever, D.M., E.A. Heinz, P.A. Lempart, and M.S. Taghon. 1990. Phylogenetic significance of the cloacal anatomy of female bolitoglossine salamanders (Plethodontidae: tribe Bolitoglossini). Herpetologica 46: 431–446.

Shaffer, H.B., J.M. Clark, and F. Kraus. 1991. When molecules and morphology clash: a phylogenetic analysis of the North American ambystomatid salamanders (Caudata: Ambystomatidae). Systematic Zoology 40: 284–303.

Sharrock, G., and J. Felsenstein. 1975. Finding all monothetic subsets of a taxonomic group. Systematic Zoology 24: 373–377. [Cited as ''1969. manuscript in preparation'' by Liem, 1970.]

Sheil, C.A., J.R. Mendelson, III, and H.R. da Silva. 2001. Phylogenetic relationships of the species of Neotropical horned frogs, genus *Hemiphractus* (Anura: Hylidae: Hemiphractinae), based on evidence from morphology. Herpetologica 57: 203–214.

Shubin, N.H., and F.A. Jenkins. 1995. An early Jurassic jumping frog. Nature. London 377: 49–52.

Silva, A.P.Z., C.F.B. Haddad, and S. Kasahara. 2003. Chromosome banding in *Macrogenioglottus alipioi* Carvalho, 1946 (Amphibia, Anura, Leptodactylidae), with comments on its taxonomic position. Boletim do Museu Nacional, Rio de Janeiro. Nova Série, Zoologia. 499: 1–9.

Silverstone, P.A. 1975. A revision of the poison-arrow frogs of the genus *Dendrobates* Wagler. Natural History Museum of Los Angeles County Science Bulletin 21: 1–55.

Simmons, M.P. 2004. Independence of alignment and tree search. Molecular Phylogenetics and Evolution 31: 874–879.

Simmons, M.P., and H. Ochoterena. 2000. Gaps as characters in sequence-based phylogenetic analyses. Systematic Biology 49: 369–381.

Sinsch, U., and N. Juraske. 1995. Reassessment of central Peruvian Telmatobiinae (genera *Batrachophrynus* and *Telmatobius*) II. Allozymes and phylogenetic relationships. Alytes 13: 52–66.

Sinsch, U., A.W. Salas, and V. Canales. 1995. Reassessment of central Peruvian Telmatobiinae (genera *Batrachophrynus* and *Telmatobius*) I. Morphometry and classification. Alytes 13: 14–44.

Sites, J.W., Jr., M. Morando, R. Highton, F. Huber, and R.E. Jung. 2004. Phylogenetic relationships of the endangered Shenandoah Salamander (*Plethodon shenandoah*) and other salamanders of the *Plethodon cinereus* group (Caudata: Plethodontidae). Journal of Herpetology 38: 96–105.

Slabbert, G.K., and W.A. Maree. 1945. The cranial morphology of the Discoglossidae and its bearing upon the phylogeny of the primitive Anura. Annals of the University of Stellenbosch 23A: 91–97.

Slowinski, J.B. 1998. The number of multiple alignments. Molecular Phylogenetics and Evolution 10: 264–266.

Smith, M.A. 1930. The Reptilia and Amphibia of the Malay Peninsula. A supplement to G.A. Boulenger's Reptilia and Batrachia, 1912. Bulletin of the Raffles Museum 3: i–xviii, 1–149.

Sokol, O. 1975. The phylogeny of anuran larvae: a new look. Copeia 1975: 1–23.

Sokol, O. 1977. A subordinal classification of frogs (Amphibia: Anura). Journal of Zoology. London 182: 505–508.

Sokol, O. 1981. The larval chondrocranium of *Pelodytes punctatus*, with a review of tadpole chondrocrania. Journal of Morphology 169: 161–183.

Starrett, P.H. 1973. Evolutionary patterns in larval morphology. *In* J.L. Vial (editor), Evolutionary biology of the anurans: contemporary research on major problems: 251–271. Columbia: University of Missouri Press.

Steindachner, F. 1867. Amphibien. *In* Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorf-Urbair, Zoologischer Theil. 1: 1–98. Wien: Kaiserlich-Königliche Hof- und Staatsdruckerei; in Commission bei K. Gerold's Sohn.

Steinfartz, S., U.W. Hwang, D. Tautz, M. Öz, and M. Veith. 2002. Molecular phylogeny of the salamandrid genus *Neurergus*: evidence for an

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intrageneric switch of reproductive biology. Amphibia-Reptilia 23: 419–431.

Stejneger, L. 1907. Herpetology of Japan and adjacent territory. Bulletin of the United States National Museum 58: i–xx, 1–577.

Stejneger, L., and T. Barbour. 1917. A check list of North American amphibians and reptiles. Cambridge, MA: Harvard University Press.

Stephenson, E.M., E.S. Robinson, and N.G. Stephenson. 1974. Inter-specific relationships of *Leiopelma* (Amphibia: Anura): further karyological evidence. Experientia 30: 1248–1250.

Stephenson, N.G. 1951. Observations on the development of the amphicoelous frogs, *Leiopelma* and *Ascaphus*. Journal of the Linnean Society of London. Zoology 42: 18–28.

Stoll, N. 1961. Introduction. *In* International Commission of Zoological Nomenclature (editors), International code of zoological nomenclature adopted by the XV International Congress of Zoology: vii–xvii. London: International Trust for Zoological Nomenclature.

Stuart, B.L., and T. Chan-ard. 2005. Two new *Huia* (Amphibia: Ranidae) from Laos and Thailand. Copeia 2005: 279–289.

Stuart, S.N., J.S. Chanson, N.A. Cox, B.E. Young, A.S.L. Rodrigues, D.L. Fischman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306: 1783–1786.

Sumida, M., A. Allison, and M. Nishioka. 2000a. Evolutionary relationships among 12 species belonging to three genera of the family Microhylidae in Papua New Guinea revealed by allozyme analysis. Biochemical Systematics and Ecology 28: 721–736.

Sumida, M., Y. Kondo, Y. Kanamori, and M. Nishioka. 2002. Inter- and intraspecific evolutionary relationships of the rice frog *Rana limnocharis* and the allied species *R. cancrivora* inferred from crossing experiements and mitochondrial DNA sequences of the 12S and 16S rRNA genes. Molecular Phylogenetics and Evolution 25: 293–305.

Sumida, M., M. Ogata, and M. Nishioka. 2000b. Molecular phylogenetic relationships of pond frogs distributed in the Palearctic Region inferred from DNA sequences of mitochondrial 12S ribosomal RNA and cytochrome b genes. Molecular Phylogenetics and Evolution 16: 278–285.

Swofford, D.L. 2002. PAUP*. Phylogenetic analysis using parsimony (*and other methods), version 4.0 beta. Sunderland, MA: Sinauer Associates.

Swofford, D.L., G.J. Olsen, P.J. Waddell, and D.M. Hillis. 1996. Phylogenetic inference. *In* D.M. Hillis, C. Moritz, and B.K. Mable (editors), Molecular systematics: 407–514. Sunderland, MA: Sinauer Associates.

Tamarunov, L.P. 1964a. Salientia. *In* Y.A. Orlov (editor), Osnovy paleontologii: spravochnik dlia paleontologov i geologov SSSR, vol. 12. Amphibia–Aves: 125–133. Moscow: Nauka.

Tamarunov, L.P. 1964b. Lepospondyli. *In* Y.A. Orlov (editor), Osnovy paleontologii: spravochnik dlia paleontologov i geologov SSSR, vol. 12. Amphibia–Aves: 144–164. Moscow: Nauka.

Tanaka-Ueno, T., M. Matsui, S.-L. Chen, O. Takenaka, and H. Ota. 1998a. Phylogenetic relationships of brown frogs from Taiwan and Japan assessed by mitochondrial cytochrome *b* gene sequences (Rana: Ranidae). Zoological Science. Tokyo 15: 283–288.

Tanaka-Ueno, T., M. Matsui, T. Sato, S. Takenaka, and O. Takenaka. 1998b. Phylogenetic relationships of brown frogs with 24 chromosomes from Far East Russia and Hokkaido assessed by mitochondrial cytochrome b gene sequences (*Rana*: Ranidae). Zoological Science. Tokyo 15: 289–294.

Tandy, M., and R. Keith. 1972. *Bufo* of Africa. *In* W.F. Blair (editor), Evolution in the genus *Bufo*: 119–170. Austin: University of Texas Press.

Taylor, E.H. 1951. Two new genera and a new family of tropical American frogs. Proceedings of the Biological Society of Washington 64: 33–40.

Taylor, E.H. 1968. The caecilians of the world: a taxonomic review. Lawrence: University of Kansas Press.

Taylor, E.H. 1969a. A new family of African Gymnophiona. University of Kansas Science Bulletin 48: 297–305.

Taylor, E.H. 1969b. Skulls of Gymnophiona and their significance in the taxonomy of the group. University of Kansas Science Bulletin 48: 585–687.

Thibaudeau, G., and R.I. Altig. 1999. Endotrophic anurans. Development and evolution. *In* R.W. McDiarmid and R. Altig (editors), Tadpoles: the biology of anuran larvae: 170–188. Chicago: University of Chicago Press.

Thompson, J.D., T.J. Gibson, F.J. Plewniak, F., and D.G. Higgins. 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Research 24 4876–4882.

Thompson, J.D., D.G. Higgins, and T.J. Gibson. 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignments through sequence weighting, position specific

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gap penalties and weight matrix choice. Nucleic Acids Research 22: 4673–4680.

Tian, W., and Q. Hu. 1985. Taxonomical studies on the primitive anurans of the Hengduan Mountains, with descriptions of a new subfamily and subdivision of *Bombina*. Acta Herpetologica Sinica, New Series 4: 219–224.

Tihen, J.A. 1958. Comments on the osteology and phylogeny of ambystomatid salamanders. Bulletin of the Florida Museum of Natural History. Biological Sciences 3: 1–50.

Tihen, J.A. 1960. Two new genera of African bufonids, with remarks on the phylogeny of related genera. Copeia 1960: 225–233.

Tihen, J.A. 1965. Evolutionary trends in frogs. American Zoologist 5: 309–318.

Tilley, S.G., and J. Bernardo. 1993. Life history evolution in plethodontid salamanders. Herpetologica 49: 154–163.

Ting, H.-P., and M.-C. T'sai. 1979. A new species of frog (*Rana minimus*) from Fujian Province. Acta Zootaxonomica Sinica 4: 297–300. [In Chinese with English abstract.]

Titus, T.A., and A. Larson. 1995. A molecular phylogenetic perspective on the evolutionary radiation of the salamander family Salamandridae. Systematic Biology 44: 125–151.

Titus, T.A., and A. Larson. 1996. Molecular phylogenetics of desmognathine salamanders (Caudata: Plethodontidae): a reevaluation of evolution in ecology, life history, and morphology. Systematic Biology 45: 451–472.

Trewevas, E. 1933. The hyoid and larynx of the Anura. Philosophical Transactions of the Royal Society of London, B, Biological Sciences 222: 401–527.

Trontelj, P., and S. Goricki. 2003. Monophyly of the family Proteidae (Amphibia: Caudata) tested by phylogenetic analysis of mitochondrial 12S rDNA sequences. Natura Croatica. Zagreb 12: 113–120.

Trueb, L. 1993. Patterns of cranial diversity among the Lissamphibia (Amphibia, Temnospondyli). *In* J. Hanken and B.K. Hall (editors), The skull: 255–343. Chicago: University of Chicago Press.

Trueb, L., and D.C. Cannatella. 1986. Systematics, morphology, and phylogeny of genus *Pipa* (Anura: Pipidae). Herpetologica 42: 412–449.

Trueb, L., and R. Cloutier. 1991. A phylogenetic investigation of the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondyli). *In* H.P. Schultze and L. Trueb (editors), Origins of the higher groups of tetrapods: controversy and consensus: 223–313. Ithaca, NY: Cornell University Press.

Tschudi, J.J., von. 1838. Classification der Batrachier mit Berücksichtigung der fossilen Thiere dieser Abtheilung der Reptilien. Neuchâtel: Petitpierre.

Tschudi, J.J., von. 1845. Reptilium conspectus quae in Republica Peruana reperiuntur et pleraquae observata vel collecta sunt in itinere a Dr. J.J. de Tschudi. Archiv für Naturgeschichte 11: 150–170.

Tyler, M.J. 1971a. The occurrence of the musculus cutaneous pectoris in the Anura. Herpetologica 27: 150–152.

Tyler, M.J. 1971b. Observations on anuran myointegumental attachments associated with the vocal sac apparatus. Journal of Natural History 5: 225–231.

Tyler, M.J. 1971c. The phylogenetic significance of vocal sac structure in hylid frogs. University of Kansas Publications. Museum of Natural History 19: 319–360.

Tyler, M.J. 1972. Superficial mandibular musculature, vocal sacs and the phylogeny of Australo-Papuan leptodactylid frogs. Records of the South Australian Museum 16: 1–20.

Tyler, M.J. 1979. Herpetofauna relationships of South America with Australia. *In* W.E. Duellman (editor), The South American herpetofauna: its origin, evolution, and dispersal. University of Kansas Museum of Natural History, Monograph 7: 73–106.

Tyler, M.J. 1982. Frogs, 2nd ed. Sydney: Collins.

Tyler, M.J. 1985. Reproductive modes in Australian Amphibia. *In* G. Grigg, R. Shine, and H. Ehman (editors), Biology of Australasian frogs and reptiles: 265–267. Sydney: Royal Zoological Society of New South Wales.

Tyler, M.J. 1989. Australian frogs. Ringwood, Victoria, Australia: Viking O'Neil.

Tyler, M.J., and M.M. Davies. 1978. Species-groups within the Australopapuan hylid frog genus *Litoria* Tschudi. Australian Journal of Zoology, Supplementary Series 63: 1–47.

Tyler, M.J., and W.E. Duellman. 1995. Superficial mandibular musculature and vocal sac structure in hemiphractine hylid frogs. Journal of Morphology 224: 65–71.

Uzzell, T., and T.J. Post. 1986. *Rana temporaria* is not a member of the *Rana boylii* group. Systematic Zoology 35: 414–421.

Vallan, D., M. Vences, and F. Glaw. 2003. Two new species of the *Boophis mandraka* complex (Anura, Mantellidae) from the Andasibe region in eastern Madagascar. Amphibia-Reptilia 24: 305–319.

Van der Hoeven, J. 1833. Handboek der dierkunde, grondbeginsels der natuurlijke geschiedenis

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van het dierenrijk, tweeden deels, tweede stuk. Amsterdam: C.G. Sulpke.

Van der Meijden, A., M. Vences, S. Hoegg, and A. Meyer. 2005. A previously unrecognized radiation of ranid frogs in southern Africa revealed by nuclear and mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 37: 674–685. [Seen as an electronic/pdf preprint available from the publisher.]

Van der Meijden, A., M. Vences, and A. Meyer. 2004. Novel phylogenetic relationships of the enigmatic brevicipitine and scaphiophrynine toads as revealed by sequences from the nuclear *Rag-1* gene. Proceedings of the Royal Society of London. B (Supplement—Biology Letters) 271: S378–S381.

Van Dijk, D.E. 2001. Osteology of the ranoid burrowing African anurans *Breviceps* and *Hemisus*. African Zoology. Pretoria 36: 137–141.

Van Gelder, R.G. 1977. Mammalian hybrids and generic limits. American Museum Novitates 2635: 1–25.

Veith, M., and S. Steinfartz. 2004. When nonmonophyly results in taxonomic consequences—the case of *Mertensiella* within the Salamandridae (Amphibia: Urodela). Salamandra 40: 67–80.

Vences, M., F. Andreone, F. Glaw, and J.E. Randrianirina. 2003a. Molecular and bioacoustic divergence in *Mantidactylus granulatus* and *M. zavona* n. sp. (Anura: Mantellidae): bearings for the biogeography of northern Madagascar. African Zoology. Pretoria 38: 67–78.

Vences, M., and F. Glaw. 2001. When molecules claim for taxonomic changes: new proposals on the classification of Old World treefrogs (Amphibia, Anura, Ranoidea). Spixiana. München 24: 85–92.

Vences, M., and F. Glaw. 2004. Revision of the subgenus *Chonomantis* (Anura: Mantellidae: *Mantidactylus*) from Madagascar, with description of two new species. Journal of Natural History. London 38: 77–118.

Vences, M., F. Glaw, F. Andreone, R. Jesu, and G. Schimmenti. 2002. Systematic revision of the enigmatic Malagasy broad-headed frogs (*Laurentomantis* Dubois, 1980) and their phylogenetic position within the endemic mantellid radiation of Madagascar. Bijdragen tot de Dierkunde 70: 191–212.

Vences, M., F. Glaw, J. Kosuch, I. Das, and M. Veith. 2000a. Polyphyly of *Tomopterna* (Amphibia: Ranidae) based on sequences of the mitochondrial 16S and 12S rRNA genes, and ecological biogeography of Malagasy relict amphibian groups. *In* W.R. Lourenço and S.M. Goodman (editors), Diversité et endéémisme à Madagascar/Diversity and endemism in Madagascar: 229–242. Mémoires de la Société de Biogéographie. Paris.

Vences, M., J. Kosuch, R. Boistel, C.F.B. Haddad, E. La Marca, and S. Lötters. 2003b. Convergent evolution of aposematic coloration in Neotropical poison frogs: a molecular phylogenetic perspective. Organisms, Diversity & Evolution 3: 215–226.

Vences, M., J. Kosuch, F. Glaw, W. Böhme, and M. Veith. 2003c. Molecular phylogeny of hyperoliid treefrogs: biogeographic origin of Malagasy and Seychellean taxa and re-analysis of familial paraphyly. Journal of Zoological Systematics and Evolutionary Research 41: 205–213.

Vences, M., J. Kosuch, S. Lötters, A. Widmer, K.H. Jungfer, J. Köhler, and M. Veith. 2000b. Phylogeny and classification of poison frogs (Amphibia: Dendrobatidae), based on mitochondrial 16S and 12S ribosomal RNA gene sequences. Molecular Phylogenetics and Evolution 15: 34–40.

Vences, M., D.R. Vieites, F. Glaw, H. Brinkmann, J. Kosuch, M. Veith, and A. Meyer. 2003d. Multiple overseas dispersal in amphibians. Proceedings of the Royal Society of London. Series B, Biological Sciences 270: 2435–2442.

Vences, M., S. Wanke, G. Odierna, J. Kosuch, and M. Veith. 2000c. Molecular and karyological data on the south Asian ranid genera *Indirana*, *Nyctibatrachus* and *Nannophrys* (Anura: Ranidae). Hamadryad 25: 75–82.

Wagler, J.G. 1828. Vorläufige Uebersicht des Geruftes, sowie Untungigung feines Systema amphibiorum. Isis von Oken 21: 859–861.

Wagler, J.G. 1830. Natürliches System der Amphibien, mit vorangehender Classification der Säugthiere und Vogel. Ein Beitrag zur vergleichenden Zoologie. München, Stuttgart and Tübingen: J.G. Cotta.

Wake, D.B. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. Memoires of the Southern California Academy of Sciences 4: 1–111.

Wake, D.B. 1993. Phylogenetic and taxonomic issues relating to salamanders of the family Plethodontidae. Herpetologica 49: 229–237.

Wake, D.B., and P. Elias. 1983. New genera and new species of Central American salamanders, with a review of the tropical genera (Amphibia, Caudata, Plethodontidae). Natural History Museum of Los Angeles County Contributions in Science. 345: 1–19.

Wake, D.B., and J.F. Lynch. 1976. The distribution, ecology and evolutionary history of pleth-

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odontid salamanders in tropical America. Natural History Museum of Los Angeles County Science Bulletin 175: 1–65.

Wake, D.B., L.R. Maxson, and G.Z. Wurst. 1978. Genetic differentiation, albumin evolution, and their biogeographic implications in plethodontid salamanders of California and southern Europe. Evolution 32: 529–539.

Wake, M.H. 1977. Fetal maintenance and its evolutionary significance in the Amphibia: Gymnophiona. Journal of Herpetology 11: 379–386.

Wake, M.H. 1980. The reproductive biology of *Nectophrynoides malcolmi* (Amphibia: Bufonidae), with comments on the evolution of reproductive modes in the genus *Nectophrynoides*. Copeia 1980: 193–209.

Wake, M.H. 1993. Non-traditional characters in the assessment of caecilian phylogenetic relationships. Herpetological Monographs 7: 42–55.

Wake, M.H., G. Parra-Olea, and J.P.-Y. Shee. 2005. Biogeography and molecular phylogeny of certain New World caecilians. *In* M.A. Donnelly, B.I. Crother, C. Guyer, M.H. Wake, and M.E. White (editors), Ecology and evolution in the tropics: a herpetological perspective: 48–64. Chicago: University of Chicago Press.

Walls, J.G. 1994. Jewels of the rainforest—poison frogs of the family Dendrobatidae. Neptune City, New Jersey: T.F.H. Publications.

Wang, L., and T. Jiang. 1994. On the complexity of multiple sequence alignment. Journal of Computational Biology 1: 337–348.

Wassersug, R.J. 1984. The *Pseudohemisus* tadpole: a morphological link between microhylid (Orton Type 2) and ranoid (Orton Type 4) larvae. Herpetologica 40: 138–148.

Wassersug, R.J., and W.R. Heyer. 1983. Morphological correlates of subaerial existence in leptodactylid tadpoles associated with flowing water. Canadian Journal of Zoology 61: 761–769.

Wassersug, R.J., and W.F. Pyburn. 1987. The biology of the Pe-ret toad, *Otophryne robusta* (Microhylidae), with special consideration of its fossorial larva and systematic relationships. Zoological Journal of the Linnean Society. London 91: 137–169.

Wei, G., N. Xu, D. Li, G. Wu, and X. Song. 1993. Karyotype C-band and Ag-NORs study of three stink frogs. Asiatic Herpetological Research 5: 45–50.

Werner, F. 1896. Beiträge zur Kenntniss der Reptilien und Batrachier von Centralamerika und Chile, sowie einiger seltenerer Schlangenarten. Verhandlungen des Zoologisch-Botanischen Vereins in Wien 46: 344–365.

Wheeler, Q.D., P.H. Raven, and E.O. Wilson. 2004. Taxonomy: impediment or expedient? Science 303: 285.

Wheeler, W.C. 1992. Extinction, sampling, and molecular phylogenetics. *In* M.J. Novacek and Q.D. Wheeler (editors), Extinction and phylogeny: 205–215. New York: Columbia University Press.

Wheeler, W.C. 1994. Sources of ambiguity in nucleic acid sequence alignment. *In* B. Schierwater, B. Streit, G.P. Wagner, and R. DeSalle (editors), Molecular ecology and evolution: approaches and applications: 323–352. Basel, Switzerland: Birkhäuser.

Wheeler, W.C. 1995. Sequence alignment, parameter sensitivity, and the phylogenetic analysis of molecular data. Systematic Biology 44: 321–331.

Wheeler, W.C. 1996. Optimization alignment: the end of multiple sequence alignment in phylogenetics? Cladistics 12: 1–9.

Wheeler, W.C. 1998. Alignment characters, dynamic programing and heuristic solutions. *In* R. DeSalle and B. Schierwater (editors), Molecular approaches to ecology and evolution, 2nd ed.: 243–251. Basel, Switzerland: Birkhäuser.

Wheeler, W.C. 1999. Fixed character states and the optimization of molecular sequence data. Cladistics 15: 379–385.

Wheeler, W.C. 2000. Heuristic reconstruction of hypothetical-ancestral DNA sequences: sequence alignment vs optimization. *In* R.W. Scotland and R.T. Pennington (editors), Homology and systematics: 106–113. New York: Taylor and Francis.

Wheeler, W.C. 2001. Homology and the optimization of DNA sequence data. Cladistics 17: S3–S11.

Wheeler, W.C. 2002. Optimization alignment: down, up, error, and improvements. *In* R. DeSalle, G. Giribet, and W.C. Wheeler (editors), Techniques in molecular systematics and evolution: 55–69. Basel, Switzerland: Birkhäuser.

Wheeler, W.C. 2003a. Iterative pass optimization of sequence data. Cladistics 19: 254–260.

Wheeler, W.C. 2003b. Implied alignment: a synapomorphy-based multiple sequence alignment method. Cladistics 19: 261–268.

Wheeler, W.C. 2003c. Search-based optimization. Cladistics 19: 348–355.

Wheeler, W.C., and D.S. Gladstein. 1992. Malign, version 1.2. New York: Computer software distributed by the authors.

Wheeler, W.C., D.S. Gladstein, and J. De Laet. 1996–2003. POY: Phylogeny reconstruction via optimization of DNA data. New York: Com-

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puter software distributed by the authors and from the American Museum of Natural History: ftp://ftp.amnh.org/pub/molecular/poy.

Widmer, A., S. Lötters, and K.-H. Jungfer. 2000. A molecular phylogenetic analysis of the Neotropical dart-poison frog genus *Phyllobates* (Amphibia: Dendrobatidae). Naturwissenschaften. Berlin 87: 559–562.

Wieczorek, A.M., A. Channing, and R.C. Drewes. 1998. A review of the taxonomy of the *Hyperolius viridiflavus* complex. Herpetological Journal. London 8: 29–34.

Wieczorek, A.M., R.C. Drewes, and A. Channing. 2000. Biogeography and evolutionary history of *Hyperolius* species: application of molecular phylogeny. Journal of Biogeography. Oxford 27: 1231–1243.

Wieczorek, A.M., R.C. Drewes, and A. Channing. 2001. Phylogenetic relationships within the *Hyperolius viridiflavus* complex (Anura: Hyperoliidae), and comments on taxonomic status. Amphibia-Reptilia 22: 155–166.

Wied-Neuwied, M.A.P., Prinz zu. 1825. Beiträge zur Naturgeschichte von Brasilien, vol. 1 (Verzeichniss der Amphibien). Weimar, Germany: Gr. H.S. priv. Landes-Industrie-Comptoir.

Wiedersheim, R. 1877. Das Kopfskelet der Urodelen (Fortsetzung). Morphologisches Jahrbuch. Leipzig 3: 459–548.

Wiens, J.J. 1989. Ontogeny of the skeleton of *Spea bombifrons* (Anura: Pelobatidae). Journal of Morphology 202: 29–51.

Wiens, J.J., R.M. Bonett, and P.T. Chippindale. 2005. Ontogeny discombobulates phylogeny: paedomorphosis and higher-level salamander relationships. Systematic Biology 54: 91–110.

Wild, E.R. 1995. New genus and species of Amazonian microhylid frog with a phylogenetic analysis of New World genera. Copeia 1995: 837–849.

Wild, E.R. 1997. Description of the adult skeleton and developmental osteology of the hyperossified horned frog, *Ceratophrys cornuta* (Anura: Leptodactylidae). Journal of Morphology 232: 169–206.

Wild, E.R. 1999. Description of the chondrocranium and osteogenesis of the chacoan burrowing frog, *Chacophrys pierotti* (Anura: Leptodactylidae). Journal of Morphology 242: 229–249.

Wiley, E.O. 1981. Phylogenetics. The theory and practice of phylogenetic systematics. New York: Wiley Interscience.

Wilkinson, J.A., and R.C. Drewes. 2000. Character assessment, genus level boundaries, and phylogenetic analysis of the family Rhacophoridae: a review and present day status. Contemporary Herpetology 2000: 1–14. [Electronic journal available at http://www.nhm.ac.uk/hosted_sites/ch/ch/index.htm.]

Wilkinson, J.A., R.C. Drewes, and O.L. Tatum. 2002. A molecular phylogenetic analysis of the family Rhacophoridae with an emphasis on the Asian and African genera. Molecular Phylogenetics and Evolution 24: 265–273.

Wilkinson, J.A., M. Matsui, and T. Terachi. 1996. Geographic variation in a Japanese tree frog (*Rhacophorus arboreus*) revealed by PCR-aided restriction site analysis of mtDNA. Journal of Herpetology 30: 418–423.

Wilkinson, M. 1991. Adult tooth crown morphology in the Typhlonectidae (Amphibia: Gymnophiona): a reinterpretation of variation and its significance. Zeitschrift für Zoologische Systematik und Evolutionsforschung 29: 304–311.

Wilkinson, M. 1997. Characters, congruence and quality: a study of neuroanatomical and traditional data in caecilian phylogeny. Biological Reviews of the Cambridge Philosophical Society 72: 423–470.

Wilkinson, M., S.P. Loader, D.J. Gower, J.A. Sheps, and B.L. Cohen. 2003. Phylogenetic relationships of African caecilians (Amphibia: Gymnophiona): insights from mitochondrial rRNA gene sequences. African Journal of Herpetology 52: 83–92.

Wilkinson, M., and R.A. Nussbaum. 1996. On the phylogenetic position of the Uraeotyphlidae (Amphibia: Gymnophiona). Copeia 1996: 550–562.

Wilkinson, M., and R.A. Nussbaum. 1999. Evolutionary relationships of the lungless caecilian *Atretochoana eiselti* (Amphibia: Gymnophiona: Typhlonectidae). Zoological Journal of the Linnean Society. London 126: 191–223.

Wilkinson, M., J.A. Sheps, O.V. Oommen, and B.L. Cohen. 2002. Phylogenetic relationships of Indian caecilians (Amphibia: Gymnophiona) inferred from mitochondrial rRNA gene sequences. Molecular Phylogenetics and Evolution 23: 401–407.

Wilkinson, M., J. Thorley, and M.J. Benton. 1997. Uncertain turtle relationships. Nature. London 387: 466.

Withgott, J. 2000. Is it ''So long, Linnaeus''? BioScience 50: 646–651.

Wogel, H., P.A. Abrunhosa, and J.P. Pombal, Jr. 2004. Vocalizations and aggressive behavior of *Phyllomedusa rohdei* (Anura: Hylidae). Herpetological Review 35: 239–243.

Wu, L., R. Xu, Q. Dong, D. Li, and J. Liu. 1983. A new species of *Rana* and records of amphibians from Guizhou Province. Acta Zoologica

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Sinica 29: 66–70. [In Chinese, with English summary.]

Wu, S.-H. 1994. Phylogenetic relationships, higher classification and historical biogeography of the microhyloid frogs (Lissampibia: Anura: Brevicipitidae and Microhylidae). Ph.D. dissertation. Department of Zoology, University of Michigan, Ann Arbor.

Xie, F., and Z. Wang. 2000. [Review of the systematics of pelobatids.] Cultum Herpetologica Sinica 8: 356–370. [In Chinese.]

Yang, D. (editor), 1991a. [The Amphibia-fauna of Yunnan.] Beijing, China: China Forestry Publishing House. [In Chinese.]

Yang, D. 1991b. Phylogenetic systematics of the *Amolops* group of ranid frogs of southeastern Asia and the Greater Sunda Islands. Fieldiana. Zoology. New Series 63: 1–42.

Yang, D., and S. Li. 1980. A new species of the genus *Rana* from Yunnan. Zoological Research. Kunming 1: 261–264.

Yokoyama, S., H. Zhang, F.B. Radlwimmer, and N.S. Blow. 1999. Adaptive evolution of color vision of the Comoran coelacanth (*Latimeria chalumnae*). Proceedings of the National Academy of Sciences of the United States of America 96: 6279–6284.

Young, B.E., K.R. Lips, J.K. Reaser, R. Ibáñez D., A.W. Salas, J.R. Cedeño, L.A. Coloma, S.R. Ron, E. La Marca, J.R. Meyer, A. Muñoz, F. Bolaños, G. Chaves, and D. Romo. 2001. Population declines and priorities for amphibian conservation in Latin America. Conservation Biology 15: 1213–1223.

Zacj, I., and J.W. Arntzen. 1999. Phylogenetic relationships of the European newts (genus *Triturus*) tested with mitochondrial DNA sequence data. Contributions to Zoology. Amsterdam 68: 78–81.

Zaldívar-Riverón, A., V. León-Regagnon, and A. Nieto-Montes de Oca. 2004. Phylogeny of the Mexican coastal leopard frogs of the *Rana berlandieri* group based on mtDNA sequences. Molecular Phylogenetics and Evolution 30: 38–49.

Zardoya, R., and A. Meyer. 1996. Evolutionary relationships of the coelacanth, lungfishes, and tetrapods based on the 28S ribosomal RNA gene. Proceedings of the National Academy of Sciences United States of America 93: 5449–5454.

Zardoya, R., and A. Meyer. 1998. Complete mitochondrial genome suggests diapsid affinities of turtles. Proceedings of the National Academy of Sciences of the United States of America 95: 14226–14231.

Zardoya, R., and A. Meyer. 2000. Mitochondrial evidence on the phylogenetic position of caecilians (Amphibia: Gymnophiona). Genetics 155: 765–775.

Zardoya, R., and A. Meyer. 2001. On the origin of and phylogenetic relationships among living amphibians. Proceedings of the National Academy of Sciences of the United States of America 98: 7380–7383.

Zhang, P., Y.Q. Chen, Y.F. Liu, H.-Y. Zhou, and L.H. Qu. 2003a. The complete mitochondrial genome of the Chinese giant salamander, *Andrias davidianus* (Amphibia: Caudata). Gene 311: 93–98.

Zhang, P., Y.Q. Chen, H.-Y. Zhou, X.L. Wang, and L.H. Qu. 2003b. The complete mitochondrial genome of a relic salamander, *Ranodon sibiricus* (Amphibia: Caudata) and implications for amphibian phylogeny. Molecular Phylogenetics and Evolution 28: 620–626.

Zhao, E. 1994. A study on vomerine teeth pattern of the genus *Liua*, with revised diagnoses of *Liua* and *Ranodon* (Caudata: Hynobiidae). Sichuan Journal of Zoology 13: 162–166.

Zhao, E., and S.-Q. Li. 1984. A new species of the genus *Platymantis* (Amphibia: Ranidae) from Xizang. Acta Herpetologica Sinica, New Series 3: 55–57. [In Chinese with English summary.]

Ziegler, M., and M. Vences. 2002. The tadpole of *Rhacophorus verrucosus* Boulenger, 1893, from Vietnam (Amphibia: Anura: Rhacophoridae). Faunistische Abhandlungen. Staatliches Museum für Tierkunde in Dresden 22: 319–327.

Zug, G.R., L.J. Vitt, and J.P. Caldwell. 2001. Herpetology: an introductory biology of amphibians and reptiles. New York: Academic Press.

Zweifel, R.G. 1955. Ecology, distribution, and systematics of frogs of the *Rana boylei* group. University of California Publications in Zoology 54: 207–292.

Zweifel, R.G. 1956. Two pelobatid frogs from the Tertiary of North America and their relationships to fossil and recent forms. American Museum Novitates 1762: 1–45.

Zweifel, R.G. 1971. Results of the Archbold Expeditions. No. 96. Relationships and distribution of *Genyophryne thomsoni*, a microhylid frog of New Guinea. American Museum Novitates 2469: 1–13.

Zweifel, R.G. 1972. Results of the Archbold Expeditions. No. 97. A revision of the frogs of the subfamily Asterophryinae, family Microhylidae. Bulletin of the American Museum of Natural History 148: 411–546.

Zweifel, R.G. 1986. A new genus and species of microhylid frog from the Cerro de la Neblina region of Venezuela and a discussion of rela-

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tionships among New World microhylid genera. American Museum Novitates 2863: 1–24.

Zweifel, R.G. 2000. Partition of the Australopapuan microhylid frog genus *Sphenophryne* with descriptions of new species. Bulletin of the American Museum of Natural History 253: 1–130.

Zwickl, D.J., and D.M. Hillis. 2002. Increased taxon sampling greatly reduces phylogenetic error. Systematic Biology 51: 588–598.

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APPENDIX 1

Voucher and DNA Locus Information

Below we provide the specimen or tissue identification (ID) numbers (or source, if ID number unavailable), localities, GenBank numbers, and total number of base pairs (bp) analyzed for each terminal in the analysis. The locus mtDNA refers to 12S, $tRNA^{Val}$, and 16S sequences, and SIA refers to the gene Seven in Absentia. Asterisks (*) mark the 85 species for which all sequence data were obtained from GenBank and not generated by us. Species for which morphological data were included from Haas (2003) are in boldface. Sequences obtained from or previously deposited in GenBank are given in bold (see appendix 2 for references); all other sequences are new. ID numbers and localities are given only for sequences generated by us. Localities for conspecific tissues are separated by a semicolon. Abbreviations are: **ABTC** (Australian Biological Tissue Collection, South Australian Museum, Adelaide), **AC** (Alan Channing field series), **ACD** (Arvin C. Deismos field series), **AH** (Alexander Haas), **AMCC** (Ambrose Monell Cryo-Collection, American Museum of Natural History, New York); **AMNH** (American Museum of Natural History, New York), **AMS** (Australian Museum, Sydney), **ARBT** (Adam Backlin field series, via Robert Fisher), **ASU** (Arizona State University, Tempe), **ATH** (Andrew T. Holycross field series), **BB** (Boris Blotto field series), **BLC** (Bruce L. Christman), **BMNH** (The Natural History Museum, London), **BPN** (Brice P. Noonan field series), **BY** (Brian Yang), **CAR** (Channing Central African Republic collection, deposited at SAM), **CAS** (California Academy of Sciences, San Francisco), **CFBH** (Célio F.B. Haddad specimen collection), **CFBH-T** (Célio F.B. Haddad tissue collection), **CG** (Caren Goldberg), **DMG** (David M. Green field series), **DPL** (Dwight P. Lawson field series), **ENS** (Eric N. Smith field series), **FMNH** (Field Museum, Chicago), **IWK** (Iwokrama collection field series, Maureen Donnelly), **IZUA** (Instituto de Zoología, Universidad Austral de Chile, Valdivia), **JAC** (Jonathan A. Campbell field series), **JF** (Julián Faivovich field series), **JLG** (João Luiz Gasparini field series), **KRL** (Karen R. Lips field series), **KU** (Natural History Museum, University of Kansas, Lawrence), **LSUMZ** (Louisiana State University Museum of Zoology, Baton Rouge), **MACN** (Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires), **MAD** (Maureen A. Donnelly field series), **MB** (Marius Burger field series), **MHNSM** (Museo de Historia Natural San Marcos, Lima, Peru), **MJH** (Martin J. Henzl field series), **MLPA** (Museo de la Plata, Buenos Aires, Argentina), **MVZ** (Museum of Vertebrate Zoology, University of California at Berkeley), **MW** (Mark Wilkinson field series), **NK** (Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia), **NTM** (Museum and Art Galleries of the Northern Territory, Darwin, Australia), **QMJ** (Queensland Museum, Brisbane), **RABI** (Marius Burger, Rabi oilfield, Gabon, field series), **RAN** (Ronald A. Nussbaum field series), **RAX** (Christopher Raxworthy field series), **RdS** (Rafael de Sá collection), **RG** (Ron Gagliardo), **RNF** (Robert N. Fisher field series), **RWM** (Roy W. McDiarmid field series), **SAM** (South African Museum, Cape Town), **SAMA** (South Australian Museum, Adelaide), **SIUC** (Southern Illinois University at Carbondale), **TAT** (Tom A. Titus field series), **TMSA** (Transvaal Museum, Pretoria, South Africa), **UAZ** (Herpetology Collection, University of Arizona, Tucson), **USNM** (National Museum of Natural History, Smithsonian Institution, Washington, D.C.), **UMFS** (University of Michigan Museum of Zoology, Ann Arbor, field series), **UMMZ** (University of Michigan Museum of Zoology, Ann Arbor), **UTA** (University of Texas at Arlington), **WAM** (Western Australia Museum, Perth), **WCS** (Wildlife Conservation Society, New York), **WR** (Wade Ryberg), **ZFMK** (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany), and **ZSM** (Zoologisches Museum, München, Germany).

			Locus/partition						
Species	ID number	Locality	mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	Total bp
*Acanthixalus spinosus**			**AJ437002 AF215214 AF465438**						1283
Acris crepitans	LSUMZ H-2164	USA, Alabama, De Kalb Co, powerline access, 0.1 mi W Lookout Mt Boys Camp Rd	**AY843559**	DQ284107	**AY844533**	**AY844762**	**AY844019**		3952
Adelotus brevis	SAMA R39251	Australia, Queensland, Nambour	DQ283298	DQ284307	DQ283948	DQ282800		DQ283638	3731
Adenomera hylaedactyla	MJH 3669	Peru, Huánuco, Río Llullapichis, Panguana	DQ283063	DQ284093	DQ283790				3063

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Species	ID number	Locality	Locus/partition						Total bp
			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Afrana angolensis	CAS 202040	Uganda, Rukungiri Dist, Bwindi Impenetrable National Park, Munyaga Falls trail	DQ284258	DQ284258				DQ283597	1600
Afrana fuscigula	AMNH A144976	South Africa, Western Cape Prov, Bainskloof, in stream at settlement at crest of pass	DQ283069	DQ284105	DQ283794		DQ282909	DQ283476	4162
Afrixalus fornasinii	AMNH A153277	Tanzania, Morogoro, Udzungwa Mts National Park, Man'gula camp site 3 on Mwaya River, 350 m, 7°50′51″S, 36°53′0″E	**U22071** DQ283401	DQ284382	DQ284013	DQ282859	DQ283003	DQ283713	4289
Afrixalus pygmaeus	CAS 214836	Kenya, Kilifi Dist, Kararacha Pond I, 03°24′54″S, 39°52′19.8″E	DQ283234	DQ284263	DQ283908	DQ282765	DQ282955	**DQ283602**	4265
Agalychnis callidryas	RdS 537	Belize, Stann Creek Dist, Cockscomb Basin Wildlife Sanctuary	**AY843563**	DQ284401	**AY844537**	**AY844765**	DQ283018		4017
Aglyptodactylus madagascariensis	UMMZ 198472	Madagascar, Toamasina, Moramanga, Mantady Park, 48.458333°S, 18.85°E	DQ283056		DQ283785		DQ282906	DQ283469	3927
Alexteroon obstetricans	MB 5515 (SAM)	Gabon, Rabi (Shell Gabon), at Rabi 059, at trap lines 1–3, 01°56′33″S, 09°51′09″E	DQ283171	DQ284209	DQ283864	DQ282723	DQ282969	DQ283561	2311
Alexteroon obstetricans	UTA A44465	Cameroon, Southwestern Prov, vicinity Ediensoa	DQ283344			DQ282820		DQ283666	3135
Alligator sinensis	WCS 850352	No data (WCS)	**NC004448**		DQ283961	DQ282809		DQ283650	3848
Allobates femoralis	LSUMZ 17552	Brazil, Rondônia, Rio Formoso, Parque Estadual Guajira-Mirim, ca. 90 km N Nova Mamore, 10°19′S, 64°33′W	DQ283045	DQ284074	DQ283774	DQ282657		DQ283465	4226
Allophryne ruthveni	MAD 1512	Guyana, Kabocali camp, 101 m, 4°17.10′N, 58°30.56′W	**AF364511 AF364512 AY843564**		**AY844538**	**AY844766**			3134
Alsodes gargola	MACN 37942	Argentina, Neuquén, Aluminé, stream 10 km W Primeros Pinos	**AY843565**	DQ284118	**AY844539**	**AY844767**		**AY844197**	4211
Alytes obstetricans	AH	Germany, Thüringen, Schnellbach, 725 m	DQ283112	DQ284158	**AY364385**	DQ282683		DQ283510	4155
Ambystoma cingulatum	AMCC 125631	USA, Florida, Wakulla Co, 30°08.96′N, 84°09.23′W	DQ283184	DQ284218					2697
Ambystoma mexicanum	AMCC 105479	No data	DQ283213	DQ284244	DQ283893				3025
Ambystoma tigrinum	AMNH A164658	USA, Arizona, Cochise Co, Hwy 80, 0.5 mi N Price Canyon Rd, ca. 50 m W Hwy 80, ca. 1401 m, 31°38′15″N, 109°11′27″W	DQ283407	DQ284388	**U36574**	DQ282864			3422

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Species	ID number	Locality	Locus/partition						Total bp
			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Amerana muscosa	BY	USA, California, Los Angeles Co, tributary of South Fork Big Rock Creek, 34.3775°N, 117.82824°W	DQ283190	DQ284224	DQ283877	DQ282735	DQ282945	DQ283575	4686
Amietia vertebralis	AMNH A144977	Lesotho, Katse	DQ283402	DQ284383		DQ282860	DQ283004	DQ283714	4382
Amnirana albilabris	UTA A44423	Cameroon, Southwestern Prov, Kumba–Mamfe rd, 6.4 km S Nguti	DQ283368	DQ284354	DQ283989			DQ283687	3273
Amnirana galamensis	KU 290412	Ghana, Muni Lagoon, Winneba, 5°21′14″N, 0°42′12″W	DQ283058		**AY341808**		**AY341749**		3250
Amolops chapaensis	AMNH A161439	Vietnam, Lai Chau Prov, Mt Fansipan, 1600 m	DQ283372	DQ284358	DQ283992	DQ282837	DQ282984	DQ283690	4695
*Amolops hongkongensis**			**AF206072 AF206453 AF206117**						1939
Amphiuma tridactylum	UMFS 10349	No data	DQ283372	DQ284358				DQ283690	3410
*Andrias davidianus**			**AJ492192**						2390
Andrias japonicus	UMFS 11734	No data (Detroit Zoo; living animal)	DQ283274	DQ284358					2714
*Aneides hardii**			**AY728226**						2342
*Anhydrophryne rattrayi**			**AF215504**						500
*Anodonthyla montana**			**AJ314812**						493
Anotheca spinosa	ENS 10039	Mexico, Oaxaca, Ixtlán de Juárez, Santiago Comaltepec, Vista Hermosa	**AY843566**	DQ284101	**AY844540**	**AY844768**	**AY844022**	**AY844198**	4730
Ansonia longidigitata	FMNH 242550	Malaysia, Sabah, Sipitang Dist, 3.3 km W Mendolong camp	DQ283341		DQ283968	DQ282817			3136
*Ansonia muelleri**			**U52740 U52784**						1200
Aphantophryne pansa	ABTC 49605	Papua New Guinea, Bolulo	DQ283195	DQ284228	DQ283879	DQ282739		DQ283578	4171
Aplastodiscus perviridis	MACN 37791	Argentina, Misiones, Guaraní, San Vicente, Campo Anexo INTA "Cuartel Río Victoria"	**AY843569**	DQ284044	**AY844543**	**AY844771**	**AY844025**	**AY844201**	4746
Aquarana catesbeiana	BLC	USA, New Mexico, Sierra Co, Las Animas Creek, Ladder Ranch	DQ283257		DQ283926	DQ282778	DQ282959	DQ283618	4363
Aquarana clamitans	AMCC 125633	USA, Florida, Walton Co, Eglin Air Force Base, Range Rd 211, ca. 1.2 mi E Indigo Pond, 30°53.28′N, 86°53.26′W	DQ283185	DQ284219	DQ283872	DQ282730		DQ283570	4160
Aquarana grylio	AMCC 125634	USA, Florida, Walton Co, Eglin Air Force Base, Range Rd 211, ca. 1.2 mi E Indigo Pond, 30°53.28′N, 86°53.26′W	DQ283186	DQ284220	DQ283873	DQ282731		DQ283571	4160
Aquarana heckscheri	AMCC 125635	USA, Florida, Wakulla Co, Smith Creek at County Rd 375	DQ283191	DQ284225	DQ283878	DQ282736	DQ282946	DQ283576	4693

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Species	ID number	Locality	Locus/partition						Total bp
			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Aquixalus gracilipes	AMNH A163897	Vietnam, Ha Giang Prov, Vi Xuyen, Cao Bo Commune, Mt Tay Conn Linh II, above Tham Ve Village, small forest pools ca. 1 km SW high camp, 1700 m, 22°45′27″N, 104°49′35″E	DQ283051		DQ283780				2712
Arenophryne rotunda	WAM R146480	Australia, Western Australia, False Entrance Well	DQ283326	DQ284322	DQ283965			DQ283656	2268
Argenteohyla siemersi pederseni	MACN 38644	Argentina, Corrientes, Bella Vista, junction R.N. 12 at Río Santa Lucía	**AY843570**	DQ284064	**AY844544**	**AY844772**	**AY844026**	**AY844202**	4734
Arthroleptella bicolor	AMNH A144967	South Africa, Western Cape Prov, Landdroskop (nr peak), ca. 15 km SW Stellenbosch (by air), ca. 1450 m	DQ283070	DQ284106	DQ283795	DQ282662	DQ282910	DQ283477	4701
Arthroleptides yakusini	RdS 862	Tanzania, Uluguru Mts, Tegetero Village, 6°56′30″S, 37°43′10″E	DQ283415	DQ284396	DQ284020	DQ282872	DQ283010	DQ283725	4729
Arthroleptis tanneri	RdS 929	Tanzania, West Usambara Mts, Mazumbai, 04°48′46.5″S, 38°30′12.0″E	DQ283427	DQ284405	DQ284028		DQ283020	DQ283736	3844
Arthroleptis variabilis	UTA A44448	Cameroon, Southwestern Prov, vicinity Babong	DQ283081	DQ284133	DQ283803		DQ282914	DQ283483	4263
Ascaphus truei	UMFS 10198	USA, Washington, Skamania Co, McCloskey Creek at Maybee Mines Rd	**AJ440760**	DQ284162				DQ283514	2905
Assa darlingtoni	SAMA R39233	Australia, New South Wales, Wiangaree	DQ283284	DQ284300	DQ283943				2128
Astylosternus schioetzi	UTA 52398	Cameroon, South Prov	DQ283349	DQ284340	DQ283976	DQ282826	DQ282974	DQ283674	4699
Atelognathus patagonicus	MACN 37905	Argentina, Neuquén, Catan Lil, Laguna del Burro	**AY843571**		**AY844545**	**AY844773**	**AY844027**	**AY844203**	4408
Atelopus flavescens	BPN 726 (UTA)	French Guiana, N side of mt just S Kaw	DQ283259	DQ284282	DQ283928	DQ282780			3462
Atelopus spumarius	BPN 754 (UTA)	French Guiana, Grand Boe of Mort (circuit trail) just SSW Saul	DQ283260	DQ284283	DQ283929	DQ282781		DQ283619	4229
Atelopus zeteki	UMFS 11492	Captive raised, Detroit Zoo (parental stock from Panama, Las Filipinas near Sora, 8°39.99′N, 80°0.249′W)	DQ283252						1518
Aubria subsigillata	MB 5855 (SAM)	Gabon, at forest stream in Gamba region, 02°46′30″S, 10°00′59″E	DQ283172 DQ283173	DQ284210	DQ283865	DQ282724		DQ283562	3689
Aubria subsigillata	DPL 4936 (UTA)	Cameroon, Southwestern Prov, Nguti–Bayenti rd	DQ283350 DQ283351 DQ283352	DQ284341	DQ283977	DQ282827	DQ282975	DQ283675	3880
Aurorana aurora	ARBT 018	USA, California, Los Angeles, San Francisquito Canyon, plunge pool, 34.545767°N, 118.51653°W	DQ283189	DQ284223	DQ283876	DQ282734	DQ282944	DQ283574	4683
Barycholos ternetzi	CFBH-T 306	Brazil, Minas Gerais, Gurinhatã	DQ283094	DQ284144	DQ283810		DQ284144	DQ283496	2938

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			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
*Batrachoseps attenuatus**			**AY728228**						2327
*Batrachoseps wrightorum**			**AY728221**						2335
Batrachuperus pinchoni	FMNH 232841	China, Sichuan, Hongya Xian, 15 km SW Bin Ling, top of Wa Shan	DQ283339	DQ284330				DQ283664	3017
Batrachyla leptopus	MACN 38008	Argentina, Chubut, Cushamen, Lago Puelo	**AY843572**	DQ284119	**AY844546**	**AY844774**	**AY844028**	**AY844204**	4726
Batrachylodes vertebralis	AMS R134887	Solomon Islands, New Georgia, Patutiva	DQ283210	DQ284242	DQ283891	DQ282753		DQ283586	4124
Bolitoglossa rufescens	JAC 21178	Mexico, Oaxaca, Coconales–Zacatepec Hwy, 1625 m	DQ283210	DQ284242		DQ282753		DQ283586	2890
Bombina bombina	AH	No data	DQ283250	DQ284275	DQ283920				3067
Bombina microdeladigitora	AMNH A163789	Vietnam, Ha Giang Prov, Vi Xuyen, Cao Bo Commune, Mt Tay Conn Linh II, above Tham Ve Village, 1900 m	DQ283408	DQ284389	DQ284017	DQ282865		DQ283718	4171
Bombina orientalis	RdS	No data	DQ283432		DQ284032			DQ283741	3474
Bombina variegata	ZSM 724/ 2000	No data	DQ283249	DQ284274	DQ283919			DQ283612	3779
Boophis albilabris	RAX 2714	Madagascar, Antsiranana, Ambanja, Antsahatelo Camp, Tsaratanana Reserve, 13°51′35″S, 48°51′59″E	DQ283033	DQ284054	DQ283762				3050
Boophis tephraeomystax	AMNH A168144	Madagascar, Antsiranana, Ambanja, Mandrizavona Village, Ramena Valley, 13°48′3″S, 48°44′47″E	DQ283032	DQ284053	DQ283761		**AF249168**		3590
Boulengerula uluguruensis	MW 3268 (BMNH)	Tanzania	DQ283087	DQ284138		DQ282670		DQ283488	3810
Brachycephalus ephippium	CFBH 2466, CFBH 2468	Brazil, São Paulo, Campinas, Joaquim Egydio	DQ283091		DQ283808 DQ283806	DQ282672 DQ282673	DQ282919 DQ282917	DQ283494 DQ283492	4263
*Brachytarsophrys feae**			**AY236799**						555
Breviceps mossambicus	RdS 903	Tanzania, Morogoro	DQ283155	DQ284397	DQ284023		DQ283013	DQ283546	4292
Buergeria japonica	UMMZ 190051	China, Taiwan, I-Lan, near Ran-Jeh spring	DQ283055		DQ283784				2710
Bufo alvarius	ATH 499	USA, Arizona Santa Cruz Co, 0.5 mi (by air) SW junction of I-19 and Ruby Rd	DQ283269	DQ284289	DQ283933	DQ282785		DQ283625	4221
Bufo amboroensis	NK A5302	Bolivia, Dept Santa Cruz, Prov Caballero, San Juán Cantón, Amboró, National Park, near San Juán del Portrero, on Río Cerro Bravo, near 17°50′08″S, 64°23′23″W, 1800–2100 m	DQ283386		DQ284003	DQ282848		DQ283701	3894

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			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Bufo andrewsi	CAS 214911	China, Yunnan, Nu Jiang Pref, small village S Gongshan, 27°42′13.7″N, 98°42′10.2″E, ca. 4760 ft	DQ283230	DQ284260	DQ283905	DQ282763		DQ283599	4216
*Bufo angusticeps**			**AF220852 AF220899**						850
Bufo arenarum	MACN 38639	Argentina, San Luís, Rte 20 between Bardas Blancas and km 330	**AY843573**	DQ284103	**AY844547**	**AY844775**		**AY844205**	4217
Bufo asper	FMNH 248147	Brunei, Dutong Dist, Tasek Merimbun, Sg Merimbun	DQ283148	DQ284188	DQ283848	DQ282704	DQ282939	DQ283539	4748
*Bufo biporcatus**			**AY325987**						2350
Bufo boreas	RNF 2416	USA, California, San Diego Co, Marron Valley Rd, 0.25 mi E Mine Canyon	DQ283180	DQ284215	DQ283871			DQ283567	3821
Bufo brauni	RdS 952	Tanzania, East Usambara Mts, adjacent to Amanai Nature Reserve, 05°07′38.0″S, 38°37′22.6″E	DQ283416		DQ284021	DQ282873	DQ283011	DQ283726	4420
*Bufo bufo**			**AY325988**		**U59921**				2672
Bufo camerunensis	UTA A44478	Cameroon, East Prov, ca. 35 km E Lipondji Village	DQ283358	DQ284345	DQ283979	DQ282830		DQ283678	4211
*Bufo celebensis**			**AF375513 AY180245**						1209
Bufo cf. *arunco*	AMNH A168401	No data (pet trade)	DQ283162	DQ284200	DQ283857	DQ282715		DQ283553	4219
Bufo cognatus	AMNH A168396	No data (pet trade)	DQ283159	DQ284197		DQ282713		DQ283550	3902
Bufo coniferus	SIUC 6913	Panama, Coclé Prov, Parque Nacional El Copé	DQ283166	DQ284204	DQ283860	DQ282719		DQ283556	4216
Bufo divergens	FMNH 242591	Malaysia, Sabah, Sipitang Dist, Mendelong camp, watershed	DQ283149	DQ284189	DQ283849	DQ282705		DQ283540	4210
Bufo galeatus	AMNH A163648	Vietnam, Quang Nam Prov, Trã My, Trã Tãp commune, stream near Thon 2 village, 920–1060 m, 15°09.622′N, 108°02.427′E	DQ283376	DQ284362	DQ283995	DQ282839	DQ282987		3994
Bufo granulosus	AMNH A139020	Guyana, southern Rupununi Savanna, Aishalton (on Kubabawau Creek), 150 m, 2°28′31″N, 59°19′16″W	DQ283332	DQ284323	DQ283966			DQ283657	3808
Bufo guttatus	AMNH A141058	Guyana, Dubulay Ranch on Berbice River, 200 ft, 5°40′55″N, 57°51′32″W	DQ283375	DQ284361	DQ283994			DQ283693	3823
Bufo gutturalis	RdS 873	Tanzania, Mumba Village, 08°10′44.9″S, 31°51′47.8″E	DQ283436		DQ284035	DQ282890		DQ283745	3863
Bufo haematiticus	SIUC 7059	Panama, Coclé Prov, Parque Nacional El Copé	DQ283167	DQ284205	DQ283861	DQ282720		DQ283557	4217

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			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Bufo latifrons	UTA A44695	Cameroon, Southwest Prov, Manyu Division, ca. 9.0 km W Bakumba Village, between Mpi River and primary forest	DQ283343	DQ284332	DQ283970	DQ282819		DQ283665	3310
Bufo lemur	UMFS 11733	No data (Detroit Zoo)	DQ283273						2424
Bufo maculatus	AMNH A163573	Mali, 12°36′45″N, 7°59′21″W	DQ283388	DQ284374	DQ284005	DQ282850		DQ283703	4213
*Bufo margaritifer**			**AF375514 AF375489**						1101
Bufo marinus	MJH 3678	Peru, Huánuco, Río Pachitea, Puerto Inca	DQ283062	DQ284092	DQ283789			DQ283472	3820
*Bufo mazatlanensis**			**U52755 U52723**						1343
Bufo melanostictus	AMNH A161135	Vietnam, Ha Tinh Prov, Huang Son Reserve, Rao An region, 200 m, 18°22′0″N, 105°13′13″E	DQ283333	DQ284324	DQ283967	DQ282815		DQ283658	4237
*Bufo nebulifer**			**AY325985**						2426
Bufo punctatus	AMNH A168398	No data (pet trade)	DQ283160	DQ284198	DQ283855	DQ282714		DQ283551	4167
Bufo quercicus	AMNH A168432	USA, Florida, Walton Co, Eglin Air Force Base, Range Rd 211, ca. 1.2 mi E Indigo Pond, 30°42′0″N, 86°19′0″W	DQ283153	DQ284192		DQ282708		DQ283544	3900
Bufo regularis	FMNH 251386	Tanzania, Kilimanjaro Region, South Pare Mts, Chome Forest Reserve, 7 km S Bombo (by air), 4°20′S, 38°00′E, 1100 m	DQ283163	DQ284201	DQ283858	DQ282716		DQ283554	4191
Bufo schneideri	BB 1224	Argentina, Santiago del Estero, Guasayán, Doña Luisa	DQ283065	DQ284102	DQ283791				3068
Bufo spinulosus	BB 1032	Argentina, Río Negro, Bariloche, Pampa Linda	DQ283046	DQ284077	DQ283775	DQ282658			3469
Bufo terrestris	AMNH A168433	USA, Florida, Marion Co, 4 mi WSW Micanopy, 29°38.56′N, 82°20.30′W	DQ283158	DQ284196	DQ283854	DQ282712		DQ283549	4214
Bufo tuberosus	UTA A52375	Cameroon, Center Prov, east bank of Nyong River, vicinity 0742952, 0382754 (UTM 32N)	DQ283362		DQ283984	DQ282832		DQ283683	3856
Bufo viridis	AMNH A168402	No data (pet trade)	DQ283279	DQ284297	DQ283940	DQ282791		DQ283630	4220
Bufo woodhousii	RNF 2417	USA, California, Imperial Co, Winterhaven, 1.5 mi (by air) N Hwy 8 on Picacho Rd, 32.75100°N, 114.61596°W	DQ283188	DQ284222	DQ283875	DQ282733		DQ283573	4217
Cacosternum platys	AC	South Africa, Western Cape Prov, Cape Town	DQ283258	DQ284281	DQ283927	DQ282779	DQ282960		3968

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Caecilia tentaculata	AMNH A145174	Guyana, Dubulay Ranch on Berbice River, 200 ft., 5°40′55″N, 57°51′32″W	DQ283406	DQ284387		DQ282863		DQ283717	2936
Calluella guttulata	FMNH 252955	Vietnam, Gia-Lai Prov, Ankhe Dist, Kannack town, Buon Luoi village, 20 km NW Kannack, Annam mts, 700–750 m, 14°20′N, 106°36′E	DQ283144	DQ284184	DQ283845	DQ282700	DQ282937	DQ283536	4714
Callulina kisiwamsitu	RdS 936	Tanzania, West Usambara Mts, Mazumbai, 04°48′46.5″S, 38°30′12.0″E	DQ283429	DQ284406		DQ282884	DQ283021	DQ283737	4333
*Callulina kreffti**			**AY326068**						2363
*Callulops slateri**			**AF095339**						541
*Capensibufo rosei**			**AF220864** **AF220911**						841
*Capensibufo tradouwi**			**AF220865** **AF220912**						842
Cardioglossa gratiosa	RABI 141 (SAM)	Gabon, Rabi (Shell Gabon), Toucan Well Head, funnel trap line 1.8, 01.4750°S, 09.5335°E	DQ283176	DQ284213	DQ283868	DQ282726		DQ283565	3699
Cardioglossa leucomystax	UTA A44591; UTA A44585	Cameroon, Southwest Prov, vicinity Ediensoa	DQ283080 DQ283079	DQ284348 DQ284132	DQ283802 DQ283982		DQ282978 DQ282913	DQ283681	4266
Caudiverbera caudiverbera	AMNH A168414	No data (pet trade)	DQ283439	DQ284415	DQ284036	DQ282893		DQ283748	4222
*Centrolene geckoideum**			**X86230** **X86264** **X86298**						1146
Centrolene prosoblepon	SIUC 7053	Panama, Coclé Prov, El Copé, Parque Nacional ''Omar Torrijos''	**AY364358** **AY364379** **AY843574**		**AY364404**	**AY844776**		**AY844206**	3871
Ceratobatrachus guentheri	AMS R137134; AMNH A161634	Solomon Islands, Malaita, Su'u Bay; Solomon Islands	DQ283197 DQ283198	DQ284230 DQ284409	DQ283881 DQ284031	DQ282741 DQ282886	DQ283024	DQ283579 DQ283740	4675
Ceratophrys cranwelli	JF 929	Argentina, Santa Fe, Vera, ''Las Gamas''	**AY843575**		**AY843797**			**AY844207**	3469
Chacophrys pierottii	AMNH A168435	No data (pet trade)	DQ283328						2421
Chalcorana chalconota	FMNH 248327	Brunei, Belait Dist, Labi, Sg Mendaram	DQ283139	DQ284179	DQ283840	DQ282695	DQ282933	DQ283531	4687
Chaperina fusca	FMNH 231111	Malaysia, Sabah, Lahad Datu Dist, Danum Valley Research Center	DQ283145	DQ284185		DQ282701	DQ282938		2307
Charadrahyla nephila	UTA A54772	Mexico, Oaxaca, Colonia Rodulfo Figueroa, El Carrizal, 1475 m	**AY843649**	DQ284100	**AY844635**	**AY844853**	**AY844094**	**AY844272**	4730
Chelydra serpentina	AMCC 101071	USA, New York, Cornwall Co, Black Rock Forest, Arthurs Pond	DQ283320			DQ282810		DQ283651	3108

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Chirixalus doriae	FMNH 255213	Laos, Huaphahn Prov, Vieng Tong Dist, Phou Louey National Biodiversity Conservation Area, near Nam Puong River, 985 m, 20°14′N, 103°16′E	DQ283135	DQ284176	DQ283836	DQ282691		DQ283528	4139
Chirixalus vittatus	FMNH 254444	Vietnam, Gia-Lai Prov, Ankhe Dist, Kannack town, Buon Luoi village, 20 km NW Kannack, Annam mts, 700–750 m, 14°20′N, 106°36′E	DQ283134	DQ284175	DQ283835	DQ282690		DQ283527	4140
Chiromantis xerampelina	AMNH A153250	Tanzania, Morogoro, Udzungwa Mts National Park, Njokamoni River drainage, 1100–1200 m	**AF215348 AF458132**	DQ284380	DQ284012				2656
Choerophryne sp.	ABTC 47720	Papua New Guinea, Mt Menawa	DQ283207	DQ284239	DQ283889	DQ282750		DQ283583	4156
*Clinotarsus curtipes**			**AF249058 AF249021**		**AF249117**		**AF249180**		2110
Cochranella bejaranoi	NK A 5292	Bolivia, Dept Santa Cruz, Prov Caballero, San Juán Cantón, Amboró, National Park, near San Juán del Portrero, on the Río Cerro Bravo, near 17°50′08″S, 64°23′23″W, 1800–2100 m	**AY843576**	DQ284066	**AY844372**	**AY844777**	**AY844029**	**AY844208**	4730
Colostethus undulatus	AMNH A159139	Venezuela, Amazonas, Cerro Yutajé, 1700 m, 5°46′N, 66°8′W	DQ283044	DQ284073	DQ283773	DQ282656		DQ283464	4223
Conraua goliath	FMNH 262216	Cameroon, Ebowala area	DQ283132	DQ284173	DQ283833	DQ282688		DQ283525	4158
Conraua robusta	UTA A44401	Cameroon, Southwest Prov, plateau NW of Ntale village, ca. 700 m	DQ283347	DQ284337	DQ283973	DQ282823	DQ282972	DQ283671	4688
Cophixalus sphagnicola	ABTC 47881	Papua New Guinea, Wau	DQ283206	DQ284238		DQ282749		DQ283582	4032
Copiula sp.	AMS R124417	Papua New Guinea, Sinyarge	DQ283208	DQ284240		DQ282751		DQ283584	3415
Crinia nimbus	ABTC 25300	Australia, Tasmania, Haast Mts	DQ283299		DQ283949	DQ282801		DQ283639	3351
Crinia signifera	SAMA R40274	Australia, New South Wales, Watagan S.F.	DQ283192 DQ283193	DQ284226		DQ282737			2695
Crossodactylus schmidti	MLPA 1414	Argentina, Misiones, Aristobulo del Valle, Balneario Cuñapirú	**AY843579**	DQ284050	**AY844552**	**AY844780**	**AY844031**		3989
Crotaphatrema tchabalmbaboensis	UTA A51667	Cameroon, Adamoua, N face of Mt Tchabal Mbabo, 1950 m	DQ283353 DQ283354	DQ284342				DQ283676	2430
Cruziohyla calcarifer	KRL 800	Panama, Coclé Prov, El Copé, Parque Nacional ''Omar Torrijos''	**AY843562**		**AY844536**		DQ282950	**AY844196**	4061
Cryptobatrachus sp.*			**AY326050**						2329
Cryptobranchus alleganiensis	TAT	USA, Arkansas, North Fork White River	DQ283263	DQ284286				DQ283621	2998

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Cryptothylax gresshoffi	CAR 381 (SAM)	Central African Republic, Pref Sangha-Mbaéré, Park National de Dzanga-Ndoki, 38.6 km 173°S Lidjombo, Camp 3, 02.2136°S, 16.0312°E	DQ283170	DQ284208	DQ283863	DQ282722		DQ283560	4184
*Cryptotriton alvarezdeltoroi**			**AF199196**						507
Ctenophryne geayei	AMNH A166444	Guyana, Berbice River camp at ca. 18 mi (linear) SW Kwakwani (ca. 2 mi downriver from Kurundi River confluence), 200 ft, 5°5′6″N, 58°14′14″W	DQ283383	DQ28436		DQ282846	DQ282993	DQ283698	4392
Cycloramphus boraceiensis	CFBH 5757	Brazil, São Paulo, Picinguaba, Ubatuba	DQ283097	DQ284147	DQ283813	DQ282675	DQ282924	DQ283498	4740
Cyclorana australis	SAMA R16906	Australia, no other data	DQ284124	DQ284124	**AY844553**				3062
Dasypops schirchi	CFBH-T 71	Brazil, Espírito Santo, Linhares, Reserva da Vale	DQ283095	DQ284145	DQ283811		DQ282922	DQ283497	4302
Dendrobates auratus	USNM 313818	Panama, Bocas del Toro	**AY843581**	DQ284072	**AY844554**	**AY844781**	**AY844032**	**AY844211**	4758
Dendrophryniscus minutus	MJH 7095	Peru, Huánuco, Río Llullapichis, Panguana	**AY843582**	DQ284096	**AY844555**				3056
Dendropsophus marmoratus	MJH 7116	Peru, Huánuco, Río Llullapichis, Panguana	**AY843640**	DQ284085	DQ283782				3071
Dendropsophus minutus	MACN 33799	Argentina, Misiones, Guaraní, San Vicente, Campo Anexo INTA ''Cuartel Río Victoria''	**AY549345**	DQ284096	DQ283758		**AY844089**	DQ283456	4309
Dendropsophus nanus	MACN 37785	Argentina, Entre Ríos, Dept Islas del Ibicuy	**AY549346**	DQ284051	**AY844634**	**AY844852**		**AY844271**	4200
Dendropsophus parviceps	AMNH A139315	Brazil, Acre, Centro Experimental da Universidade do Acre at km 23 on Rio Branco–Porto Velho Rd	**AY843652**		**AY844638**	**AY844856**	**AY844097**	**AY844274**	4410
*Dendrotriton rabbi**			**AF199232**						516
Dermatonotus muelleri	AMNH A168436	No data (pet trade)	DQ283329 DQ283330						2069
Dermophis oaxacae	UTA 56550	Mexico, Guerrero, Tierra Colorada–Ayutla Hwy, 424 m	DQ283455	DQ284428		DQ282897			2710
Desmognathus quadramaculatus	UMMZ 221202	USA, North Carolina, Macon Co, Blue Ridge Parkway	DQ283253	DQ284278	DQ283923	DQ282775		DQ283614	3628
*Desmognathus wrighti**			**AY728225**						2320
Dicamptodon aterrimus	RAN 31288	USA, Idaho, Beneweh Co, Mannering Creek	DQ283118	DQ284164				DQ283516	3394
Dicamptodon tenebrosus	TAT 1043	USA, Oregon, Lane Co, Thompson Creek	DQ283261	DQ284284					2705
Didelphis marsupialis	AMNH A272836	Peru, Loreto, Río Galvez, Nuevo San Juán	DQ283321			DQ282811			1897
*Didynamipus sjostedti**			**AY325991**						2289

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Species	ID number	Locality	Locus/partition						Total bp
			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Dimorphognathus africanus	SAM 51540	Gabon, Loango National Park, near pitfall trap line #3, 02°20′27″S, 09°35′50″E	DQ283175	DQ284212	DQ283867	DQ282725	DQ282943	DQ283564	4240
Discodeles guppyi	AMS R137175	Solomon Islands, Malaita, Su'u Bay	DQ283200	DQ284232	DQ283883	DQ282743	DQ282947		3521
Discoglossus galganoi	ZSM 725/2000	Portugal, Alamada City	DQ283243	DQ284270	DQ283915	DQ282770		DQ283609	3774
Discoglossus pictus	AH	Spain, Barcelona	DQ283435	DQ284412	DQ284034	DQ282889		DQ283744	3796
Duellmanohyla rufioculis	MVZ 207193	Costa Rica, Guanacaste Prov, Volcán Cacao	**AY549315**	DQ284059	**AY844556**		**AY844033**	**AY844212**	4295
Dyscophus guineti	RdS	No data (pet trade)	DQ283434	DQ284411		DQ282888	DQ283025	DQ283743	4419
Eburana chloronota	AMNH A163935	Vietnam, Ha Giang Prov, Vi Xuyen, Cao Bo Commune, Mt Tay Conn Linh II, Bac Trao River, near camp, just upstream, 600 m, 22°45′39″N, 104°52′23″E	DQ283394		DQ284008	DQ282854	DQ282999	DQ283707	4359
Ecnomiohyla miliaria	SIUC 6998	Panama, Coclé Prov, El Copé, Parque Nacional ''Omar Torrijos''	**AY843776 AY843777**	DQ284115	**AY844629**	**AY844847**	**AY844088**	**AY844268**	3846
Edalorhina perezi	MJH 7082	Peru, Huánuco, Río Llullapichis, Panguana	**AY843585**	DQ284095	**AY844558**	**AY844764**		DQ283474	4200
Elachistocleis ovalis	AMNH A141136	Guyana, Dubulay Ranch on Berbice River, 200 ft, 5°40′55″N, 57°51′32″W	DQ283405	DQ284386					2728
Eleutherodactylus alfredi	JAC 21987	Mexico, Veracruz, Municipio Córdoba, Cruz de los Naranjos, 1100 m	DQ283318	DQ284318				DQ283649	3483
Eleutherodactylus augusti	CG (now UAZ unnumbered)	Mexico, Sonora, Alamos	DQ283271	DQ284291	DQ283935	DQ282786	DQ282963	DQ283627	4738
Eleutherodactylus binotatus	CFBH 5813	Brazil, São Paulo, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, São Luiz do Paraitinga	DQ283092	DQ284142	DQ283807		DQ282918	DQ283493	4288
Eleutherodactylus bufoniformis	SIUC 7062	Panama, Coclé Prov, Parque Nacional El Copé	DQ283165	DQ284203		DQ282718	DQ282942	DQ283555	4404
Eleutherodactylus juipoca	CFBH 4450	Brazil, Minas Gerais, Poços de Caldas	DQ283093	DQ284143	DQ283809		DQ282920	DQ283495	4271
Eleutherodactylus marnockii	USNM 331345	USA, Texas, Travis Co, Austin, Univ of Texas Campus, near football stadium	DQ283101 DQ283102	DQ284151	DQ283817	DQ282677		DQ283502	3324
Eleutherodactylus nitidus	UTA A54771	Mexico, Oaxaca, Municipio Cuicatlán, Tutepetongo, 1619 m	DQ283316	DQ284316	DQ283959	DQ282807		DQ283647	2855
Eleutherodactylus planirostris	USNM 547959; P. Moler, unnumbered	USA, Florida, Collier, Naples, Parkshore subdivision, Parkview Way, 26°11′24″N, 81°48′16″W; USA, Florida, Duval Co, 2826 Rosselle St	DQ283107 DQ283108	DQ284155 DQ284294	DQ283821 DQ283937	DQ282680 DQ282788	DQ282929 DQ282964	DQ283506 DQ283629	4740

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Eleutherodactylus pluvicanorus	AMNH A165195	Bolivia, Santa Cruz, Caballero, San Juán Canton, Amboró National Park, 2050 m, 17°50′17″S, 64°23′30″W	**AY843586**	DQ284372	**AY844559**	**AY844785**	**AY844035**	**AY844213**	4790
Eleutherodactylus punctariolus	SIUC 7066	Panama, Coclé, Parque Nacional El Copé	DQ283168	DQ284206	DQ283862			DQ283558	3804
Eleutherodactylus ranoides	USNM-FS 195393	Panama, Bocas del Toro, Isla Escudo de Veraguas, West Point	DQ283105 DQ283106	DQ284154	DQ283820		DQ282928	DQ283505	4004
Eleutherodactylus rhodopis	JAC 22721	Mexico, Oaxaca, El Mirador, Municipio Santa María Chilchotla	DQ283317	DQ284317	DQ283960	DQ282808	DQ282968	DQ283648	4702
*Ensatina eschscholtzii**			**AY728216**						2311
Epicrionops sp.	UMMZ 185825	Ecuador, Cotopaxi, San Francisco de Las Pampas	DQ283130	DQ284171				DQ283523	3074
Epipedobates boulengeri	UMMZ 227952	Pet trade, imported from Ecuador	DQ283037	DQ284063	DQ283768	DQ282653	DQ282902	DQ283461	4761
*Euphlyctis cyanophlyctis**			**AF249053 AF249015**		**AF249111**		**AF249174**		2069
*Euproctus asper**			**U04694 U04695**						840
Eupsophus calcaratus	MACN 37980	Argentina, Neuquén, Huiliches, Termas de Epulafquen	**AY843587**	DQ284120	**AY844560**	**AY844786**	**AY844036**	**AY844214**	4749
Eurycea wilderae	UMMZ 221205	USA, North Carolina, Macon Co, Deep Gap	DQ283254					DQ283615	3040
Exerodonta chimalapa	JAC 21736	Mexico, Chiapas, Colonia Rodulfo Figueroa, El Carrizal, 1475 m	**AY843619**	DQ284099	**AY844596**	**AY844815**	**AY844062**	**AY844240**	4738
*Fejervarya cancrivorus**			**AB070731 AF206473 AF206092 AF206137**						2391
*Fejervarya kirtisinghei**			**AY014380**						502
Fejervarya limnocharis	AMNH A161230	Vietnam, Nghe An Prov, Con Cuong Dist, Bong Khe Commune, 19°2′24″N, 104°54′24″E	**AY843588**	DQ284356	**AY844561**	**AY844787**	**AY844037**		3991
*Fejervarya syhadrensis**			**AY141843 AF249011**		**AF249107**		**AF249170**		2484
Flectonotus sp.	CFBH 5720	Brazil, Santa Catarina, Santo Amaro da Imperatriz	**AY843589**		**AY844562**	**AY844788**	**AY844038**	**AY844215**	4004
Gastrophryne elegans	RdS 726	Belize, Stann Creek Dist, Cockscomb Basin Wildlife Sanctuary	DQ283426	DQ284404		DQ282883	DQ283019	DQ283735	4387
Gastrophryne olivacea	ATH 476	USA, Arizona, Santa Cruz Co, Ruby Rd, vicinity Calabasas Canyon	DQ283268	DQ284288	DQ283932	DQ282784	DQ282961	DQ283624	4703

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			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Gastrotheca cf. *marsupiata*	NK A5286	Bolivia, Dept Santa Cruz, Prov Caballero, San Juán Cantón, Amboró, National Park, near San Juán del Potrero, on Río Cerro Bravo, near 17°50′08″S, 64°23′23″W, 1800–2100 m	**AY843590**	DQ284069	**AY844563**	**AY844789**	**AY844039**		3995
Gastrotheca fissipes	JLG 09	Brazil, Espírito Santo, Setiba, Guarapari	**AY843592**		**AY844564**	**AY844790**			3130
Gazella thomsoni	WCS 851199	No data	**M86501**			DQ282812		DQ283652	3556
*Gegeneophis ramaswamii**			**AF461136** **AF461137**						972
Genyophryne thomsoni	ABTC 49624	Papua New Guinea, Bolulo	DQ283209	DQ284241	DQ283890	DQ282752		DQ283585	4171
Geocrinia victoriana	ABTC 7145	Australia, Victoria, Tanjil Bren	DQ283294 DQ283295 DQ283296	DQ284306	DQ283947	DQ282799	DQ282965	DQ283637	3858
Geotrypetes seraphini	FMNH 256782	Gabon, Prov de Woleu-Ntem, 31 km ESE Minvoul, along IOBT trail (PK 29), 600 m, 2°4.8′N, 12°24.4′E	DQ283337	DQ284328				DQ283662	2816
*Glandirana minima**			**AF315127** **AF315153**						882
Gyrinophilus porphyriticus	UMMZ 221207	USA, North Carolina, Macon Co, Deep Gap	DQ283255	DQ284279	DQ283924	DQ282776		DQ283616	3630
Hamptophryne boliviana	RdS	Peru (no other data)	DQ283438	DQ284414		DQ282892		DQ283747	3891
Heleioporus australiacus	ABTC 76692	Australia, New South Wales, Mona Vale	DQ283306 DQ283307	DQ284311	DQ283953	DQ282804		DQ283642	3694
Heleophryne purcelli	TMSA 84157	South Africa, Western Cape Prov, Cedarberg Range, head of Krom River	**AY843593**	DQ284113	**AY844565**	**AY844791**			3458
Heleophryne regis	AC 2544	South Africa, Western Cape Prov, Montague Pass	DQ283115	DQ284161	DQ283828	DQ282684		DQ283513	3758
Hemidactylium scutatum	UMFS 11564	USA, Michigan, Saint Clair Co, Woodlot just S Marysville along Hwy 29/Busha Hwy, about 1 km NW jct Davis Rd, 42°53.3′N, 82°29.3′W	DQ283120 DQ283121						1587
Hemiphractus helioi	MJH 3689	Peru, Ucayali, 3 km S, km 65 on Hwy Federico Basadre at Ivita	**AY843594**	DQ284084	**AY844566**	**AY844792**			3431
Hemisus marmoratus	RdS 916	Tanzania, Arusha, Masai Camp	**AY326070**	DQ284407	DQ284029	DQ282885	DQ283022	DQ283738	4619
Herpele squalostoma	UTA A52349	Cameroon, Southwestern Prov, Nguti	DQ283359	DQ284346	DQ283980			DQ283679	3746
Heterixalus sp.	UMMZ 219330	Madagascar, Mahajanga, Antsalova, Bemaraha Reserve Antranopasasy, 44.71635°N, 18.708016°E	DQ283448	DQ284422			DQ283027	DQ283752	4004
*Heterixalus tricolor**			**AY341630** **AY341697** **AY341725**				**AY341759**		2392

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			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Hoplobatrachus occipitalis	KU 290425	Ghana, Muni Lagoon, Winneba, 5°21′14″N, 0°42′12″W	DQ283059	DQ284090	DQ283787		DQ282907	DQ283471	4303
Hoplobatrachus rugulosus	FMNH 255191	Laos, Champasak Prov, Mounlapamok Dist, Dong Khanthung National Biodiversity Conservation Area, near Houay Khiem stream, 60 m, 14°08′N, 105°22′E	DQ283141	DQ284181	DQ283842	DQ282697	DQ282934	DQ283533	4696
Hoplophryne rogersi	RdS 949	Tanzania, East Usambara Mts, adjacent to Amanai Nature Reserve, 05°07′38.0″S, 38°37′22.6″E	DQ283419	DQ284398		DQ282876	DQ283015	DQ283730	3946
Huia nasica	AMNH A161169	Vietnam, Ha Tinh Prov, Huang Son Reserve, Rao An region, top of Pomu Mt, 900–1200 m, 18°20′53″N, 105°14′38″E	DQ283345	DQ284333	DQ283971	DQ282821	DQ282970	DQ283667	4694
Hyalinobatrachium fleischmanni	JAC 21365	Mexico, Oaxaca, San José Pacífico–Candelaria Loxicha Hwy, 480 m	DQ283453	DQ284	DQ284043			DQ283756	3800
Hydromantes platycephalus	CAS 206495	USA, California, Inyo Co, Elderberry Canyon, 37.37749°N, 118.63851°W	DQ283227	DQ28425					2248
*Hyla arborea**	ZFMK	Germany (live specimen)	**AY843601**		**AY843822**		**AY844046**		3270
Hyla cinerea	MVZ 145385	USA, Texas, Travis Co, Austin, municipal golf course	**AY549327**	DQ284057	**AY844597**	**AY844816**	**AY844063**	**AY844241**	4736
Hylarana erythraea	FMNH 257285	Cambodia, Siem Reap Prov, Siem Reap Dist, Siem Reap town, <10 m, 13°22′29″N, 103°50′44″E	DQ283138		DQ283839	DQ282694			3121
Hylarana taipehensis	AMNH A163972	Vietnam, Ha Giang Prov, Yen Minh, Du Gia Commune, Khau Ria Village, rice paddy on edge of limestone forest S village, 934 m, 22°53′49″N, 105°14′48″E	DQ283396		DQ284010	DQ282856	DQ283000	DQ283710	4358
Hylodes phyllodes	CFBH-T 249	Brazil, São Paulo, Picinguaba, Ubatuba	DQ283096	DQ284146	DQ283812	DQ282674	DQ282923		3989
*Hylorina sylvatica**			**AY389153**						718
Hyloscirtus armatus	AMNH A165163	Bolivia, Dept Santa Cruz, Caballero, San Juán Canton, Amboró National Park, near base camp on Río Cerro Bravo, 17°50′17″S, 64°23′30″W	**AY549321**	DQ284070	**AY844579**		**AY844050**	**AY844224**	4367
Hyloscirtus palmeri	SIUC 6924	Panama, Coclé Prov, El Copé, Parque Nacional ''Omar Torrijos''	**AY843650**	DQ284088	**AY844636**		**AY844095**	**AY844273**	4354
*Hymenochirus boettgeri**			**AY341634 AY341700 AY341726**				**AY341763**		2339

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Species	ID number	Locality	Locus/partition						Total bp
			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Hyperolius alticola	CAS 202047	Uganda, Rukungiri Dist, Bwindi Impenetrable National Park, Munyaga River, ca. 100 m downstream from Munyaga Falls	DQ283225	DQ284255	DQ283902	DQ282762	DQ282952	DQ283595	3781
Hyperolius punticulatus	AMNH A153299	Tanzania, Morogoro, Udzungwa Mts National Park, Njokamoni River drainage, 1100–1200 m	DQ283389	DQ284375		DQ282851	DQ282997	DQ283704	3963
Hyperolius tuberilinguis	AMNH A153257	Tanzania, Morogoro, Udzungwa Mts National Park, Man'gula Camp Site 3 on Mwaya River, 350 m, 7°50′51″S, 36°53′0″E	DQ283399 DQ283400	DQ284381		DQ282858	DQ283002	DQ283712	3492
Hypogeophis rostratus	UMMZ 181332	Seychelles, Silhouette Island, Trail from La Passe to Jardin Marron	DQ283131	DQ284172		DQ282687		DQ283524	3890
Hypsiboas albomarginatus	USNM 284519	Brazil, Pernambuco, near Carauruçu, on way to Serra dos Cavalos	**AY549316**		**AY549369**	**AY844794**		**AY844218**	3901
Hypsiboas boans	RWM 17746	Venezuela, Amazonas, Caño Agua Blanca, 3.5 km SE Neblina base camp on Río Baria	**AY843610**	DQ284086	**AY844588**	**AY844809**	**AY844055**	**AY844231**	4746
Hypsiboas cinerascens	MAD 085	Guyana, Iwokrama, Muri Scrub camp, 80 m	**AY549336**	DQ284076	**AY844610**	**AY844828**		DQ283466	4218
Hypsiboas multifasciatus	AMNH A141040	Guyana, Demerara, Ceiba Station, Madewini River, ca. 3 mi (linear) E Timehri airport	**AY843648**		**AY844633**	**AY844851**	**AY844093**	**AY844270**	4437
Ichthyophis cf. *peninsularis*	MW 375 (Univ of Kerala)	India	DQ283086	DQ284137		DQ282669		DQ283487	3847
Ichthyophis sp.	FMNH 256425	Laos, Khammouan Nakai Dist, Nakai Nam Theun National Biodiversity Conservation Area, Annamite Mts, disturbed evergreen forest along Houay Ting Tou stream, 700 m, 17°58′N, 105°34′E	DQ283336	DQ284327				DQ283661	2988
Iguana iguana	WCS	No data	**NC002793**	DQ284249				DQ283590	3416
Indirana sp.*			**AF249051**		**AF249122**		**AF249185**		1399
Indirana sp.*			**AF249064**		**AF249123**		**AF249186**		1406
Ingerana baluensis	FMNH 231085	Malaysia, Sabah, Lahad Datu Dist, Danum Valley Research Center	DQ283142	DQ284182	DQ283843	DQ282698	DQ282935	DQ283534	4636
Ischnocnema quixensis	MJH 7057	Peru, Huánuco, Panguana, Río Llullapichis	**DQ283061 DQ283060**	DQ284091	DQ283788	DQ282661			2950
Isthmohyla rivularis	MVZ 149750	Costa Rica, Heredia Prov, ''Chompipe'', vicinity Volcán Barba	**AY843659**	DQ284058	**AY844649**		**AY844117**		3598
*Ixalotriton niger**			**AF451248**						518

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Kalophrynus pleurostigma	FMNH 230844	Malaysia, Sabah, Lahad Datu Dist, Danum Valley Research Center	DQ283146	DQ284186	DQ283846	DQ282702		DQ283537	4168
Kaloula pulchra	AMCC 106697; RdS 02	Vietnam, Ha Tinh Prov, Huong Son Dist, Huong Son Reserve, Ngai Doi region, headquarters of Huong Son Reserve, 100 m, 18°27′08″N, 105°17′43″E; No data (pet trade)	DQ283397 DQ283398	DQ284379	DQ284011	DQ282857 DQ282874	DQ283001 DQ283012	DQ283711 DQ283727	4745
Kassina senegalensis	RdS 803	Tanzania, Iringa, Kibebe Farm, 07°48′12.4″S, 35°45′24.2″E	DQ283437	DQ284413		DQ282891	DQ283026	DQ283746	4401
Kurixalus eiffingeri	UMFS 5969	China, Taiwan, Nan-Tou, Lu-Gu Chi-Tou, 900–1100 m	DQ283122	DQ284166	DQ283830		DQ282931	DQ283518	4272
Kurixalus idiootocus	UMFS 5702	China, Taiwan, Nan-Tou, Tung Fu, 750 m	DQ283054	DQ284087	DQ283783		DQ282905	DQ283468	4287
Kyarranus sphagnicolus	ABTC 25186	Australia, New South Wales, Dorrigo Mountain	DQ283313		DQ283957			DQ283646	3442
Laliostoma labrosum	UMMZ 213554	Madagascar, Toliara, Sakaraha, Zombitsy Forest, 44.711666°S, 22.843333°E	DQ283057	DQ284089	DQ283786		**AF249169**	DQ283470	4295
*Lankanectes corrugatus**			**AF215393 AF249019 AF249043**		**AF249115**		**AF249178**		2102
Latimeria chalumnae	AMNH A59196	Comoros, Grande Comore	**NC_001804**	DQ284319	**AF131253**			DQ283653	3865
Lechriodus fletcheri	ABTC 24921	Australia, New South Wales, Border Ranges National Park	DQ283282 DQ283283	DQ284299	DQ283942	DQ282793		DQ283632	3753
Leiopelma archeyi	DMG 5123	New Zealand, North Island, Coromandel Peninsula, Tapu Summit	DQ283216 DQ283215	DQ284246	DQ283895			DQ283588	3395
Leiopelma hochstetteri	DMG 5135	New Zealand, Waitakere Mts, Cowan Stream	DQ283217	DQ284247		DQ282755		DQ283589	3894
Lepidobatrachus laevis	AMNH A168407	No data (pet trade)	DQ283152	DQ284191	DQ283851	DQ282707		DQ283543	4192
Leptobrachium chapaense	AMNH A163791	Vietnam, Ha Giang Prov, Vi Xuyen, Cao Bo Commune, Mount Tay Conn Linh II, above Tham Ve Village, spring camp, 1420 m, 22°45′59″N, 104°49′56″E	DQ283052	DQ284081				DQ283467	3053
Leptobrachium hasselti	CAS 222293	Myanmar, Rakhine State, Gwa Township, Rakhine Yoma Elephant Sanctuary, Kyat stream camp, 17°42′14.0″N, 94°38′54.3″E	DQ283239	DQ284265	DQ283911	DQ282767		DQ283605	4176
Leptodactylodon bicolor	UTA A44492	Cameroon, Southwest Prov, plateau NW Ntale Village	DQ283364	DQ284351	DQ283986		DQ282980		3587

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Species	ID number	Locality	Locus/partition						Total bp
			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Leptodactylus fuscus	AMNH A139088	Guyana, Southern Rupununi savanna, Aishalton (on Kubabawau Creek), 150 m, 2°28′31″N, 59°19′16″W	DQ283404	DQ284385	DQ284015	DQ282862	**AY341760**	DQ283716	4744
Leptodactylus ocellatus	MACN 38648	Argentina, Buenos Aires, Escobar, Loma Verde, Establecimiento ‘‘Los Cipreses’’	**AY843688**	DQ284104	**AY844681**			**AY844302**	3809
Leptolalax bourretti	AMNH A163810	Vietnam, Ha Giang Prov, Vi Xuyen, Cao Bo Commune, Mount Tay Conn Linh II, above Tham Ve village, stream 2 km SW base camp, 1420 m, 22°46′8″N, 104°49′51″E	DQ283381	DQ284367	DQ284000	DQ282844		DQ283696	3246
Leptopelis argenteus	CAS 169938	Kenya, Kilifi Dist, 14.4 km W Kakayuni, towards Lake Jilore, on Kakayuni Rd roadside pond	DQ283226	DQ284256	DQ283903			DQ283596	3760
Leptopelis bocagei	RdS 802	Tanzania, Iringa, Kibebe Farm, 07°48′12.4″S, 35°45′24.2″E	DQ283418				DQ283014	DQ283729	3639
Leptopelis sp.	AMNH A168408	No data (pet trade)	DQ283161	DQ284199	DQ283856			DQ283552	3766
Leptopelis vermiculatus	CAS 168661	Tanzania, Tanga Region, Muheza Dist, East Usambara Mts, Amani-Muheza Rd 3–5 km SE Amani	DQ283242	DQ284268				DQ283608	3450
Limnodynastes depressus	NTM R26241	Australia, Northern Territory, Elizabeth Downs, Daly River region	DQ283308	DQ284312	DQ283954	DQ282805		DQ283643	4174
Limnodynastes dumerilli	SAMA R34734	Australia, New South Wales, Langothlin	DQ283285 DQ283286	DQ284301	DQ283944	DQ282794		DQ283633	3743
Limnodynastes ornatus	QMJ 57109	Australia, Queensland, Heathlands	DQ283280 DQ283281	DQ284298	DQ283941	DQ282792		DQ283631	3756
Limnodynastes peronii	AH	No data	DQ283245 DQ283246	DQ284272	DQ283917	DQ282772			2962
*Limnodynastes salmini**			**AY326071**						2408
Limnomedusa macroglossa	MACN 38641	Argentina, Misiones, Aristobulo del Valle, Balneario Cuñapirú	**AY843689**	DQ284127	**AY844682**		**AY844128**		3594
*Limnonectes acanthi**			**AY313724**						2399
Limnonectes grunniens	ABTC 47812	Papua New Guinea, Utai	DQ283202	DQ284234	DQ283885	DQ282745			3443
*Limnonectes heinrichi**			**AY313749**						2402
Limnonectes kuhlii	AMNH A161202	Vietnam, Quang Binh Prov, Minh Hoa, Cha Lo	**AY313686**	DQ284234	DQ283885	DQ282745	DQ282982	DQ283688	4686
Limnonectes poilani	AMNH A163717	Vietnam, Quang Nam Prov, Trã My, Trã Tâp Commune, stream near Thon 2 Village, 920–1060 m, 15°9′37″N, 108°2′26″E	DQ283378	DQ284364	DQ283997	DQ282841	DQ282989		3981
*Limnonectes visayanus**			**AY313719**						2358

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			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
*Lineatriton lineolus**			**AF380808**						516
Liophryne rhododactyla	ABTC 49566	Papua New Guinea, Bulolo	DQ283199	DQ284231	DQ283882	DQ282742		DQ283580	4171
Lithobates palmipes	AMNH A166454	Guyana, Magdalen's Creek camp, ±300 yd NW bank of Konawaruk River ca. 25 mi (linear) WSW Mabura Hill, 400 ft, 5°13′7″N, 59°2′43″W	DQ283384	DQ284369	DQ284001	DQ282847	DQ282994	DQ283699	4686
Lithodytes lineatus	AMNH A166426	Guyana, Berebice River camp at ca. 18 mi (linear) SW Kwakwani (ca. 2 mi downriver from Kurundi River confluence), 200 ft, 5°5′6″N, 58°14′14″W	**AY843690**	DQ284112	**AY844683**		**AY844129**	**AY844303**	4345
Litoria aurea	AMS 52744	New Caledonia, Prov Nord, Valle Phaaye, Nomac River, 8 km E Poum	**AY843691**	DQ284098	**AY844684**	**AY844130**	**AY844892**		3989
Litoria freycineti	SAMA R12260	Australia, New South Wales, 16 km E Retreat	**AY843693**	DQ284122	**AY844686**	**AY844894**			3460
Litoria genimaculata	SAMA R41068	Australia, Northern Territory, Mt Lewis	DQ283222	DQ284252	DQ283899	DQ282759		DQ283592	4144
Litoria inermis	SAMA R53945	Australia, Western Australia, 24 km N Tunnel Creek Gorge	DQ283211 DQ283212	DQ284243	DQ283892				2718
Litoria lesueurii	SAMA R35012	Australia, New South Wales, Murrumbidgee River	DQ283204	DQ284236	DQ283887	DQ282747			3456
Litoria meiriana	SAMA R17215	Australia, Western Australia, Black Rock, near Kununurra	**AY843695**	DQ284125	**AY844688**	**AY844895**	**AY844132**		3988
Litoria nannotis	SAMA R40266	Australia, Queensland, Paluma	DQ283218	DQ284248	DQ283896	DQ282756			3459
Lysapsus laevis	AMCC 10720	Guyana, Southern Rupununi Savannah, Aishalton (on Kubanawan Creek)	**AY843696**	DQ284110	**AY844689**	**AY844896**	**AY844133**	**AY844305**	4746
Mannophryne trinitatis	MVZ 199838	Trinidad and Tobago, Nariva Parish, Tamana Cave, Charuma Ward	DQ283071	DQ284108	DQ283796				3052
Mantella aurantiaca	UMMZ 201411	Madagascar, Toamasina, Moramanga, Andasibe Region	DQ283035	DQ284061	DQ283766	DQ282651	DQ282901	DQ283460	4666
Mantella nigricans	AMNH A167477	Madagascar, Antsiranana, Ambanja, Antsaravy Ridge, Tsaratanana Reserve, 13°55′34″S, 48°54′21″E	DQ283034	DQ284056	DQ283764			DQ283458	3730
Mantidactylus cf. *femoralis*	AMNH A167581	Madagascar, Antsiranana, Ambanja, Ramena River Camp, Tsaratanana Reserve, 13°55′4″S, 48°53′16″E	**AY843698**	DQ284055	DQ283763	**AY844898**	DQ282900		3978
Mantidactylus peraccae	UMMZ 213278	Madagascar, Fianarantsoa, Ivohibe, Andringitra Volotsangana River (Camp 3), 47.016666°S, 22.277777°E	DQ283036	DQ284062	DQ283767	DQ282652			3445

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			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Megaelosia goeldii	MZUSP 95879	Brazil, Rio de Janeiro, Teresópolis, Rio Beija Flor, 910 m, 22°24′S, 42°69′W	DQ283072	DQ284109	DQ283797		DQ282911		3590
Megistolotis lignarius	SAMA R37834	Australia, Western Australia, Kununurra	DQ283289	DQ284303		DQ282796		DQ283634	3846
Megophrys nasuta	FMNH 236525	Malaysia, Sabah, Tenom Dist, Crocker Range National Park, Purulon camp, Sungai Kilampun	DQ283342	DQ284331	DQ283969	DQ282818			3437
Melanophryniscus klappenbachi	MACN 38531	Argentina, Chaco, vicinity Resistencia	**AY843699**	DQ284060	DQ283765	**AY844899**		**AY844306**	4207
Meristogenys orphnocnemis	FMNH 230531	Malaysia, Sabah, Lahad Datu Dist, Danum Valley Research Center, Sungai Palum Tambun	DQ283147	DQ284187	DQ283847	DQ282703		DQ283538	4176
Metacrinia nichollsi	WAM R106065	Australia, Western Australia, 9.5 km ENE Mt Frankland	DQ283292 DQ283293	DQ284305	DQ283946	DQ282798		DQ283636	3077
Micrixalus borealis	CAS 205064	Myanmar, Rakhine State, Gwa Township, ca. 0.5 mi S Pleasant Beach Resort, 17°43′3.7″N, 94°31′55.6″E	DQ283235 DQ283236		DQ283909	DQ282766		DQ283603	2517
*Micrixalus fuscus**			**AF249024 AF249056**		**AF249120**		**AF249183**		2105
*Micrixalus kottigeharensis**			**AF249025 AF249041**		**AF249121**		**AF249184**		2103
Microhyla heymonsi	AMNH A163850	Vietnam, Ha Giang Prov, Yen Minh, Du Gia Commune, Khau Ria Village, stream 1, below cascade, 22°54′27″N, 105°13′52″E	DQ283382			DQ282845	DQ282992	DQ283697	4052
Microhyla sp.	RdS 05	No data (pet trade)	DQ283422	DQ284400	DQ284025	DQ282879	DQ283017	DQ283732	4678
*Micryletta inornata**			**AF285207**						502
Minyobates claudiae	USNM-FS 59980	Panama, Bocas del Toro, S end of Isla Popa, 1 km E Sumwood Channel	DQ283042	DQ284071	DQ283772	DQ282654		DQ283462	4224
Mixophyes carbinensis	ABTC 25115	Australia, Queensland, Mt Lewis area	DQ283314 DQ283315	DQ284315	DQ283958				2148
Myobatachus gouldii	WAM R116075	Australia, Western Australia, Spalding Park Geraldton	DQ283309 DQ283310	DQ284313	DQ283955			DQ283644	3337
*Nannophrys ceylonensis**			**AF249016 AF249047**		**AF249112**		**AF249175**		2112
*Nanorana pleskei**			**AF206111 AF206156 AF206492**						1979
Nasikabatrachidae sp.*			**AY425725 AY425726**						902
*Nasikabatrachus sahyadrensis**			**AY364360 AY364381**		**AY364406**				1532
*Natalobatrachus bonebergi**			**AF215396 AF215198**						784
Nectophryne afra	UTA A44673	Cameroon, Southwest Prov, vicinity Edienosa	DQ283360	DQ284347	DQ283981	DQ282831	DQ282977	DQ283680	4705

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			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Nectophryne batesi	RABI 031	Gabon, Rabi (Shell Gabon), near Toucan Well Head, 01.47°S, 09.53°E	DQ283169	DQ284207		DQ282721		DQ283559	3863
Nectophrynoides tornieri	RdS 951	Tanzania, East Usambara Mts, adjacent to Amanai Nature Reserve, 05°07′38.0″S, 38°37′22.6″E	DQ283413	DQ284394	DQ284018	DQ282870		DQ283723	3774
Necturus cf. *beyeri*	AMCC 125608	USA, Florida, Jackson Co, Econfina Creek, 30°34.17′N, 85°21.72′W	DQ283151	DQ284190				DQ283542	2952
Necturus maculosus	AMCC 105652	USA, New York, Suffolk Co, Cold Spring Harbor, Cold Spring Harbor Fish Hatchery	DQ283412					DQ283722	2622
*Nelsonophryne aequatorialis**			**AY326067**						2414
Neobatrachus pictus	SAMA R50636	Australia, South Australia, 10 km S Robe	DQ283290 DQ283291	DQ284304		DQ282797		DQ283635	3430
Neobatrachus sudelli	SAMA R12391	Australia, New South Wales, 30 km N Kenmore	**AY843700**	DQ284123	**AY844691**			**AY844307**	3779
Nesionixalus thomensis	CAS 218925	São Tome and Principe, São Tome I, forest at radio tower S Bom Sucesso, 00°16′64.0″N, 06°36′20.0″E	DQ284123	DQ284261	DQ283906	DQ282764	DQ282953	DQ283600	4213
Nesomantis thomasseti	RAN 25162	Seychelles, Mahe, junction of Foret Noir Rd with Grand Bois River and Congo Rouge Trail	DQ283452	DQ284425	DQ284042		**AY341761**	DQ283755	3776
*Neurergus crocatus**			**AY147246 AY147247**						719
Nidirana adenopleura	UMMZ 189963	China, Taiwan, Taipei, Wu-Lai, Shao-Yi, trail along Tung-Ho Creek	DQ283117	DQ284163	DQ283829	DQ282685	DQ282930	DQ283515	4684
Nidirana chapaensis	AMNH A161183	Vietnam, Ha Tinh Prov, Huang Son Reserve, Rao An region, top of Pomu Mountain, 900–1200 m, 18°20′53″N, 105°14′38″E	DQ283365 DQ283366	DQ284352	DQ283987	DQ282833	DQ282981	DQ283685	3791
Notaden melanoscaphus	QMJ 57130	Australia, Queensland, Hervey Range	DQ283287 DQ283288	DQ284302	DQ283945	DQ282795			3026
Notophthalmus viridiscens	AMCC 106084	No data	DQ283421	DQ284399	DQ284024	DQ282878			3001
*Nototriton abscondens**			**AF199199**						514
Nyctibates corrugatus	UTA A44461	Cameroon, Southwestern Prov, vicinity Ediensoa	DQ283361	DQ284349	DQ283983		DQ282979	DQ283682	3876
Nyctibatrachus cf. *aliciae**			**AF249018 AF249063**		**AF249114**				1578
*Nyctibatrachus major**			**AF249017 AF249052 AY341687**		**AF249113**		**AF249176**		2688
Nyctimistes pulchra	SAMA R45336	Papua New Guinea, Magidobo, SHP	**AY843701**	DQ284126	**AY844692**		**AY844134**		3588

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			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Nyctimystes dayi	SAMA R41010; ZSM 748/2000	Australia, Queensland, Pilgrim Sands; Australia, Queensland, Tully River tributary, 100 m, 50 km (by rd) NW Tully	DQ283220	DQ284250 DQ284276	DQ283921 DQ283897	DQ282757		DQ283591	4145
Nyctixalus pictus	FMNH 231095	Malaysia, Sabah, Lahad Datu Dist, Danum Valley Research Center	DQ283133	DQ284174	DQ283834	DQ282689		DQ283526	4150
Nyctixalus spinosus	ACD 1043	Philippines, Mindanao	DQ283114	DQ284160	DQ283827			DQ283512	3768
Occidozyga baluensis	FMNH 242747	Malaysia, Sabah, Sipitang Dist, Mendolong camp, km 6.8	DQ283143	DQ284183	DQ283844	DQ282699	DQ282936	DQ283535	4262
Occidozyga lima	CAS 213254	Myanmar, Yangon Division, Hlaw Ga Park, Mingalardon Township, 17°02′36.5″N, 96°06′41.5″E	**AF161027**	DQ284254	DQ283901	DQ282761	DQ282951	DQ283594	4143
Occidozyga martensii	AMNH A161171	Vietnam, Ha Tinh Prov, Huang Son Reserve, Rao An region, 160 m, 18°29′54″N, 105°13′51″E	DQ283357	DQ284344	DQ283978	DQ282829	DQ282976		3560
Odontophrynus achalensis	ZSM 733/2000; BB 1324	Argentina, Prov Córdoba, Pampa de Achala; Argentina, Prov Córdoba, proximity of Pampilla, near Parador El Cóndor	DQ283247 DQ283248	DQ284273	DQ283918	DQ282773		DQ283611	4243
Odontophrynus americanus	JF 1946	Argentina, Buenos Aires, Escobar, Loma Verde, Ea. ''Los Cipreses''	**AY843704**		**AY844695**	**AY844901**		**AY844309**	3913
Odorrana grahami	CAS 207504	China, Yunnan, Baoshan Pref, Qushi, ca. 25°17′N, 98°36′E	DQ283241	DQ284267	DQ283913	DQ282769		DQ283607	4163
*Oedipina uniformis**			**AF199230**						515
Ophryophryne hansi	AMNH A163669	Vietnam, Quang Nam Prov, Trà My, Trà Don Commune, near Camp 1, 980–1020 m, 15°11′41″N, 108°2′25″E	DQ283377	DQ284363	DQ283996	DQ282840	DQ282988		3995
Ophryophryne microstoma	AMNH A163859	Vietnam, Ha Giang Prov, Yen Minh, Du Gia Commune, Khau Ria Village, stream 1, above cascade, 900 m, 22°54′8″N, 105°13′52″E	DQ283391	DQ284376	DQ284006	DQ282852		DQ283705	4190
Opisthothylax immaculatus	MB 5513 (SAM); DPL 3968	Gabon, Rabi (Shell Gabon), at Rabi 059, trap lines 1–3, 01.5633°S, 09.5109°E; Cameroon, Southwest Prov, Kumba–Mamfe rd, within 15 km N and S of Nguti	DQ283174	DQ284211	DQ283866		DQ282971	DQ283563	4274
Oreophryne brachypus	AMS R129618	Papua New Guinea, 8 km NNE Amelei	DQ283194	DQ284227		DQ282738		DQ283577	3446
*Osornophryne guacamayo**			**AY326036**						2412

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Osteocephalus taurinus	AMNH A131254	Venezuela, Amazonas, Neblina base camp on Río Mawarinuma (=Río Baria), 140 m	**AY843709**	DQ284075	**AY844700**	**AY844905**	**AY844140**	**AY844313**	4731
Osteopilus septentrionalis	USNM 317830	Cuba, Guantanamo, Guantanamo Bay	**AY843712**	DQ284049		**AY844906**		**AY844316**	3886
Pachytriton brevipes	AMNH A168416	No data (pet trade)	DQ283446 DQ283447	DQ284421					1749
*Pantherana berlandieri**			**AY115111**						856
Pantherana capito	AMCC 125632	USA, Florida, Hernando Co, Croom Wildlife Management Area, Seed Orchard	DQ283187	DQ284221	DQ283874	DQ282732		DQ283572	4158
Pantherana chiricahuensis	ASU 33310	USA, Arizona, Greenlee Co, Coleman Creek	DQ283270	DQ284290	DQ283934		DQ282962	DQ283626	4291
Pantherana forreri	USNM 534222	Honduras, El Paraiso, 12 km NNW Ojo de Agua	DQ283103	DQ284152	DQ283818	DQ282678		DQ283503	4156
Pantherana pipiens	UMMZ 227023	USA, Michigan, Kent Co, Grand Rapids Ada Township Park	DQ283123	DQ284167	DQ283831	DQ282686		DQ283519	4161
Pantherana yavapaiensis	CG	USA, Arizona, Pima Co, Cienega Creek	DQ283272	DQ284292	DQ283936	DQ282787		DQ283628	4158
Papurana daemeli	SAMA R40355	Australia, Northern Territory, Cape Tribulation	DQ283201	DQ284233	DQ283884	DQ282744	DQ282948	DQ283581	4682
Paracrinia haswelli	SAMA R40951	Australia, Victoria, near Marlo	DQ283304 DQ283305	DQ284310	DQ283952			DQ283641	3327
Paramesotriton sp.	RdS	Vietnam (no other data)	DQ283428						1950
Paratelmatobius sp.	CFBH-T 240	Brazil, Paraná, Piraquara	DQ283098	DQ284148	DQ283814	DQ282676	DQ282925	DQ283499	4726
*Parvimolge townsendi**			**AF451247**						512
Pedostibes hosei	FMNH 231190	Malaysia, Sabah, Lahad Datu Dist, Danum Valley Research Center, Sungai Palum Tambun	DQ283164	DQ284202	DQ283859	DQ282717			3463
*Pelobates cultripes**			**AY236801 AY364341 AY364363**		**AY364386**				1586
Pelobates fuscus	AH	Germany, Thüringen, Geroda (Triptis)	DQ283113	DQ284159	DQ283826			DQ283511	3788
Pelodytes punctatus	AH	Spain, Barcelona	DQ283111	DQ284157	DQ283824	DQ282682		DQ283509	4175
Pelomedusa subrufa	RAX 2055 (now KU)	Ghana, Muni Lagoon, Winneba, 5°21′14″N, 0°42′12″W	**NC001947**			DQ282782		DQ283622	3545
*Pelophryne brevipes**			**AF375503 AF375530**						1093
Pelophylax nigromaculata	FMNH 232879	China, Sichuan, Hongya Xian, Bin Ling	DQ283137	DQ284178	DQ283838	DQ282693	DQ282932	DQ283530	4694
*Pelophylax ridibunda**			**AB023397 AY147983**						918
Petropedetes cameronensis	UTA A44399	Cameroon, Southwest Prov, vicinity Ediensoa	DQ283075 DQ283076	DQ284130	DQ283800	DQ282665		DQ283481	3671
Petropedetes newtoni	RABI 033	Gabon, Rabi (Shell Gabon), Toucan Well Head, 01.4750°S, 09.5335°E	DQ283177 DQ283178	DQ284214	DQ283869	DQ282727			3045

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Petropedetes palmipes	UTA A52407	Cameroon, South Prov, near Bipindi, vicinity 0658198, 0342287 (UTM 32 N)	DQ283074	DQ284129	DQ283799	DQ282664		DQ283480	3747
*Petropedetes parkeri**			**AY341694 AY364348 AY364369**		**AY364394**		**AY341757**		2830
*Phaeognathus hubrichti**			**AY728233**						2363
Phasmahyla guttata	CFBH 5756	Brazil, São Paulo, Ubatuba, Picinguaba	**AY843716**		**AY844703**	**AY844909**	**AY844145**		3661
Philautus rhododiscus	AMNH A163892	Vietnam, Ha Giang Prov, Vi Xuyen, Cao Bo Commune, Mount Tay Conn Linh II, above Tham Ve Village, base camp, 1420 m, 22°46′8″N, 104°49′51″E	DQ283392 DQ283393		DQ284007	DQ282853	DQ282998	DQ283706	3945
Phlyctimantis leonardi	DPL 4057	Cameroon, Southwestern Prov, Kumba–Mamfe	DQ283355 DQ283356	DQ284343		DQ282828		DQ283677	3446
Phobobates silverstonei	RG	No data (Atlanta Botanical Garden, captive bred)	DQ283073	DQ284116	DQ283798	DQ282663		DQ283479	4223
Phrynobatrachus auritus	UTA A44704	Cameroon, Southwest Prov, vicinity Edienosa	DQ283084	DQ284135		DQ282668	DQ282916	DQ283485	3901
Phrynobatrachus calcaratus	CAS 199268	Cameroon, East Prov, Dja Reserve, Boumir Camp, 3°11′26″N, 12°48′42″E, 665 m	DQ283240	DQ28426	DQ283912	DQ282768		DQ283606	4157
Phrynobatrachus dendrobates	CAS 202048	Uganda, Rukunguri Prov Dist, Bwindi Impenetrable National Park, Munyaga River, ca. 100 m downstream Munyaga Falls	DQ283228 DQ283229	DQ2842	DQ283904			DQ283598	3312
Phrynobatrachus dispar	CAS 218995	São Tome and Principe, São Tome Id., Java, 00°15′39.9″N, 06°39′03.2″E	DQ283223	DQ284253	DQ283900	DQ282760		DQ283593	3742
Phrynobatrachus mababiensis	RdS 805	Tanzania, Iringa, Kibebe Farm, Netting Pond, 07°48′12.4″S, 35°45′24.2″E	DQ283424	DQ284402	DQ284026	DQ282881		DQ283733	4158
Phrynobatrachus natalensis	RdS 881	Tanzania, Tatanda Village, 08°29′27.2″S, 31°30′18.3″E	DQ283414	DQ284395	DQ284019	DQ282871	DQ283009	DQ283724	4628
Phrynodon sandersoni	UTA A44599; UTA A44600	Cameroon, Southwest Prov, plateau NW Ntale Village. ca. 567 m	DQ283082 DQ283083	DQ284339 DQ284134	DQ283804 DQ283975	DQ282825 DQ282667	DQ282915 DQ282973	DQ283673 DQ283484	4662
Phrynomantis bifasciatus	RdS	No data (pet trade)	DQ283154	DQ28419		DQ282709	DQ282940	DQ283545	3945
Phrynopus sp.	AMNH A165108	Bolivia, La Paz, Bautista Saavedra, Canton Charazani, ca. 4 km E Chullina, 3590 m, 15°10′12″S, 68°53′12″W	**AY843720**	DQ284371			DQ282995	**AY844323**	3901
Phrynopus sp.*	KU 202652		**AY326010**						3446
Phyllobates lugubris	USNM-FS 195116	Panama, Bocas del Toro, S end of Isla Popa, 1 km E Sumwood Channel	DQ283043			DQ282655		DQ283463	4157
Phyllodytes luteolus	JLG17	Brazil, Espírito Santo, Setiba, Guarapari	**AY843721**		**AY844708**	**AY844913**	**AY844150**		3312

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Species	ID number	Locality	Locus/partition						Total bp
			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Phyllomedusa vaillanti	AMNH A166288	Guyana, Berbice River camp at ca. 18 mi (linear) SW Kwakwani, ca. 2 mi downriver from Kurundi River confluence, 200 ft, 5°5′6″N, 58°14′14″W	**AY549363**		**AY844716**	**AY844921**	**AY844158**	**AY844329**	3742
Physalaemus gracilis	RdS 788	Uruguay, Flores	DQ283417		DQ284022	DQ282875		DQ283728	3885
Pipa carvalhoi	AH	No data	DQ283251	DQ284277	DQ283922	DQ282774		DQ283613	4009
Pipa pipa	USNM 562560	Venezuela, Amazonas, Dept Río Negro, Neblina Base Camp on the Río Baria, 00°49′50″N, 66°09′40″W, 140 m	DQ283053		DQ283781	DQ282660			3168
Platymantis pelewensis	USNM 546385	Palau Islands, Ngerekebesang I, Echang village, rd to Japanese bunkers just N Image Restaurant and Palau Sunrise Hotel, 7°21′N, 134°27′E	DQ283104	DQ2841	DQ283819	DQ282679		DQ283504	4134
Platymantis weberi	AMS R134894	Solomon Islands, New Georgia, Patutiva	DQ283196	DQ284229	DQ283880	DQ282740			3436
Platypelis grandis	AMNH A167214	Madagascar, Antsiranana, Vohemar, Bezavona Mountain, 13°31′58″S, 49°51′57″E	DQ283410	DQ284392		DQ282868	DQ283007	DQ283721	4336
Plectrohyla guatemalensis	UTA A-55140	Guatemala, Guatemala, Don Justo, Santa Rosalia, km 12.5 on the hwy to El Salvador	**AY843731**		**AY844719**	**AY844924**	**AY844160**		3663
Plethodon dunni	TAT 1040	USA, Oregon, Lane Co, Richardson Creek Rd	DQ283262	DQ284285	DQ283930			DQ283620	3226
Plethodon jordani	UMMZ 210798	North Carolina, Macon Co, Coweeta Middle Elevation	DQ283125 DQ283126	DQ284169				DQ283521	2431
Plethodontohyla sp.	AMNH A167315	Madagascar, Antsiranana, Vohemar, Camp 1, Sorata Mountain, 13°41′9″S, 49°26′31″E	DQ283409	DQ284390		DQ282866	DQ283006	DQ283719	3914
Pleurodeles waltl	AMNH A168418	No data (pet trade)	DQ283445	DQ284420				DQ283751	3442
Pleurodema brachyops	AMNH A139118	Guyana, Southern Rupununi Savanna, Aishalton (on Kubabawau Creek), 150 m, 2°28′31″N, 59°19′16″W	**AY843733**	DQ28411	**AY844721**	**AY844926**			3466
*Polypedates cruciger**			**AF249028 AY341685**		**AF249124**		**AF249187**		2167
Polypedates leucomystax	AMNH A161395	Vietnam, Ha Tinh, Huong Son, Huong Son Reserve, Rao An region, top of Pomu Mountain, 900–1200 m, 18°20′53″N, 105°14′38″E	DQ283048	DQ284079	DQ283777				3040
Probreviceps macrodactylus	RdS 942	Tanzania, East Usambara Mts, adjacent to Amanai Nature Reserve, 05°07′38.0″S, 38°37′22.6″E	DQ283420			DQ282877	DQ283016	DQ283731	3149

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			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Proceratophrys avelinoi	JF 1947	Argentina, Misiones, Guarani, San Vicente, Campo Anexo INTA "Cuartel Río Victoria"	DQ283038 DQ283039	DQ2840	DQ283769		DQ282903		3255
Pseudacris crucifer	JF	No data (pet trade)	**AY843735**	DQ284114	**AY844723**	**AY844927**	**AY844163**	DQ283478	4695
Pseudacris ocularis	AMNH A168472	USA, Florida, Columbia Co, SR 250 2 mi W I-10	**AY843736**		**AY844724**		**AY844164**		4416
Pseudis paradoxa	MACN 37786	Argentina, Corrientes, Dept Bellavista, San Roque–Bellavista rd	**AY843740**	DQ284128	**AY844727**		**AY844167**	**AY844337**	4357
Pseudoamolops sauteri	UMMZ 189938	China, Taiwan, Tai-Chung, Ha-Pin trout pond near Wu-Lin	DQ283124	DQ284168	DQ283832			DQ283520	3762
Pseudobranchus striatus	AMCC 125629	USA, Georgia, Long Co, 15.5 km E Glennville	DQ283182 DQ283183	DQ284217				DQ283569	2935
Pseudoeurycea conanti	JAC 21252	Mexico, Oaxaca, Sierra Madre del Sur, San José Pacífico–Portillo del Rayo Hwy, 1850 m, 16°1.701′N, 96°31.176′W	DQ283454	DQ284427				DQ283757	2917
Pseudopaludicola falcipes	MACN 38647	Argentina, Corrientes, Yapeyu	**AY843741**	DQ284117	**AY844728**	**AY844930**	**AY844168**		3989
Pseudophryne bibroni	SAMA R73293	Australia, New South Wales, S Para Reservoir Reserve	**AY843988**					**AY844338**	3118
Pseudophryne coriacea	ABTC 25573	Australia, New South Wales, Sheepstation Creek, Border Ranges	DQ283311 DQ283312	DQ284314	DQ283956	DQ282806		DQ283645	3276
Pseudorana johnsi	AMNH A161191	Vietnam, Nghe An Prov, Con Cuong, Chau Khe Commune, Ngun Stream, 300 m, 19°2′17″N, 104°42′6″E	DQ283214	DQ284245	DQ283894	DQ282754		DQ283587	4148
*Ptychadena anchietae**			**AF261249 AF261267**						1650
Ptychadena cooperi	AMNH A158394	Ethiopia, Bale Prov, creek just E Dinsho	DQ283066 DQ283067		DQ283792			DQ283475	2497
Ptychadena mascareniensis	AMNH A167415	Madagascar, Antsiranana, Ambanja, Mandrizavona Village, Ramena Valley, 13°48′3″S, 48°44′47″E	DQ283031	DQ284052	DQ283760		DQ282899		3670
Ptychohyla leonhardlschultei	UTA A-54782	Mexico, Oaxaca, Sierra Madre del Sur, Pochutla Hwy, 681 m	**AY843746**		**AY844733**	**AY844934**	**AY844171**		3660
Pyxicephalus edulis	AMNH A168412	No data (pet trade)	DQ283157	DQ284195	DQ283853	DQ282711	DQ282941	DQ283548	4685
Quasipaa verrucospinosa	AMNH A163740	Vietnam, Quang Nam Prov, Trà My, Trà Don Commune, near Camp 1, 980–1020 m, 15°11′41″N, 108°2′25″E	DQ283379	DQ284365	DQ283998	DQ282842	DQ282990	DQ283694	4263
Quasipaa exilispinosa	ZSM 759/ 2000	China, Hong Kong, Lantau Island, Sunset Peak	DQ283244	DQ284271	DQ283916	DQ282771	DQ282957	DQ283610	4698
*Ramanella obscura**			**AF215382**						499
Rana japonica	FMNH 232896	China, Sichuan, Hongya Xian, Bin Ling	DQ283136	DQ284177	DQ283837	DQ282692		DQ283529	4153

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			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Rana sylvatica	AMCC 108286	USA, New Jersey, Monmouth Co, 2 mi N Manalapan, 40.27910°N, 74.38136°W	DQ283387	DQ284373	DQ284004	DQ282849	DQ282996	DQ283702	4687
Rana temporaria	ZSM 762/ 2000; UMFS 8005	Germany, Thuringia, Schnellbach, 725 m elevation; Ireland, Kells, Meath	DQ283127 DQ283128 DQ283129	DQ284170 DQ284269	DQ283914		DQ282956	DQ283522	4284
*Ranodon sibiricus**			**NC004021**						2428
Rhacophorus annamensis	AMNH A161414	Vietnam, Quang Binh Prov, Minh Hoa, Cha Lo	DQ283047		DQ283776				2729
Rhacophorus bipunctatus	AMNH A161418	Vietnam, Ha Tinh Prov, Huong Son Dist, Huon Son Reserve, Rao An region, top of Pomu Mountain	**AY843750**	DQ284078	**AY844737**				3756
Rhacophorus calcaneus	AMNH A163749	Vietnam, Quang Nam Prov, Trà My, Trà Don Commune, near Camp 1, 980–1020 m, 15°11′41″N, 108°2′25″E	DQ283380	DQ284366	DQ283999	DQ282843	DQ282991	DQ283695	4692
Rhacophorus orlovi	AMNH A161405	Vietnam, Ha Tinh Prov, Huong Son Dist, Huon Son Reserve, Nga Doi region, tributary of Nga Doi River, 240–350 m, 18°29′50″N, 105°13′49″E	DQ283049		DQ283778				2716
*Rhamphophryne festae**			**AF375504 AF375531**						1583
Rheobatrachus silus	ABTC 7317	Australia, Queensland, Connondale Ranges	DQ283275 DQ283276	DQ284295	DQ283938	DQ282789			3007
Rhinatrema bivittatum	AMNH A166059	Guyana, Magdalen's Creek camp, ±300 yd NW bank of Konawaruk River ca. 25 mi (linear) WSW Mabura Hill, 400 ft, 5°13′7″N, 59°2′43″W	DQ283385	DQ284370	DQ284002			DQ283700	2897
Rhinoderma darwinii	IZUA 3504	Chile, X Región, Valdivia, Reserva Forestal de Oncol	DQ283324	DQ284320	DQ283963	DQ282813		DQ283654	4202
Rhinophrynus dorsalis	WR	USA, Texas, Starr Co, near McAllen (living specimen)	DQ283109	DQ284156	DQ283822	DQ282681		DQ283507	4198
Rhyacotriton cascadae	UMFS 11729	USA, Oregon, Multnomah Co, 122.114°W, 45.569°N	DQ283110		DQ283823			DQ283508	2924
Salamandra salamandra	AMNH A168419	No data (pet trade)	DQ283440	DQ284416	DQ284037				2604
Scaphiophryne marmorata	AMNH A-167395	Madagascar, Antsiranana, Vohemnar, Sorata Mtn (1320 m)	**AY843751**	DQ284391	**AY364390**	DQ282867	AY844175	DQ283720	4706
Scaphiopus couchii	AMNH A168413	No data (pet trade)	DQ283150		DQ283850	DQ282706		DQ283541	3860
Scaphiopus holbrooki	AMNH A168434	USA, Florida, Alachua Co, Rd 346, 1.2 mi W jct Florida Hwy 121	DQ283156	DQ284194	DQ283852	DQ282710		DQ283547	4101
Scarthyla goinorum	KU 215427	Peru, Madre de Dios, Cusco Amazónico, 15 km E Puerto Maldonado	**AY843752**		**AY844738**	**AY844938**			3124

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			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Schismaderma carens	RdS 796	Tanzania, Iringa, Kibebe Farm, 07°48′12.4″S, 35°45′24.2″E	DQ283425	DQ284403	DQ284027	DQ282882		DQ283734	4218
Schistometopum gregorii	BMNH 2002.98	Tanzania	DQ283089	DQ284140	DQ283805			DQ283490	3749
Schoutedenella schubotzi	CAS 201752	Uganda, Rukungiri Dist, Bwindi Impenetrable National Park, Buhoma Rd (E side), ca. 25 m S Bizenga River, 00°59′33.9″S, 29°36′56.6″E	DQ283237 DQ283238	DQ284264	DQ283910			DQ283604	2964
Schoutedenella sylvatica	UTA A44685	Cameroon, Southwest Prov, vicinity Babong	DQ283077 DQ283078	DQ284131	DQ283801	DQ282666	DQ282912	DQ283482	4028
Schoutedenella taeniata	CAS 207926	Equatorial Guinea, Bioko I, vicinity Moka Malabo, along road cut of Moka Rd, 03°21′39.5″N, 08°40′02.7″E	DQ283232	DQ284262	DQ283907		DQ282954	DQ283601	3892
Schoutedenella xenodactyloides	RdS 864	Tanzania, Uluguru Mts, Tegetero Village, 6°56′30″S, 37°43′10″E	DQ283431	DQ284408	DQ284030		DQ283023	DQ283739	3911
Scinax garbei	MHNSM 7311	Peru, Madre de Dios, Prov Tambopata, Cusco Amazónico, ca. 15 km E Puerto Maldonado, 200 m	DQ283030		DQ283759	DQ282650	DQ282898	DQ283457	4446
Scinax ruber	IWK 109	Guyana, Iwokrama, Muri Scrub camp	**AY549365**	DQ284045	**AY844746**	**AY844944**	**AY844181**		3993
Scolecomorphus vittatus	FMNH 251843	Tanzania, Tanga Region, Muheza Dist, western edge Kwangumi Forest Reserve, 4.4 km W Mt Mhinduro, 2 km S Kwamtili Estate offices, 230 m, 4°56′30″S, 38°44′E	DQ283338	DQ284329		DQ282816		DQ283663	3792
Scotobleps gabonicus	UTA A44772	Cameroon, SW Prov, vicinity Ediensoa	DQ283367	DQ284353	DQ283988	DQ282834		DQ283686	3743
Scythrophrys sawayae	CFBH 6072	Brazil, Paraná, Piraquara	DQ283099	DQ284149	DQ283815		DQ282926	DQ283500	4334
Sierrana maculata	USNM 559483	Honduras, Atlantida, Parque Nacional Pico Bonito, Quebrada de Oro (tributary of Río Viejo), 15°38′N, 86°48′W, 945 m	DQ283303	DQ284309	DQ283951	DQ282803	DQ282967		3975
Silurana tropicalis	UTA A47158	Cameroon, East Prov, vicinity Lipondji Village	DQ283363	DQ284350	DQ283985			DQ283684	3834
Siphonops hardyi	MW 1032 (BM)	Brazil	DQ283088	DQ284139				DQ283489	2535
*Siren intermedia**			**Y10946**						2410
Siren lacertina	AMCC 125630	USA, Florida, Putnam Co, Rodman Reservoir at FL Hwy 310, 29°32.5′N, 81°50.2′W	DQ283181	DQ284216		DQ282729		DQ283568	3825
Smilisca phaeota	RdS 786	No data (Baltimore Natl Aquarium; captive bred)	**AY843764**	DQ284083	**AY844751**	**AY844948**	**AY844185**	**AY844351**	4733
Sooglossus sechellensis	UMMZ (#15)	No data	DQ283449 DQ283450	DQ284423	DQ284040	DQ282895	DQ283028	DQ283753	4337

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			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Spea hammondii	RNF 3221	USA, California, San Diego Co, Del Mar Mesa, 32.94738333°N, 117.15688333°W	DQ283179		DQ283870	DQ282728		DQ283566	3857
*Speleomantes italicus**			**AY728215**						2069
Sphaenorhynchus lacteus	USNM 152136	Peru, Madre de Dios, 30 km (by air) SSW Puerto Maldonado, Tambopata Reserve	**AY549367**	DQ28404	**AY844754**		**AY844188**	**AY844352**	4344
Sphaerotheca breviceps	USNM 524017	Myanmar, Sagaing, Kanbular Township, Chatthin, ca. 2 km WNW Chatthin Wildlife Sancturary, San Myaung Camp, 23°34′46″N, 95°44′26″E, 200 m	DQ283100	DQ28415	DQ283816		DQ282927	DQ283501	3883
*Sphaerotheca pluvialis**			**AF249014** **AF249042**		**AF249110**		**AF249173**		2110
Sphenophryne sp.	AMS R122221	Papua New Guinea, Namosado	DQ283205	DQ284237		DQ282748			3134
Spicospina flammocaerulea	WAM R119457	Australia, Western Australia, 30 km NE Walpole	DQ283301 DQ283302	DQ284308	DQ283950	DQ282802	DQ282966	DQ283640	4267
Staurois tuberlinguis	FMNH 243096	Malaysia, Sabah, Sipitang Dist, Mendolong camp, Sungai Mendolong	DQ283140	DQ284180	DQ283841	DQ282696		DQ283532	4150
Stefania evansi	AMNH A164211	Guyana, Iwokrama, Pakatau Creek, 85 m, 4°45′N, 59°01′W	**AY843767**		**AY844755**	**AY844950**	**AY844189**	**AY844353**	4032
*Stephopaedes anotis**			**AF220910**						511
Strongylopus grayii	AMNH A144979	South Africa, Western Cape Prov, Bainskloof, at settlement at crest of pass in stream	DQ283068		DQ283793				2719
Stumpffia cf. *psologlossa*	AMNH A167359	Madagascar, Antsiranana, Vohemar, Bezavona Mountain, 13°31′58″S, 49°51′57″E	DQ283411	DQ284393		DQ282869	DQ283008		3580
Sylvirana guentheri	AMNH A161190; AMNH A163940	Vietnam, Ha Tinh Prov, Ke Go Natural Reserve, Rao Cai; Vietnam, Ha Tinh, Yen Minh, Du Gia Commune, Khau Ria Village, rice paddy on edge of limestone forest south of village, 934 m, 22°53′49″N, 105°14′48″E	DQ283265 DQ283266 DQ283267	DQ284287 DQ284377	DQ283931 DQ284009	DQ282783 DQ282855		DQ283623 DQ283708	4155
Sylvirana maosonensis	AMNH A161487	Vietnam, Vinh Phu Prov, ca. 17 km NW Tam Dao Hill Station near Buddhist temple (E Tinh Sinh)	DQ283373	DQ284359	DQ283993	DQ282838	DQ282985	DQ283691	4687
Sylvirana nigrovittata	AMNH A161280	Vietnam, Ha Tinh Prov, Ke Go Natural Reserve, Rao Cai	DQ283371	DQ284357	DQ283991	DQ282836	DQ282983	DQ283689	4284
*Sylvirana temporalis**			**AF249022** **AF249054**		**AF249118**		**AF249181**		2163
Synapturanus mirandaribeiroi	MJH 3986	No data	DQ283064	DQ284094			DQ282908	DQ283473	2032

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Tachycnemis seychellensis	UMMZ 189382	Seychelles, Praslin, near entrance Vallee de Mai	DQ283451	DQ284424	DQ284041	DQ282896	DQ283029	DQ283754	4719
Taricha sp.	AMNH A168420	No data (pet trade)	DQ283444	DQ284419	DQ284039				2607
Taudactylus acutirostris	SAMA R41092	Australia, Queensland, Mt Lewis	DQ283277 DQ283278	DQ284296	DQ283939	DQ282790			2987
*Taylorana limborgi**			**AF261251**						490
Telmatobius jahuira	AMNH A165110	Bolivia, La Paz, Bautista Saavedra, Charazani Canton, stream 4, 15°7′49″S, 68°53′17″W	DQ283040		DQ283770				2740
Telmatobius marmoratus	AMNH A165114	Bolivia, La Paz, Bautista Saavedra, Charazani Canton, stream, 2700–2750 m, 15°7′49″S, 68°53′17″W	**AY843769**	DQ284068	**AY844757**	**AY844952**		**AY844355**	4192
Telmatobius sp.	AMNH A165130	Bolivia, La Paz, Bautista Saavedra, Charazani Canton, stream 4, 15°7′49″S, 68°53′17″W	DQ283041	DQ284067	DQ283771				3066
Telmatobufo venustus	IZUA 3054	Chile, VII Región, Altos de Vilches, Río Licay	DQ283325	DQ284321	DQ283964	DQ282814		DQ283655	3216
Theloderma corticale	AMNH A161499	Vietnam, Vinh Phu Prov, ca. 500 m W Institute of Ecology and Biological Resources Station on SW outskirts of Tam Dao	DQ283050	DQ284080	DQ283779	DQ282659	DQ282904		3969
Thorius sp.	JAC 21291	Mexico, Oaxaca, Sierra Miahuatlán, 2943 m	DQ283334	DQ284325				DQ283659	2925
Thoropa miliaris	CFBH 3239	Brazil, São Paulo, Picinguaba, Ubatuba	DQ283331						2752
Tlalocohyla picta	RdS 606	Belize, Stann Creek Dist, Cockscomb Basin Wildlife Sanctuary	**AY843654**	DQ284121	**AY844640**	**AY844858**	**AY844099**	**AY844276**	4739
Tomopterna delalandii	AMNH A144981	South Africa, Western Cape Prov, Stellenbosch air field	DQ283403	DQ284384	DQ284014	DQ282861	DQ283005	DQ283715	4694
*Torrentophryne aspinia**			**AF160770 AF160787**						897
Trachycephalus jordani	UMMZ 218914	No data	**AY843771**	DQ284097	**AY844758**	**AY844953**	**AY844190**	**AY844356**	4735
Trachycephalus venulosus	AMNH A141142	Guyana, Dubulay Ranch on Berbice River, 200 ft, 5°40′55″N, 57°51′32″W	**AY549362**		**AY844707**	**AY844912**	**AY844149**	**AY844322**	4735
Trichobatrachus robustus	DPL 3932	Cameroon, Southwest Prov, Kumba–Mamfe	**AY843773**	DQ284335	**AY844760**	**AY844954**	**AY844192**	DQ283669	4684
Triprion petasatus	RdS	Belize, Hummingbird Hwy, 9.5 km from Western Hwy turnpoint	**AY843774**	DQ284082	**AY844761**	**AY844955**	**AY844193**	**AY844357**	4729
Triturus cristatus	AMNH A168421	No data (pet trade)	DQ283441	DQ284417	DQ284038	DQ282894		DQ283749	3695
Trypheropsis warszewitschii	KRL 823 (voucher at Univ of Panama)	Panama, Coclé Prov, Parque Nacional El Copé	DQ283256	DQ284280	DQ283925	DQ282777	DQ282958	DQ283617	4682

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Species	ID number	Locality	Locus/partition						Total bp
			mtDNA	Histone H3	Rhodopsin	SIA	Tyrosinase	28S	
Tylerana arfaki	AMS R114913	Papua New Guinea, near Haia	DQ283203	DQ284235	DQ283886	DQ282746			3982
Tylototriton shanjing	AMCC 105494	No data	DQ283395	DQ284378				DQ283709	3433
Typhlonectes natans	BMNH 2000.218	Venezuela (no other data)	DQ283085	DQ284136				DQ283486	2992
Uperoleia laevigata	SAMA R42629	Australia, New South Wales, Ourimbah State Forest	DQ283221	DQ284251	DQ283898	DQ282758			3445
Uraeotyphlus narayani	MW 1418 (Univ of Kerala)	India (no other data)	DQ283090	DQ284141		DQ282671		DQ283491	3822
Vanzolinius discodactylus	RdS	Ecuador (no other data)	DQ283433	DQ284410	DQ284033	DQ282887		DQ283742	4204
Werneria mertensi	DPL 5107	Cameroon (no other data)	DQ283348	DQ284338	DQ283974	DQ282824		DQ283672	4217
Wolterstorffina parvipalmata	DPL 5101	Cameroon (no other data)	DQ283346	DQ284334	DQ283972	DQ282822		DQ283668	3778
*Xenophrys lateralis** (=*X. major*)			**AY236800**						553
Xenophrys major	AMNH A161506	Vietnam, Vinh Phu Prov, ca. 17 km NW Tam Dao Hill Station near Buddhist temple (E Tinh Sinh)	DQ283374	DQ284360			DQ282986	DQ283692	3572
Xenopus gilli	AMNH A153027	South Africa, Western Cape Prov, 5 km E of Betty's Bay, 34°22′S, 19°7′E	DQ283442 DQ283443	DQ284418				DQ283750	3161
Xenopus laevis*			**NC001573 Y10943**		**BC054145**		AY341764	**X59734**	4044

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APPENDIX 2

Accession Numbers and Publication References for GenBank Sequences Used

Accession numbers and publication references are provided for all 199 GenBank sequences included in this study. The locus mtDNA refers to 12S, $tRNA^{Val}$, and 16S sequences.

Species	Locus	GenBank accession number	Reference
Acanthixalus spinosus	mtDNA	AJ437002, AF215214, AF465438	Vences, unpubl. data; Rödel et al., 2003; Vences et al., 2003c
Afrixalus fornasini	mtDNA	U22071	Richards and Moore, 1996
Alligator sinensis	mtDNA	NC004448	Wu et al., unpubl. data
Allophryne ruthveni	mtDNA	AF364511, AF364512	Austin et al., 2002
Alytes obstetricans	Rhodopsin	AY364385	Biju and Bossuyt, 2003
Ambystoma tigrinum	Rhodopsin	U36574	N. Chen et al., 1996
Amnirana galamensis	Rhodopsin	AY341808	Vences et al., 2003d
Amolops hongkongensis	mtDNA	AF206072, AF206453, AF206117	L.Q. Chen et al., 2005
Andrias davidianus	mtDNA	AJ492192	Zhang et al., 2003a
Aneides hardii	mtDNA	AY728226	Mueller et al., 2004
Anhydrophryne rattrayi	mtDNA	AF215504	Vences, unpubl. data
Anodonthyla montana	mtDNA	AJ314812	Odierna et al., unpubl. data
Ansonia muelleri	mtDNA	U52740, U52784	Graybeal, 1997
Ascaphus truei	mtDNA	AJ440760	Hertwig et al., 2004
Batrachoseps attenuatus	mtDNA	AY728228	Mueller et al., 2004
Batrachoseps wrightorum	mtDNA	AY728221	Mueller et al., 2004
Boophis tephraeomystax	Tyrosinase	AF249168	Bossuyt and Milinkovitch, 2000
Brachytarsophrys feae	mtDNA	AY236799	García-París et al., 2003
Bufo angusticeps	mtDNA	AF220852, AF220899	Cunningham and Cherry, 2000
Bufo biporcatus	mtDNA	AY325987	Darst and Cannatella, 2004
Bufo bufo	mtDNA	AY325988	Darst and Cannatella, 2004
Bufo bufo	Rhodopsin	U59921	Fyhrquist et al., unpubl. data
Bufo celebensis	mtDNA	AF375513, AY180245	Darst and Cannatella, 2004; B.J. Evans et al., 2004
Bufo margaritifer	mtDNA	AF375514, AF375489	A. Gluesenkamp, unpubl. data
Bufo mazatlanensis	mtDNA	U52755, U52723	Graybeal, 1997
Bufo nebulifer	mtDNA	AY325985	Darst and Cannatella, 2004
Callulina kreffti	mtDNA	AY326068	Darst and Cannatella, 2004
Callulops slateri	mtDNA	AF095339	Emerson et al., 2000b
Capensibufo rosei	mtDNA	AF220864, AF220911	Cunningham and Cherry, 2000
Capensibufo tradouwi	mtDNA	AF220865, AF220912	Cunningham and Cherry, 2000
Centrolene geckoideum	mtDNA	X86230, X86264, X86298	Hay et al., 1995
Centrolene prosoblepon	mtDNA	AY364358, AY364379	Biju and Bossuyt, 2003
Centrolene prosoblepon	Rhodopsin	AY364404	Biju and Bossuyt, 2003
Chiromantis xerampelina	mtDNA	AF215348, AF458132	Vences, unpubl. data; J.A. Wilkinson et al., 2002
Clinotarsus curtipes	mtDNA	AF249058, AF249021	Bossuyt and Milinkovitch, 2000
Clinotarsus curtipes	Rhodopsin	AF249117	Bossuyt and Milinkovitch, 2000
Clinotarsus curtipes	Tyrosinase	AF249180	Bossuyt and Milinkovitch, 2000
Cryptobatrachus sp.	mtDNA	AY326050	Darst and Cannatella, 2004
Cryptotriton alvarezdeltoroi	mtDNA	AF199196	García-París and Wake, 2000
Dendrotriton rabbi	mtDNA	AF199232	García-París and Wake, 2000
Desmognathus wrighti	mtDNA	AY728225	Mueller et al., 2004
Didynamipus sjostedti	mtDNA	AY325991	Darst and Cannatella, 2004
Ensatina eschscholtzii	mtDNA	AY728216	Mueller et al., 2004
Euphlyctis cyanophlyctis	mtDNA	AF249053, AF249015	Bossuyt and Milinkovitch, 2000; Biju and Bossuyt, 2003
Euphlyctis cyanophlyctis	Rhodopsin	AF249111	Bossuyt and Milinkovitch, 2000
Euphlyctis cyanophlyctis	Tyrosinase	AF249174	Bossuyt and Milinkovitch, 2000
Euproctus asper	mtDNA	U04694, U04695	Caccone et al., 1994
Fejervarya cancrivorus	mtDNA	AB070731, AF206473, AF206092, AF206137	Chen et al., unpubl. data; Sumida et al., 2002
Fejervarya kirtisinghei	mtDNA	AY014380	Kosuch et al., 2001
Fejervarya syhadrensis	mtDNA	AY141843, AF249011	Bossuyt and Milinkovitch, 2000; Meegaskumbura et al., 2002
Fejervarya syhadrensis	Rhodopsin	AF249107	Bossuyt and Milinkovitch, 2000
Fejervarya syhadrensis	Tyrosinase	AF249170	Bossuyt and Milinkovitch, 2000
Gazella thomsoni	mtDNA	M86501	Allard et al., 1992
Gegeneophis ramaswamii	mtDNA	AF461136, AF461137	M. Wilkinson et al., 2002
Glandirana minima	mtDNA	AF315127, AF315153	Jiang and Zhou, 2001
Hemisus marmoratus	mtDNA	AY326070	Darst and Cannatella, 2004
Heterixalus tricolor	mtDNA	AY341630, AY341697, AY341725	Vences et al., 2003d
Heterixalus tricolor	Tyrosinase	AY341759	Vences et al., 2003d
Hydrophylax galamensis	Tyrosinase	AY341749	Vences et al., 2003d
Hylorina sylvatica	mtDNA	AY389153	Nuñez, unpubl. data
Hymenochirus boettgeri	mtDNA	AY341634, AY341700, AY341726	Vences et al., 2003d
Hymenochirus boettgeri	Tyrosinase	AY341763	Vences et al., 2003d
Iguana iguana	mtDNA	NC_002793	Janke et al., 2001
Indirana sp. 1	mtDNA	AF249051	Bossuyt and Milinkovitch, 2000
Indirana sp. 1	Rhodopsin	AF249122	Bossuyt and Milinkovitch, 2000
Indirana sp. 1	Tyrosinase	AF249185	Bossuyt and Milinkovitch, 2000
Indirana sp. 2	mtDNA	AF249064	Bossuyt and Milinkovitch, 2000
Indirana sp. 2	Rhodopsin	AF249123	Bossuyt and Milinkovitch, 2000

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Species	Locus	GenBank accession number	Reference
Indirana sp. 2	Tyrosinase	AF249186	Bossuyt and Milinkovitch, 2000
Ixalotriton niger	mtDNA	AF451248	Parra-Olea, 2002
Laliostoma labrosum	Tyrosinase	AF249169	Bossuyt and Milinkovitch, 2000
Lankanectes corrugatus	mtDNA	AF215393, AF249019, AF249043	Vences, unpubl. data; Bossuyt and Milinkovitch, 2000
Lankanectes corrugatus	Rhodopsin	AF249115	Bossuyt and Milinkovitch, 2000
Lankanectes corrugatus	Tyrosinase	AF249178	Bossuyt and Milinkovitch, 2000
Latimeria chalumnae	mtDNA	NC_001804	Zardoya and Meyer, 1996
Latimeria chalumnae	Rhodopsin	AF131253	Yokoyama et al., 1999
Leptodactylus fuscus	Tyrosinase	AY341760	Vences et al., 2003d
Limnodynastes salmini	mtDNA	AY326071	Darst and Cannatella, 2004
Limnonectes acanthi	mtDNA	AY313724	B.J. Evans et al., 2004
Limnonectes heinrichi	mtDNA	AY313749	B.J. Evans et al., 2004
Limnonectes kuhlii	mtDNA	AY313686	B.J. Evans et al., 2004
Limnonectes visayanus	mtDNA	AY313719	B.J. Evans et al., 2004
Lineatriton lineolus	mtDNA	AF380808	Parra-Olea and Wake, 2001
Micrixalus fuscus	mtDNA	AF249024	Bossuyt and Milinkovitch, 2000
Micrixalus fuscus	mtDNA	AF249056	Bossuyt and Milinkovitch, 2000
Micrixalus fuscus	Rhodopsin	AF249120	Bossuyt and Milinkovitch, 2000
Micrixalus fuscus	Tyrosinase	AF249183	Bossuyt and Milinkovitch, 2000
Micrixalus kottigeharensis	mtDNA	AF249025, AF249041	Bossuyt and Milinkovitch, 2000
Micrixalus kottigeharensis	Rhodopsin	AF249121	Bossuyt and Milinkovitch, 2000
Micrixalus kottigeharensis	Tyrosinase	AF249184	Bossuyt and Milinkovitch, 2000
Micryletta inornata	mtDNA	AF285207	Ziegler, unpubl. data
Nannophrys ceylonensis	mtDNA	AF249016, AF249047	Bossuyt and Milinkovitch, 2000
Nannophrys ceylonensis	Rhodopsin	AF249112	Bossuyt and Milinkovitch, 2000
Nannophrys ceylonensis	Tyrosinase	AF249175	Bossuyt and Milinkovitch, 2000
Nanorana pleskei	mtDNA	AF206111, AF206156, AF206492	L.Q. Chen et al., 2005
Nasikabatrachus sahyadrensis	mtDNA	AY364360, AY364381	Biju and Bossuyt, 2003
Nasikabatrachus sahyadrensis	Rhodopsin	AY364406	Biju and Bossuyt, 2003
Nasikobatrachidae sp.	mtDNA	AY425725, AY425726	Dutta et al., 2004
Natalobatrachus bonebergi	mtDNA	AF215396, AF215198	Vences, unpubl. data
Nelsonophryne aequatorialis	mtDNA	AY326067	Darst and Cannatella, 2004
Nesomantis thomasseti	Tyrosinase	AY341761	Vences et al., 2003d
Neurergus crocatus	mtDNA	AY147246, AY147247	Steinfartz et al., 2002
Nototriton abscondens	mtDNA	AF199199	García-París and Wake, 2000
Nyctibatrachus cf. *aliciae*	mtDNA	AF249018, AF249063	Bossuyt and Milinkovitch, 2000
Nyctibatrachus cf. *aliciae*	Rhodopsin	AF249114	Bossuyt and Milinkovitch, 2000
Nyctibatrachus major	mtDNA	AF249017, AF249052, AY341687	Bossuyt and Milinkovitch, 2000; Vences et al., 2003d
Nyctibatrachus major	Rhodopsin	AF249113	Bossuyt and Milinkovitch, 2000
Nyctibatrachus major	Tyrosinase	AF249176	Bossuyt and Milinkovitch, 2000
Occidozyga lima	mtDNA	AF161027	Marmayou et al., 2000
Oedipina uniformis	mtDNA	AF199230	García-París and Wake, 2000
Osornophryne guacamayo	mtDNA	AY326036	Darst and Cannatella, 2004
Parvimolge townsendi	mtDNA	AF451247	Parra-Olea, 2002
Pelobates cultripes	mtDNA	AY236801, AY364341, AY364363	García-París et al., 2003; Biju and Bossuyt, 2003
Pelobates cultripes	Rhodopsin	AY364386	Biju and Bossuyt, 2003
Pelomedusa subrufa	mtDNA	NC_001947	Zardoya and Meyer, 1998
Pelophryne brevipes	mtDNA	AF375503, AF375530	Gluesenkamp, unpubl. data
Pelophylax ridibunda	mtDNA	AB023397, AY147983	Sumida et al., 2000b
Petropedetes parkeri	mtDNA	AY341694, AY364348, AY364369	Biju and Bossuyt, 2003
Petropedetes parkeri	Rhodopsin	AY364394	Biju and Bossuyt, 2003
Petropedetes parkeri	Tyrosinase	AY341757	Vences et al., 2003d
Phaeognathus hubrichti	mtDNA	AY728233	Mueller et al., 2004
Phrynopus sp. KU 202652	mtDNA	AY326010	Darst and Cannatella, 2004
Polypedates cruciger	mtDNA	AF249028, AY341685	Bossuyt and Milinkovitch, 2000; Vences et al., 2003d
Polypedates cruciger	Rhodopsin	AF249124	Bossuyt and Milinkovitch, 2000
Polypedates cruciger	Tyrosinase	AF249187	Bossuyt and Milinkovitch, 2000
Ptychadena anchietae	mtDNA	AF261249, AF261267	Richards et al., 2000
Ramanella obscura	mtDNA	AF215382	Vences, unpubl. data
Rana berlandieri	mtDNA	AY115111	Zaldívar-Riverón et al., 2004
Ranodon sibiricus	mtDNA	NC_004021	Zhang et al., 2003b
Rhamphophryne festae	mtDNA	AF375504, AF375531	Gluesenkamp, unpubl. data
Scaphiophryne marmorata	Rhodopsin	AY364390	Biju and Bossuyt, 2003
Siren intermedia	mtDNA	Y10946	Feller and Hedges, 1998
Speleomantes italicus	mtDNA	AY728215	Mueller et al., 2004
Sphaerotheca pluvialis	mtDNA	AF249014, AF249042	Bossuyt and Milinkovitch, 2000
Sphaerotheca pluvialis	Rhodopsin	AF249110	Bossuyt and Milinkovitch, 2000
Sphaerotheca pluvialis	Tyrosinase	AF249173	Bossuyt and Milinkovitch, 2000
Stephopaedes anotis	mtDNA	AF220910	Cunningham and Cherry, 2000
Sylvirana temporalis	mtDNA	AF249022, AF249054	Bossuyt and Milinkovitch, 2000
Sylvirana temporalis	Rhodopsin	AF249118	Bossuyt and Milinkovitch, 2000
Sylvirana temporalis	Tyrosinase	AF249181	Bossuyt and Milinkovitch, 2000
Taylorana limborgi	mtDNA	AF261251	Richards et al., 2000
Torrentophryne aspinia	mtDNA	AF160770, AF160787	W. Liu et al., 2000
Xenophrys major	mtDNA	AY236800	García-París et al., 2003
Xenopus laevis	Rhodopsin	BC054145	Klein et al., 2002
Xenopus laevis	Tyrosinase	AY341764	Vences et al., 2003d

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APPENDIX 3

Base-Pair Length of 28S Fragment

Higher taxon and family	Species	Length (bp)
Marsupialia		
Didelphidae	*Didelphis marsupialis*	1092
Diapsida		
Alligatoridae	*Alligator sinensis*	696
Iguanidae	*Iguana iguana*	699
Testudines		
Chelydridae	*Chelydra serpentina*	694
Pelomedusidae	*Pelomedusa subrufa*	694
Coelocantha		
Latimeriidae	*Latimeria chalumnae*	691
Anura		
Alytidae	*Alytes obstetricans*	706
Alytidae	*Discoglossus galganoi*	706
Alytidae	*Discoglossus pictus*	706
Amphignathodontidae	*Flectonotus* sp.	762
Arthroleptidae	*Arthroleptis tanneri*	721
Arthroleptidae	*Arthroleptis variabilis*	722
Arthroleptidae	*Astylosternus schioetzi*	716
Arthroleptidae	*Cardioglossa gratiosa*	717
Arthroleptidae	*Cardioglossa leucomystax*	719
Arthroleptidae	*Leptopelis argenteus*	717
Arthroleptidae	*Leptopelis bocagei*	717
Arthroleptidae	*Leptopelis* sp.	717
Arthroleptidae	*Nyctibates corrugatus*	717
Arthroleptidae	*Schoutedenella schubotzi*	744
Arthroleptidae	*Schoutedenella xenodactyloides*	762
Arthroleptidae	*Scotobleps gabonicus*	718
Arthroleptidae	*Trichobatrachus robustus*	714
Batrachophrynidae	*Caudiverbera caudiverbera*	709
Batrachophrynidae	*Telmatobufo venustus*	710
Bombinatoridae	*Bombina microdeladigitora*	710
Bombinatoridae	*Bombina orientalis*	710
Bombinatoridae	*Bombina variegata*	710
Brachycephalidae	*Barycholos ternetzi*	744
Brachycephalidae	*Brachycephalus ephippium*	740
Brachycephalidae	*Craugastor alfredi*	759
Brachycephalidae	*Craugastor augusti*	760
Brachycephalidae	*Craugastor bufoniformis*	744
Brachycephalidae	*Craugastor pluvicanorus*	830
Brachycephalidae	*Craugastor punctariolus*	756
Brachycephalidae	*Craugastor rhodopis*	756
Brachycephalidae	*Eleutherodactylus binotatus*	747
Brachycephalidae	*Eleutherodactylus juipoca*	738
Brachycephalidae	*Eleutherodactylus rugulosus*	757
Brachycephalidae	*Euhyas planirostris*	768
Brachycephalidae	*Phrynopus* sp.	743
Brachycephalidae	*Syrrhophus marnockii*	769
Brachycephalidae	*Syrrhophus nitidus*	769
Brevicipitidae	*Breviceps mossambicus*	712
Brevicipitidae	*Callulina kisiwamsitu*	710
Brevicipitidae	*Probreviceps macrodactylus*	710
Bufonidae	*Atelopus spumarius*	766
Bufonidae	*Bufo alvarius*	751
Bufonidae	*Bufo amboroensis*	751
Bufonidae	*Bufo andrewsi*	752
Bufonidae	*Bufo arenarum*	752
Bufonidae	*Bufo asper*	751
Bufonidae	*Bufo boreas*	751
Bufonidae	*Bufo brauni*	751
Bufonidae	*Bufo camerunensis*	732
Bufonidae	*Bufo* cf. *chilensis*	752
Bufonidae	*Bufo cognatus*	751
Bufonidae	*Bufo divergens*	750
Bufonidae	*Bufo granulosus*	742
Bufonidae	*Bufo guttatus*	752
Bufonidae	*Bufo gutturalis*	732
Bufonidae	*Bufo haematiticus*	752
Bufonidae	*Bufo latifrons*	751
Bufonidae	*Bufo maculatus*	751
Bufonidae	*Bufo punctatus*	700
Bufonidae	*Bufo quercicus*	751
Bufonidae	*Bufo terrestris*	751
Bufonidae	*Bufo tuberosus*	721
Anura (*continued*)		
Bufonidae	*Bufo viridis*	751
Bufonidae	*Bufo woodhousii*	751
Bufonidae	*Dendrophryniscus minutus*	752
Bufonidae	*Melanophryniscus klappenbachi*	740
Bufonidae	*Nectophryne afra*	752
Bufonidae	*Nectophryne batesi*	752
Bufonidae	*Nectophrynoides tornieri*	753
Bufonidae	*Schismaderma carens*	754
Bufonidae	*Werneria mertensi*	751
Bufonidae	*Wolterstorffina parvipalmata*	750
Centrolenidae	*Centrolene prosoblepon*	732
Centrolenidae	*Cochranella bejaranoi*	732
Centrolenidae	*Hyalinobatrachium fleischmanni*	732
Ceratobatrachidae	*Batrachylodes vertebralis*	714
Ceratobatrachidae	*Ceratobatrachus guentheri*	720
Ceratobatrachidae	*Playmantis pelewensis*	713
Ceratophryidae	*Atelognatus patagonicus*	732
Ceratophryidae	*Batrachyla leptopus*	732
Ceratophryidae	*Ceratophrys cranwelli*	728
Ceratophryidae	*Telmatobius* sp.	728
Cryptobatrachidae	*Stefania evansi*	786
Cycloramphidae	*Alsodes gargola*	757
Cycloramphidae	*Cycloramphus boraceiensis*	742
Cycloramphidae	*Eupsophus calcaratus*	757
Cycloramphidae	*Odontophrynus achalensis*	780
Cycloramphidae	*Odontophrynus americanus*	778
Cycloramphidae	*Rhinoderma darwinii*	744
Dendrobatidae	*Allobates boulengeri*	774
Dendrobatidae	*Ameerega femoralis*	782
Dendrobatidae	*Colostethus undulatus*	775
Dendrobatidae	*Dendrobates auratus*	759
Dendrobatidae	*Minyobates claudiae*	760
Dendrobatidae	*Phobobates silverstonei*	771
Dendrobatidae	*Phyllobates lugubris*	769
Dicroglossidae	*Hoplobatrachus occipitalis*	708
Dicroglossidae	*Hoplobatrachus rugulosus*	708
Dicroglossidae	*Limnonectes kuhlii*	709
Dicroglossidae	*Occidozyga lima*	708
Dicroglossidae	*Paa exilispinosa*	714
Dicroglossidae	*Quasipaa verrucospinosa*	708
Dicroglossidae	*Phrynoglossus baluensis*	708
Dicroglossidae	*Phrynoglossus borealis*	708
Dicroglossidae	*Sphaerotheca breviceps*	709
Heleophrynidae	*Heleophryne regis*	719
Hemisotidae	*Hemisus marmoratus*	709
Hylidae	*Anotheca spinosa*	743
Hylidae	*Hypsiboas albomarginatus*	764
Hylidae	*Aplastodiscus perviridis*	757
Hylidae	*Argenteohyla siemersi pederseni*	740
Hylidae	*Charadrahyla nephila*	741
Hylidae	*Cruziohyla calcarifer*	789
Hylidae	*Dendropsophus minutus*	713
Hylidae	*Dendropsophus nanus*	745
Hylidae	*Duellmanohyla rufioculis*	738
Hylidae	*Ecnomiohyla miliaria*	744
Hylidae	*Exerodonta chimalapa*	743
Hylidae	*Hyla cinerea*	742
Hylidae	*Hyloscirtus armatus*	764
Hylidae	*Hyloscirtus palmeri*	767
Hylidae	*Hypsiboas boans*	757
Hylidae	*Hypsiboas granosus*	767
Hylidae	*Hypsiboas multifasciatus*	762
Hylidae	*Litoria genimaculata*	690
Hylidae	*Lysapsus laevis*	757
Hylidae	*Nyctimistes dayi*	694
Hylidae	*Osteocephalus taurinus*	740
Hylidae	*Osteopilus septentrionalis*	742
Hylidae	*Phrynohyas venulosa*	744
Hylidae	*Phyllomedusa vaillanti*	795
Hylidae	*Plectrohyla guatemalensis*	744
Hylidae	*Pseudacris crucifer*	743
Hylidae	*Pseudacris triseriata*	747
Hylidae	*Pseudis paradoxa*	758
Hylidae	*Scinax garbei*	778

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Higher taxon and family	Species	Length (bp)
Anura (*continued*)		
Hylidae	*Smilisca phaeota*	745
Hylidae	*Sphaenorhynchus lacteus*	753
Hylidae	*Tlalacohyla picta*	747
Hylidae	*Trachycephalus jordani*	742
Hylidae	*Triprion petasatus*	743
Hyperoliidae	*Afrixalus fornasinii*	714
Hyperoliidae	*Afrixalus pygmaeus*	714
Hyperoliidae	*Alexteroon obstetricans*	716
Hyperoliidae	*Cryptothylax gresshoffi*	714
Hyperoliidae	*Heterixalus* sp.	735
Hyperoliidae	*Hyperolius alticola*	714
Hyperoliidae	*Hyperolius punticulatus*	713
Hyperoliidae	*Hyperolius tuberilinguis*	713
Hyperoliidae	*Kassina senegalensis*	714
Hyperoliidae	*Nesionixalus thomensis*	714
Hyperoliidae	*Opisthothylax immaculatus*	714
Hyperoliidae	*Phlyctimantis leonardi*	714
Hyperoliidae	*Tachycnemis seychellensis*	733
Leiopelmatidae	*Ascaphus truei*	703
Leiopelmatidae	*Leiopelma archeyi*	703
Leiopelmatidae	*Leiopelma hochstetteri*	703
Leptodactylidae	*Edalorhina perezi*	756
Leptodactylidae	*Leptodactylus fuscus*	750
Leptodactylidae	*Leptodactylus ocellatus*	742
Leptodactylidae	*Lithodytes lineatus*	746
Leptodactylidae	*Paratelmatobius* sp.	730
Leptodactylidae	*Physalaemus cuvieri*	761
Leptodactylidae	*Scythrophrys sawayae*	728
Leptodactylidae	*Vanzolinius discodactylus*	745
Limnodynastidae	*Adelotus brevis*	721
Limnodynastidae	*Heleioporus australiacus*	720
Limnodynastidae	*Lechriodus fletcheri*	727
Limnodynastidae	*Limnodynastes depressus*	724
Limnodynastidae	*Limnodynastes dumerilli*	719
Limnodynastidae	*Limnodynastes lignarius*	720
Limnodynastidae	*Limnodynastes ornatus*	730
Limnodynastidae	*Neobatrachus pictus*	721
Limnodynastidae	*Neobatrachus sudelli*	721
Limnodynastidae	*Philoria sphagnicola*	724
Mantellidae	*Aglyptodactylus madagascariensis*	710
Mantellidae	*Laliostoma labrosum*	712
Mantellidae	*Mantella aurantiaca*	685
Mantellidae	*Mantella nigricans*	685
Megophryidae	*Leptobrachium chapaense*	728
Megophryidae	*Leptobrachium hasselti*	726
Megophryidae	*Leptolalax pelodytoides*	726
Megophryidae	*Ophryophryne microstoma*	725
Megophryidae	*Xenophrys major*	726
Microhylidae	*Aphantophryne pansa*	719
Microhylidae	*Calluella guttulata*	725
Microhylidae	*Choerophryne* sp.	719
Microhylidae	*Cophixalus sphagnicola*	718
Microhylidae	*Ctenophryne geayei*	727
Microhylidae	*Dasypops schirchi*	719
Microhylidae	*Dyscophus guineti*	716
Microhylidae	*Gastrophryne elegans*	720
Microhylidae	*Gastrophryne olivacea*	721
Microhylidae	*Genyophryne thomsoni*	728
Microhylidae	*Hoplophryne rogersi*	718
Microhylidae	*Kalophrynus pleurostigma*	716
Microhylidae	*Kaloula pulchra*	732
Microhylidae	*Liophryne rhododactyla*	718
Microhylidae	*Microhyla heymonsi*	725
Microhylidae	*Microhyla* sp.	698
Microhylidae	*Oreophryne brachypus*	719
Microhylidae	*Phrynomantis bifasciatus*	726
Microhylidae	*Platyelis* sp.	716
Microhylidae	*Plethodontohyla* sp.	717
Microhylidae	*Scaphiophryne marmorata*	716
Microhylidae	*Synapturanus mirandaribeiroi*	718
Myobatrachidae	*Arenophryne rotunda*	726
Myobatrachidae	*Crinia nimba*	724
Myobatrachidae	*Metacrinia nichollsi*	726
Myobatrachidae	*Myobatachus gouldii*	726
Myobatrachidae	*Pseudophryne bibroni*	726
Myobatrachidae	*Pseudophryne coriacea*	726
Myobatrachidae	*Spicospina flammocaerulea*	726
Pelobatidae	*Pelobates fuscus*	713
Anura (*continued*)		
Pelodytidae	*Pelodytes puntatus*	703
Petropedetidae	*Arthroleptides* sp.	747
Petropedetidae	*Conraua goliath*	708
Petropedetidae	*Conraua robusta*	708
Petropedetidae	*Petropedetes cameronensis*	718
Petropedetidae	*Petropedetes palmipes*	726
Phrynobatrachidae	*Dimorphognathus africanus*	708
Phrynobatrachidae	*Phrynobatrachus auritus*	707
Phrynobatrachidae	*Phrynobatrachus calcaratus*	719
Phrynobatrachidae	*Phrynobatrachus dendrobates*	708
Phrynobatrachidae	*Phrynobatrachus dispar*	719
Phrynobatrachidae	*Phrynobatrachus mababiensis*	708
Phrynobatrachidae	*Phrynobatrachus natalensis*	708
Phrynobatrachidae	*Phrynodon sandersoni*	710
Pipidae	*Silurana tropicalis*	713
Pipidae	*Xenopus gilli*	713
Ptychadenidae	*Ptychadena cooperi*	714
Pyxicephalidae	*Amietia angolensis*	718
Pyxicephalidae	*Amietia fuscigula*	721
Pyxicephalidae	*Amietia vertebralis*	718
Pyxicephalidae	*Arthroleptella bicolor*	731
Pyxicephalidae	*Aubria subsigillata*	708
Pyxicephalidae	*Aubria subsigillata*	708
Pyxicephalidae	*Pyxicephalus edulis*	708
Pyxicephalidae	*Tomopterna delalandii*	713
Ranidae	*Amerana mucosa*	708
Ranidae	*Amnirana albilabris*	708
Ranidae	*Amolops chapaensis*	709
Ranidae	*Aquarana catesbeiana*	708
Ranidae	*Aquarana clamitans*	709
Ranidae	*Aquarana grylio*	708
Ranidae	*Aquarana heckscheri*	708
Ranidae	*Aquarana aurora*	708
Ranidae	*Chalcorana chalconota*	708
Ranidae	*Huia nasica*	709
Ranidae	*Hylarana taipehensis*	708
Ranidae	*Lithobates palmipes*	708
Ranidae	*Meristogenys orphnocnemis*	708
Ranidae	*Nidirana adenopleura*	714
Ranidae	*Nidirana chapaensis*	708
Ranidae	*Odorrana grahami*	709
Ranidae	*Odorrana livida*	709
Ranidae	*Pantherana capito*	708
Ranidae	*Pantherana chiricahuensis*	708
Ranidae	*Pantherana forreri*	708
Ranidae	*Pantherana pipiens*	708
Ranidae	*Pantherana yavapaiensis*	708
Ranidae	*Papurana daemeli*	708
Ranidae	*Pelophylax nigromaculata*	708
Ranidae	*Pseudoamalops sauteri*	713
Ranidae	*Pseudorana johnsi*	708
Ranidae	*Rana japonica*	709
Ranidae	*Rana sylvatica*	707
Ranidae	*Rana temporaria*	707
Ranidae	*Staurois tuberlinguis*	710
Ranidae	*Sylvirana guentheri*	708
Ranidae	*Sylvirana maosonensis*	708
Ranidae	*Sylvirana nigrovittata*	708
Ranidae	*Trypheropsis warszewitschii*	708
Rhacophoridae	*Chirixalus doriae*	709
Rhacophoridae	*Chirixalus vittatus*	710
Rhacophoridae	*Kurixalus eiffingeri*	709
Rhacophoridae	*Kurixalus idiooticus*	709
Rhacophoridae	*Nyctixalus pictus*	709
Rhacophoridae	*Nyctixalus spinosus*	709
Rhacophoridae	*Philautus rhododiscus*	709
Rhacophoridae	*Rhacophorus bipunctatus*	709
Rhacophoridae	*Rhacophorus calcaneus*	709
Rhinophrynidae	*Rhinophrynus dorsalis*	705
Scaphiopodidae	*Scaphiopus couchii*	703
Scaphiopodidae	*Scaphiopus holbrooki*	703
Scaphiopodidae	*Spea hammondii*	703
Sooglossidae	*Nesomantis thomasseti*	737
Sooglossidae	*Sooglossus seychellensis*	741
Artiodactyla		
Bovidae	*Gazella thomsoni*	748

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Higher taxon and family	Species	Length (bp)
Caudata		
Ambystomatidae	*Dicamptodon ensatus*	694
Amphiumidae	*Amphiuma tridactylum*	694
Cryptobranchidae	*Cryptobranchus alleganiensis*	694
Hynobiidae	*Batrachuperus pinchoni*	694
Plethodontidae	*Bolitoglossa rufescens*	694
Plethodontidae	*Desmognathus quadramaculatus*	695
Plethodontidae	*Eurycea wilderae*	694
Plethodontidae	*Gyrinophilus porphyriticus*	694
Plethodontidae	*Plethodon dunni*	694
Plethodontidae	*Plethodon jordani*	694
Plethodontidae	*Pseudoeurycea conanti*	695
Plethodontidae	*Thorius* sp.	694
Proteidae	*Necturus* cf. *beyeri*	694
Proteidae	*Necturus maculosus*	694
Rhyacotritonidae	*Rhyacotriton cascadae*	694
Salamandridae	*Pleurodeles waltl*	694
Salamandridae	*Triturus* sp.	695
Salamandridae	*Tylototriton shanjing*	694
Caudata (*continued*)		
Sirenidae	*Pseudobranchus striatus*	694
Sirenidae	*Siren lacertina*	694
Gymnophiona		
Caeciliidae	*Boulengerula uluguruensis*	701
Caeciliidae	*Caecilia tentaculata*	709
Caeciliidae	*Crotaphatrema tchabalmboensis*	727
Caeciliidae	*Geotrypetes seraphini*	710
Caeciliidae	*Herpele squalostoma*	700
Caeciliidae	*Hypogeophis rostratus*	702
Caeciliidae	*Schistometopum gregorii*	701
Caeciliidae	*Siphonops hardyi*	700
Caeciliidae	*Typhlonectes natans*	684
Ichthyophiidae	*Ichthyophis peninsularis*	683
Ichthyophiidae	*Ichthyophis* sp.	697
Ichthyophiidae	*Uraeotyphlus narayani*	683
Rhinatrematidae	*Epicrionops* sp.	714
Rhinatrematidae	*Rhinatrema bivittatum*	695

APPENDIX 4

Branch Lengths, Bremer Support, and Jackknife Values

Values given correspond to branches numbered in figures 50, 52, 53, 54, 56, 58, 59, 60, 61, 62, 63, and 65.

Branch	Taxon	Branch length	Bremer support	Jackknife
1	Amniota	117	96	100
2	Mammalia	81	67	100
3	Sauropsida	103	83	100
4	Testudines	105	83	100
5	Diapsida	94	75	100
6	Amphibia	78	49	100
7	Gymnophiona	89	78	100
8	Rhinatrematidae	49	30	100
9	Stegokrotaphia	58	47	100
10	Ichthyophiidae	89	82	100
11	Unnamed	56	33	100
12	Caeciliidae	60	44	100
13	Unnamed	63	41	100
14	Unnamed	34	21	100
15	Unnamed	98	90	100
16	Unnamed	44	27	100
17	Scolecomorphinae	47	40	100
18	Unnamed	73	32	100
19	Unnamed	31	23	100
20	Unnamed	55	39	100
21	Unnamed	24	19	100
22	Unnamed	25	17	100
23	Batrachia	72	109	100
24	Caudata	114	107	99
25	Cryptobranchoidei	58	40	100
26	Hynobiidae	91	80	100
27	Cryptobranchidae	122	115	100
28	*Andrias*	71	64	100
29	Diadectosalamandroidei	43	30	99
30	Hydatinosalamandroidei	38	29	100
31	Perennibranchia	43	35	100
32	Proteidae	166	163	100
33	Sirenidae	108	98	100
34	*Siren*	57	49	100
35	Treptobranchia	43	29	100
36	Ambystomatidae	78	69	100
37	*Dicamptodon*	168	165	100
38	*Ambystoma*	135	128	100
39	Unnamed	54	52	100
40	Salamandridae	72	63	100
41	Pleurodelinae	35	28	100
42	Unnamed	37	24	100
43	Unnamed	21	9	100
44	Unnamed	20	6	92
45	Unnamed	22	9	99
46	Unnamed	26	21	100
47	Unnamed	11	9	99
48	Unnamed	7	2	78
49	Plethosalamandroidei	50	41	99
50	Xenosalamandroidei	48	31	99
51	Plethodontidae	94	85	99
52	Plethodontinae	36	24	100
53	Unnamed	26	15	100
54	Unnamed	45	38	100
55	Unnamed	29	19	99
56	Unnamed	39	26	100
57	*Desmognathus*	37	26	100
58	Unnamed	26	13	100
59	Unnamed	77	66	100
60	Unnamed	34	13	97
61	*Batrachoseps*	85	43	100
62	Unnamed	15	6	88
63	Unnamed	25	15	99
64	Unnamed	48	34	100
65	Unnamed	24	21	99
66	Unnamed	9	4	97
67	Unnamed	7	1	51
68	Unnamed	10	4	87
69	Unnamed	9	6	94
70	Unnamed	60	11	99
71	Unnamed	5	2	62
72	*Pseudoeurycea*	7	3	76
73	Unnamed	12	9	99
74	Anura	125	109	99
75	Leiopelmatidae	55	41	100
76	*Leiopelma*	72	65	100
77	Lalagobatrachia	82	57	99
78	Xenoanura	68	55	100
79	Pipidae	45	48	100
80	Unnamed	36	130	100
81	*Pipa*	85	198	100
82	Unnamed	145	17	100
83	*Xenopus*	24	24	100
84	Sokolanura	36	20	99

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Branch	Taxon	Branch length	Bremer support	Jackknife
85	Costata	69	55	100
86	Alytidae	68	48	100
87	*Discoglossus*	138	130	100
88	Bombinatoridae	200	198	100
89	Unnamed	27	17	100
90	Unnamed	28	24	100
91	Acosmanura	81	65	99
92	Anomocoela	85	65	100
93	Pelodytoidea	57	33	100
94	Scaphiopodidae	101	87	100
95	*Scaphiopus*	82	72	100
96	Pelobatoidea	74–75	53	100
97	Pelobatidae	69	66	100
98	Megophryidae	100	39	100
99	Unnamed	65–66	27	100
100	*Leptobrachium*	61–62	37	100
101	Unnamed	18–92	16	100
102	*Xenophrys*	31–35	31	100
103	Unnamed	39–42	10	100
104	*Ophryophryne*	99	81	100
105	Neobatrachia	127	108	100
106	Heleophrynidae	187	186	100
107	Phthanobatrachia	66	31	99
108	Ranoides	110	31	99
109	Allodapanura	45	31	100
110	Microhylidae	72	34	100
111	Unnamed	7	2	71
112	Unnamed	17	3	90
113	Unnamed	4	3	85
114	Unnamed	36	33	97
115	Unnamed	28	13	99
116	Unnamed	50	9	98
117	Unnamed	8	5	93
118	Cophylinae	118	24	100
119	Unnamed	71	6	99
120	Unnamed	8	11	98
121	Gastrophryninae	36	13	99
122	Unnamed	67	58	100
123	Unnamed	44	15	99
124	Unnamed	54	34	100
125	Unnamed	39	23	100
126	Unnamed	29	18	99
127	*Gastrophryne*	58	47	100
128	Unnamed	27	16	99
129	Unnamed	29	18	100
130	Microhylinae	54	42	100
131	Unnamed	24	45	98
132	Unnamed	43	50	100
133	Unnamed	115	92	100
134	Unnamed	45	31	99
135	Asterophryinae	100	24	100
136	Unnamed	44	7	100
137	Unnamed	22	13	98
138	Unnamed	21	40	91
139	Unnamed	54	22	100
140	Unnamed	32	14	100
141	Unnamed	38	7	98
142	Unnamed	10	7	98
143	Afrobatrachia	52	37	100
144	Xenosyneunitanura	96	81	100
145	Brevicipitidae	79	49	100
146	Unnamed	77	53	100
147	*Callulina*	103	103	100
148	Laurentobatrachia	61	42	100
149	Hyperoliidae	114	64	100
150	Unnamed	14	9	98
151	Unnamed	31	21	100
152	Unnamed	76	29	100
153	Unnamed	52	27	100
154	Unnamed	43	32	100
155	*Afrixalus*	36	16	99
156	Unnamed	98	68	100
157	*Heterixalus*	20	8	97
158	Unnamed	42	23	100
159	Unnamed	82	37	100
160	*Alexteroon*	19	19	100
161	*Hyperolius*	21	9	98
162	Unnamed	14	8	98
163	Unnamed	28	10	97
164	Arthroleptidae	57	37	100
165	Leptopelinae	112	100	100
166	Unnamed	53	37	100
167	Unnamed	72	72	100
168	Arthroleptinae	56	44	100
169	Astylosternini	54	39	100
170	Unnamed	45	21	99
171	Unnamed	78	60	100
172	Arthroleptini	38	28	100
173	Unnamed	109	92	100
174	*Cardioglossa*	79	70	100
175	*Arthroleptis*	55	42	100
176	Unnamed	45	32	100
177	Unnamed	26	14	100
178	Unnamed	46	32	100
179	Unnamed	68	62	100
180	Natatanura	65	34	99
181	Ptychadenidae	135	100	100
182	Unnamed	37	85	100
183	Victoranura	39	20	99
184	Ceratobatrachidae	114	43	100
185	Unnamed	129	120	100
186	Unnamed	41	22	100
187	Unnamed	56	35	100
188	*Platymantis*	100	82	100
189	Telmatobatrachia	19	10	99
190	Micrixalidae	105	42	100
191	Ametrobatrachia	17	12	99
192	Africanura	32	21	99
193	Phrynobatrachidae	87	51	100
194	Unnamed	45	26	100
195	Unnamed	85	70	100
196	Unnamed	74	103	100
197	Unnamed	62	35	100
198	Unnamed	115	61	100
199	Unnamed	52	31	100
200	Pyxicephaloidea	25	14	99
201	Petropedetidae	33	15	99
202	*Conraua*	89	24	100
203	Unnamed	17	13	99
204	*Indirana*	30	22	100
205	Unnamed	51	39	100
206	*Petropedetes*	77	54	100
207	Unnamed	29	19	100
208	Unnamed	10	5	89
209	Pyxicephalidae	36	21	100
210	Pyxicephalinae	117	105	100
211	*Aubria*	189	187	100
212	Cacosterninae	56	44	99
213	Unnamed	43	6	94
214	Unnamed	8	5	92
215	Unnamed	28	9	99
216	Unnamed	33	10	98
217	Unnamed	8	2	85
218	*Amietia*	33	6	99
219	Unnamed	4	3	85
220	Saukrobatrachia	26	17	99
221	Dicroglossidae	39	31	100
222	Occidozyginae	42	36	100
223	Unnamed	24	15	99
224	Unnamed	57	21	99
225	Dicroglossinae	37	27	100
226	Limnonectini	84	20	100
227	Unnamed	45	14	100
228	Unnamed	34	14	99
229	Unnamed	9	6	98
230	Unnamed	13	9	99
231	Unnamed	30	10	99
232	Dicroglossini	43	32	100
233	*Quasipaa*	56	46	100
234	Unnamed	26	20	100
235	Unnamed	71	65	100
236	*Fejervarya 1*	60	39	100
237	Unnamed	43	32	100
238	*Sphaerotheca*	57	53	100
239	Unnamed	26	6	86
240	*Fejervarya 2*	16	15	100
241	Unnamed	29	19	100
242	Unnamed	28	16	100

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Branch	Taxon	Branch length	Bremer support	Jackknife
243	*Hoplobatrachus*	27	14	99
244	Aglaioanura	33	19	99
245	Rhacophoroidea	36	24	100
246	Mantellidae	52	40	100
247	Boophinae	81	67	100
248	Mantellinae	38	21	100
249	Laliostomini	50	30	100
250	Mantellini	52	44	100
251	*Mantidactylus*	52	35	100
252	*Mantella*	83	68	100
253	Rhacophoridae	57	46	100
254	Rhacophorinae	61	42	100
255	Unnamed	33	16	57
256	*Kurixalus*	137	127	100
257	Unnamed	15	2	100
258	Unnamed	54	42	100
259	Unnamed	74	54	100
260	*Nyctixalus*	47	38	100
261	Unnamed	38	27	100
262	*Rhacophorus*	44	32	100
263	Unnamed	30	10	96
264	Unnamed	40	25	100
265	Unnamed	41	29	100
266	*Polypedates*	66	60	100
267	*Chiromantis*	55	37	100
268	Unnamed	57	39	100
269	Ranoidea	23	17	99
270	Nyctibatrachidae	18	8	97
271	*Nyctibatrachus*	75	64	100
272	Ranidae	57	37	99
273	Unnamed	53	36	99
274	*Hylarana*	37	21	100
275	Unnamed	96	85	100
276	Unnamed	36	13	99
277	Unnamed	28	22	99
278	*Hydrophylax*	45	10	99
279	Unnamed	42	26	100
280	*Sylvirana*	27	13	99
281	Unnamed	37	22	100
282	Unnamed	17	12	99
283	Unnamed	39	31	100
284	Unnamed	26–27	3	87
285	Unnamed	32–34	15	100
286	Unnamed	7–23	13	69
287	Unnamed	25–26	23	52
288	*Pelophylax*	12	2	58
289	Unnamed	10–19	7	98
290	Unnamed	32	10	99
291	*Babina*	56	32	100
292	*Huia*	70	55	100
293	Unnamed	28	19	99
294	Unnamed	43	16	99
295	Unnamed	39	30	100
296	*Rana*	50	39	100
297	Unnamed	52	39	100
298	Unnamed	34	26	100
299	Unnamed	31	16	100
300	Unnamed	18	8	98
301	*Lithobates*	33	27	100
302	Unnamed	59	45	100
303	Unnamed	18	6	88
304	Unnamed	8	2	56
305	Unnamed	24	1	52
306	Unnamed	42	28	100
307	Unnamed	28	12	99
308	Unnamed	32	9	90
309	Unnamed	71	35	100
310	Unnamed	19	5	78
311	Unnamed	44	34	100
312	Unnamed	9	7	99
313	Unnamed	4	1	66
314	Hyloides	60	35	100
315	Sooglossidae	50	42	100
316	*Nasikabatrachus*	122	117	100
317	*Sooglossus*	62	62	100
318	Notogaeanura	51	24	100
319	Australobatrachia	62	54	100
320	Batrachophrynidae	93	86	100
321	Myobatrachoidea	48	31	100
322	Limnodynastidae	72	61	100
323	Unnamed	47	30	100
324	Unnamed	22	16	100
325	Unnamed	26	18	100
326	*Neobatrachus*	80	75	100
327	Unnamed	33	20	100
328	Unnamed	79	67	100
329	Unnamed	35	17	99
330	*Limnodynastes*	57	47	100
331	Unnamed	20	13	99
332	Unnamed	31	22	100
333	Unnamed	48	41	100
334	Myobatrachidae	38	24	100
335	Unnamed	30	12	98
336	Unnamed	49	36	100
337	Unnamed	63	53	100
338	Unnamed	27	20	100
339	Unnamed	58	32	100
340	Unnamed	45	47	100
341	Unnamed	23	16	100
342	Unnamed	36	27	100
343	Unnamed	37	24	100
344	Unnamed	55	48	100
345	*Pseudophryne*	35	30	100
346	Unnamed	56	27	100
347	Unnamed	5	3	85
348	Nobleobatrachia	96	88	100
349	Meridianura	51	35	100
350	Brachycephalidae	49	43	100
351	Unnamed	52	38	100
352	Unnamed	54	38	100
353	Unnamed	35	27	100
354	Unnamed	44	26	100
355	Unnamed	38	26	100
356	Unnamed	77	51	100
357	Unnamed	110	96	100
358	*Syrrhophus*	78	72	100
359	Unnamed	32	25	100
360	*Phrynopus*	61	42	100
361	*Craugastor*	51	34	100
362	Unnamed	102	85	100
363	Unnamed	95	77	100
364	Unnamed	75	50	100
365	Unnamed	119	107	100
366	Cladophrynia	58	45	100
367	Cryptobatrachidae	34	22	100
368	Tinctanura	43	29	100
369	Amphignathodontidae	44	33	100
370	*Gastrotheca*	67	47	100
371	Athesphatanura	41	37	100
372	Hylidae	35	37	100
373	Unnamed (Phyllomedusinae + Pelodryadinae)	76	65	100
374	Phyllomedusinae	87	45	100
375	Unnamed	42	24	99
376	Unnamed	34	16	99
377	Pelodryadinae	45	33	100
378	Unnamed	49	37	100
379	Unnamed	74	24	100
380	Unnamed	40	25	100
381	Unnamed	39	27	100
382	Unnamed	58	40	100
383	Unnamed	16	10	98
384	Unnamed	20	11	99
385	Unnamed	22	12	98
386	Hylinae	32	24	100
387	Unnamed	28	20	100
388	Unnamed	49	29	100
389	*Scinax*	115	97	100
390	Cophomantini	61	52	100
391	*Hyloscirtus*	61	40	100
392	Unnamed	61	33	100
393	Unnamed	44	30	100
394	Unnamed	48	24	100
395	Unnamed	37	30	100
396	Unnamed	23	14	99
397	Unnamed	32	24	100
398	Unnamed	82	69	100
399	Unnamed	64	48	100

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Branch	Taxon	Branch length	Bremer support	Jackknife	Branch	Taxon	Branch length	Bremer support	Jackknife
400	*Dendropsophus*	69	55	100	464	Unnamed	56	32	100
401	Unnamed	49	25	100	465	Unnamed	39	24	100
402	Unnamed	53	37	100	466	Unnamed	53	29	100
403	Unnamed	29	22	100	467	Unnamed	47	35	100
404	Lophiohylini	65	42	100	468	Unnamed	68	45	100
405	Unnamed	23	14	90	469	Bufonidae	51	33	99
406	*Osteocephalus*	18	8	87	470	Unnamed	83	38	99
407	Unnamed	22	12	91	471	Unnamed	39	22	100
408	*Trachycephalus*	45	25	100	472	*Atelopus*	54	43	100
409	Hylini	85	78	100	473	Unnamed	114	114	100
410	Unnamed	29	15	100	474	Unnamed	40	25	100
411	Unnamed	43	32	100	475	Unnamed	58	20	100
412	Unnamed	27	19	99	476	*Rhaebo*	51	42	100
413	Unnamed	16	4	75	477	Unnamed	43	20	100
414	Unnamed	24	9	96	478	Unnamed	30	25	100
415	Unnamed	23	5	89	479	Unnamed	30	14	98
416	Unnamed	42	32	100	480	*Nectophryne*	134	107	100
417	*Pseudacris*	54	37	100	481	Unnamed	15	9	97
418	Unnamed	54	5	100	482	Unnamed	37	18	100
419	Unnamed	34	19	99	483	Unnamed	12	8	97
420	Unnamed	15	5	85	484	Unnamed	20	9	95
421	Unnamed	44	30	100	485	Unnamed	27	10	94
422	Unnamed	23	14	99	486	Unnamed	24	9	94
423	Unnamed	45	28	100	487	*Ansonia*	25	9	90
424	Leptodactyliformes	24	17	100	488	Unnamed	13	8	93
425	Diphyabatrachia	35	29	98	489	Unnamed	9	6	94
426	Centrolenidae	41	12	99	490	Unnamed	14	6	95
427	Centroleninae	67	22	100	491	*Ingerophrynus*	16	10	99
428	Unnamed	23	13	99	492	Unnamed	15	11	100
429	Unnamed	20	11	99	493	Unnamed	30	14	99
430	Leptodactylidae	30	23	99	494	Unnamed	12	8	92
431	Unnamed	50	41	98	495	Unnamed	18	12	99
432	Unnamed	70	47	100	496	Unnamed	31	16	99
433	Unnamed	26	10	97	497	Unnamed	35	15	99
434	Unnamed	30	15	99	498	Unnamed	15	10	98
435	Unnamed	65	40	100	499	*Bufo* (sensu stricto)	59	28	100
436	*Leptodactylus*	61	47	100	500	Unnamed	6	3	90
437	Unnamed	64	42	100	501	Unnamed	18	5	71
438	Unnamed	46	34	100	502	Unnamed	12	9	94
439	Unnamed	64	31	100	503	*Capensibufo*	11	10	99
440	Chthonobatrachia	18	13	100	504	Unnamed	10	7	94
441	Ceratophryidae	34	18	98	505	Unnamed	7	2	61
442	Telmatobiinae	70	62	100	506	*Amietophrynus*	9	2	65
443	Unnamed	26	18	100	507	Unnamed	36	2	65
444	Ceratophryinae	22	2	62	508	Unnamed	22	15	99
445	Batrachylini	54	37	100	509	Unnamed	22	17	99
446	Ceratophryini	46	38	100	510	Unnamed	30	22	99
447	Unnamed	24	8	94	511	Unnamed	100	98	100
448	Hesticobatrachia	34	26	98	512	Unnamed	25	27	94
449	Cycloramphidae	21	9	98	513	*Anaxyrus*	22	15	99
450	Hylodinae	70	5	91	514	Unnamed	44	33	100
451	Unnamed	71	43	100	515	Unnamed	23	8	90
452	Cycloramphinae	19	9	82	516	Unnamed	28	21	100
453	Cycloramphini	42	30	96	517	Unnamed	30	26	100
454	Alsodini	28	4	80	518	Unnamed	13	6	81
455	Unnamed	8	4	81	519	*Cranopsis*	25	11	99
456	Unnamed	19	14	99	520	Unnamed	14	1	58
457	Unnamed	44	10	100	521	Unnamed	16	11	99
458	Unnamed	76	52	100	522	*Chaunus*	22	16	98
459	*Odontophrynus*	48	38	100	523	Unnamed	13	7	78
460	Agastorophrynia	39	30	98	524	Unnamed	14	9	80
461	Dendrobatoidea	51	39	100	525	Unnamed	13	6	75
462	Dendrobatidae	74	61	100	526	Unnamed	55	51	100
463	Unnamed	66	51	100	527	Unnamed	21	17	99

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APPENDIX 5

DNA Sequence Transformations for Selected Branches/Taxa

Evidence is presented for taxa recognized solely on the basis of DNA sequence transformations, or taxa whose molecular evidence was specifically noted in the text. The table is organized by branch number, with those taxa lacking branch numbers following in alphabetical order. Optimization ambiguous transformations are excluded. Locus abbreviations are 28S (large nuclear ribosomal subunit), H1 (mitochondrial transcription unit H1), H3 (histone H3), rhod (rhodopsin exon 1), SIA (seven in absentia), and tyr (tyrosinase). Other abbreviations are Br/Taxon/Frag (branch, taxon, and DNA fragment), Pos (position in aligned sequence), Anc (ancestral character), Der (derived character), A (adenine), C (cytosine), G (guanine), T (thymine), and ‘‘—’’ (gap).

Br/Taxon/Frag	Pos	Anc	Der
29 (Diadectosalamandroidei)			
28S frag. 4	71	T	C
H1 frag. 10	7	G	C
H1 frag. 10	23	T	A
H1 frag. 11	315	A	—
H1 frag. 11	409	T	—
H1 frag. 13	198	C	A
H1 frag. 14	143	C	T
H1 frag. 14	217	T	A
H1 frag. 16	94	A	G
H1 frag. 16	313	A	—
H1 frag. 17	47	C	A
H1 frag. 17	210	C	T
H1 frag. 18	276	A	C
H1 frag. 18	349	C	A
H1 frag. 19	136	G	A
H1 frag. 19	195	C	A
H1 frag. 19	331	G	T
H1 frag. 19	376	G	—
H1 frag. 19	509	A	—
H1 frag. 19	531	A	—
H1 frag. 2	218	C	A
H1 frag. 2	277	A	—
H1 frag. 2	285	A	—
H1 frag. 20	78	G	A
H1 frag. 21	124	C	—
H1 frag. 22	70	A	T
H1 frag. 23	33	C	—
H1 frag. 23	260	C	T
H1 frag. 23	283	C	—
H1 frag. 23	981	T	A
H1 frag. 23	1114	A	T
H1 frag. 23	1338	C	A
H1 frag. 23	1405	A	—
H1 frag. 23	1684	T	—
H1 frag. 23	1687	T	—
H1 frag. 23	1940	T	—
H1 frag. 3	415	A	T
H1 frag. 4	169	C	A
H1 frag. 8	159	G	C
H1 frag. 8	250	T	A
H1 frag. 9	84	C	A
H1 frag. 9	85	C	A
H3 frag. 2	26	T	C
30 (Hydatinosalamandroidei)			
H1 frag. 11	31	T	C
H1 frag. 11	595	A	C
H1 frag. 11	694	C	—
H1 frag. 11	1294	T	A
H1 frag. 13	91	A	—
H1 frag. 14	45	C	T
H1 frag. 14	144	G	A
H1 frag. 14	182	—	T
H1 frag. 15	22	C	T
H1 frag. 16	466	—	T
H1 frag. 17	38	A	T
H1 frag. 17	133	—	A
H1 frag. 18	838	A	T
H1 frag. 18	878	A	T
H1 frag. 19	294	A	—
H1 frag. 19	369	A	T
H1 frag. 19	453	A	—
H1 frag. 19	496	C	—
H1 frag. 19	668	A	—
H1 frag. 2	73	T	A
H1 frag. 23	743	—	T
H1 frag. 23	956	—	A
H1 frag. 23	1051	—	A
H1 frag. 23	1090	—	C
H1 frag. 23	1169	G	A
H1 frag. 23	1328	G	A
H1 frag. 23	1750	T	—
H1 frag. 4	205	—	T
H1 frag. 4	640	—	A
H1 frag. 6	23	T	C
H1 frag. 6	75	A	—
H1 frag. 7	35	C	A
H1 frag. 8	156	C	—
H1 frag. 8	628	A	T
H1 frag. 8	796	T	A
SIA frag. 1	9	A	T
SIA frag. 1	12	T	C
SIA frag. 2	20	C	T
31 (Perennibranchia)			
28S frag. 2	312	C	T
H1 frag. 10	199	C	T
H1 frag. 11	36	T	A
H1 frag. 11	72	C	T
H1 frag. 11	249	—	G
H1 frag. 11	819	T	C
H1 frag. 11	1327	T	—
H1 frag. 14	93	A	T
H1 frag. 14	166	C	A
H1 frag. 14	244	G	A
H1 frag. 15	60	T	A
H1 frag. 16	94	G	—
H1 frag. 16	127	T	—
H1 frag. 16	170	T	—
H1 frag. 16	191	T	—
H1 frag. 16	221	A	C
H1 frag. 16	563	T	G
H1 frag. 18	488	C	T
H1 frag. 18	628	T	—
H1 frag. 19	131	A	T
H1 frag. 20	25	A	T
H1 frag. 21	76	T	C
H1 frag. 23	43	T	A
H1 frag. 23	1015	A	T
H1 frag. 23	1118	—	A
H1 frag. 23	1303	A	T
H1 frag. 23	1759	A	T
H1 frag. 23	1763	T	A
H1 frag. 23	1962	A	T
H1 frag. 8	28	A	C
H1 frag. 8	57	C	T
H1 frag. 8	69	A	T
H1 frag. 8	110	C	T
H1 frag. 8	589	C	T
H1 frag. 8	634	T	A
H1 frag. 8	714	A	G
H1 frag. 9	54	T	C
H1 frag. 9	73	C	A
H1 frag. 9	333	A	C
H3 frag. 1	48	G	A
H3 frag. 1	103	C	A
H3 frag. 1	135	C	G
H3 frag. 1	204	C	A
35 (Treptobranchia)			
28S frag. 4	150	T	C
H1 frag. 11	141	A	T
H1 frag. 11	264	C	T
H1 frag. 11	822	A	—
H1 frag. 11	1101	—	C
H1 frag. 12	41	A	T
H1 frag. 13	71	C	A
H1 frag. 13	130	C	A
H1 frag. 14	31	T	A
H1 frag. 14	89	T	A
H1 frag. 14	106	A	C
H1 frag. 15	25	G	A
H1 frag. 16	152	A	T
H1 frag. 16	429	C	A
H1 frag. 17	47	A	T
H1 frag. 17	182	T	A
H1 frag. 18	79	A	G
H1 frag. 18	116	T	C
H1 frag. 18	366	—	C
H1 frag. 18	756	T	C
H1 frag. 19	259	A	—
H1 frag. 19	749	A	T
H1 frag. 2	342	A	T
H1 frag. 2	407	A	C
H1 frag. 20	146	T	A
H1 frag. 21	93	C	T
H1 frag. 23	67	G	A
H1 frag. 23	670	—	T
H1 frag. 23	1676	A	—
H1 frag. 23	1707	A	T
H1 frag. 3	169	T	A
H1 frag. 4	64	T	C
H1 frag. 4	262	A	G
H1 frag. 4	263	G	A
H1 frag. 4	458	A	C
H1 frag. 4	487	—	T
H1 frag. 9	288	C	T
H1 frag. 9	763	T	A
H3 frag. 1	192	C	G
SIA frag. 1	3	T	C
SIA frag. 3	66	A	G
SIA frag. 3	72	C	T
SIA frag. 3	147	A	G
41 (Pleurodelinae)			
H1 frag. 10	101	G	A
H1 frag. 11	89	C	T
H1 frag. 11	264	T	—
H1 frag. 11	1191	T	A
H1 frag. 11	1327	T	—
H1 frag. 12	6	A	G
H1 frag. 12	90	T	A
H1 frag. 14	208	A	C
H1 frag. 16	4	C	T
H1 frag. 17	22	T	C
H1 frag. 17	38	T	C
H1 frag. 17	136	A	T
H1 frag. 18	45	A	—
H1 frag. 18	479	A	C
H1 frag. 18	741	C	—
H1 frag. 18	750	G	A
H1 frag. 18	759	A	T
H1 frag. 18	854	T	A
H1 frag. 19	729	T	C
H1 frag. 21	50	—	A
H1 frag. 21	260	T	A
H1 frag. 22	11	T	C
H1 frag. 23	293	T	C
H1 frag. 23	1130	—	G
H1 frag. 23	1726	A	C
H1 frag. 6	89	—	C
H1 frag. 8	57	C	T
H1 frag. 8	316	T	C
H1 frag. 8	335	T	C
H1 frag. 8	628	T	C
H1 frag. 8	790	T	C
H1 frag. 9	89	A	G
H1 frag. 9	409	T	C
H3 frag. 1	66	C	G
H3 frag. 1	81	C	A
46 (unnamed taxon)			
H1 frag. 18	479	C	A
H1 frag. 18	536	—	A
H1 frag. 18	732	A	T
H1 frag. 19	42	A	C
H1 frag. 19	254	G	—
H1 frag. 19	278	C	A
H1 frag. 19	331	T	A
H1 frag. 19	431	C	A
H1 frag. 19	612	T	C
H1 frag. 19	796	C	T
H1 frag. 19	808	C	T
H1 frag. 20	54	A	T
H1 frag. 20	176	A	G
H1 frag. 20	182	T	C
H1 frag. 21	57	A	C
H1 frag. 21	239	—	T
H1 frag. 23	22	T	C
H1 frag. 23	293	C	T
H1 frag. 23	668	C	A
H1 frag. 23	1346	A	C
H1 frag. 6	31	C	T
H1 frag. 7	11	G	A
H1 frag. 8	250	A	T
H1 frag. 8	628	C	T
H1 frag. 8	675	—	T
H1 frag. 8	735	T	C
49 (Plethosalamandroidei)			
H1 frag. 10	24	A	G
H1 frag. 10	101	G	A
H1 frag. 11	57	A	T
H1 frag. 11	89	C	T
H1 frag. 11	1191	T	A
H1 frag. 12	52	T	A
H1 frag. 13	172	C	T
H1 frag. 14	124	T	C
H1 frag. 15	58	A	G
H1 frag. 16	4	C	T
H1 frag. 16	681	T	A
H1 frag. 17	46	A	T
H1 frag. 17	160	T	A
H1 frag. 18	479	A	T
H1 frag. 18	750	G	A
H1 frag. 18	854	T	—
H1 frag. 19	417	T	A
H1 frag. 19	432	—	C
H1 frag. 20	140	A	T
H1 frag. 21	134	G	—
H1 frag. 21	177	C	A
H1 frag. 21	260	T	C
H1 frag. 23	49	T	A
H1 frag. 23	102	A	T
H1 frag. 23	182	T	—

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Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 23	521	A	—
H1 frag. 23	623	A	—
H1 frag. 23	789	A	—
H1 frag. 23	902	C	—
H1 frag. 23	951	G	—
H1 frag. 23	953	G	—
H1 frag. 23	1108	A	—
H1 frag. 23	1124	A	—
H1 frag. 23	1158	T	—
H1 frag. 23	1173	A	—
H1 frag. 23	1657	T	A
H1 frag. 23	1766	T	A
H1 frag. 6	77	—	T
H1 frag. 8	184	T	C
H1 frag. 8	331	—	C
H1 frag. 8	345	G	A
H1 frag. 8	369	A	T
H1 frag. 8	562	G	A
H1 frag. 8	634	T	C
H1 frag. 9	209	T	—
H1 frag. 9	520	A	—
H1 frag. 9	672	A	T
rhod frag. 1	94	G	A
rhod frag. 1	151	C	T
rhod frag. 2	93	C	G
50 (Xenosalamandroidei)			
H1 frag. 11	40	G	—
H1 frag. 11	77	C	T
H1 frag. 11	213	C	—
H1 frag. 11	577	—	C
H1 frag. 11	1217	A	C
H1 frag. 11	1311	C	—
H1 frag. 12	59	A	T
H1 frag. 12	74	A	T
H1 frag. 13	70	T	C
H1 frag. 14	250	C	A
H1 frag. 15	15	T	A
H1 frag. 15	23	T	A
H1 frag. 15	25	G	A
H1 frag. 15	60	T	A
H1 frag. 16	5	A	G
H1 frag. 16	39	T	A
H1 frag. 16	201	T	A
H1 frag. 16	359	T	C
H1 frag. 16	672	A	T
H1 frag. 17	221	—	A
H1 frag. 18	322	A	C
H1 frag. 18	488	C	T
H1 frag. 18	748	T	C
H1 frag. 18	802	—	A
H1 frag. 19	15	A	G
H1 frag. 19	97	T	C
H1 frag. 19	99	T	C
H1 frag. 19	460	T	G
H1 frag. 19	573	G	T
H1 frag. 19	635	T	—
H1 frag. 20	60	A	G
H1 frag. 20	146	T	A
H1 frag. 20	176	A	G
H1 frag. 21	17	—	A
H1 frag. 21	243	T	C
H1 frag. 23	167	A	C
H1 frag. 23	293	T	C
H1 frag. 23	965	—	T
H1 frag. 23	1081	A	G
H1 frag. 23	1703	T	C
H1 frag. 23	1752	A	—
H1 frag. 23	1796	T	—
H1 frag. 25	34	C	A
H1 frag. 6	27	G	A
H1 frag. 6	91	T	A
H1 frag. 8	316	T	A
H1 frag. 8	598	A	—
H1 frag. 8	667	C	T
72 (*Pseudoeurycea*)			
H1 frag. 21	57	A	C
H1 frag. 23	49	A	G
H1 frag. 23	1376	T	C
H1 frag. 23	1776	C	—
H1 frag. 23	1798	T	—

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 23	1816	A	G
H1 frag. 23	1833	—	A
86 (Alytidae)			
28S frag. 2	753	C	—
28S frag. 2	764	A	T
28S frag. 3	217	C	G
28S frag. 3	424	G	C
28S frag. 3	582	G	C
H1 frag. 11	409	T	A
H1 frag. 11	457	C	A
H1 frag. 11	565	C	A
H1 frag. 11	694	C	—
H1 frag. 11	983	T	A
H1 frag. 11	1161	A	C
H1 frag. 11	1217	A	C
H1 frag. 13	121	A	T
H1 frag. 14	35	A	C
H1 frag. 14	166	C	—
H1 frag. 16	7	A	C
H1 frag. 16	46	—	T
H1 frag. 16	429	C	—
H1 frag. 17	56	—	T
H1 frag. 17	231	T	A
H1 frag. 17	320	—	G
H1 frag. 18	306	A	C
H1 frag. 18	447	T	C
H1 frag. 18	746	T	A
H1 frag. 19	91	C	—
H1 frag. 19	203	A	C
H1 frag. 19	415	A	C
H1 frag. 19	439	A	G
H1 frag. 19	771	A	C
H1 frag. 20	20	T	—
H1 frag. 21	10	T	C
H1 frag. 21	57	A	T
H1 frag. 21	218	C	T
H1 frag. 23	52	C	T
H1 frag. 23	199	A	C
H1 frag. 23	452	C	—
H1 frag. 23	942	A	T
H1 frag. 23	1154	A	G
H1 frag. 23	1186	—	A
H1 frag. 23	1256	T	C
H1 frag. 23	1376	T	C
H1 frag. 23	1496	—	C
H1 frag. 23	1919	C	—
H1 frag. 23	1962	A	T
H1 frag. 25	15	C	T
H1 frag. 25	86	G	A
H1 frag. 6	49	T	A
H1 frag. 6	81	A	C
H1 frag. 6	183	—	T
H1 frag. 8	132	T	A
H1 frag. 8	634	T	C
H1 frag. 9	520	A	—
H1 frag. 9	768	—	A
H3 frag. 1	51	T	A
H3 frag. 1	81	A	C
H3 frag. 1	114	T	C
H3 frag. 1	126	G	T
H3 frag. 2	39	G	T
H3 frag. 2	42	C	G
rhod frag. 1	90	T	C
rhod frag. 1	99	T	C
rhod frag. 1	101	G	A
rhod frag. 2	3	A	G
rhod frag. 2	69	T	C
SIA frag. 4	7	T	C
SIA frag. 4	61	T	A
88 (Bombinatoridae/*Bombina*)			
28S frag. 2	132	T	C
28S frag. 2	467	—	T
28S frag. 2	711	—	G
28S frag. 2	763	—	A
28S frag. 3	370	G	C
28S frag. 3	420	—	A
28S frag. 3	535	C	T
28S frag. 4	83	T	C
H1 frag. 1	18	T	C
H1 frag. 1	20	A	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 1	40	T	A
H1 frag. 1	41	A	G
H1 frag. 1	64	A	G
H1 frag. 10	72	A	T
H1 frag. 10	261	T	A
H1 frag. 11	10	A	—
H1 frag. 11	17	—	G
H1 frag. 11	31	T	C
H1 frag. 11	47	T	C
H1 frag. 11	67	C	A
H1 frag. 11	79	A	G
H1 frag. 11	88	T	C
H1 frag. 11	141	A	T
H1 frag. 11	213	C	T
H1 frag. 11	230	C	T
H1 frag. 11	778	A	—
H1 frag. 11	910	C	A
H1 frag. 11	953	C	G
H1 frag. 11	1135	C	—
H1 frag. 11	1316	A	T
H1 frag. 12	4	T	A
H1 frag. 12	29	A	C
H1 frag. 12	52	G	A
H1 frag. 12	122	G	A
H1 frag. 14	9	G	A
H1 frag. 14	93	A	C
H1 frag. 14	100	T	C
H1 frag. 14	144	G	T
H1 frag. 14	146	A	G
H1 frag. 14	149	G	A
H1 frag. 14	208	A	C
H1 frag. 15	19	C	T
H1 frag. 15	22	C	A
H1 frag. 15	40	C	T
H1 frag. 16	5	A	G
H1 frag. 16	18	T	C
H1 frag. 16	23	G	A
H1 frag. 16	94	T	—
H1 frag. 16	127	T	—
H1 frag. 16	241	A	G
H1 frag. 16	509	A	G
H1 frag. 16	535	A	C
H1 frag. 16	576	A	C
H1 frag. 16	590	A	C
H1 frag. 16	648	A	G
H1 frag. 16	696	G	A
H1 frag. 17	2	C	T
H1 frag. 17	60	G	A
H1 frag. 17	125	T	C
H1 frag. 17	187	A	T
H1 frag. 17	372	T	C
H1 frag. 18	164	T	—
H1 frag. 18	185	C	—
H1 frag. 18	380	—	A
H1 frag. 18	433	A	C
H1 frag. 18	501	A	T
H1 frag. 18	579	—	T
H1 frag. 18	604	A	T
H1 frag. 18	656	A	—
H1 frag. 18	717	A	C
H1 frag. 18	748	T	C
H1 frag. 18	766	C	T
H1 frag. 18	830	C	A
H1 frag. 18	863	G	A
H1 frag. 18	866	C	A
H1 frag. 18	883	C	T
H1 frag. 19	109	C	T
H1 frag. 19	244	A	C
H1 frag. 19	250	—	G
H1 frag. 19	259	A	C
H1 frag. 19	283	—	T
H1 frag. 19	313	—	C
H1 frag. 19	350	A	G
H1 frag. 19	449	T	A
H1 frag. 19	531	A	T
H1 frag. 19	823	C	A
H1 frag. 19	826	A	T
H1 frag. 2	79	—	G
H1 frag. 2	88	A	C
H1 frag. 2	108	C	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 2	133	C	T
H1 frag. 2	210	G	A
H1 frag. 2	301	C	A
H1 frag. 2	407	A	C
H1 frag. 20	61	A	G
H1 frag. 21	44	—	A
H1 frag. 21	177	C	A
H1 frag. 21	178	C	A
H1 frag. 21	251	A	G
H1 frag. 23	49	T	C
H1 frag. 23	100	T	A
H1 frag. 23	102	T	A
H1 frag. 23	105	A	C
H1 frag. 23	236	A	G
H1 frag. 23	283	C	T
H1 frag. 23	981	T	A
H1 frag. 23	1097	G	—
H1 frag. 23	1150	—	T
H1 frag. 23	1169	G	A
H1 frag. 23	1181	C	G
H1 frag. 23	1270	T	C
H1 frag. 23	1607	C	A
H1 frag. 23	1695	A	G
H1 frag. 23	1722	A	C
H1 frag. 23	1745	C	T
H1 frag. 23	1759	T	C
H1 frag. 23	1824	T	—
H1 frag. 23	1940	T	A
H1 frag. 24	1	C	T
H1 frag. 24	10	A	C
H1 frag. 24	17	C	T
H1 frag. 24	35	G	A
H1 frag. 25	16	A	C
H1 frag. 25	24	T	C
H1 frag. 25	38	A	G
H1 frag. 3	48	A	T
H1 frag. 3	58	C	T
H1 frag. 3	160	T	C
H1 frag. 3	214	T	C
H1 frag. 3	251	C	T
H1 frag. 3	283	A	G
H1 frag. 3	384	T	C
H1 frag. 3	391	A	G
H1 frag. 3	402	C	A
H1 frag. 3	407	C	A
H1 frag. 4	8	C	A
H1 frag. 4	26	A	G
H1 frag. 4	169	C	A
H1 frag. 4	260	T	C
H1 frag. 4	268	T	C
H1 frag. 4	283	T	A
H1 frag. 4	286	A	G
H1 frag. 4	298	A	T
H1 frag. 4	363	T	A
H1 frag. 4	365	T	C
H1 frag. 4	386	T	A
H1 frag. 4	404	A	G
H1 frag. 4	408	A	C
H1 frag. 4	434	A	G
H1 frag. 4	439	C	A
H1 frag. 4	452	A	—
H1 frag. 4	467	G	T
H1 frag. 4	481	A	G
H1 frag. 4	489	T	C
H1 frag. 4	517	A	G
H1 frag. 4	592	T	C
H1 frag. 4	637	T	C
H1 frag. 4	649	A	C
H1 frag. 6	35	T	C
H1 frag. 6	52	T	A
H1 frag. 6	75	A	C
H1 frag. 6	85	T	A
H1 frag. 6	137	C	A
H1 frag. 6	176	—	C
H1 frag. 7	83	A	—
H1 frag. 7	84	A	—
H1 frag. 8	316	T	C
H1 frag. 8	582	T	C
H1 frag. 8	628	A	C
H1 frag. 8	644	A	G

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Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 8	647	A	C
H1 frag. 8	711	G	A
H1 frag. 8	735	C	—
H1 frag. 8	787	C	—
H1 frag. 8	792	C	T
H1 frag. 8	807	—	G
H1 frag. 8	828	T	A
H1 frag. 9	42	G	T
H1 frag. 9	281	T	C
H1 frag. 9	453	A	T
H3 frag. 1	84	G	C
H3 frag. 1	222	C	T
H3 frag. 2	5	T	G
H3 frag. 2	33	G	A
H3 frag. 2	63	C	T
H3 frag. 2	66	C	T
rhod frag. 1	78	G	A
rhod frag. 1	104	T	A
rhod frag. 1	110	C	T
rhod frag. 1	122	C	T
rhod frag. 1	131	T	C
rhod frag. 1	134	G	C
rhod frag. 1	135	T	C
rhod frag. 1	137	C	T
rhod frag. 1	150	C	T
rhod frag. 2	21	C	T
rhod frag. 2	31	C	T
rhod frag. 2	54	C	T
rhod frag. 2	67	T	G
rhod frag. 2	112	C	T
92 (Anomocoela)			
H1 frag. 11	622	C	—
H1 frag. 11	897	—	T
H1 frag. 11	898	—	C
H1 frag. 11	1076	—	T
H1 frag. 11	1294	T	C
H1 frag. 13	69	C	A
H1 frag. 14	154	G	—
H1 frag. 14	166	C	A
H1 frag. 14	208	A	T
H1 frag. 14	250	C	T
H1 frag. 16	59	—	G
H1 frag. 16	292	A	G
H1 frag. 16	485	G	C
H1 frag. 16	590	A	C
H1 frag. 16	668	—	C
H1 frag. 17	5	T	A
H1 frag. 17	46	A	C
H1 frag. 17	407	T	A
H1 frag. 18	7	C	T
H1 frag. 18	388	C	T
H1 frag. 18	784	—	C
H1 frag. 18	838	A	—
H1 frag. 19	5	—	C
H1 frag. 19	109	C	T
H1 frag. 19	249	—	A
H1 frag. 19	278	C	T
H1 frag. 19	668	C	T
H1 frag. 19	808	C	T
H1 frag. 2	73	T	C
H1 frag. 2	256	A	C
H1 frag. 2	301	C	—
H1 frag. 20	68	G	A
H1 frag. 20	146	T	A
H1 frag. 20	176	A	G
H1 frag. 21	113	A	T
H1 frag. 23	250	G	T
H1 frag. 23	606	—	C
H1 frag. 23	737	—	T
H1 frag. 23	762	C	A
H1 frag. 23	1097	G	C
H1 frag. 23	1160	—	G
H1 frag. 23	1256	T	A
H1 frag. 23	1338	C	A
H1 frag. 23	1358	A	T
H1 frag. 23	1444	G	—
H1 frag. 23	1460	G	T
H1 frag. 23	1669	C	T
H1 frag. 23	1951	A	T
H1 frag. 3	120	T	A

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 3	248	G	A
H1 frag. 3	266	C	T
H1 frag. 3	366	C	T
H1 frag. 3	391	A	G
H1 frag. 3	402	C	T
H1 frag. 3	410	A	T
H1 frag. 4	280	C	T
H1 frag. 4	375	—	C
H1 frag. 4	391	A	C
H1 frag. 6	137	C	A
H1 frag. 7	35	C	G
H1 frag. 8	306	C	T
H1 frag. 8	629	—	T
H1 frag. 9	453	A	T
H3 frag. 1	18	G	C
H3 frag. 1	72	C	T
H3 frag. 1	99	C	T
H3 frag. 1	138	C	T
H3 frag. 1	195	G	T
H3 frag. 1	204	C	T
H3 frag. 2	29	T	C
rhod frag. 1	78	G	A
rhod frag. 1	120	C	T
rhod frag. 1	122	C	A
rhod frag. 1	153	G	A
rhod frag. 2	9	A	G
rhod frag. 2	33	G	C
rhod frag. 2	73	G	T
SIA frag. 1	12	T	C
SIA frag. 1	36	T	C
SIA frag. 2	14	A	G
SIA frag. 3	43	T	A
SIA frag. 3	44	C	G
SIA frag. 3	171	G	C
SIA frag. 4	49	T	G
SIA frag. 4	67	T	C
93 (Pelodytoidea)			
28S frag. 2	442	C	—
28S frag. 2	613	C	—
28S frag. 2	714	G	—
28S frag. 2	753	C	—
28S frag. 2	764	A	—
H1 frag. 11	16	A	T
H1 frag. 11	230	C	T
H1 frag. 12	116	G	A
H1 frag. 14	106	A	C
H1 frag. 14	142	C	T
H1 frag. 14	146	A	G
H1 frag. 14	260	G	T
H1 frag. 15	21	T	C
H1 frag. 16	31	A	G
H1 frag. 16	94	T	—
H1 frag. 16	127	T	A
H1 frag. 16	201	T	A
H1 frag. 16	382	A	C
H1 frag. 16	509	A	—
H1 frag. 16	690	A	T
H1 frag. 17	437	C	A
H1 frag. 18	95	A	C
H1 frag. 18	138	A	—
H1 frag. 18	315	—	A
H1 frag. 18	545	—	C
H1 frag. 18	830	C	T
H1 frag. 19	273	—	T
H1 frag. 19	274	—	T
H1 frag. 19	600	C	T
H1 frag. 2	100	A	C
H1 frag. 2	203	A	G
H1 frag. 20	16	T	A
H1 frag. 20	77	G	A
H1 frag. 23	25	A	T
H1 frag. 23	38	C	T
H1 frag. 23	96	A	T
H1 frag. 23	902	C	T
H1 frag. 23	963	A	—
H1 frag. 23	1019	—	T
H1 frag. 23	1169	G	T
H1 frag. 23	1334	A	T
H1 frag. 3	92	C	T
H1 frag. 3	117	G	A

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 4	120	T	C
H1 frag. 4	232	C	T
H1 frag. 4	268	T	C
H1 frag. 4	286	A	G
H1 frag. 4	481	A	G
H1 frag. 6	164	—	A
H1 frag. 8	316	T	C
H1 frag. 8	488	C	T
H1 frag. 9	652	T	C
H1 frag. 9	775	A	T
rhod frag. 1	69	C	T
SIA frag. 3	48	G	T
SIA frag. 3	66	G	A
SIA frag. 3	153	A	G
96 (Pelobatoidea)			
28S frag. 2	589	—	C
28S frag. 2	590	—	G
28S frag. 2	721	—	C
H1 frag. 1	2	T	C
H1 frag. 10	72	A	—
H1 frag. 10	76	A	—
H1 frag. 11	116	—	C
H1 frag. 11	138	A	C
H1 frag. 11	565	C	T
H1 frag. 11	988	—	C
H1 frag. 11	1217	A	—
H1 frag. 11	1248	C	—
H1 frag. 13	168	C	A
H1 frag. 14	51	A	G
H1 frag. 14	102	T	C
H1 frag. 14	129	C	T
H1 frag. 14	217	A	T
H1 frag. 15	54	G	A
H1 frag. 16	32	C	T
H1 frag. 16	319	—	A
H1 frag. 16	429	C	T
H1 frag. 17	52	A	T
H1 frag. 17	231	C	—
H1 frag. 18	209	A	—
H1 frag. 18	615	C	T
H1 frag. 18	727	C	T
H1 frag. 19	66	A	T
H1 frag. 19	376	G	C
H1 frag. 19	531	A	C
H1 frag. 2	108	C	T
H1 frag. 2	360	T	—
H1 frag. 21	133	A	T
H1 frag. 21	219	—	T
H1 frag. 23	105	A	T
H1 frag. 23	789	A	T
H1 frag. 23	1221	C	T
H1 frag. 23	1478	G	—
H1 frag. 23	1518	A	—
H1 frag. 23	1607	C	—
H1 frag. 23	1657	C	—
H1 frag. 23	1676	C	—
H1 frag. 23	1787	T	—
H1 frag. 23	1962	A	—
H1 frag. 3	58	C	A
H1 frag. 3	108	A	C
H1 frag. 3	214	T	A
H1 frag. 4	26	A	T
H1 frag. 4	148	A	T
H1 frag. 4	211	A	T
H1 frag. 4	263	G	A
H1 frag. 4	271	T	A
H1 frag. 4	441	A	C
H1 frag. 4	493	C	T
H1 frag. 6	66	C	—
H1 frag. 6	167	A	T
H1 frag. 6	181	A	C
H1 frag. 7	81	C	T
H1 frag. 7	84	A	C
H1 frag. 8	232	A	C
H1 frag. 8	628	A	T
H1 frag. 8	696	A	G
H1 frag. 8	711	G	A
H1 frag. 8	804	A	G
H1 frag. 8	818	C	T
H1 frag. 9	89	G	A

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 9	226	A	T
H1 frag. 9	788	A	C
H3 frag. 1	108	C	A
H3 frag. 1	147	A	G
rhod frag. 1	33	G	A
rhod frag. 1	168	C	T
rhod frag. 1	169	A	G
rhod frag. 1	174	G	A
rhod frag. 2	106	A	T
97 (Pelobatidae)			
H1 frag. 10	174	—	C
H1 frag. 11	53	T	G
H1 frag. 11	134	A	C
H1 frag. 11	141	A	T
H1 frag. 11	409	T	C
H1 frag. 11	517	—	C
H1 frag. 11	795	—	C
H1 frag. 11	901	—	A
H1 frag. 11	991	—	T
H1 frag. 11	1081	—	A
H1 frag. 11	1161	A	T
H1 frag. 11	1266	A	T
H1 frag. 11	1311	C	A
H1 frag. 11	1333	T	C
H1 frag. 12	41	A	G
H1 frag. 22	70	A	G
H1 frag. 23	18	—	A
H1 frag. 23	25	A	—
H1 frag. 23	50	C	T
H1 frag. 23	72	C	T
H1 frag. 23	89	G	A
H1 frag. 23	490	T	C
H1 frag. 23	559	T	A
H1 frag. 23	602	T	A
H1 frag. 23	762	A	T
H1 frag. 23	1015	A	C
H1 frag. 23	1161	—	A
H1 frag. 23	1181	C	A
H1 frag. 23	1316	C	T
H1 frag. 23	1711	A	C
H1 frag. 23	1793	A	C
H1 frag. 23	1799	—	C
H1 frag. 23	1908	—	A
H1 frag. 25	15	C	T
H1 frag. 25	86	G	A
H1 frag. 6	84	—	C
H1 frag. 6	199	C	T
H1 frag. 6	213	A	C
H1 frag. 8	28	A	C
H1 frag. 8	41	A	T
H1 frag. 8	69	C	T
H1 frag. 8	179	C	T
H1 frag. 8	192	G	A
H1 frag. 8	565	A	T
H1 frag. 8	667	C	T
H1 frag. 8	828	T	A
H1 frag. 9	46	T	C
H1 frag. 9	202	C	—
H1 frag. 9	256	C	T
H1 frag. 9	367	A	T
H1 frag. 9	618	A	C
H1 frag. 9	781	—	C
H1 frag. 9	782	—	C
rhod frag. 1	6	T	C
rhod frag. 1	94	G	A
rhod frag. 1	134	G	C
rhod frag. 1	140	A	T
rhod frag. 1	159	G	A
rhod frag. 2	6	C	T
rhod frag. 2	24	C	T
rhod frag. 2	37	C	T
rhod frag. 2	41	C	T
rhod frag. 2	54	C	T
rhod frag. 2	66	G	C
rhod frag. 2	100	G	T
rhod frag. 2	101	C	A
rhod frag. 2	115	C	T
rhod frag. 2	136	T	C
rhod frag. 2	139	G	A

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Br/Taxon/Frag	Pos	Anc	Der
99 (unnamed taxon)			
H1 frag. 10	93	A	G
H1 frag. 11	16	A	T
H1 frag. 11	77	C	T
H1 frag. 11	86	A	G
H1 frag. 11	95	T	C
H1 frag. 11	116	C	A
H1 frag. 11	124	C	—
H1 frag. 11	264	C	T
H1 frag. 11	315	A	G
H1 frag. 11	392	C	—
H1 frag. 11	852	C	T
H1 frag. 12	112	G	A
H1 frag. 13	39	A	—
H1 frag. 13	73	A	—
H1 frag. 13	107	G	A
H1 frag. 14	13	T	A
H1 frag. 14	64	A	T
H1 frag. 16	1	A	G
H1 frag. 16	7	A	G
H1 frag. 16	127	T	C
H1 frag. 16	359	C	T
H1 frag. 16	563	C	—
H1 frag. 16	576	C	T
H1 frag. 16	658	C	T
H1 frag. 17	47	C	T
H1 frag. 17	182	T	A
H1 frag. 17	416	—	G
H1 frag. 18	52	A	C
H1 frag. 18	164	T	C
H1 frag. 18	276	A	C
H1 frag. 18	581	C	T
H1 frag. 18	746	T	C
H1 frag. 18	756	T	C
H1 frag. 18	830	C	A
H1 frag. 19	278	T	C
H1 frag. 20	20	C	G
H1 frag. 20	140	T	C
H1 frag. 21	8	C	T
H1 frag. 23	789	T	—
H1 frag. 23	944	G	A
H1 frag. 23	963	A	—
H1 frag. 23	968	C	—
H1 frag. 23	1027	A	—
H1 frag. 23	1097	C	—
H1 frag. 23	1320	C	T
H1 frag. 23	1376	T	A
H1 frag. 23	1695	A	G
H1 frag. 23	1704	C	T
H1 frag. 25	14	G	A
H1 frag. 25	87	C	T
H3 frag. 1	72	T	C
H3 frag. 1	120	T	C
H3 frag. 2	39	G	C
rhod frag. 1	33	A	C
rhod frag. 1	78	A	G
rhod frag. 1	135	T	C
rhod frag. 2	61	G	A
rhod frag. 2	85	C	G
rhod frag. 2	108	A	T
SIA frag. 2	32	G	A
SIA frag. 2	41	A	G
SIA frag. 2	59	C	T
SIA frag. 3	48	G	C
SIA frag. 3	54	C	T
SIA frag. 3	78	A	G
SIA frag. 4	88	T	G
101 (unnamed taxon)			
H1 frag. 10	7	A	C
H1 frag. 10	9	T	C
H1 frag. 10	23	T	G
H1 frag. 10	192	—	T
H1 frag. 10	199	C	A
H1 frag. 10	261	T	C
H1 frag. 11	19	A	G
H1 frag. 11	130	A	C
H1 frag. 11	469	—	T
H1 frag. 11	887	A	T
H1 frag. 11	1336	T	C
H1 frag. 12	14	A	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 12	125	A	T
H1 frag. 13	18	G	T
H1 frag. 13	172	C	A
H1 frag. 14	83	A	T
H1 frag. 14	108	C	T
H1 frag. 14	193	T	C
H1 frag. 14	250	T	A
H1 frag. 16	54	—	G
H1 frag. 16	292	G	T
H1 frag. 16	319	A	T
H1 frag. 16	333	A	T
H1 frag. 16	648	A	C
H1 frag. 17	46	C	A
H1 frag. 17	52	T	C
H1 frag. 17	120	T	—
H1 frag. 17	122	A	—
H1 frag. 17	136	A	—
H1 frag. 17	160	A	—
H1 frag. 17	187	A	—
H1 frag. 17	210	T	C
H1 frag. 17	251	T	C
H1 frag. 18	138	A	—
H1 frag. 18	218	C	T
H1 frag. 18	433	A	C
H1 frag. 18	501	A	C
H1 frag. 18	539	A	—
H1 frag. 18	656	A	G
H1 frag. 18	698	A	G
H1 frag. 18	707	T	G
H1 frag. 19	109	T	—
H1 frag. 19	123	A	C
H1 frag. 19	286	C	A
H1 frag. 19	715	A	T
H1 frag. 19	749	C	T
H1 frag. 20	25	A	G
H1 frag. 20	66	T	C
H1 frag. 21	171	A	T
H1 frag. 21	179	C	T
H1 frag. 22	20	T	C
H1 frag. 23	48	A	G
H1 frag. 23	299	G	—
H1 frag. 23	898	—	T
H1 frag. 23	922	—	T
H1 frag. 23	1160	G	T
H1 frag. 23	1181	C	T
H1 frag. 23	1303	C	A
H1 frag. 23	1686	—	C
H1 frag. 23	1781	A	T
H1 frag. 23	1824	T	C
H1 frag. 23	1882	A	T
H1 frag. 23	1968	T	A
H1 frag. 25	32	G	A
H1 frag. 6	62	A	—
H1 frag. 6	67	T	—
H1 frag. 6	75	A	—
H1 frag. 6	85	T	—
H1 frag. 6	98	A	—
H1 frag. 6	104	C	—
H1 frag. 6	115	A	—
H1 frag. 6	181	C	—
H1 frag. 6	213	A	—
H1 frag. 8	40	T	C
H1 frag. 8	173	T	G
H1 frag. 8	184	T	C
H1 frag. 8	232	C	—
H1 frag. 8	525	C	A
H1 frag. 8	619	—	C
H1 frag. 9	28	A	G
H1 frag. 9	48	T	C
H1 frag. 9	281	T	C
H1 frag. 9	309	—	C
H1 frag. 9	558	A	C
H1 frag. 9	618	A	—
H1 frag. 9	739	A	G
H1 frag. 9	818	T	C
H3 frag. 1	0	C	T
H3 frag. 1	27	C	T
H3 frag. 1	28	C	A
H3 frag. 1	81	A	C
H3 frag. 1	216	G	A

Br/Taxon/Frag	Pos	Anc	Der
102 (unnamed taxon)			
H1 frag. 21	57	A	T
H1 frag. 21	113	T	C
H1 frag. 21	133	T	C
H1 frag. 21	190	A	G
H1 frag. 21	277	C	A
H1 frag. 22	55	T	C
H1 frag. 23	5	T	C
H1 frag. 23	17	G	A
H1 frag. 23	25	A	G
H1 frag. 23	40	T	C
H1 frag. 23	67	G	A
H1 frag. 23	114	A	T
H1 frag. 23	195	—	C
H1 frag. 23	224	A	T
H1 frag. 23	260	C	T
H1 frag. 23	283	C	T
H1 frag. 23	606	C	T
H1 frag. 23	762	A	C
H1 frag. 23	854	C	T
H1 frag. 23	1027	A	C
H1 frag. 23	1074	T	C
H1 frag. 23	1081	A	T
H1 frag. 23	1114	A	T
H1 frag. 23	1135	T	—
H1 frag. 23	1160	T	—
H1 frag. 23	1169	G	—
H1 frag. 23	1201	G	A
H1 frag. 23	1226	T	A
H1 frag. 23	1256	A	T
H1 frag. 23	1458	—	T
H1 frag. 23	1687	A	T
H1 frag. 23	1825	T	C
H1 frag. 24	8	C	T
H1 frag. 24	17	C	T
H1 frag. 25	20	A	T
108 (Ranoides)			
28S frag. 2	720	G	—
H1 frag. 10	14	C	T
H1 frag. 10	19	G	A
H1 frag. 11	27	G	A
H1 frag. 12	14	C	T
H1 frag. 12	21	G	A
H1 frag. 12	127	A	T
H1 frag. 13	151	C	T
H1 frag. 14	72	—	A
H1 frag. 14	142	C	T
H1 frag. 14	147	G	A
H1 frag. 14	149	G	A
H1 frag. 15	19	C	T
H1 frag. 15	20	C	T
H1 frag. 15	60	T	A
H1 frag. 16	72	—	G
H1 frag. 16	152	A	T
H1 frag. 16	249	—	T
H1 frag. 16	467	G	—
H1 frag. 16	665	T	C
H1 frag. 17	160	C	—
H1 frag. 17	306	—	A
H1 frag. 18	93	C	T
H1 frag. 18	185	C	T
H1 frag. 19	155	T	C
H1 frag. 19	215	A	G
H1 frag. 19	216	T	C
H1 frag. 19	286	C	A
H1 frag. 19	826	A	T
H1 frag. 2	16	C	A
H1 frag. 2	196	T	C
H1 frag. 2	200	G	A
H1 frag. 2	301	C	A
H1 frag. 2	419	A	C
H1 frag. 22	10	T	C
H1 frag. 23	250	G	A
H1 frag. 23	274	C	A
H1 frag. 23	729	C	T
H1 frag. 23	1386	—	A
H1 frag. 23	1607	C	A
H1 frag. 23	1695	A	T
H1 frag. 23	1759	T	A
H1 frag. 23	1828	C	A

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 23	1962	A	T
H1 frag. 3	124	T	A
H1 frag. 3	342	G	T
H1 frag. 4	308	—	G
H1 frag. 4	391	A	C
H1 frag. 4	673	T	A
H1 frag. 6	46	C	A
H1 frag. 6	81	A	C
H1 frag. 7	76	C	T
H1 frag. 7	83	A	—
H1 frag. 7	84	A	—
H1 frag. 8	162	C	A
H1 frag. 8	179	C	T
H1 frag. 8	192	G	A
H1 frag. 8	352	—	A
H1 frag. 8	369	G	T
H1 frag. 8	488	C	A
H1 frag. 8	544	A	C
H1 frag. 8	580	C	A
H1 frag. 8	647	A	C
H1 frag. 8	726	A	T
H1 frag. 8	822	—	A
H1 frag. 9	73	C	A
H1 frag. 9	281	T	A
H1 frag. 9	633	C	—
rhod frag. 1		A	C
rhod frag. 1	3	T	C
rhod frag. 1	12	T	C
rhod frag. 1	21	C	T
rhod frag. 1	107	T	C
rhod frag. 1	117	T	A
rhod frag. 1	157	T	C
rhod frag. 2	3	A	G
rhod frag. 2	51	T	C
rhod frag. 2	73	G	A
rhod frag. 2	82	G	C
rhod frag. 2	126	C	A
SIA frag. 2	41	A	G
SIA frag. 2	59	C	T
SIA frag. 3	12	C	A
SIA frag. 3	108	T	C
SIA frag. 3	117	C	T
SIA frag. 3	129	C	T
tyr frag. 1	40	C	T
tyr frag. 2	14	G	A
tyr frag. 2	93	A	C
tyr frag. 2	96	A	C
tyr frag. 2	100	G	C
tyr frag. 2	108	G	A
tyr frag. 2	128	G	A
tyr frag. 2	138	T	G
tyr frag. 2	172	C	T
tyr frag. 2	207	C	T
tyr frag. 2	270	G	C
tyr frag. 3	63	C	A
tyr frag. 3	85	A	G
tyr frag. 3	88	C	T
tyr frag. 3	91	A	T
tyr frag. 3	103	C	T
tyr frag. 3	119	C	T
tyr frag. 3	127	A	T
tyr frag. 3	128	C	T
tyr frag. 3	140	G	A
tyr frag. 3	164	G	A
tyr frag. 3	173	C	T
109 (Allodapanura)			
H1 frag. 1	68	C	T
H1 frag. 11	536	C	T
H1 frag. 11	622	C	T
H1 frag. 11	868	—	A
H1 frag. 11	872	—	A
H1 frag. 11	938	—	C
H1 frag. 11	1089	C	A
H1 frag. 12	65	—	A
H1 frag. 16	221	C	—
H1 frag. 16	313	C	—
H1 frag. 16	509	A	T
H1 frag. 18	371	A	T
H1 frag. 19	54	T	A
H1 frag. 19	185	G	A

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Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 19	208	C	T
H1 frag. 19	244	A	C
H1 frag. 19	796	A	G
H1 frag. 21	277	C	T
H1 frag. 22	37	T	C
H1 frag. 23	762	C	A
H1 frag. 23	1041	T	—
H1 frag. 23	1905	T	—
H1 frag. 3	407	A	—
H1 frag. 4	578	—	T
H1 frag. 4	639	—	C
H1 frag. 6	51	—	A
H1 frag. 6	181	A	T
H1 frag. 8	241	—	C
H1 frag. 8	316	T	A
H1 frag. 8	335	T	A
H1 frag. 8	423	C	T
H1 frag. 9	580	C	A
rhod frag. 1	99	T	C
SIA frag. 3	33	C	T
SIA frag. 3	64	T	C
tyr frag. 2	210	C	T
tyr frag. 3	35	G	T
tyr frag. 3	64	A	G
tyr frag. 3	79	C	T
tyr frag. 3	122	G	A
tyr frag. 3	181	G	A
110 (Microhylidae)			
28S frag. 2	473	T	C
28S frag. 2	644	—	C
28S frag. 2	719	C	G
28S frag. 2	790	C	A
28S frag. 3	424	G	C
H1 frag. 10	261	C	T
H1 frag. 11	144	T	C
H1 frag. 11	726	—	G
H1 frag. 11	1045	A	T
H1 frag. 11	1217	A	C
H1 frag. 12	52	C	—
H1 frag. 13	8	G	A
H1 frag. 13	125	A	C
H1 frag. 14	44	T	C
H1 frag. 15	50	T	C
H1 frag. 16	16	A	G
H1 frag. 16	25	T	C
H1 frag. 16	414	A	T
H1 frag. 16	556	—	T
H1 frag. 16	557	—	T
H1 frag. 17	231	C	T
H1 frag. 17	423	A	G
H1 frag. 18	116	A	T
H1 frag. 18	397	—	A
H1 frag. 18	607	—	C
H1 frag. 18	727	C	T
H1 frag. 18	872	A	C
H1 frag. 19	376	T	A
H1 frag. 19	668	A	T
H1 frag. 2	7	C	A
H1 frag. 2	407	A	T
H1 frag. 20	129	T	A
H1 frag. 23	190	—	C
H1 frag. 23	213	A	G
H1 frag. 23	1532	—	C
H1 frag. 23	1607	A	T
H1 frag. 23	1846	C	T
H1 frag. 23	1946	—	A
H1 frag. 4	120	T	—
H1 frag. 4	201	—	A
H1 frag. 4	308	G	C
H1 frag. 4	330	T	—
H1 frag. 4	637	T	C
H1 frag. 5	12	A	G
H1 frag. 6	167	A	—
H1 frag. 8	24	A	T
H1 frag. 8	28	A	T
H1 frag. 8	122	A	C
H1 frag. 8	260	C	A
H1 frag. 8	313	C	T
H1 frag. 8	523	A	C
H1 frag. 9	216	—	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 9	226	A	G
H1 frag. 9	652	T	C
H1 frag. 9	775	C	T
H3 frag. 1	114	T	C
H3 frag. 1	117	G	C
H3 frag. 1	193	C	A
H3 frag. 2	29	T	C
H3 frag. 2	39	G	C
rhod frag. 1	36	A	G
rhod frag. 1	66	T	C
rhod frag. 1	117	A	C
rhod frag. 1	135	C	T
rhod frag. 1	162	T	C
rhod frag. 2	43	T	A
rhod frag. 2	53	A	T
rhod frag. 2	130	G	—
SIA frag. 3	9	T	C
SIA frag. 3	120	G	C
SIA frag. 3	168	T	C
SIA frag. 3	177	A	G
111 (unnamed taxon)			
28S frag. 2	369	—	C
H1 frag. 2	66	—	C
H1 frag. 2	438	T	A
H1 frag. 3	355	A	T
H1 frag. 4	337	C	T
H1 frag. 4	351	G	A
H3 frag. 1	55	C	A
118 (Cophylinae)			
28S frag. 2	567	C	—
H1 frag. 11	16	A	G
H1 frag. 11	47	T	—
H1 frag. 11	67	C	—
H1 frag. 11	409	T	—
H1 frag. 11	663	A	C
H1 frag. 11	726	G	C
H1 frag. 11	778	C	—
H1 frag. 11	910	C	T
H1 frag. 11	938	C	—
H1 frag. 11	983	T	—
H1 frag. 11	1342	T	A
H1 frag. 12	6	A	C
H1 frag. 13	6	A	—
H1 frag. 13	33	T	—
H1 frag. 13	75	T	—
H1 frag. 13	127	A	T
H1 frag. 13	132	G	A
H1 frag. 14	13	T	C
H1 frag. 14	91	T	A
H1 frag. 14	193	T	C
H1 frag. 14	243	G	A
H1 frag. 14	263	T	C
H1 frag. 15	23	C	A
H1 frag. 16	33	C	T
H1 frag. 16	86	—	T
H1 frag. 16	355	—	C
H1 frag. 16	547	C	—
H1 frag. 16	557	A	C
H1 frag. 17	38	A	T
H1 frag. 18	45	T	C
H1 frag. 18	93	T	C
H1 frag. 18	94	A	C
H1 frag. 18	408	—	C
H1 frag. 18	581	C	T
H1 frag. 18	707	T	C
H1 frag. 18	821	T	C
H1 frag. 18	872	C	A
H1 frag. 19	83	C	A
H1 frag. 19	331	G	—
H1 frag. 19	338	A	—
H1 frag. 19	350	G	—
H1 frag. 19	356	C	—
H1 frag. 19	376	A	T
H1 frag. 19	439	G	—
H1 frag. 19	715	T	C
H1 frag. 20	66	A	G
H1 frag. 20	176	A	G
H1 frag. 21	10	C	T
H1 frag. 21	171	G	A
H1 frag. 21	238	—	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 22	36	G	A
H1 frag. 23	9	A	C
H1 frag. 23	22	T	C
H1 frag. 23	102	A	T
H1 frag. 23	190	C	—
H1 frag. 23	250	T	—
H1 frag. 23	265	A	C
H1 frag. 23	559	C	T
H1 frag. 23	1015	A	C
H1 frag. 23	1181	C	A
H1 frag. 23	1292	—	C
H1 frag. 23	1310	T	C
H1 frag. 23	1316	T	C
H1 frag. 23	1532	C	—
H1 frag. 23	1739	A	T
H1 frag. 23	1750	A	C
H1 frag. 23	1846	T	C
H1 frag. 24	20	T	C
H1 frag. 6	25	T	C
H1 frag. 6	27	G	A
H1 frag. 8	23	T	C
H1 frag. 8	24	T	A
H1 frag. 8	41	A	T
H1 frag. 8	90	—	C
H1 frag. 8	139	C	T
H1 frag. 8	568	A	C
H1 frag. 8	611	A	T
H1 frag. 8	667	A	C
H1 frag. 8	828	T	C
H1 frag. 9	132	T	—
H1 frag. 9	138	C	—
H1 frag. 9	173	A	—
H1 frag. 9	185	A	—
H1 frag. 9	202	A	—
H1 frag. 9	226	G	—
H1 frag. 9	315	C	—
H1 frag. 9	333	C	—
H1 frag. 9	343	A	—
H1 frag. 9	367	A	—
H1 frag. 9	506	C	—
H1 frag. 9	520	A	—
H1 frag. 9	533	A	—
H1 frag. 9	558	A	—
H1 frag. 9	580	A	—
H1 frag. 9	693	A	—
H1 frag. 9	798	C	—
H1 frag. 9	818	T	C
H3 frag. 1	45	C	T
H3 frag. 1	69	G	A
H3 frag. 1	192	C	G
H3 frag. 1	195	A	C
SIA frag. 1	36	T	C
SIA frag. 2	44	C	T
SIA frag. 3	33	T	C
SIA frag. 3	42	T	G
SIA frag. 3	60	A	G
SIA frag. 3	64	C	T
SIA frag. 3	159	C	G
SIA frag. 4	76	T	G
tyr frag. 1	50	A	G
tyr frag. 2	92	G	A
tyr frag. 2	191	G	A
tyr frag. 2	194	A	G
tyr frag. 3	91	T	A
tyr frag. 3	113	T	A
tyr frag. 3	126	C	A
tyr frag. 3	153	G	A
121 (Gastrophryninae)			
H1 frag. 1	71	A	T
H1 frag. 11	67	C	A
H1 frag. 11	595	A	T
H1 frag. 11	778	C	A
H1 frag. 11	1000	A	T
H1 frag. 13	69	C	A
H1 frag. 13	151	T	C
H1 frag. 14	124	T	C
H1 frag. 15	58	A	G
H1 frag. 16	191	C	T
H1 frag. 16	414	T	C
H1 frag. 16	590	A	—

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 17	118	G	T
H1 frag. 17	300	—	G
H1 frag. 18	322	A	G
H1 frag. 18	393	—	C
H1 frag. 18	447	C	—
H1 frag. 19	119	A	T
H1 frag. 2	154	T	C
H1 frag. 21	57	A	—
H1 frag. 3	398	C	A
H1 frag. 4	672	T	A
H1 frag. 8	41	A	C
H1 frag. 8	428	—	T
H1 frag. 8	545	C	T
H1 frag. 9	46	A	T
H1 frag. 9	349	—	T
H1 frag. 9	383	C	A
H1 frag. 9	440	—	C
H3 frag. 1	198	G	A
SIA frag. 2	38	C	T
SIA frag. 3	9	C	T
tyr frag. 1	46	T	C
tyr frag. 2	47	T	G
tyr frag. 2	83	T	C
tyr frag. 3	47	G	A
129 (unnamed taxon)			
H1 frag. 11	872	C	A
H1 frag. 11	1161	A	—
H1 frag. 13	159	T	C
H1 frag. 16	201	T	—
H1 frag. 17	33	A	T
H1 frag. 17	176	—	A
H1 frag. 18	267	—	T
H1 frag. 18	276	A	T
H1 frag. 18	349	C	T
H1 frag. 18	821	T	C
H1 frag. 19	600	C	T
H1 frag. 2	152	C	—
H1 frag. 20	20	C	A
H1 frag. 21	90	C	A
H1 frag. 23	942	C	T
H1 frag. 23	981	A	—
H1 frag. 23	997	A	T
H1 frag. 23	1103	—	A
H1 frag. 3	2	A	G
H1 frag. 3	398	C	A
H1 frag. 3	402	C	T
H1 frag. 4	191	T	C
H1 frag. 8	84	—	C
H1 frag. 8	241	C	T
H1 frag. 8	568	A	C
H1 frag. 9	216	T	C
rhod frag. 1	51	T	C
SIA frag. 2	59	T	C
SIA frag. 3	42	T	C
130 (Microhylinae)			
28S frag. 2	434	—	G
28S frag. 2	682	—	C
28S frag. 3	491	—	G
28S frag. 3	603	A	G
H1 frag. 1	50	A	G
H1 frag. 1	57	A	G
H1 frag. 10	52	C	T
H1 frag. 11	368	A	C
H1 frag. 11	595	A	T
H1 frag. 11	868	A	C
H1 frag. 11	1089	A	T
H1 frag. 11	1327	T	A
H1 frag. 12	65	A	G
H1 frag. 13	125	C	A
H1 frag. 16	170	T	A
H1 frag. 16	556	T	C
H1 frag. 16	614	T	C
H1 frag. 17	31	T	—
H1 frag. 17	182	T	A
H1 frag. 17	296	T	A
H1 frag. 17	423	G	A
H1 frag. 18	185	C	T
H1 frag. 19	278	C	A
H1 frag. 20	1	C	T
H1 frag. 20	68	G	A

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Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 20	73	A	G
H1 frag. 21	10	C	T
H1 frag. 21	171	G	A
H1 frag. 23	52	C	T
H1 frag. 23	602	T	—
H1 frag. 23	1221	C	T
H1 frag. 23	1331	C	T
H1 frag. 23	1518	A	C
H1 frag. 23	1616	C	A
H1 frag. 4	13	A	T
H1 frag. 6	181	C	T
H1 frag. 6	199	A	T
H1 frag. 8	41	A	T
H1 frag. 8	313	T	A
H1 frag. 8	523	C	T
H1 frag. 9	609	C	A
H3 frag. 1		T	C
H3 frag. 1	124	A	C
rhod frag. 1	57	T	C
rhod frag. 1	66	C	T
rhod frag. 1	125	T	C
SIA frag. 1	4	T	C
SIA frag. 2	32	G	C
SIA frag. 3	3	A	G
SIA frag. 3	111	A	G
SIA frag. 3	153	A	G
tyr frag. 1	21	T	G
tyr frag. 2	130	T	C
tyr frag. 3	50	T	A
134 (unnamed taxon)			
28S frag. 2	567	C	T
H1 frag. 10	199	C	A
H1 frag. 11	53	T	G
H1 frag. 11	439	C	A
H1 frag. 11	852	C	A
H1 frag. 11	938	C	T
H1 frag. 11	1294	T	C
H1 frag. 11	1333	T	A
H1 frag. 13	69	C	A
H1 frag. 16	19	C	A
H1 frag. 16	27	T	A
H1 frag. 16	648	A	G
H1 frag. 16	681	C	T
H1 frag. 17	333	C	T
H1 frag. 18	13	A	G
H1 frag. 18	539	T	—
H1 frag. 18	724	—	C
H1 frag. 19	42	A	T
H1 frag. 19	61	G	—
H1 frag. 19	119	A	T
H1 frag. 2	65	T	—
H1 frag. 2	154	T	C
H1 frag. 2	180	A	T
H1 frag. 2	439	C	T
H1 frag. 21	57	A	—
H1 frag. 21	163	—	A
H1 frag. 23	452	C	T
H1 frag. 23	623	A	C
H1 frag. 23	1169	C	T
H1 frag. 3	58	C	T
H1 frag. 3	362	G	A
H1 frag. 4	283	T	C
H1 frag. 4	316	C	A
H1 frag. 5	17	C	A
H1 frag. 6	91	T	C
H1 frag. 8	40	A	T
H1 frag. 8	74	A	T
H1 frag. 8	260	A	C
H1 frag. 8	441	A	C
H1 frag. 8	696	A	G
H1 frag. 8	735	A	G
H1 frag. 9	343	A	C
H1 frag. 9	645	—	T
H1 frag. 9	818	T	C
SIA frag. 1	39	C	T
135 (Asterophryinae)			
28S frag. 2	453	C	T
28S frag. 2	650	—	G
H1 frag. 1	22	G	A
H1 frag. 10	52	C	A

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 10	217	T	—
H1 frag. 10	269	C	T
H1 frag. 11	7	G	A
H1 frag. 11	88	T	C
H1 frag. 11	778	C	—
H1 frag. 11	870	—	C
H1 frag. 11	887	A	T
H1 frag. 11	1314	—	T
H1 frag. 11	1315	—	T
H1 frag. 11	1336	T	—
H1 frag. 11	1342	T	—
H1 frag. 12	41	A	G
H1 frag. 12	143	A	C
H1 frag. 13	130	C	T
H1 frag. 14	9	G	A
H1 frag. 14	238	A	T
H1 frag. 16	33	C	T
H1 frag. 16	72	G	A
H1 frag. 16	115	—	C
H1 frag. 16	241	A	—
H1 frag. 16	573	—	T
H1 frag. 16	665	C	T
H1 frag. 16	677	G	A
H1 frag. 16	680	G	T
H1 frag. 17	54	C	T
H1 frag. 17	210	A	C
H1 frag. 18	1	G	A
H1 frag. 18	116	C	T
H1 frag. 18	306	A	C
H1 frag. 18	530	C	—
H1 frag. 18	563	A	C
H1 frag. 18	597	—	A
H1 frag. 18	717	A	C
H1 frag. 18	741	C	—
H1 frag. 18	792	A	T
H1 frag. 18	883	C	T
H1 frag. 19	24	G	—
H1 frag. 19	66	A	T
H1 frag. 19	369	C	A
H1 frag. 19	439	G	A
H1 frag. 2	7	A	C
H1 frag. 2	285	A	—
H1 frag. 20	9	A	T
H1 frag. 20	60	G	—
H1 frag. 21	8	C	T
H1 frag. 21	172	G	A
H1 frag. 21	270	G	C
H1 frag. 22	10	C	T
H1 frag. 22	11	C	T
H1 frag. 22	13	C	T
H1 frag. 22	23	G	A
H1 frag. 22	61	G	A
H1 frag. 23	52	C	T
H1 frag. 23	67	G	A
H1 frag. 23	103	A	C
H1 frag. 23	190	C	—
H1 frag. 23	274	A	C
H1 frag. 23	283	C	T
H1 frag. 23	440	—	A
H1 frag. 23	693	A	—
H1 frag. 23	1131	G	A
H1 frag. 23	1303	C	T
H1 frag. 23	1816	A	C
H1 frag. 23	1946	A	—
H1 frag. 3	2	A	T
H1 frag. 3	8	T	C
H1 frag. 3	251	C	T
H1 frag. 3	252	C	T
H1 frag. 3	321	G	A
H1 frag. 3	398	C	T
H1 frag. 4	391	A	C
H1 frag. 4	441	C	A
H1 frag. 4	592	C	A
H1 frag. 4	670	A	C
H1 frag. 5	12	G	A
H1 frag. 5	35	G	A
H1 frag. 8	41	A	C
H1 frag. 8	86	—	A
H1 frag. 8	313	T	C
H1 frag. 8	488	T	A

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 8	824	—	C
H1 frag. 9	226	G	A
H1 frag. 9	281	C	A
H1 frag. 9	725	C	T
H3 frag. 1	12	C	T
H3 frag. 1	84	C	G
H3 frag. 1	189	G	C
SIA frag. 3	6	A	G
SIA frag. 3	51	T	C
SIA frag. 3	60	A	C
SIA frag. 3	84	G	C
SIA frag. 3	123	T	C
SIA frag. 4	22	G	T
SIA frag. 4	23	T	C
SIA frag. 4	46	T	C
SIA frag. 4	76	T	C
143 (Afrobatrachia)			
28S frag. 2	386	C	G
28S frag. 2	639	G	—
28S frag. 2	655	G	—
28S frag. 2	768	C	A
H1 frag. 1	59	T	A
H1 frag. 10	43	A	—
H1 frag. 11	264	C	T
H1 frag. 11	429	—	A
H1 frag. 11	565	C	A
H1 frag. 11	819	C	A
H1 frag. 11	1327	T	G
H1 frag. 12	80	C	—
H1 frag. 12	112	G	A
H1 frag. 12	116	G	A
H1 frag. 13	91	T	A
H1 frag. 16	333	A	C
H1 frag. 17	118	G	—
H1 frag. 17	333	C	T
H1 frag. 18	388	C	T
H1 frag. 19	3	C	T
H1 frag. 2	152	C	T
H1 frag. 2	171	A	C
H1 frag. 2	437	C	A
H1 frag. 20	176	A	G
H1 frag. 21	133	A	T
H1 frag. 23	22	T	C
H1 frag. 23	59	G	A
H1 frag. 23	822	—	T
H1 frag. 23	981	T	A
H1 frag. 23	1169	C	A
H1 frag. 3	22	C	A
H1 frag. 3	169	A	T
H1 frag. 3	176	A	T
H1 frag. 3	338	—	C
H1 frag. 3	396	—	T
H1 frag. 4	592	T	A
H1 frag. 6	23	C	T
H1 frag. 8	69	C	T
H1 frag. 8	352	A	G
H1 frag. 8	550	G	A
H1 frag. 8	626	C	A
H1 frag. 9	397	—	A
H1 frag. 9	506	A	T
H1 frag. 9	558	A	—
H1 frag. 9	818	T	C
rhod frag. 2	126	A	G
tyr frag. 1		G	A
tyr frag. 1	12	A	C
tyr frag. 2	157	A	C
tyr frag. 2	195	G	A
tyr frag. 2	258	A	G
tyr frag. 3	53	T	C
144 (Xenosyneunitanura)			
28S frag. 2	330	G	—
28S frag. 2	719	C	—
H1 frag. 11	67	C	T
H1 frag. 11	139	A	C
H1 frag. 11	368	A	C
H1 frag. 11	852	C	T
H1 frag. 11	937	—	C
H1 frag. 11	1071	C	A
H1 frag. 11	1217	A	T
H1 frag. 11	1259	T	—

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 12	148	T	—
H1 frag. 12	186	A	C
H1 frag. 14	72	A	—
H1 frag. 16	39	T	A
H1 frag. 16	535	A	—
H1 frag. 16	672	A	T
H1 frag. 17	274	A	—
H1 frag. 18	276	A	C
H1 frag. 18	306	A	T
H1 frag. 18	349	C	T
H1 frag. 18	508	—	T
H1 frag. 18	648	C	A
H1 frag. 19	123	A	C
H1 frag. 19	216	C	A
H1 frag. 19	439	G	T
H1 frag. 19	509	C	T
H1 frag. 2	32	G	A
H1 frag. 2	67	—	C
H1 frag. 2	133	C	T
H1 frag. 2	277	A	—
H1 frag. 20	60	G	A
H1 frag. 20	115	T	—
H1 frag. 21	218	C	—
H1 frag. 23	52	C	T
H1 frag. 23	1074	T	—
H1 frag. 23	1131	G	C
H1 frag. 23	1338	C	—
H1 frag. 23	1444	G	—
H1 frag. 23	1825	A	T
H1 frag. 3	58	C	T
H1 frag. 3	184	A	T
H1 frag. 3	297	C	A
H1 frag. 3	351	—	C
H1 frag. 3	365	T	C
H1 frag. 4	94	A	T
H1 frag. 4	292	T	—
H1 frag. 4	351	G	A
H1 frag. 6	181	T	C
H1 frag. 7	96	A	T
H1 frag. 8	46	T	C
H1 frag. 8	51	C	T
H1 frag. 8	52	A	G
H1 frag. 8	74	A	T
H1 frag. 8	181	A	G
H1 frag. 8	369	T	—
H1 frag. 8	458	—	T
H1 frag. 8	556	T	C
H1 frag. 8	558	G	A
H1 frag. 8	565	A	C
H1 frag. 8	611	A	T
H1 frag. 8	816	T	C
H1 frag. 8	828	T	A
H1 frag. 9	5	C	A
H1 frag. 9	457	—	G
H1 frag. 9	538	—	C
H1 frag. 9	539	—	C
H1 frag. 9	693	A	—
H1 frag. 9	840	C	A
rhod frag. 1	2	A	C
rhod frag. 2	3	G	A
rhod frag. 2	42	C	G
rhod frag. 2	80	G	A
rhod frag. 2	127	C	G
rhod frag. 2	129	A	T
SIA frag. 1	36	T	C
SIA frag. 1	39	C	T
SIA frag. 2	53	A	G
SIA frag. 3	24	C	T
SIA frag. 3	54	C	T
SIA frag. 3	78	G	A
SIA frag. 3	114	G	T
SIA frag. 4	22	G	A
SIA frag. 4	73	G	T
tyr frag. 1	7	C	G
tyr frag. 1	46	T	C
tyr frag. 1	82	C	T
tyr frag. 2	11	C	T
tyr frag. 2	39	A	C
tyr frag. 2	138	G	A
tyr frag. 2	177	C	T

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Br/Taxon/Frag	Pos	Anc	Der
tyr frag. 2	204	C	A
tyr frag. 2	213	T	A
tyr frag. 3	44	G	A
tyr frag. 3	51	G	A
tyr frag. 3	52	A	C
tyr frag. 3	123	C	T
148 (Laurentobatrachia)			
28S frag. 2	714	G	C
28S frag. 2	764	A	C
28S frag. 3	306	—	C
H1 frag. 11	392	C	A
H1 frag. 11	868	A	C
H1 frag. 11	1089	A	—
H1 frag. 12	103	A	—
H1 frag. 12	127	T	A
H1 frag. 14	91	T	A
H1 frag. 16	31	A	G
H1 frag. 16	359	C	A
H1 frag. 16	547	C	A
H1 frag. 16	590	A	T
H1 frag. 17	11	A	C
H1 frag. 17	47	C	T
H1 frag. 17	182	T	A
H1 frag. 17	318	—	C
H1 frag. 18	93	T	C
H1 frag. 18	371	T	—
H1 frag. 18	766	C	T
H1 frag. 18	782	A	—
H1 frag. 18	863	G	A
H1 frag. 19	24	G	T
H1 frag. 19	91	C	T
H1 frag. 19	247	C	T
H1 frag. 19	403	C	A
H1 frag. 19	816	G	A
H1 frag. 2	16	A	C
H1 frag. 2	118	C	A
H1 frag. 2	210	A	G
H1 frag. 2	238	C	T
H1 frag. 2	345	—	C
H1 frag. 20	73	A	G
H1 frag. 20	182	C	T
H1 frag. 21	76	C	T
H1 frag. 22	55	T	C
H1 frag. 23	250	A	T
H1 frag. 23	1238	—	G
H1 frag. 23	1359	G	A
H1 frag. 23	1427	A	C
H1 frag. 23	1556	—	A
H1 frag. 3	124	A	T
H1 frag. 3	165	—	A
H1 frag. 4	370	—	A
H1 frag. 4	673	A	C
H1 frag. 6	199	C	A
H1 frag. 7	55	C	T
H1 frag. 8	249	A	—
H1 frag. 8	735	T	A
H1 frag. 9	729	—	A
rhod frag. 2	6	C	G
rhod frag. 2	27	C	T
rhod frag. 2	82	C	G
rhod frag. 2	118	T	C
SIA frag. 3	51	T	C
SIA frag. 3	156	T	A
tyr frag. 1	14	T	G
tyr frag. 1	29	C	G
tyr frag. 2	53	C	T
tyr frag. 3	47	T	A
tyr frag. 3	134	A	G
161 (*Hyperolius*)			
28S frag. 2	567	G	A
H1 frag. 16	401	—	C
H1 frag. 18	24	C	T
H1 frag. 18	254	T	A
H1 frag. 18	509	A	T
H1 frag. 19	54	A	T
H1 frag. 19	178	C	T
H1 frag. 19	331	G	A
H1 frag. 19	396	A	T
H1 frag. 19	651	A	C
H1 frag. 19	729	C	A

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 19	749	T	C
H1 frag. 23	693	A	T
H1 frag. 23	1074	T	A
H1 frag. 23	1221	C	—
H1 frag. 23	1911	—	T
tyr frag. 2	23	C	T
tyr frag. 2	65	C	T
tyr frag. 2	67	C	G
tyr frag. 2	222	T	C
tyr frag. 3	79	C	G
164 (Arthroleptidae)			
28S frag. 2	319	—	G
28S frag. 3	370	G	C
H1 frag. 1	G	A	
H1 frag. 1	30	C	T
H1 frag. 10	54	—	T
H1 frag. 10	101	G	A
H1 frag. 10	266	C	T
H1 frag. 11	12	G	A
H1 frag. 11	89	C	T
H1 frag. 11	910	T	—
H1 frag. 11	927	A	C
H1 frag. 13	168	A	C
H1 frag. 14	65	G	—
H1 frag. 14	129	T	C
H1 frag. 15	54	A	G
H1 frag. 16	127	T	C
H1 frag. 16	614	T	A
H1 frag. 17	31	T	A
H1 frag. 17	429	A	C
H1 frag. 18	52	A	C
H1 frag. 18	95	A	C
H1 frag. 18	388	T	A
H1 frag. 18	503	—	A
H1 frag. 19	119	A	T
H1 frag. 19	338	A	—
H1 frag. 19	560	A	T
H1 frag. 2	15	C	A
H1 frag. 20	60	G	T
H1 frag. 20	180	C	T
H1 frag. 23	17	G	A
H1 frag. 23	693	A	C
H1 frag. 23	1214	T	—
H1 frag. 23	1221	C	A
H1 frag. 3	262	T	C
H1 frag. 3	355	A	G
H1 frag. 3	362	G	A
H1 frag. 4	120	T	A
H1 frag. 4	630	T	A
H1 frag. 7	15	T	C
H1 frag. 8	139	C	T
H1 frag. 8	263	—	A
H1 frag. 8	545	A	T
H1 frag. 9	73	A	C
H1 frag. 9	202	C	A
H1 frag. 9	492	A	C
H3 frag. 1	42	C	T
H3 frag. 1	57	G	C
H3 frag. 1	66	C	T
H3 frag. 1	126	A	C
rhod frag. 2	21	C	T
rhod frag. 2	61	G	A
tyr frag. 1	55	T	C
tyr frag. 2	17	C	T
tyr frag. 2	20	G	A
tyr frag. 2	56	G	A
tyr frag. 2	92	A	G
tyr frag. 2	207	T	A
165 (Leptopelinae)			
28S frag. 2	606	—	C
28S frag. 3	603	A	G
H1 frag. 1	22	G	A
H1 frag. 10	6	C	T
H1 frag. 10	24	G	A
H1 frag. 10	261	C	T
H1 frag. 11	16	A	G
H1 frag. 11	72	C	A
H1 frag. 11	130	A	C
H1 frag. 11	146	C	T
H1 frag. 11	663	A	G

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 11	1226	—	T
H1 frag. 12	6	A	G
H1 frag. 12	7	G	T
H1 frag. 12	12	T	C
H1 frag. 12	84	—	C
H1 frag. 12	186	A	C
H1 frag. 13	18	G	T
H1 frag. 13	91	A	T
H1 frag. 13	130	C	T
H1 frag. 13	156	T	A
H1 frag. 14	28	C	A
H1 frag. 14	60	—	T
H1 frag. 14	143	C	A
H1 frag. 14	238	A	T
H1 frag. 14	250	C	A
H1 frag. 14	260	G	T
H1 frag. 15	42	A	T
H1 frag. 16	141	—	A
H1 frag. 16	170	T	A
H1 frag. 16	333	C	T
H1 frag. 16	450	A	C
H1 frag. 16	648	A	T
H1 frag. 16	691	A	G
H1 frag. 17	5	T	C
H1 frag. 17	12	A	T
H1 frag. 17	296	C	T
H1 frag. 17	372	T	—
H1 frag. 18	164	T	C
H1 frag. 18	306	A	C
H1 frag. 18	530	C	A
H1 frag. 18	648	C	T
H1 frag. 18	673	A	C
H1 frag. 18	717	A	T
H1 frag. 18	825	—	A
H1 frag. 19	14	—	A
H1 frag. 19	54	A	T
H1 frag. 19	66	A	T
H1 frag. 19	172	A	C
H1 frag. 19	318	T	—
H1 frag. 19	439	G	A
H1 frag. 19	826	T	A
H1 frag. 2	44	G	A
H1 frag. 2	176	—	A
H1 frag. 2	207	G	A
H1 frag. 2	237	C	T
H1 frag. 2	240	G	A
H1 frag. 2	425	C	T
H1 frag. 2	437	A	C
H1 frag. 20	23	C	A
H1 frag. 21	76	T	—
H1 frag. 21	113	A	T
H1 frag. 21	243	T	—
H1 frag. 22	37	C	T
H1 frag. 22	47	—	T
H1 frag. 22	55	C	—
H1 frag. 23	2	G	C
H1 frag. 23	52	C	A
H1 frag. 23	100	A	T
H1 frag. 23	182	T	G
H1 frag. 23	1131	G	C
H1 frag. 23	1154	A	T
H1 frag. 23	1181	C	A
H1 frag. 23	1321	A	G
H1 frag. 23	1460	G	T
H1 frag. 23	1554	T	C
H1 frag. 23	1704	C	A
H1 frag. 24	8	C	T
H1 frag. 25	44	A	T
H1 frag. 3	8	A	C
H1 frag. 3	44	A	T
H1 frag. 3	249	A	T
H1 frag. 3	266	C	A
H1 frag. 4	211	A	T
H1 frag. 4	254	T	C
H1 frag. 4	280	C	T
H1 frag. 4	298	A	T
H1 frag. 4	316	C	T
H1 frag. 4	337	C	A
H1 frag. 4	343	G	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 4	346	C	A
H1 frag. 4	349	C	A
H1 frag. 4	351	G	T
H1 frag. 4	577	—	C
H1 frag. 4	637	T	—
H1 frag. 5	9	A	G
H1 frag. 5	33	A	T
H1 frag. 6	25	T	C
H1 frag. 7	42	A	C
H1 frag. 7	97	C	A
H1 frag. 8	69	T	C
H1 frag. 8	177	A	C
H1 frag. 8	181	A	G
H1 frag. 8	298	G	A
H1 frag. 8	488	A	C
H1 frag. 8	544	C	T
H1 frag. 8	550	A	G
H1 frag. 8	694	—	A
H1 frag. 8	716	—	T
H1 frag. 8	735	A	G
H1 frag. 9	67	T	C
H1 frag. 9	126	C	T
168 (Arthroleptinae)			
H1 frag. 11	67	C	A
H1 frag. 11	264	T	C
H1 frag. 11	368	A	C
H1 frag. 11	409	T	—
H1 frag. 11	938	C	A
H1 frag. 11	1191	T	—
H1 frag. 12	113	—	G
H1 frag. 12	116	A	G
H1 frag. 14	93	A	C
H1 frag. 14	208	A	T
H1 frag. 16	94	T	—
H1 frag. 16	382	A	C
H1 frag. 16	436	—	A
H1 frag. 16	629	A	C
H1 frag. 17	182	A	G
H1 frag. 17	383	A	T
H1 frag. 17	424	—	C
H1 frag. 18	155	—	T
H1 frag. 18	628	T	A
H1 frag. 18	720	A	C
H1 frag. 18	866	A	G
H1 frag. 19	3	T	C
H1 frag. 19	449	T	C
H1 frag. 19	485	—	A
H1 frag. 19	531	A	C
H1 frag. 19	715	A	T
H1 frag. 2	328	C	T
H1 frag. 23	25	C	T
H1 frag. 23	59	A	G
H1 frag. 23	216	—	G
H1 frag. 23	602	T	—
H1 frag. 23	997	A	T
H1 frag. 23	1097	G	A
H1 frag. 23	1169	A	C
H1 frag. 23	1518	A	C
H1 frag. 23	1951	A	C
H1 frag. 3	58	C	A
H1 frag. 3	169	T	—
H1 frag. 3	176	T	G
H1 frag. 3	338	C	T
H1 frag. 4	292	T	—
H1 frag. 4	325	A	T
H1 frag. 4	386	T	C
H1 frag. 6	55	T	G
H1 frag. 6	62	A	T
H1 frag. 8	74	A	T
H1 frag. 8	441	A	C
H1 frag. 8	523	A	C
H1 frag. 8	667	A	T
H1 frag. 9	27	A	G
H1 frag. 9	343	A	—
H1 frag. 9	409	A	C
tyr frag. 2	23	C	T
tyr frag. 2	35	C	T
tyr frag. 3	50	T	C
tyr frag. 3	52	A	C

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Br/Taxon/Frag	Pos	Anc	Der
169 (Astylosternini)			
H1 frag. 10	55	T	A
H1 frag. 11	40	G	—
H1 frag. 11	656	—	G
H1 frag. 11	657	—	C
H1 frag. 11	694	T	C
H1 frag. 11	778	A	C
H1 frag. 11	1113	A	C
H1 frag. 11	1311	A	C
H1 frag. 12	148	T	A
H1 frag. 13	159	A	C
H1 frag. 14	64	T	C
H1 frag. 14	72	A	C
H1 frag. 14	214	—	C
H1 frag. 15	50	T	C
H1 frag. 16	333	C	—
H1 frag. 16	590	T	C
H1 frag. 16	626	—	C
H1 frag. 16	660	—	G
H1 frag. 17	11	C	T
H1 frag. 17	251	T	—
H1 frag. 17	350	A	C
H1 frag. 17	407	T	C
H1 frag. 17	435	—	A
H1 frag. 18	816	—	C
H1 frag. 19	24	T	A
H1 frag. 19	217	A	C
H1 frag. 19	364	—	A
H1 frag. 2	65	T	C
H1 frag. 20	129	T	C
H1 frag. 21	133	T	A
H1 frag. 23	299	G	A
H1 frag. 23	785	—	T
H1 frag. 23	1074	T	—
H1 frag. 23	1088	A	C
H1 frag. 23	1124	A	T
H1 frag. 23	1226	T	C
H1 frag. 23	1346	A	C
H1 frag. 23	1750	T	A
H1 frag. 23	1962	T	A
H1 frag. 3	342	T	C
H1 frag. 3	391	A	G
H1 frag. 4	434	A	G
H1 frag. 5	35	A	G
H1 frag. 8	28	A	C
H1 frag. 8	407	C	—
H1 frag. 8	611	A	C
H1 frag. 8	626	A	C
H1 frag. 9	511	A	T
H1 frag. 9	703	—	C
tyr frag. 1	29	G	A
tyr frag. 2	83	C	A
tyr frag. 2	240	C	T
tyr frag. 2	243	C	A
tyr frag. 3	153	A	G
172 (Arthroleptini)			
H1 frag. 10	204	—	C
H1 frag. 11	15	A	T
H1 frag. 11	149	T	C
H1 frag. 11	762	A	C
H1 frag. 11	1327	G	A
H1 frag. 11	1336	T	C
H1 frag. 12	21	A	G
H1 frag. 12	41	A	T
H1 frag. 13	117	C	A
H1 frag. 14	35	A	T
H1 frag. 14	44	T	A
H1 frag. 14	75	—	T
H1 frag. 14	106	A	T
H1 frag. 14	243	G	A
H1 frag. 17	18	A	T
H1 frag. 17	437	C	T
H1 frag. 18	276	A	T
H1 frag. 19	216	C	T
H1 frag. 19	278	C	T
H1 frag. 19	460	A	C
H1 frag. 19	788	A	C
H1 frag. 19	796	G	A
H1 frag. 20	10	T	C
H1 frag. 20	73	G	A

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 23	40	C	T
H1 frag. 23	1338	C	T
H1 frag. 23	1427	C	A
H1 frag. 8	711	G	A
H1 frag. 8	796	C	A
H1 frag. 8	804	A	T
H1 frag. 9	17	A	G
H1 frag. 9	22	A	G
H1 frag. 9	52	T	C
H1 frag. 9	54	T	C
H1 frag. 9	256	C	T
H1 frag. 9	432	T	—
SIA frag. 2	32	C	A
SIA frag. 3	39	C	T
175 (*Arthroleptis*)			
28S frag. 2	790	C	A
28S frag. 3	187	G	C
28S frag. 3	263	—	C
28S frag. 3	264	—	C
H1 frag. 10	54	T	A
H1 frag. 11	368	C	—
H1 frag. 11	505	A	—
H1 frag. 11	536	T	—
H1 frag. 11	1245	A	C
H1 frag. 12	41	T	C
H1 frag. 12	113	G	A
H1 frag. 15	50	T	C
H1 frag. 15	58	A	G
H1 frag. 16	681	T	C
H1 frag. 17	54	C	T
H1 frag. 17	306	A	T
H1 frag. 17	333	T	A
H1 frag. 18	155	T	C
H1 frag. 18	539	A	C
H1 frag. 18	821	T	A
H1 frag. 18	830	A	C
H1 frag. 18	865	A	T
H1 frag. 19	460	C	—
H1 frag. 19	796	A	—
H1 frag. 20	115	T	C
H1 frag. 20	129	T	C
H1 frag. 23	133	G	A
H1 frag. 23	1074	T	C
H1 frag. 23	1303	C	A
H1 frag. 23	1607	A	C
H1 frag. 23	1732	T	A
H1 frag. 23	1992	C	T
H1 frag. 6	59	—	C
H1 frag. 7	24	C	T
H1 frag. 7	40	A	C
H1 frag. 7	43	G	A
H1 frag. 7	78	C	T
H1 frag. 7	95	C	T
H1 frag. 8	28	A	T
H1 frag. 8	41	A	C
H1 frag. 8	710	A	T
H1 frag. 9	14	A	G
H1 frag. 9	57	T	C
H1 frag. 9	79	G	A
H1 frag. 9	85	C	A
H1 frag. 9	90	G	A
tyr frag. 2	19	A	G
tyr frag. 2	41	C	T
tyr frag. 2	126	C	G
tyr frag. 2	219	T	C
tyr frag. 2	273	T	C
tyr frag. 3	61	G	C
tyr frag. 3	70	T	C
tyr frag. 3	114	T	A
tyr frag. 3	134	G	A
180 (Natatanura)			
28S frag. 2	768	C	—
H1 frag. 1	38	C	T
H1 frag. 1	64	A	T
H1 frag. 10	23	T	C
H1 frag. 11	368	A	C
H1 frag. 11	778	A	—
H1 frag. 13	127	A	T
H1 frag. 14	93	A	T
H1 frag. 16	450	A	—

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 16	590	A	C
H1 frag. 17	350	A	T
H1 frag. 18	654	A	T
H1 frag. 18	746	T	C
H1 frag. 18	838	A	T
H1 frag. 18	866	A	G
H1 frag. 19	24	G	A
H1 frag. 19	91	C	T
H1 frag. 19	278	C	A
H1 frag. 19	415	A	T
H1 frag. 19	560	A	T
H1 frag. 19	635	C	—
H1 frag. 2	133	C	A
H1 frag. 2	371	—	C
H1 frag. 2	432	C	T
H1 frag. 2	437	C	T
H1 frag. 2	443	G	A
H1 frag. 20	62	—	G
H1 frag. 20	77	G	—
H1 frag. 23	2	G	C
H1 frag. 23	25	C	T
H1 frag. 23	184	—	C
H1 frag. 23	299	G	C
H1 frag. 23	1108	C	—
H1 frag. 23	1840	T	A
H1 frag. 23	1940	T	—
H1 frag. 3	8	A	C
H1 frag. 3	160	T	A
H1 frag. 4	64	T	—
H1 frag. 4	223	A	C
H1 frag. 4	280	C	—
H1 frag. 4	439	C	A
H1 frag. 6	229	C	A
H1 frag. 7	24	C	—
H1 frag. 8	74	A	T
H1 frag. 8	407	C	T
H1 frag. 8	554	G	A
H1 frag. 8	735	T	G
H1 frag. 9	693	A	C
H3 frag. 1	57	G	C
H3 frag. 1	162	G	C
H3 frag. 1	189	G	C
H3 frag. 2	39	G	A
rhod frag. 2	42	C	G
rhod frag. 2	97	A	C
tyr frag. 1	18	T	C
tyr frag. 1	46	T	G
tyr frag. 2	23	C	T
tyr frag. 2	101	A	G
tyr frag. 2	159	T	C
tyr frag. 2	183	C	T
tyr frag. 2	208	G	T
tyr frag. 2	249	T	G
tyr frag. 3	52	A	G
tyr frag. 3	137	T	G
181 (Ptychadenidae/*Ptychadena*)			
H1 frag. 1	20	A	G
H1 frag. 1	54	T	A
H1 frag. 1	76	C	T
H1 frag. 10	43	A	—
H1 frag. 14	89	T	C
H1 frag. 14	106	A	C
H1 frag. 14	208	A	T
H1 frag. 15	42	A	T
H1 frag. 16	7	A	G
H1 frag. 16	201	T	C
H1 frag. 16	249	T	C
H1 frag. 16	292	A	G
H1 frag. 16	359	C	A
H1 frag. 16	548	—	A
H1 frag. 16	549	—	A
H1 frag. 17	356	—	C
H1 frag. 17	446	C	A
H1 frag. 18	38	T	A
H1 frag. 18	52	A	G
H1 frag. 18	209	A	G
H1 frag. 18	232	C	T
H1 frag. 18	282	—	G
H1 frag. 18	411	A	T
H1 frag. 18	514	A	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 18	530	C	T
H1 frag. 18	563	A	T
H1 frag. 18	727	C	T
H1 frag. 18	766	C	T
H1 frag. 18	863	G	A
H1 frag. 19	148	A	T
H1 frag. 19	197	A	T
H1 frag. 19	201	A	T
H1 frag. 19	213	T	C
H1 frag. 19	461	—	C
H1 frag. 2	118	C	A
H1 frag. 2	140	C	T
H1 frag. 2	215	A	T
H1 frag. 2	277	A	G
H1 frag. 2	389	T	C
H1 frag. 2	420	A	G
H1 frag. 20	68	G	A
H1 frag. 20	146	T	G
H1 frag. 22	72	T	A
H1 frag. 23	265	A	T
H1 frag. 23	883	C	—
H1 frag. 23	983	—	G
H1 frag. 23	997	A	T
H1 frag. 23	1201	G	A
H1 frag. 23	1245	C	T
H1 frag. 23	1346	A	T
H1 frag. 23	1356	A	G
H1 frag. 23	1444	G	A
H1 frag. 23	1555	—	A
H1 frag. 23	1704	C	T
H1 frag. 23	1951	A	C
H1 frag. 23	1977	C	T
H1 frag. 24	5	T	C
H1 frag. 24	16	C	T
H1 frag. 24	33	A	G
H1 frag. 25	16	A	G
H1 frag. 3	41	G	A
H1 frag. 3	129	—	T
H1 frag. 3	138	—	G
H1 frag. 3	142	—	A
H1 frag. 3	170	—	G
H1 frag. 3	190	—	T
H1 frag. 3	193	—	C
H1 frag. 3	194	—	T
H1 frag. 3	195	—	T
H1 frag. 3	200	—	C
H1 frag. 3	206	—	T
H1 frag. 3	207	—	T
H1 frag. 3	226	—	T
H1 frag. 3	227	—	T
H1 frag. 3	241	—	T
H1 frag. 3	243	—	T
H1 frag. 3	249	A	G
H1 frag. 3	258	C	A
H1 frag. 3	291	—	T
H1 frag. 3	292	—	A
H1 frag. 3	293	—	A
H1 frag. 3	294	—	A
H1 frag. 3	295	—	C
H1 frag. 3	298	—	A
H1 frag. 3	306	—	C
H1 frag. 3	343	—	C
H1 frag. 3	344	—	G
H1 frag. 3	346	—	G
H1 frag. 3	347	—	G
H1 frag. 3	348	—	G
H1 frag. 4	13	A	G
H1 frag. 4	214	—	T
H1 frag. 4	335	A	G
H1 frag. 4	338	T	A
H1 frag. 4	447	A	G
H1 frag. 5	20	A	C
H1 frag. 5	29	G	A
H1 frag. 6	12	C	T
H1 frag. 6	49	T	—
H1 frag. 6	104	C	—
H1 frag. 6	137	C	T
H1 frag. 6	163	C	A
H1 frag. 7	11	G	A
H1 frag. 7	54	C	T

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Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 8	47	C	A
H1 frag. 8	148	C	T
H1 frag. 8	300	A	G
H1 frag. 8	352	A	T
H1 frag. 8	488	A	T
H1 frag. 8	557	—	G
H1 frag. 8	568	A	—
H1 frag. 8	569	A	G
H1 frag. 8	714	A	C
H1 frag. 8	752	—	A
H1 frag. 8	818	C	A
H1 frag. 9	71	T	—
H1 frag. 9	202	C	T
H1 frag. 9	227	—	G
H1 frag. 9	258	—	A
H1 frag. 9	383	C	—
H1 frag. 9	432	T	—
H1 frag. 9	618	A	T
H1 frag. 9	739	A	T
H1 frag. 9	798	A	G
rhod frag. 1		C	T
rhod frag. 1	27	G	A
rhod frag. 1	107	C	G
rhod frag. 1	128	C	T
rhod frag. 1	129	C	T
rhod frag. 1	135	C	T
rhod frag. 1	165	C	T
rhod frag. 1	171	C	T
rhod frag. 2	41	C	T
rhod frag. 2	54	C	T
rhod frag. 2	86	A	T
183 (Victoranura)			
28S frag. 2	764	A	—
H1 frag. 11	392	C	A
H1 frag. 11	663	A	T
H1 frag. 12	120	A	C
H1 frag. 13	168	A	C
H1 frag. 17	118	G	A
H1 frag. 17	231	C	T
H1 frag. 17	333	C	A
H1 frag. 18	276	A	T
H1 frag. 18	388	C	T
H1 frag. 19	737	—	C
H1 frag. 2	88	A	—
H1 frag. 2	100	A	T
H1 frag. 2	162	—	A
H1 frag. 2	342	A	—
H1 frag. 21	76	C	T
H1 frag. 23	182	T	C
H1 frag. 23	1376	T	C
H1 frag. 23	1816	A	G
H1 frag. 23	1968	T	C
H1 frag. 4	106	—	C
H1 frag. 4	211	A	—
H1 frag. 4	308	G	A
H1 frag. 6	91	T	C
H1 frag. 8	41	A	C
H1 frag. 8	260	C	—
H1 frag. 8	313	C	T
H1 frag. 8	423	C	—
H1 frag. 9	256	C	T
H1 frag. 9	495	—	T
H1 frag. 9	517	T	A
H1 frag. 9	755	A	C
H3 frag. 1	3	C	T
rhod frag. 2	100	G	C
tyr frag. 1		G	A
tyr frag. 1	28	T	C
tyr frag. 2	258	A	G
tyr frag. 2	276	C	T
tyr frag. 3	98	G	C
184 (Ceratobatrachidae)			
28S frag. 3	134	T	G
H1 frag. 10	269	C	T
H1 frag. 11	7	G	A
H1 frag. 11	16	A	T
H1 frag. 11	505	C	T
H1 frag. 11	852	C	T
H1 frag. 12	128	T	C
H1 frag. 13	91	T	C

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 13	121	A	—
H1 frag. 13	125	A	T
H1 frag. 13	132	G	A
H1 frag. 14	7	T	G
H1 frag. 14	13	T	C
H1 frag. 14	69	—	T
H1 frag. 14	126	A	G
H1 frag. 14	166	C	T
H1 frag. 14	244	G	A
H1 frag. 14	263	T	C
H1 frag. 15	6	A	G
H1 frag. 15	33	A	C
H1 frag. 15	34	G	A
H1 frag. 15	57	T	C
H1 frag. 16	337	—	T
H1 frag. 17	372	T	C
H1 frag. 18	164	T	C
H1 frag. 18	185	T	A
H1 frag. 18	488	T	A
H1 frag. 18	530	C	A
H1 frag. 18	655	—	C
H1 frag. 18	761	T	C
H1 frag. 18	878	T	C
H1 frag. 18	885	A	C
H1 frag. 19	278	A	T
H1 frag. 19	427	T	C
H1 frag. 19	596	C	A
H1 frag. 19	622	A	G
H1 frag. 2	438	T	C
H1 frag. 20	61	A	G
H1 frag. 21	57	A	C
H1 frag. 21	270	G	—
H1 frag. 23	69	T	C
H1 frag. 23	83	A	G
H1 frag. 23	96	A	T
H1 frag. 23	213	A	G
H1 frag. 23	236	A	—
H1 frag. 23	260	C	—
H1 frag. 23	1097	G	A
H1 frag. 23	1131	G	A
H1 frag. 23	1338	C	A
H1 frag. 23	1346	A	C
H1 frag. 23	1364	A	C
H1 frag. 23	1427	A	T
H1 frag. 23	1478	A	—
H1 frag. 23	1743	A	C
H1 frag. 23	1776	A	G
H1 frag. 23	1798	T	C
H1 frag. 23	1840	A	C
H1 frag. 23	1905	T	—
H1 frag. 24	6	T	C
H1 frag. 24	29	A	G
H1 frag. 3	44	A	T
H1 frag. 3	303	C	T
H1 frag. 3	315	—	A
H1 frag. 3	362	G	A
H1 frag. 4	306	A	G
H1 frag. 4	330	T	C
H1 frag. 4	475	—	A
H1 frag. 5	17	A	C
H1 frag. 7	42	A	C
H1 frag. 7	76	T	C
H1 frag. 8	62	T	A
H1 frag. 8	122	A	T
H1 frag. 8	221	—	C
H1 frag. 8	223	—	C
H1 frag. 8	345	G	A
H1 frag. 8	488	A	—
H1 frag. 8	514	C	T
H1 frag. 8	551	A	T
H1 frag. 8	568	A	C
H1 frag. 8	696	A	—
H1 frag. 8	732	—	C
H1 frag. 8	735	G	A
H1 frag. 8	796	C	G
H1 frag. 8	804	A	T
H1 frag. 8	831	G	A
H1 frag. 9	104	C	A
H1 frag. 9	326	—	C
H1 frag. 9	453	A	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 9	467	G	A
H1 frag. 9	522	—	T
H1 frag. 9	618	A	—
rhod frag. 1	3	C	T
rhod frag. 1	9	T	C
rhod frag. 1	161	A	T
rhod frag. 2	42	G	T
rhod frag. 2	61	G	A
SIA frag. 2	20	C	T
SIA frag. 2	71	A	C
SIA frag. 3	109	C	A
SIA frag. 3	123	T	C
SIA frag. 3	126	C	T
SIA frag. 4	52	C	T
SIA frag. 4	55	G	A
tyr frag. 1	52	T	C
tyr frag. 2	26	C	T
tyr frag. 2	66	A	G
tyr frag. 2	67	C	T
tyr frag. 2	80	C	T
tyr frag. 2	285	G	A
tyr frag. 3	13	C	T
tyr frag. 3	14	G	T
tyr frag. 3	53	T	A
tyr frag. 3	56	G	A
tyr frag. 3	67	C	T
189 (Telmatobatrachia)			
H1 frag. 11	598	—	T
H1 frag. 11	600	—	G
H1 frag. 11	1093	—	A
H1 frag. 21	251	T	A
H1 frag. 22	62	A	G
H1 frag. 23	644	—	C
H1 frag. 23	762	C	A
H1 frag. 23	1041	T	A
H1 frag. 23	1233	A	G
H1 frag. 23	1411	—	C
H1 frag. 23	1518	A	C
H1 frag. 23	1657	T	C
H1 frag. 23	1865	A	G
H1 frag. 23	1970	T	—
H1 frag. 6	50	—	A
H1 frag. 8	249	A	T
H1 frag. 9	98	C	T
rhod frag. 2	86	A	C
tyr frag. 3	181	G	T
190 (Micrixalidae)			
H1 frag. 10	159	A	C
H1 frag. 11	16	A	G
H1 frag. 11	27	A	G
H1 frag. 11	36	T	C
H1 frag. 11	67	C	A
H1 frag. 11	79	A	G
H1 frag. 11	112	—	A
H1 frag. 11	113	—	C
H1 frag. 11	138	A	T
H1 frag. 11	312	—	A
H1 frag. 11	910	C	A
H1 frag. 11	1190	—	C
H1 frag. 11	1248	A	T
H1 frag. 11	1316	A	T
H1 frag. 11	1327	T	C
H1 frag. 12	74	T	A
H1 frag. 21	124	A	C
H1 frag. 21	133	A	C
H1 frag. 21	155	T	C
H1 frag. 22	8	T	A
H1 frag. 22	20	T	C
H1 frag. 22	53	C	T
H1 frag. 22	54	T	C
H1 frag. 22	55	T	C
H1 frag. 22	63	G	A
H1 frag. 23	25	T	A
H1 frag. 23	38	T	C
H1 frag. 23	103	A	C
H1 frag. 23	129	C	T
H1 frag. 23	149	A	G
H1 frag. 23	152	A	G
H1 frag. 23	184	C	A
H1 frag. 23	258	—	G

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 23	293	T	A
H1 frag. 23	727	—	C
H1 frag. 23	729	T	A
H1 frag. 23	940	—	A
H1 frag. 23	1014	—	T
H1 frag. 23	1124	A	—
H1 frag. 23	1214	T	C
H1 frag. 23	1288	T	C
H1 frag. 23	1295	T	C
H1 frag. 23	1378	G	A
H1 frag. 23	1676	C	T
H1 frag. 23	1766	C	A
H1 frag. 23	1770	A	G
H1 frag. 23	1802	T	C
H1 frag. 23	1803	G	A
H1 frag. 23	1811	C	T
H1 frag. 23	1977	C	T
H1 frag. 23	1995	G	A
H1 frag. 24	10	A	T
H1 frag. 24	24	G	A
H1 frag. 6	85	T	C
H1 frag. 8	49	—	C
H1 frag. 8	59	T	—
H1 frag. 8	62	T	C
H1 frag. 8	469	T	A
H1 frag. 8	553	A	G
H1 frag. 8	554	A	T
H1 frag. 8	714	A	G
H1 frag. 8	816	T	C
H1 frag. 8	828	T	—
H1 frag. 9	28	A	G
H1 frag. 9	33	T	C
H1 frag. 9	43	A	C
H1 frag. 9	48	T	C
H1 frag. 9	71	T	A
H1 frag. 9	170	—	G
H1 frag. 9	171	—	A
H1 frag. 9	453	A	G
H1 frag. 9	467	G	C
H1 frag. 9	495	T	C
H1 frag. 9	672	T	A
H1 frag. 9	755	C	—
rhod frag. 1	12	C	T
rhod frag. 1	159	G	C
rhod frag. 1	162	T	C
rhod frag. 2	57	C	T
rhod frag. 2	112	C	T
rhod frag. 2	132	A	T
tyr frag. 1	19	C	A
tyr frag. 1	21	T	G
tyr frag. 1	43	C	T
tyr frag. 1	46	G	A
tyr frag. 2	36	T	C
tyr frag. 2	41	T	C
tyr frag. 2	46	G	A
tyr frag. 2	47	C	T
tyr frag. 2	92	A	G
tyr frag. 2	98	C	T
tyr frag. 2	100	C	G
tyr frag. 2	174	G	A
tyr frag. 2	189	C	G
tyr frag. 2	201	T	C
tyr frag. 2	208	T	G
tyr frag. 2	216	C	T
tyr frag. 2	222	T	C
tyr frag. 2	233	A	G
tyr frag. 2	266	A	G
tyr frag. 3	4	G	A
tyr frag. 3	56	G	T
tyr frag. 3	94	C	T
tyr frag. 3	128	T	C
tyr frag. 3	173	T	C
191 (Ametrobatrachia)			
H1 frag. 10	261	C	T
H1 frag. 11	467	—	A
H1 frag. 11	963	—	T
H1 frag. 23	963	A	T
H1 frag. 23	1062	—	T
H1 frag. 23	1077	—	A
H1 frag. 23	1781	C	T

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Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 7	36	—	T
H1 frag. 8	232	A	C
H1 frag. 8	352	A	G
H1 frag. 8	387	—	C
H1 frag. 9	202	C	T
H1 frag. 9	315	A	T
H1 frag. 9	492	A	T
H1 frag. 9	788	A	T
H1 frag. 9	798	A	T
tyr frag. 3	155	A	G
193 (Phrynobatrachidae)			
H1 frag. 1	50	A	G
H1 frag. 1	66	C	T
H1 frag. 10	55	T	A
H1 frag. 10	260	C	A
H1 frag. 11	27	A	G
H1 frag. 11	57	A	—
H1 frag. 11	457	C	T
H1 frag. 11	694	C	—
H1 frag. 11	983	C	A
H1 frag. 11	1045	A	T
H1 frag. 11	1093	A	C
H1 frag. 12	120	C	A
H1 frag. 13	110	—	C
H1 frag. 13	127	T	—
H1 frag. 14	31	T	A
H1 frag. 14	104	T	C
H1 frag. 16	72	G	A
H1 frag. 16	576	A	T
H1 frag. 17	210	A	C
H1 frag. 17	333	A	—
H1 frag. 17	392	—	G
H1 frag. 18	254	T	A
H1 frag. 18	447	T	A
H1 frag. 18	766	C	T
H1 frag. 18	767	C	T
H1 frag. 18	861	G	A
H1 frag. 18	863	G	A
H1 frag. 19	172	A	C
H1 frag. 19	542	A	C
H1 frag. 19	651	T	C
H1 frag. 19	822	A	C
H1 frag. 2	118	C	A
H1 frag. 2	162	A	C
H1 frag. 21	76	T	A
H1 frag. 23	40	T	C
H1 frag. 23	182	C	T
H1 frag. 23	299	C	T
H1 frag. 23	559	C	T
H1 frag. 23	729	T	C
H1 frag. 23	1074	T	A
H1 frag. 23	1097	G	A
H1 frag. 23	1427	A	—
H1 frag. 23	1554	T	—
H1 frag. 3	155	G	—
H1 frag. 3	266	C	A
H1 frag. 3	339	—	C
H1 frag. 4	673	A	C
H1 frag. 6	49	T	A
H1 frag. 6	137	C	—
H1 frag. 6	213	A	C
H1 frag. 8	10	T	C
H1 frag. 8	93	C	—
H1 frag. 8	122	A	C
H1 frag. 8	249	T	—
H1 frag. 8	554	A	G
H1 frag. 8	569	A	G
H1 frag. 8	714	A	—
H1 frag. 8	816	T	—
H1 frag. 8	838	C	T
H1 frag. 9	432	T	A
H1 frag. 9	453	A	T
H1 frag. 9	708	A	C
H1 frag. 9	739	A	G
H3 frag. 1	168	C	A
rhod frag. 1	54	A	G
rhod frag. 1	171	C	T
rhod frag. 2	79	C	T
SIA frag. 3	51	T	C

Br/Taxon/Frag	Pos	Anc	Der
SIA frag. 3	78	G	A
SIA frag. 3	99	G	A
SIA frag. 3	105	A	G
SIA frag. 3	120	G	T
SIA frag. 3	153	A	G
SIA frag. 4	61	T	C
tyr frag. 1	4	A	C
tyr frag. 1	13	C	T
tyr frag. 1	28	C	T
tyr frag. 1	46	G	T
tyr frag. 2	80	C	T
tyr frag. 2	157	A	C
tyr frag. 2	159	C	T
tyr frag. 2	171	C	T
tyr frag. 2	193	C	A
tyr frag. 2	213	C	T
tyr frag. 2	241	T	A
tyr frag. 3	39	A	G
tyr frag. 3	134	A	G
200 (Pyxicephaloidea)			
28S frag. 2	473	T	C
H1 frag. 1	38	T	C
H1 frag. 11	887	A	T
H1 frag. 11	953	C	A
H1 frag. 11	1232	A	C
H1 frag. 16	359	C	T
H1 frag. 17	81	A	—
H1 frag. 18	411	A	T
H1 frag. 18	628	T	C
H1 frag. 18	741	C	A
H1 frag. 19	147	C	T
H1 frag. 20	68	G	A
H1 frag. 23	789	A	T
H1 frag. 23	1346	A	T
H1 frag. 23	1951	A	T
H1 frag. 3	26	T	C
H1 frag. 4	100	T	A
H1 frag. 4	191	C	A
H1 frag. 6	62	A	T
H1 frag. 6	91	C	T
H1 frag. 8	568	A	C
H1 frag. 8	628	A	T
H1 frag. 9	188	—	C
H1 frag. 9	202	T	A
H1 frag. 9	609	C	T
201 (Petropedetidae)			
H1 frag. 1	52	C	T
H1 frag. 11	57	A	T
H1 frag. 11	130	T	C
H1 frag. 11	392	A	C
H1 frag. 11	483	—	T
H1 frag. 12	80	C	A
H1 frag. 13	87	—	A
H1 frag. 13	172	C	A
H1 frag. 16	333	A	C
H1 frag. 16	535	A	C
H1 frag. 17	118	A	T
H1 frag. 18	153	—	T
H1 frag. 18	276	T	A
H1 frag. 18	322	C	T
H1 frag. 18	539	A	C
H1 frag. 23	1427	A	G
H1 frag. 23	1607	A	T
H1 frag. 23	1811	C	T
H1 frag. 3	8	C	A
H1 frag. 3	370	G	A
H1 frag. 3	415	T	C
H1 frag. 4	4	T	C
H1 frag. 4	292	T	A
H1 frag. 4	505	—	A
H1 frag. 8	29	T	C
H1 frag. 9	226	A	T
H1 frag. 9	564	—	C
H3 frag. 2	39	A	C
SIA frag. 3	42	T	A
SIA frag. 3	120	G	A
tyr frag. 1	52	T	A
tyr frag. 2	104	T	C
tyr frag. 2	165	T	C

Br/Taxon/Frag	Pos	Anc	Der
209 (Pyxicephalidae)			
28S frag. 3	424	G	C
H1 frag. 10	52	T	A
H1 frag. 10	101	G	A
H1 frag. 11	89	C	T
H1 frag. 11	264	C	T
H1 frag. 13	127	T	A
H1 frag. 14	85	C	A
H1 frag. 14	142	T	C
H1 frag. 15	25	A	G
H1 frag. 16	513	—	T
H1 frag. 17	388	—	G
H1 frag. 17	437	C	T
H1 frag. 18	260	—	C
H1 frag. 19	369	T	—
H1 frag. 19	771	C	T
H1 frag. 2	162	A	T
H1 frag. 21	133	A	C
H1 frag. 23	152	A	G
H1 frag. 23	644	C	A
H1 frag. 23	1088	G	C
H1 frag. 23	1288	T	C
H1 frag. 23	1776	A	T
H1 frag. 3	209	—	T
H1 frag. 3	313	—	A
H1 frag. 3	342	T	C
H1 frag. 6	26	A	T
H1 frag. 8	272	A	—
H3 frag. 1	193	C	A
rhod frag. 1	21	T	C
rhod frag. 1	104	C	T
rhod frag. 1	165	C	G
tyr frag. 2	64	A	T
tyr frag. 2	67	C	G
tyr frag. 2	97	A	T
tyr frag. 3	51	G	A
tyr frag. 3	120	C	T
210 (Pyxicephalinae)			
H1 frag. 1	20	A	G
H1 frag. 11	67	C	—
H1 frag. 11	141	A	T
H1 frag. 11	467	A	—
H1 frag. 11	983	C	—
H1 frag. 11	1327	T	A
H1 frag. 12	153	T	A
H1 frag. 13	69	C	A
H1 frag. 13	117	C	T
H1 frag. 14	72	A	—
H1 frag. 14	78	A	—
H1 frag. 14	149	A	G
H1 frag. 14	217	T	A
H1 frag. 15	5	G	T
H1 frag. 15	19	T	C
H1 frag. 15	23	C	A
H1 frag. 16	2	T	C
H1 frag. 16	221	C	T
H1 frag. 16	266	T	G
H1 frag. 16	292	A	C
H1 frag. 16	563	A	C
H1 frag. 17	231	T	A
H1 frag. 17	274	A	T
H1 frag. 17	372	T	A
H1 frag. 18	164	T	C
H1 frag. 18	254	T	C
H1 frag. 18	349	T	—
H1 frag. 18	411	T	C
H1 frag. 18	870	C	T
H1 frag. 19	42	T	C
H1 frag. 19	160	A	T
H1 frag. 19	175	A	C
H1 frag. 19	213	T	A
H1 frag. 19	216	T	A
H1 frag. 19	278	A	C
H1 frag. 19	496	A	T
H1 frag. 20	176	A	G
H1 frag. 21	57	A	C
H1 frag. 23	22	T	C
H1 frag. 23	140	T	C
H1 frag. 23	224	C	G
H1 frag. 23	299	C	—

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 23	623	A	C
H1 frag. 23	729	T	C
H1 frag. 23	883	C	—
H1 frag. 23	1077	A	T
H1 frag. 23	1097	G	A
H1 frag. 23	1154	C	T
H1 frag. 23	1181	C	A
H1 frag. 23	1214	T	C
H1 frag. 23	1334	T	C
H1 frag. 23	1376	C	T
H1 frag. 23	1386	A	T
H1 frag. 23	1554	T	—
H1 frag. 23	1569	A	—
H1 frag. 23	1722	G	A
H1 frag. 23	1798	T	A
H1 frag. 23	1803	G	—
H1 frag. 23	1816	G	A
H1 frag. 23	1824	T	C
H1 frag. 24	17	C	T
H1 frag. 24	19	C	A
H1 frag. 3	58	T	A
H1 frag. 3	262	C	T
H1 frag. 3	268	C	T
H1 frag. 3	362	G	A
H1 frag. 3	391	A	G
H1 frag. 4	13	A	G
H1 frag. 4	137	—	A
H1 frag. 4	325	T	C
H1 frag. 4	383	—	C
H1 frag. 4	404	T	A
H1 frag. 4	414	A	—
H1 frag. 4	452	A	C
H1 frag. 4	585	—	C
H1 frag. 4	649	A	C
H1 frag. 4	673	A	C
H1 frag. 5	3	C	A
H1 frag. 6	34	G	A
H1 frag. 6	167	T	C
H3 frag. 1	6	G	A
H3 frag. 1	45	C	T
H3 frag. 1	57	C	T
H3 frag. 1	99	C	T
H3 frag. 1	189	C	G
H3 frag. 2	42	C	G
rhod frag. 1	9	T	C
rhod frag. 1	36	A	G
rhod frag. 1	125	C	T
rhod frag. 2	21	C	T
rhod frag. 2	28	C	T
rhod frag. 2	33	G	A
rhod frag. 2	112	C	T
SIA frag. 3	82	G	A
SIA frag. 3	102	C	T
SIA frag. 3	153	A	G
SIA frag. 4	22	A	T
SIA frag. 4	55	G	A
tyr frag. 1	4	A	C
tyr frag. 1	18	C	T
tyr frag. 1	28	C	T
tyr frag. 1	29	A	G
tyr frag. 1	46	G	T
tyr frag. 1	55	C	T
tyr frag. 2	20	G	A
tyr frag. 2	47	C	T
tyr frag. 2	83	C	T
tyr frag. 2	144	G	A
tyr frag. 2	153	G	A
tyr frag. 2	159	C	T
tyr frag. 2	194	C	A
tyr frag. 2	213	C	T
tyr frag. 2	234	C	T
tyr frag. 2	237	C	T
tyr frag. 3	31	C	T
tyr frag. 3	70	T	A
tyr frag. 3	167	C	T
212 (Cacosterninae)			
28S frag. 2	315	—	G
28S frag. 2	496	—	T
28S frag. 2	613	C	G
28S frag. 2	724	—	C

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Br/Taxon/Frag	Pos	Anc	Der
28S frag. 2	727	—	C
28S frag. 2	729	—	A
H1 frag. 1	50	A	G
H1 frag. 1	70	A	G
H1 frag. 11	762	A	—
H1 frag. 11	819	C	T
H1 frag. 12	21	A	G
H1 frag. 16	301	—	T
H1 frag. 18	116	A	C
H1 frag. 18	488	T	A
H1 frag. 18	604	A	C
H1 frag. 18	648	C	A
H1 frag. 19	145	A	T
H1 frag. 19	148	T	G
H1 frag. 19	406	—	T
H1 frag. 19	695	A	T
H1 frag. 2	171	C	T
H1 frag. 2	312	—	T
H1 frag. 2	407	T	A
H1 frag. 21	190	A	G
H1 frag. 23	25	T	C
H1 frag. 23	182	C	T
H1 frag. 23	602	T	A
H1 frag. 23	1245	C	T
H1 frag. 23	1732	T	C
H1 frag. 23	1743	A	G
H1 frag. 3	8	C	T
H1 frag. 3	47	C	T
H1 frag. 4	283	C	T
H1 frag. 4	343	A	G
H1 frag. 6	213	A	C
H1 frag. 7	13	A	T
H1 frag. 7	39	C	T
H1 frag. 8	69	C	T
H1 frag. 8	122	A	C
H1 frag. 8	313	T	C
H1 frag. 8	628	T	G
H1 frag. 9	73	C	A
H1 frag. 9	212	—	G
H1 frag. 9	226	A	C
H1 frag. 9	716	—	G
H1 frag. 9	739	A	G
rhod frag. 1	78	G	A
rhod frag. 1	85	A	C
rhod frag. 1	131	C	T
rhod frag. 2	147	T	G
SIA frag. 1	12	A	G
SIA frag. 2	14	A	G
tyr frag. 1	75	T	C
tyr frag. 2	66	A	G
tyr frag. 2	68	T	C
tyr frag. 2	183	T	C
218 (*Amietia*)			
H1 frag. 1	70	G	A
H1 frag. 11	642	—	C
H1 frag. 11	819	T	C
H1 frag. 11	963	T	C
H1 frag. 14	144	A	G
H1 frag. 15	42	A	T
H1 frag. 16	359	T	C
H1 frag. 16	614	T	A
H1 frag. 17	167	—	T
H1 frag. 18	260	C	A
H1 frag. 18	411	T	C
H1 frag. 18	488	A	T
H1 frag. 18	891	T	A
H1 frag. 19	201	A	G
H1 frag. 19	449	T	C
H1 frag. 2	215	C	—
H1 frag. 21	133	C	G
H1 frag. 23	114	A	T
H1 frag. 23	294	—	C
H1 frag. 23	559	C	T
H1 frag. 23	1464	—	T
H1 frag. 23	1828	A	T
H1 frag. 24	10	A	T
H1 frag. 3	20	T	C
H1 frag. 3	51	G	A
H1 frag. 3	126	C	T
H1 frag. 4	298	A	G

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 4	649	A	G
H1 frag. 5	7	T	C
H1 frag. 7	96	A	C
H1 frag. 8	511	A	G
tyr frag. 2	183	C	T
tyr frag. 3	2	C	A
220 (Saukrobatrachia)			
H1 frag. 11	663	T	A
H1 frag. 11	1161	A	C
H1 frag. 16	313	C	T
H1 frag. 18	254	T	—
H1 frag. 18	411	A	C
H1 frag. 18	877	T	C
H1 frag. 19	560	T	A
H1 frag. 19	749	C	A
H1 frag. 2	210	A	G
H1 frag. 2	328	C	A
H1 frag. 2	437	T	C
H1 frag. 23	452	C	T
H1 frag. 23	1181	C	A
H1 frag. 23	1245	C	T
H1 frag. 23	1358	C	T
H1 frag. 3	214	T	G
H1 frag. 4	223	C	A
H1 frag. 4	306	A	C
H1 frag. 8	211	—	A
H1 frag. 8	711	G	T
H1 frag. 9	228	—	G
H1 frag. 9	383	C	—
H1 frag. 9	672	T	C
H3 frag. 1	114	T	C
H3 frag. 2	33	G	C
H3 frag. 2	60	G	C
221 (Dicroglossidae)			
H1 frag. 10	14	T	C
H1 frag. 10	19	A	G
H1 frag. 11	320	—	T
H1 frag. 11	409	T	A
H1 frag. 11	983	C	T
H1 frag. 12	103	A	T
H1 frag. 13	172	C	A
H1 frag. 14	25	—	C
H1 frag. 14	63	A	G
H1 frag. 14	89	T	C
H1 frag. 16	382	A	T
H1 frag. 17	210	A	C
H1 frag. 17	407	T	—
H1 frag. 18	116	A	T
H1 frag. 18	490	—	C
H1 frag. 18	868	A	C
H1 frag. 19	449	T	C
H1 frag. 19	729	C	—
H1 frag. 21	251	A	T
H1 frag. 21	270	G	A
H1 frag. 23	1060	C	A
H1 frag. 23	1169	C	T
H1 frag. 23	1427	A	G
H1 frag. 23	1518	C	—
H1 frag. 25	53	C	T
H1 frag. 25	69	G	A
H1 frag. 7	40	A	—
H1 frag. 8	116	T	A
H1 frag. 9	343	A	T
H1 frag. 9	521	—	C
H1 frag. 9	693	C	A
rhod frag. 1	10	A	G
rhod frag. 1	72	G	A
rhod frag. 2	57	C	T
SIA frag. 3	120	G	A
SIA frag. 3	156	T	A
tyr frag. 1	85	C	T
tyr frag. 3	53	T	C
tyr frag. 3	167	C	T
222 (Occidozyginae)			
H1 frag. 10	55	T	C
H1 frag. 10	205	—	A
H1 frag. 11	57	A	T
H1 frag. 11	92	T	C
H1 frag. 11	392	A	—
H1 frag. 11	595	A	—

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 11	622	A	T
H1 frag. 11	1035	—	C
H1 frag. 12	52	C	A
H1 frag. 12	143	A	C
H1 frag. 13	8	G	T
H1 frag. 13	130	C	T
H1 frag. 14	13	T	A
H1 frag. 14	127	A	G
H1 frag. 14	208	A	T
H1 frag. 15	34	G	A
H1 frag. 15	56	T	C
H1 frag. 16	94	T	C
H1 frag. 16	305	—	C
H1 frag. 16	658	A	G
H1 frag. 22	6	G	T
H1 frag. 22	8	T	G
H1 frag. 22	17	C	G
H1 frag. 22	20	T	C
H1 frag. 23	67	G	A
H1 frag. 23	81	G	A
H1 frag. 23	1041	A	T
H1 frag. 23	1221	C	T
H1 frag. 23	1811	C	T
H1 frag. 23	1825	A	T
H1 frag. 23	1919	A	T
H1 frag. 24	19	C	A
rhod frag. 1	78	G	A
rhod frag. 1	134	G	C
rhod frag. 2	80	G	A
SIA frag. 3	9	T	C
SIA frag. 3	42	T	C
SIA frag. 3	54	T	C
SIA frag. 3	138	T	C
SIA frag. 3	160	C	T
SIA frag. 4	76	T	C
SIA frag. 4	79	T	G
225 (Dicroglossinae)			
H1 frag. 11	53	T	G
H1 frag. 12	80	C	A
H1 frag. 13	16	A	T
H1 frag. 13	43	—	G
H1 frag. 13	55	A	C
H1 frag. 14	6	C	T
H1 frag. 14	90	T	A
H1 frag. 14	177	C	T
H1 frag. 15	15	A	T
H1 frag. 17	333	A	C
H1 frag. 18	138	A	T
H1 frag. 18	550	A	C
H1 frag. 18	886	G	A
H1 frag. 19	42	A	T
H1 frag. 19	212	C	T
H1 frag. 19	757	—	C
H1 frag. 21	277	C	A
H1 frag. 22	15	A	G
H1 frag. 23	293	T	—
H1 frag. 23	623	A	C
H1 frag. 23	1154	A	G
H1 frag. 23	1183	—	C
H1 frag. 23	1569	A	T
H1 frag. 23	1732	T	C
H1 frag. 23	1846	C	T
H1 frag. 6	213	A	—
H1 frag. 7	13	A	T
H1 frag. 8	47	C	A
H1 frag. 8	306	C	T
H1 frag. 8	553	A	G
H1 frag. 8	568	A	C
H1 frag. 9	432	T	C
H1 frag. 9	545	C	—
SIA frag. 3	3	G	A
SIA frag. 3	141	T	C
tyr frag. 2	31	T	C
tyr frag. 3	98	C	T
226 (Limnonectini)			
H1 frag. 1	64	T	C
H1 frag. 10	101	G	A
H1 frag. 11	89	C	T
H1 frag. 11	146	C	T
H1 frag. 11	320	T	A

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 11	1316	A	T
H1 frag. 11	1327	T	G
H1 frag. 12	136	—	C
H1 frag. 12	148	T	—
H1 frag. 12	153	A	C
H1 frag. 12	187	G	A
H1 frag. 13	125	A	T
H1 frag. 14	93	T	C
H1 frag. 16	382	T	C
H1 frag. 16	585	—	C
H1 frag. 17	47	T	A
H1 frag. 18	110	—	C
H1 frag. 18	322	C	A
H1 frag. 18	488	T	A
H1 frag. 18	530	C	A
H1 frag. 18	717	C	T
H1 frag. 18	767	C	T
H1 frag. 18	861	G	A
H1 frag. 19	771	C	T
H1 frag. 2	360	T	C
H1 frag. 20	73	A	G
H1 frag. 22	23	G	A
H1 frag. 23	38	T	C
H1 frag. 23	52	C	T
H1 frag. 23	69	T	C
H1 frag. 23	83	A	G
H1 frag. 23	113	T	C
H1 frag. 23	224	C	T
H1 frag. 23	602	T	A
H1 frag. 23	896	—	A
H1 frag. 23	1233	G	A
H1 frag. 23	1478	A	C
H1 frag. 23	1882	A	G
H1 frag. 23	1962	T	C
H1 frag. 3	22	A	C
H1 frag. 3	150	A	T
H1 frag. 3	160	A	G
H1 frag. 3	252	C	T
H1 frag. 3	342	T	C
H1 frag. 3	361	G	A
H1 frag. 3	365	T	C
H1 frag. 4	673	A	C
H1 frag. 5	6	C	T
H1 frag. 6	25	T	C
H1 frag. 6	27	G	A
H1 frag. 8	29	T	C
H1 frag. 8	37	C	A
H1 frag. 8	52	A	C
H1 frag. 8	69	C	T
H1 frag. 8	556	T	G
H1 frag. 8	667	A	T
H1 frag. 8	816	T	A
H1 frag. 9	42	G	A
H1 frag. 9	71	T	A
H1 frag. 9	460	—	T
H3 frag. 2	33	C	G
H3 frag. 2	36	A	C
H3 frag. 2	42	C	G
H3 frag. 2	60	C	G
rhod frag. 1	142	A	G
rhod frag. 2	91	C	T
SIA frag. 1	42	G	A
SIA frag. 3	48	G	A
SIA frag. 3	78	G	A
SIA frag. 3	108	C	T
SIA frag. 3	168	A	C
SIA frag. 4	31	G	A
tyr frag. 1	4	A	C
tyr frag. 1	11	A	G
tyr frag. 1	44	T	A
tyr frag. 1	73	C	T
tyr frag. 2	87	A	C
tyr frag. 2	100	C	T
tyr frag. 2	124	T	C
tyr frag. 2	285	G	T
tyr frag. 3	64	A	C
tyr frag. 3	88	T	G
tyr frag. 3	115	C	T
tyr frag. 3	128	T	C

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Br/Taxon/Frag	Pos	Anc	Der
228 (unnamed taxon)			
H1 frag. 10	55	T	A
H1 frag. 10	217	T	C
H1 frag. 11	561	—	T
H1 frag. 11	1093	A	C
H1 frag. 12	127	T	A
H1 frag. 13	82	T	C
H1 frag. 13	172	A	C
H1 frag. 14	127	A	G
H1 frag. 14	128	G	A
H1 frag. 16	39	T	C
H1 frag. 16	672	A	G
H1 frag. 17	26	A	G
H1 frag. 17	38	A	T
H1 frag. 18	322	A	T
H1 frag. 18	514	A	C
H1 frag. 18	746	C	T
H1 frag. 19	695	A	C
H1 frag. 2	218	T	C
H1 frag. 2	371	C	T
H1 frag. 22	43	C	T
H1 frag. 22	62	G	A
H1 frag. 23	559	C	—
H1 frag. 23	1077	A	T
H1 frag. 23	1338	C	A
H1 frag. 23	1478	C	T
H1 frag. 23	1834	A	C
H1 frag. 3	214	G	A
H1 frag. 4	100	T	C
H1 frag. 7	39	C	T
H1 frag. 8	816	A	C
H1 frag. 9	281	A	T
H1 frag. 9	609	C	T
H1 frag. 9	618	A	T
H1 frag. 9	693	A	T
232 (Dicroglossini)			
H1 frag. 11	409	T	G
H1 frag. 11	513	—	A
H1 frag. 11	598	T	C
H1 frag. 11	606	—	C
H1 frag. 11	831	—	C
H1 frag. 11	983	T	C
H1 frag. 11	1146	—	A
H1 frag. 12	21	A	G
H1 frag. 12	52	A	C
H1 frag. 21	133	C	A
H1 frag. 23	2	C	G
H1 frag. 23	644	C	T
H1 frag. 23	981	C	T
H1 frag. 23	1411	C	T
H1 frag. 6	22	C	T
H1 frag. 8	233	A	T
H1 frag. 8	281	T	—
H1 frag. 8	298	T	—
H1 frag. 9	43	T	C
H1 frag. 9	54	C	T
H1 frag. 9	202	A	C
H1 frag. 9	367	A	T
H1 frag. 9	798	G	A
rhod frag. 2	139	T	C
tyr frag. 1	4	A	G
tyr frag. 1	67	C	T
tyr frag. 2	84	G	A
tyr frag. 2	261	T	C
tyr frag. 3	119	T	C
214 (Aglaioanura)			
H1 frag. 11	457	C	T
H1 frag. 11	762	A	C
H1 frag. 12	4	A	G
H1 frag. 12	14	T	C
H1 frag. 14	208	A	C
H1 frag. 14	217	T	A
H1 frag. 16	535	A	T
H1 frag. 17	333	A	T
H1 frag. 18	143	—	C
H1 frag. 18	371	A	—
H1 frag. 2	118	C	T
H1 frag. 2	162	A	T
H1 frag. 2	238	C	T
H1 frag. 20	68	G	A

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 23	644	C	T
H1 frag. 24	5	T	C
H1 frag. 24	33	A	G
H1 frag. 4	94	A	T
H1 frag. 4	169	C	A
H1 frag. 4	561	—	T
H1 frag. 6	49	T	A
H1 frag. 8	122	A	T
H1 frag. 8	369	T	—
H1 frag. 8	488	A	C
H1 frag. 8	735	G	A
H1 frag. 9	233	—	C
H1 frag. 9	533	A	C
H1 frag. 9	708	A	G
H3 frag. 1	15	C	A
H3 frag. 2	18	A	T
H3 frag. 2	19	G	C
245 (Rhacophoroidea)			
H1 frag. 11	467	A	T
H1 frag. 11	1139	—	T
H1 frag. 13	35	—	A
H1 frag. 16	127	T	C
H1 frag. 16	313	T	A
H1 frag. 16	429	C	A
H1 frag. 16	509	A	C
H1 frag. 18	322	C	T
H1 frag. 18	563	A	T
H1 frag. 18	830	A	C
H1 frag. 18	838	T	C
H1 frag. 23	452	T	A
H1 frag. 23	623	A	—
H1 frag. 23	1015	A	T
H1 frag. 23	1776	A	G
H1 frag. 3	108	A	T
H1 frag. 3	124	C	A
H1 frag. 3	331	—	T
H1 frag. 4	120	T	A
H1 frag. 4	191	C	T
H1 frag. 4	404	T	C
H1 frag. 4	408	A	T
H1 frag. 4	439	A	T
H1 frag. 8	201	—	T
H1 frag. 8	249	T	A
H1 frag. 8	568	A	C
H1 frag. 9	104	C	A
H3 frag. 1	168	C	A
H3 frag. 1	184	C	A
H3 frag. 1	186	C	A
tyr frag. 1	29	A	G
tyr frag. 2	53	C	T
tyr frag. 2	98	C	A
tyr frag. 2	198	C	T
tyr frag. 3	32	T	G
tyr frag. 3	98	C	T
246 (Mantellidae)			
H1 frag. 11	602	—	T
H1 frag. 12	80	C	A
H1 frag. 13	40	—	C
H1 frag. 14	72	A	—
H1 frag. 16	2	T	C
H1 frag. 16	170	T	C
H1 frag. 16	221	C	A
H1 frag. 16	547	C	T
H1 frag. 18	144	—	A
H1 frag. 18	752	A	G
H1 frag. 18	758	G	A
H1 frag. 18	761	T	C
H1 frag. 18	870	C	T
H1 frag. 18	877	C	T
H1 frag. 19	54	T	A
H1 frag. 19	148	A	T
H1 frag. 19	154	A	G
H1 frag. 19	164	A	C
H1 frag. 19	181	G	A
H1 frag. 19	209	C	T
H1 frag. 19	216	T	C
H1 frag. 2	20	C	A
H1 frag. 2	90	—	A
H1 frag. 2	362	—	A
H1 frag. 20	23	C	A

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 21	57	A	C
H1 frag. 21	90	A	T
H1 frag. 22	61	A	G
H1 frag. 23	105	A	T
H1 frag. 23	963	T	A
H1 frag. 23	1181	A	C
H1 frag. 23	1233	G	C
H1 frag. 23	1386	A	—
H1 frag. 23	1743	A	C
H1 frag. 23	1816	G	A
H1 frag. 23	1846	C	T
H1 frag. 25	34	C	A
H1 frag. 4	223	A	T
H1 frag. 4	592	T	C
H1 frag. 7	54	C	T
H1 frag. 8	544	T	C
H1 frag. 9	392	—	C
H1 frag. 9	493	—	A
H3 frag. 1	78	C	A
rhod frag. 1	104	C	T
rhod frag. 1	144	C	T
rhod frag. 2	80	G	A
rhod frag. 2	134	C	G
tyr frag. 1	28	C	T
tyr frag. 1	40	T	A
tyr frag. 1	55	T	C
tyr frag. 2	100	C	T
247 (Boophinae/*Boophis*)			
H1 frag. 1	36	A	G
H1 frag. 1	48	A	T
H1 frag. 10	261	T	C
H1 frag. 11	134	A	T
H1 frag. 11	317	—	C
H1 frag. 11	887	A	T
H1 frag. 11	1071	C	T
H1 frag. 13	82	T	C
H1 frag. 13	126	A	G
H1 frag. 14	193	T	—
H1 frag. 15	40	C	T
H1 frag. 16	36	T	C
H1 frag. 16	94	T	C
H1 frag. 16	361	—	A
H1 frag. 16	676	A	G
H1 frag. 17	38	A	G
H1 frag. 18	93	T	C
H1 frag. 18	185	T	C
H1 frag. 18	283	—	A
H1 frag. 18	868	A	C
H1 frag. 19	531	A	T
H1 frag. 19	542	A	T
H1 frag. 2	16	A	C
H1 frag. 2	118	T	C
H1 frag. 2	241	C	T
H1 frag. 20	66	A	G
H1 frag. 20	68	A	G
H1 frag. 20	73	A	G
H1 frag. 20	151	A	G
H1 frag. 20	180	C	T
H1 frag. 23	21	G	A
H1 frag. 23	23	T	C
H1 frag. 23	38	T	C
H1 frag. 23	40	T	C
H1 frag. 23	43	T	C
H1 frag. 23	52	C	T
H1 frag. 23	224	C	T
H1 frag. 23	293	T	C
H1 frag. 23	764	—	T
H1 frag. 23	1041	A	T
H1 frag. 23	1062	T	G
H1 frag. 23	1124	A	G
H1 frag. 23	1226	T	A
H1 frag. 23	1722	G	A
H1 frag. 23	1811	C	T
H1 frag. 23	1828	A	T
H1 frag. 23	1951	A	T
H1 frag. 3	58	T	A
H1 frag. 3	372	T	A
H1 frag. 3	402	T	C
H1 frag. 4	215	—	A
H1 frag. 4	271	T	C

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 4	292	T	A
H1 frag. 4	325	T	A
H1 frag. 4	365	T	C
H1 frag. 4	434	A	G
H1 frag. 4	458	A	C
H1 frag. 7	11	G	A
H1 frag. 8	94	—	T
H1 frag. 8	174	A	G
H1 frag. 8	201	T	A
H1 frag. 8	249	A	C
H1 frag. 8	294	T	C
H1 frag. 8	300	G	A
H1 frag. 8	313	T	C
H1 frag. 8	545	T	C
H1 frag. 8	726	T	C
H1 frag. 8	788	—	T
H1 frag. 8	804	A	G
H1 frag. 8	838	C	T
H1 frag. 9	42	G	T
H1 frag. 9	54	T	C
H1 frag. 9	67	C	T
H1 frag. 9	506	A	—
H3 frag. 1	81	A	G
H3 frag. 1	126	A	G
H3 frag. 1	195	C	A
H3 frag. 1	243	T	C
H3 frag. 2	5	T	G
H3 frag. 2	18	T	G
rhod frag. 1	165	C	T
248 (Mantellinae)			
H1 frag. 11	315	A	T
H1 frag. 11	368	C	T
H1 frag. 11	422	—	A
H1 frag. 11	457	T	C
H1 frag. 11	983	C	—
H1 frag. 11	1135	C	—
H1 frag. 12	9	C	A
H1 frag. 13	156	T	A
H1 frag. 14	144	A	G
H1 frag. 14	208	C	T
H1 frag. 15	22	T	C
H1 frag. 18	145	—	T
H1 frag. 18	411	C	—
H1 frag. 18	530	C	A
H1 frag. 18	654	T	A
H1 frag. 19	42	A	T
H1 frag. 19	449	T	C
H1 frag. 2	240	G	A
H1 frag. 2	425	C	T
H1 frag. 23	420	—	T
H1 frag. 23	710	—	T
H1 frag. 23	789	A	T
H1 frag. 23	1334	A	C
H1 frag. 23	1704	C	T
H1 frag. 4	106	C	—
H1 frag. 4	149	—	A
H1 frag. 5	10	—	G
H1 frag. 5	16	A	T
H1 frag. 7	36	T	G
H1 frag. 8	33	C	T
H1 frag. 8	387	C	A
H1 frag. 8	425	—	C
H1 frag. 9	71	T	A
H3 frag. 1	18	G	C
H3 frag. 1	117	G	C
H3 frag. 1	204	C	A
H3 frag. 2	20	C	A
tyr frag. 1	21	T	C
249 (Laliostomini)			
28S frag. 2	714	G	C
H1 frag. 10	159	A	G
H1 frag. 11	23	T	C
H1 frag. 11	79	A	G
H1 frag. 11	1217	A	C
H1 frag. 13	127	T	A
H1 frag. 14	89	T	C
H1 frag. 14	177	C	T
H1 frag. 16	1	A	G
H1 frag. 16	201	T	C
H1 frag. 16	566	—	T

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Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 17	33	A	T
H1 frag. 17	103	A	T
H1 frag. 17	306	A	C
H1 frag. 18	125	—	G
H1 frag. 18	126	—	T
H1 frag. 18	209	A	G
H1 frag. 18	322	T	—
H1 frag. 18	494	C	T
H1 frag. 18	581	C	A
H1 frag. 18	717	C	T
H1 frag. 19	83	C	A
H1 frag. 19	181	A	T
H1 frag. 19	278	A	T
H1 frag. 19	286	A	C
H1 frag. 19	424	A	G
H1 frag. 19	749	A	C
H1 frag. 19	771	C	T
H1 frag. 2	171	C	A
H1 frag. 2	360	T	C
H1 frag. 21	260	A	T
H1 frag. 23	1427	A	T
H1 frag. 23	1478	A	G
H1 frag. 23	1919	A	T
H1 frag. 3	26	T	C
H1 frag. 4	316	C	T
H1 frag. 4	373	G	A
H1 frag. 6	25	T	C
H1 frag. 8	177	A	G
H1 frag. 8	211	A	C
H1 frag. 8	441	A	T
H1 frag. 8	469	C	A
H1 frag. 8	696	A	G
H1 frag. 9	84	C	T
H1 frag. 9	229	—	T
H1 frag. 9	546	—	T
H1 frag. 9	609	C	—
H1 frag. 9	739	A	G
tyr frag. 2	273	C	T
tyr frag. 3	155	G	A
253 (Rhacophoridae)			
H1 frag. 10	52	T	A
H1 frag. 11	663	A	C
H1 frag. 11	694	C	A
H1 frag. 11	819	C	T
H1 frag. 11	1093	A	—
H1 frag. 13	163	A	T
H1 frag. 15	34	G	A
H1 frag. 16	31	A	G
H1 frag. 16	72	G	A
H1 frag. 16	242	—	T
H1 frag. 16	333	A	T
H1 frag. 16	590	C	—
H1 frag. 16	665	C	T
H1 frag. 17	306	A	T
H1 frag. 18	52	A	T
H1 frag. 18	232	C	T
H1 frag. 18	306	A	T
H1 frag. 18	349	C	A
H1 frag. 18	457	—	A
H1 frag. 18	604	A	T
H1 frag. 18	615	C	T
H1 frag. 18	650	—	A
H1 frag. 18	732	C	T
H1 frag. 18	878	T	C
H1 frag. 19	24	A	T
H1 frag. 19	271	T	A
H1 frag. 19	356	C	T
H1 frag. 19	796	A	T
H1 frag. 19	826	T	A
H1 frag. 2	140	C	A
H1 frag. 2	154	T	C
H1 frag. 2	191	—	T
H1 frag. 2	196	C	A
H1 frag. 2	218	T	A
H1 frag. 23	163	C	—
H1 frag. 23	199	A	T
H1 frag. 23	250	A	G
H1 frag. 23	521	T	A
H1 frag. 23	1214	T	C
H1 frag. 23	1256	T	C

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 23	1342	A	T
H1 frag. 23	1676	C	T
H1 frag. 4	100	T	A
H1 frag. 4	306	C	A
H1 frag. 5	9	A	T
H1 frag. 5	28	G	A
H1 frag. 6	25	T	A
H1 frag. 6	213	A	C
H1 frag. 8	47	C	A
H1 frag. 9	27	A	G
H1 frag. 9	46	T	A
H1 frag. 9	49	T	C
H1 frag. 9	59	T	A
H1 frag. 9	73	A	T
H1 frag. 9	256	T	C
H1 frag. 9	281	A	C
H1 frag. 9	498	—	C
254 (Rhacophorinae)			
H1 frag. 11	600	G	—
H1 frag. 11	963	T	C
H1 frag. 11	1056	—	T
H1 frag. 11	1113	A	T
H1 frag. 11	1217	A	—
H1 frag. 11	1324	A	T
H1 frag. 12	148	T	A
H1 frag. 13	69	C	T
H1 frag. 13	123	A	T
H1 frag. 13	168	C	A
H1 frag. 14	106	A	C
H1 frag. 15	3	A	T
H1 frag. 16	7	A	G
H1 frag. 16	243	—	G
H1 frag. 16	400	—	C
H1 frag. 16	535	T	C
H1 frag. 16	614	T	—
H1 frag. 17	47	T	A
H1 frag. 18	140	—	C
H1 frag. 18	185	T	A
H1 frag. 18	838	C	A
H1 frag. 18	866	G	A
H1 frag. 19	91	T	A
H1 frag. 19	376	T	A
H1 frag. 19	427	T	C
H1 frag. 19	622	A	G
H1 frag. 2	16	A	C
H1 frag. 2	180	A	C
H1 frag. 2	287	—	A
H1 frag. 20	146	T	C
H1 frag. 21	133	A	C
H1 frag. 23	25	T	C
H1 frag. 23	529	—	C
H1 frag. 23	602	T	A
H1 frag. 23	644	T	C
H1 frag. 23	854	A	C
H1 frag. 23	1015	T	—
H1 frag. 23	1781	T	C
H1 frag. 23	1793	A	T
H1 frag. 24	1	C	T
H1 frag. 24	35	G	A
H1 frag. 24	38	T	C
H1 frag. 3	407	T	A
H1 frag. 4	106	C	T
H1 frag. 4	191	T	A
H1 frag. 4	439	T	C
H1 frag. 4	562	—	C
H1 frag. 7	36	T	—
H1 frag. 7	97	C	A
H1 frag. 8	201	T	C
H1 frag. 8	313	T	C
H1 frag. 8	335	T	G
H1 frag. 8	469	C	A
H1 frag. 8	488	C	A
H1 frag. 8	523	T	A
H1 frag. 9	16	—	T
H1 frag. 9	28	A	—
H1 frag. 9	48	T	—
H1 frag. 9	55	—	A
H1 frag. 9	432	T	C
H1 frag. 9	558	A	C

Br/Taxon/Frag	Pos	Anc	Der
256 (*Kurixalus*)			
28S frag. 2	753	C	T
H1 frag. 1	68	T	C
H1 frag. 10	43	A	C
H1 frag. 10	143	A	—
H1 frag. 11	23	T	C
H1 frag. 11	368	C	A
H1 frag. 11	439	T	A
H1 frag. 11	536	G	T
H1 frag. 11	663	C	—
H1 frag. 11	762	C	—
H1 frag. 11	852	C	—
H1 frag. 11	958	—	T
H1 frag. 11	959	—	T
H1 frag. 11	1138	—	T
H1 frag. 11	1248	A	T
H1 frag. 11	1327	T	G
H1 frag. 12	80	C	T
H1 frag. 12	103	A	T
H1 frag. 12	174	A	G
H1 frag. 13	198	C	T
H1 frag. 14	68	—	A
H1 frag. 14	208	C	—
H1 frag. 14	217	A	T
H1 frag. 14	260	G	A
H1 frag. 16	191	C	A
H1 frag. 16	464	A	C
H1 frag. 16	672	A	T
H1 frag. 16	700	C	A
H1 frag. 17	16	C	A
H1 frag. 17	306	T	A
H1 frag. 17	350	T	A
H1 frag. 18	13	A	G
H1 frag. 18	143	C	T
H1 frag. 18	433	T	—
H1 frag. 18	488	T	A
H1 frag. 18	539	T	A
H1 frag. 18	767	C	T
H1 frag. 18	861	G	A
H1 frag. 19	197	A	T
H1 frag. 19	203	A	T
H1 frag. 19	212	C	T
H1 frag. 19	224	A	T
H1 frag. 19	350	A	G
H1 frag. 19	369	C	A
H1 frag. 19	379	—	T
H1 frag. 19	396	A	T
H1 frag. 19	823	C	A
H1 frag. 2	7	C	T
H1 frag. 2	20	C	A
H1 frag. 2	154	C	T
H1 frag. 2	187	C	A
H1 frag. 2	192	—	A
H1 frag. 2	207	G	A
H1 frag. 2	237	C	T
H1 frag. 2	301	A	C
H1 frag. 2	430	—	T
H1 frag. 2	439	C	—
H1 frag. 21	57	A	T
H1 frag. 22	5	G	A
H1 frag. 22	18	C	T
H1 frag. 22	20	T	C
H1 frag. 23	48	C	A
H1 frag. 23	81	G	A
H1 frag. 23	902	C	T
H1 frag. 23	942	C	A
H1 frag. 23	997	A	C
H1 frag. 23	1154	C	A
H1 frag. 23	1256	C	T
H1 frag. 23	1359	G	A
H1 frag. 23	1386	A	C
H1 frag. 23	1478	A	T
H1 frag. 23	1758	G	A
H1 frag. 23	1811	C	T
H1 frag. 23	1840	A	C
H1 frag. 23	1974	C	T
H1 frag. 23	1977	C	T
H1 frag. 24	5	C	T
H1 frag. 24	16	C	T
H1 frag. 24	17	C	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 24	33	G	A
H1 frag. 25	30	C	T
H1 frag. 25	34	C	A
H1 frag. 25	41	A	G
H1 frag. 3	26	T	C
H1 frag. 3	141	T	C
H1 frag. 3	150	A	G
H1 frag. 3	266	C	T
H1 frag. 3	268	C	T
H1 frag. 3	321	G	A
H1 frag. 4	316	C	T
H1 frag. 4	373	G	A
H1 frag. 4	380	C	T
H1 frag. 4	463	A	T
H1 frag. 5	32	T	C
H1 frag. 7	35	C	T
H1 frag. 7	43	G	A
H1 frag. 7	79	—	T
H1 frag. 7	80	—	A
H1 frag. 7	87	A	C
H1 frag. 7	96	A	T
H1 frag. 8	37	C	T
H1 frag. 8	59	T	C
H1 frag. 8	62	T	C
H1 frag. 8	122	T	A
H1 frag. 8	352	G	A
H1 frag. 8	553	A	G
H1 frag. 8	568	C	T
H1 frag. 8	626	C	A
H1 frag. 8	711	T	A
H1 frag. 8	816	T	A
H1 frag. 8	838	C	T
H1 frag. 9	52	C	T
H1 frag. 9	409	C	—
H1 frag. 9	498	C	A
H1 frag. 9	558	C	T
H1 frag. 9	693	C	T
H1 frag. 9	755	C	A
H1 frag. 9	798	T	C
H1 frag. 9	840	T	C
rhod frag. 1	161	A	T
rhod frag. 2	134	C	G
tyr frag. 1	29	G	C
tyr frag. 2	8	T	A
tyr frag. 2	36	T	C
tyr frag. 2	50	G	T
tyr frag. 2	77	C	T
tyr frag. 2	168	C	T
tyr frag. 2	213	C	T
tyr frag. 2	266	A	G
tyr frag. 2	277	C	T
tyr frag. 3	2	C	T
tyr frag. 3	28	T	A
tyr frag. 3	31	C	T
tyr frag. 3	63	A	C
tyr frag. 3	70	T	C
tyr frag. 3	158	G	C
tyr frag. 3	170	C	T
267 (*Chiromantis*)			
H1 frag. 11	264	T	C
H1 frag. 11	409	G	—
H1 frag. 11	648	—	C
H1 frag. 11	963	C	—
H1 frag. 11	1089	T	—
H1 frag. 12	74	T	A
H1 frag. 12	120	C	A
H1 frag. 14	64	C	T
H1 frag. 14	102	T	C
H1 frag. 16	27	T	C
H1 frag. 16	31	G	C
H1 frag. 16	266	T	C
H1 frag. 17	200	—	A
H1 frag. 17	306	T	—
H1 frag. 17	350	T	A
H1 frag. 17	446	C	T
H1 frag. 18	1	G	A
H1 frag. 18	140	C	T
H1 frag. 18	185	A	—
H1 frag. 18	209	A	T
H1 frag. 18	581	C	A

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Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 18	628	C	A
H1 frag. 18	868	A	T
H1 frag. 19	651	C	T
H1 frag. 2	7	C	A
H1 frag. 2	16	C	A
H1 frag. 2	44	G	A
H1 frag. 2	154	C	T
H1 frag. 2	237	C	T
H1 frag. 2	328	T	—
H1 frag. 2	419	T	C
H1 frag. 20	7	G	A
H1 frag. 20	25	A	T
H1 frag. 22	15	A	G
H1 frag. 22	45	T	C
H1 frag. 22	70	C	T
H1 frag. 23	103	C	A
H1 frag. 23	1131	G	A
H1 frag. 23	1169	C	A
H1 frag. 23	1359	G	A
H1 frag. 3	55	C	A
H1 frag. 4	263	G	A
H1 frag. 4	408	T	A
H1 frag. 4	493	C	T
H1 frag. 4	670	A	C
H1 frag. 6	62	A	—
H1 frag. 8	10	T	C
H1 frag. 8	569	A	G
H1 frag. 8	626	C	A
H1 frag. 9	17	A	G
H1 frag. 9	263	—	A
H1 frag. 9	570	—	A
rhod frag. 2	132	A	C
rhod frag. 2	134	C	A
rhod frag. 2	136	T	A
270 (Nyctibatrachidae)			
H1 frag. 12	112	A	G
H1 frag. 21	113	A	C
H1 frag. 21	124	A	C
H1 frag. 23	105	A	C
H1 frag. 23	641	—	T
H1 frag. 23	1676	C	T
H1 frag. 23	1977	C	T
H1 frag. 25	14	G	A
H1 frag. 25	87	C	T
H1 frag. 7	13	A	T
H1 frag. 8	172	T	C
H1 frag. 9	492	T	C
H1 frag. 9	506	A	T
rhod frag. 2	139	T	A
tyr frag. 2	250	A	C
tyr frag. 3	13	C	T
tyr frag. 3	28	T	C
tyr frag. 3	120	C	A
272 (Ranidae)			
H1 frag. 10	35	—	T
H1 frag. 11	409	T	C
H1 frag. 11	467	A	—
H1 frag. 11	852	C	T
H1 frag. 11	953	C	—
H1 frag. 11	1000	A	T
H1 frag. 12	160	C	A
H1 frag. 14	109	C	A
H1 frag. 14	238	A	G
H1 frag. 16	7	A	G
H1 frag. 16	17	A	G
H1 frag. 16	24	T	C
H1 frag. 16	563	A	T
H1 frag. 17	33	A	C
H1 frag. 17	182	T	A
H1 frag. 17	251	T	G
H1 frag. 17	274	A	G
H1 frag. 17	383	A	T
H1 frag. 18	433	T	A
H1 frag. 18	758	G	T
H1 frag. 18	766	C	T
H1 frag. 18	767	C	T
H1 frag. 18	861	G	A
H1 frag. 18	863	G	A
H1 frag. 19	178	T	C
H1 frag. 19	518	—	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 19	560	A	T
H1 frag. 19	771	C	T
H1 frag. 23	182	C	A
H1 frag. 23	199	A	T
H1 frag. 23	224	C	T
H1 frag. 23	238	—	T
H1 frag. 23	789	A	C
H1 frag. 23	1062	T	—
H1 frag. 23	1181	A	—
H1 frag. 23	1221	C	A
H1 frag. 23	1233	G	A
H1 frag. 23	1245	T	C
H1 frag. 23	1378	G	—
H1 frag. 23	1607	A	C
H1 frag. 23	1867	—	A
H1 frag. 6	25	T	C
H1 frag. 6	46	A	C
H1 frag. 6	91	C	T
H1 frag. 7	35	C	—
H1 frag. 7	39	C	A
H1 frag. 8	139	C	T
H1 frag. 8	161	C	A
H1 frag. 8	748	A	G
H1 frag. 9	71	T	C
H1 frag. 9	84	C	T
H1 frag. 9	233	C	A
rhod frag. 1	3	C	T
rhod frag. 1	9	T	C
rhod frag. 1	134	G	T
rhod frag. 2	33	G	A
rhod frag. 2	112	C	T
274 (*Hylarana*)			
H1 frag. 10	73	—	T
H1 frag. 11	368	C	T
H1 frag. 11	409	C	A
H1 frag. 11	457	T	C
H1 frag. 11	663	A	C
H1 frag. 13	69	C	G
H1 frag. 14	177	C	T
H1 frag. 16	152	T	A
H1 frag. 16	259	—	G
H1 frag. 16	629	A	T
H1 frag. 18	411	C	A
H1 frag. 18	504	—	T
H1 frag. 18	838	T	C
H1 frag. 19	61	G	—
H1 frag. 19	338	A	C
H1 frag. 19	449	T	C
H1 frag. 2	301	A	C
H1 frag. 21	90	A	C
H1 frag. 23	152	A	G
H1 frag. 23	250	A	T
H1 frag. 23	439	—	T
H1 frag. 23	613	—	C
H1 frag. 23	729	T	—
H1 frag. 23	902	C	A
H1 frag. 23	1041	A	T
H1 frag. 23	1288	T	C
H1 frag. 23	1303	A	T
H1 frag. 23	1356	A	G
H1 frag. 23	1834	A	T
H1 frag. 3	268	C	T
H1 frag. 4	289	—	A
H1 frag. 4	541	—	G
H1 frag. 4	548	A	T
H1 frag. 5	18	C	A
H1 frag. 6	229	A	G
H1 frag. 9	409	T	C
SIA frag. 4	79	T	G
285 (unnamed taxon)			
H1 frag. 10	3	A	G
H1 frag. 10	24	A	C
H1 frag. 10	26	T	C
H1 frag. 10	261	C	T
H1 frag. 11	12	G	A
H1 frag. 11	505	C	T
H1 frag. 11	565	C	T
H1 frag. 11	600	G	A
H1 frag. 11	973	—	T
H1 frag. 11	1217	T	A

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 11	1266	A	C
H1 frag. 21	83	—	C
H1 frag. 23	942	C	T
H1 frag. 23	1169	C	T
H1 frag. 23	1338	C	A
H1 frag. 23	1607	C	T
H1 frag. 24	10	A	G
H1 frag. 6	81	C	T
H1 frag. 6	199	C	T
H1 frag. 7	13	A	T
H1 frag. 8	249	T	C
H1 frag. 8	457	—	A
H1 frag. 8	542	G	A
H1 frag. 8	548	C	T
H1 frag. 8	792	A	C
H1 frag. 9	247	—	T
H1 frag. 9	533	C	—
H1 frag. 9	681	—	C
H1 frag. 9	739	A	G
rhod frag. 1	94	G	A
rhod frag. 2	9	A	G
rhod frag. 2	61	G	A
287 (unnamed taxon)			
H1 frag. 11	27	A	G
H1 frag. 11	72	C	T
H1 frag. 11	88	T	—
H1 frag. 11	392	A	T
H1 frag. 11	1071	C	—
H1 frag. 13	151	T	C
H1 frag. 15	40	T	A
H1 frag. 17	210	A	T
H1 frag. 17	306	A	C
H1 frag. 18	328	—	T
H1 frag. 18	433	A	T
H1 frag. 18	615	C	A
H1 frag. 18	648	A	T
H1 frag. 18	870	T	A
H1 frag. 19	369	A	T
H1 frag. 19	376	A	T
H1 frag. 21	251	A	T
H1 frag. 23	105	A	C
H1 frag. 23	587	—	G
H1 frag. 23	693	C	T
H1 frag. 23	789	C	A
H1 frag. 23	1015	A	G
H1 frag. 8	773	T	C
H1 frag. 9	409	T	C
H1 frag. 9	455	—	G
H1 frag. 9	708	A	G
288 (*Pelophylax*)			
H1 frag. 16	201	T	A
H1 frag. 16	241	A	G
H1 frag. 16	313	A	C
H1 frag. 16	547	C	A
H1 frag. 17	350	T	C
H1 frag. 17	372	T	C
H1 frag. 18	164	T	C
H1 frag. 18	232	C	—
H1 frag. 18	330	A	T
H1 frag. 19	350	A	C
H1 frag. 19	523	—	C
H1 frag. 20	5	A	C
296 (*Rana*)			
H1 frag. 10	60	—	C
H1 frag. 11	7	G	T
H1 frag. 11	1179	—	A
H1 frag. 11	1217	T	C
H1 frag. 13	168	C	A
H1 frag. 14	93	T	C
H1 frag. 17	33	C	A
H1 frag. 17	58	C	A
H1 frag. 17	118	T	C
H1 frag. 18	276	A	T
H1 frag. 18	654	T	C
H1 frag. 18	758	T	A
H1 frag. 19	146	G	A
H1 frag. 19	181	G	A
H1 frag. 19	217	A	T
H1 frag. 19	531	A	C
H1 frag. 19	596	C	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 19	749	A	C
H1 frag. 2	389	T	C
H1 frag. 2	397	C	T
H1 frag. 20	62	G	A
H1 frag. 22	61	A	G
H1 frag. 22	62	G	A
H1 frag. 23	11	C	T
H1 frag. 23	96	T	C
H1 frag. 23	584	—	G
H1 frag. 23	1834	A	—
H1 frag. 24	19	C	A
H1 frag. 3	47	T	C
H1 frag. 3	266	C	A
H1 frag. 3	342	G	—
H1 frag. 4	575	A	C
H1 frag. 6	229	G	—
H1 frag. 8	40	A	T
H1 frag. 8	792	A	C
H1 frag. 9	315	T	—
H1 frag. 9	400	A	T
H1 frag. 9	638	T	C
H3 frag. 1	117	G	C
rhod frag. 2	86	A	T
SIA frag. 2	53	A	G
SIA frag. 2	59	T	C
SIA frag. 3	45	T	C
tyr frag. 1	25	G	A
tyr frag. 1	58	C	T
tyr frag. 2	41	C	T
tyr frag. 2	85	T	A
tyr frag. 3	22	A	G
tyr frag. 3	109	C	T
tyr frag. 3	155	A	C
314 (Hyloides)			
28S frag. 2	354	—	C
28S frag. 2	483	—	C
28S frag. 3	379	—	C
28S frag. 3	385	—	C
28S frag. 3	389	—	C
28S frag. 3	487	—	G
H1 frag. 11	1294	T	C
H1 frag. 12	103	A	T
H1 frag. 14	208	A	T
H1 frag. 16	94	T	A
H1 frag. 16	414	A	C
H1 frag. 17	54	C	A
H1 frag. 17	372	T	C
H1 frag. 18	232	C	—
H1 frag. 18	322	A	C
H1 frag. 18	632	—	A
H1 frag. 18	727	C	A
H1 frag. 18	782	A	T
H1 frag. 19	109	C	T
H1 frag. 19	376	T	C
H1 frag. 2	154	T	C
H1 frag. 2	333	—	A
H1 frag. 20	68	G	A
H1 frag. 21	251	T	C
H1 frag. 23	52	C	T
H1 frag. 23	283	C	A
H1 frag. 23	559	C	A
H1 frag. 23	981	T	—
H1 frag. 23	1131	G	—
H1 frag. 23	1569	A	—
H1 frag. 3	258	C	A
H1 frag. 3	327	—	C
H1 frag. 4	94	A	C
H1 frag. 4	529	—	C
H1 frag. 4	548	A	C
H1 frag. 4	603	—	A
H1 frag. 4	637	T	A
H1 frag. 6	137	C	—
H1 frag. 8	741	C	A
H1 frag. 8	828	T	A
H1 frag. 9	609	C	A
H1 frag. 9	755	A	C
H1 frag. 9	788	A	C
H3 frag. 1	69	G	A
H3 frag. 1	117	G	C
H3 frag. 2	5	T	C

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Br/Taxon/Frag	Pos	Anc	Der
rhod frag. 2	103	T	C
SIA frag. 2	66	T	C
SIA frag. 3	48	G	A
SIA frag. 3	75	G	A
tyr frag. 1	7	C	G
tyr frag. 1	18	T	A
tyr frag. 1	55	T	C
tyr frag. 1	58	C	T
tyr frag. 2	8	T	G
tyr frag. 2	195	G	A
tyr frag. 2	261	T	C
tyr frag. 3	25	T	C
tyr frag. 3	49	G	A
tyr frag. 3	98	G	C
315 (Sooglossidae)			
H1 frag. 10	3	A	G
H1 frag. 10	20	G	A
H1 frag. 10	26	T	C
H1 frag. 10	141	—	A
H1 frag. 11	13	A	T
H1 frag. 11	144	T	C
H1 frag. 11	409	T	—
H1 frag. 11	595	A	—
H1 frag. 11	663	A	C
H1 frag. 11	887	A	—
H1 frag. 11	1000	A	—
H1 frag. 12	74	T	C
H1 frag. 12	153	A	C
H1 frag. 21	155	T	C
H1 frag. 22	13	C	T
H1 frag. 23	149	A	G
H1 frag. 23	236	A	G
H1 frag. 23	452	C	T
H1 frag. 23	762	C	T
H1 frag. 23	1201	G	—
H1 frag. 23	1225	—	A
H1 frag. 23	1268	—	C
H1 frag. 23	1270	A	C
H1 frag. 23	1295	T	C
H1 frag. 23	1348	A	C
H1 frag. 23	1359	G	—
H1 frag. 23	1444	G	A
H1 frag. 23	1726	C	A
H1 frag. 23	1940	T	C
H1 frag. 8	30	C	A
H1 frag. 8	59	T	C
H1 frag. 8	115	—	A
H1 frag. 8	441	A	—
H1 frag. 8	523	A	T
H1 frag. 8	551	A	T
H1 frag. 8	565	A	C
H1 frag. 8	583	—	C
H1 frag. 8	584	—	C
H1 frag. 8	593	T	C
H1 frag. 8	598	A	C
H1 frag. 8	643	A	G
H1 frag. 8	687	G	A
H1 frag. 8	726	A	C
H1 frag. 9	432	T	C
H1 frag. 9	467	G	A
H1 frag. 9	579	—	T
H1 frag. 9	739	A	C
H1 frag. 9	840	T	A
rhod frag. 1	60	T	C
rhod frag. 1	110	C	T
318 (Notogaeanura)			
28S frag. 3	370	G	C
H1 frag. 1	68	C	T
H1 frag. 10	43	A	—
H1 frag. 11	96	T	C
H1 frag. 11	457	C	A
H1 frag. 11	1327	T	A
H1 frag. 13	130	C	T
H1 frag. 13	159	A	T
H1 frag. 14	177	C	T
H1 frag. 16	16	A	G
H1 frag. 16	25	T	C
H1 frag. 17	118	G	A
H1 frag. 18	358	—	A
H1 frag. 18	628	T	C

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 18	717	A	C
H1 frag. 18	741	C	G
H1 frag. 18	775	T	—
H1 frag. 19	201	A	C
H1 frag. 19	729	C	A
H1 frag. 2	118	C	A
H1 frag. 20	129	T	A
H1 frag. 21	90	A	—
H1 frag. 23	67	G	A
H1 frag. 23	963	A	—
H1 frag. 23	1154	A	C
H1 frag. 23	1607	C	T
H1 frag. 3	321	G	A
H1 frag. 4	120	T	A
H1 frag. 4	148	A	C
H1 frag. 4	619	—	C
H1 frag. 4	624	—	C
H1 frag. 6	169	—	C
H1 frag. 7	84	A	T
H1 frag. 8	10	T	C
H1 frag. 8	369	G	C
H1 frag. 8	569	A	G
H1 frag. 8	626	C	T
H1 frag. 9	71	T	A
H1 frag. 9	558	A	—
rhod frag. 1	97	A	T
rhod frag. 2	42	C	G
SIA frag. 1	39	C	T
SIA frag. 3	156	T	G
SIA frag. 4	55	G	A
tyr frag. 1	31	C	T
tyr frag. 1	43	C	T
tyr frag. 2	68	T	C
tyr frag. 3	10	C	T
tyr frag. 3	50	T	C
tyr frag. 3	51	G	C
tyr frag. 3	61	G	A
319 (Australobatrachia)			
28S frag. 2	567	C	T
28S frag. 2	639	G	—
28S frag. 2	719	C	—
H1 frag. 1	52	T	G
H1 frag. 10	250	G	A
H1 frag. 11	53	T	G
H1 frag. 11	146	C	T
H1 frag. 11	671	—	T
H1 frag. 11	677	—	G
H1 frag. 11	685	—	C
H1 frag. 12	153	A	—
H1 frag. 12	186	A	C
H1 frag. 12	187	G	A
H1 frag. 13	74	—	A
H1 frag. 13	156	T	C
H1 frag. 14	268	T	G
H1 frag. 16	266	C	—
H1 frag. 16	398	A	C
H1 frag. 16	629	A	—
H1 frag. 17	333	C	A
H1 frag. 17	383	A	G
H1 frag. 18	254	T	C
H1 frag. 18	378	—	C
H1 frag. 18	563	A	C
H1 frag. 18	842	—	C
H1 frag. 19	531	A	C
H1 frag. 2	20	C	G
H1 frag. 2	171	A	T
H1 frag. 2	218	T	A
H1 frag. 22	15	A	G
H1 frag. 23	40	T	C
H1 frag. 23	602	T	C
H1 frag. 23	1027	A	G
H1 frag. 23	1612	—	A
H1 frag. 23	1796	A	C
H1 frag. 3	51	G	A
H1 frag. 3	126	C	T
H1 frag. 3	370	A	T
H1 frag. 4	238	—	T
H1 frag. 4	408	A	C
H1 frag. 4	504	—	A
H1 frag. 4	637	A	C

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 5	9	A	G
H1 frag. 5	28	G	A
H1 frag. 6	13	C	T
H1 frag. 6	43	—	C
H1 frag. 6	62	A	T
H1 frag. 8	24	A	G
H1 frag. 8	177	A	G
H1 frag. 8	232	A	—
H1 frag. 8	354	—	C
H1 frag. 8	580	C	T
H1 frag. 9	28	A	G
H1 frag. 9	87	T	A
H1 frag. 9	124	A	G
H1 frag. 9	580	C	T
H1 frag. 9	659	—	A
H3 frag. 1	81	A	C
H3 frag. 1	117	C	T
rhod frag. 2	79	C	G
SIA frag. 1	21	G	A
SIA frag. 4	19	A	T
320 (Batrachophrynidae)			
28S frag. 2	354	C	—
28S frag. 2	386	C	—
28S frag. 2	505	C	—
28S frag. 2	655	G	—
28S frag. 2	671	G	—
28S frag. 2	692	G	—
28S frag. 3	332	C	—
28S frag. 3	370	C	—
28S frag. 3	385	C	G
28S frag. 3	424	G	—
28S frag. 3	487	G	—
H1 frag. 11	67	C	A
H1 frag. 11	92	T	C
H1 frag. 11	144	T	C
H1 frag. 11	409	T	C
H1 frag. 11	536	C	A
H1 frag. 11	684	—	C
H1 frag. 11	983	T	C
H1 frag. 11	1129	—	C
H1 frag. 12	14	C	T
H1 frag. 12	74	T	C
H1 frag. 12	143	A	T
H1 frag. 13	168	A	C
H1 frag. 14	141	T	C
H1 frag. 14	144	A	G
H1 frag. 14	243	A	C
H1 frag. 15	22	T	C
H1 frag. 15	27	A	G
H1 frag. 16	7	A	G
H1 frag. 16	19	T	A
H1 frag. 16	191	C	T
H1 frag. 16	230	—	T
H1 frag. 16	414	C	A
H1 frag. 16	505	—	G
H1 frag. 16	614	T	—
H1 frag. 16	691	A	G
H1 frag. 16	696	A	G
H1 frag. 17	5	T	C
H1 frag. 17	38	A	G
H1 frag. 17	54	A	C
H1 frag. 17	160	C	A
H1 frag. 17	289	—	G
H1 frag. 17	296	C	T
H1 frag. 18	13	A	G
H1 frag. 18	604	A	C
H1 frag. 18	648	C	T
H1 frag. 18	746	T	C
H1 frag. 18	821	T	C
H1 frag. 19	3	C	T
H1 frag. 19	42	A	C
H1 frag. 19	140	C	T
H1 frag. 19	155	T	C
H1 frag. 19	197	A	C
H1 frag. 19	215	A	G
H1 frag. 19	350	A	G
H1 frag. 19	788	A	T
H1 frag. 20	61	A	G
H1 frag. 20	68	A	G
H1 frag. 21	121	—	C

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 22	23	G	A
H1 frag. 23	59	G	A
H1 frag. 23	224	C	T
H1 frag. 23	452	C	T
H1 frag. 23	784	—	A
H1 frag. 23	872	—	C
H1 frag. 23	874	—	C
H1 frag. 23	875	—	C
H1 frag. 23	1097	G	A
H1 frag. 23	1154	C	T
H1 frag. 23	1245	C	T
H1 frag. 23	1316	C	T
H1 frag. 23	1321	A	G
H1 frag. 23	1328	G	A
H1 frag. 23	1351	C	T
H1 frag. 23	1508	—	G
H1 frag. 23	1704	C	T
H1 frag. 23	1776	A	G
H1 frag. 25	17	T	C
H1 frag. 25	20	C	A
H3 frag. 1	42	C	G
H3 frag. 2	8	G	T
H3 frag. 2	31	C	T
rhod frag. 2	15	C	T
rhod frag. 2	118	T	C
SIA frag. 1	18	T	C
SIA frag. 3	60	A	G
SIA frag. 3	90	C	T
SIA frag. 3	153	A	G
SIA frag. 3	165	T	C
SIA frag. 3	177	A	G
SIA frag. 3	183	C	G
SIA frag. 4	13	C	G
SIA frag. 4	49	T	G
321 (Myobatrachoidea)			
28S frag. 3	93	—	C
28S frag. 3	297	—	C
28S frag. 3	575	G	C
H1 frag. 10	115	C	T
H1 frag. 10	269	C	T
H1 frag. 11	7	G	A
H1 frag. 11	457	A	—
H1 frag. 11	1017	—	A
H1 frag. 11	1217	A	C
H1 frag. 12	160	T	C
H1 frag. 14	217	A	T
H1 frag. 14	252	A	C
H1 frag. 17	437	C	A
H1 frag. 18	349	C	A
H1 frag. 18	447	T	A
H1 frag. 18	514	A	C
H1 frag. 2	140	C	T
H1 frag. 23	789	A	—
H1 frag. 23	883	C	—
H1 frag. 23	902	C	—
H1 frag. 23	942	C	T
H1 frag. 23	1074	T	A
H1 frag. 23	1334	A	C
H1 frag. 23	1364	A	C
H1 frag. 23	1444	G	A
H1 frag. 23	1554	T	C
H1 frag. 3	22	C	A
H1 frag. 4	191	T	A
H1 frag. 4	280	C	T
H1 frag. 6	23	C	T
H1 frag. 8	37	C	T
H1 frag. 8	40	A	T
H1 frag. 8	132	T	C
H1 frag. 8	173	T	C
H1 frag. 8	274	—	A
H1 frag. 8	275	—	A
H1 frag. 8	316	T	A
H1 frag. 8	726	A	C
H1 frag. 8	748	A	G
H1 frag. 9	17	A	G
H1 frag. 9	54	T	C
H1 frag. 9	739	A	T
H3 frag. 1	51	C	T
H3 frag. 1	111	G	A
rhod frag. 1	169	A	G

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Br/Taxon/Frag	Pos	Anc	Der
SIA frag. 2	62	C	G
SIA frag. 3	48	A	C
SIA frag. 3	120	G	C
322 (Limnodynastidae)			
28S frag. 2	129	A	G
28S frag. 2	330	G	C
28S frag. 2	354	C	T
28S frag. 2	442	C	G
28S frag. 2	692	G	A
28S frag. 2	790	C	A
28S frag. 2	797	G	A
28S frag. 3	8	T	C
28S frag. 3	53	G	A
28S frag. 3	74	—	A
28S frag. 3	75	G	C
28S frag. 3	134	T	G
28S frag. 3	187	G	—
28S frag. 3	478	—	G
28S frag. 3	586	C	G
28S frag. 4	130	—	T
H1 frag. 10	76	A	C
H1 frag. 11	15	A	C
H1 frag. 11	1045	A	C
H1 frag. 11	1135	C	A
H1 frag. 11	1336	T	C
H1 frag. 12	52	C	T
H1 frag. 13	160	—	A
H1 frag. 14	13	T	A
H1 frag. 14	64	A	C
H1 frag. 14	83	A	C
H1 frag. 14	142	C	T
H1 frag. 15	15	A	C
H1 frag. 16	4	C	T
H1 frag. 16	31	A	C
H1 frag. 16	106	—	T
H1 frag. 16	414	C	T
H1 frag. 16	429	C	A
H1 frag. 16	683	T	C
H1 frag. 17	33	A	C
H1 frag. 17	274	A	T
H1 frag. 17	350	A	C
H1 frag. 17	446	C	A
H1 frag. 18	750	G	A
H1 frag. 18	756	T	C
H1 frag. 18	821	T	A
H1 frag. 18	872	A	C
H1 frag. 2	198	—	A
H1 frag. 21	124	A	C
H1 frag. 23	274	C	T
H1 frag. 23	1181	C	T
H1 frag. 23	1607	T	C
H1 frag. 23	1743	A	C
H1 frag. 23	1763	T	C
H1 frag. 23	1940	T	A
H1 frag. 4	75	—	C
H1 frag. 4	169	C	A
H1 frag. 4	408	C	T
H1 frag. 4	529	C	—
H1 frag. 7	42	A	C
H1 frag. 8	545	A	C
H1 frag. 8	667	C	A
H1 frag. 9	84	A	C
H1 frag. 9	173	A	G
rhod frag. 1	9	T	C
rhod frag. 1	69	C	T
rhod frag. 1	90	T	C
rhod frag. 1	97	T	C
rhod frag. 1	131	T	G
rhod frag. 1	137	C	T
rhod frag. 1	140	A	C
rhod frag. 2	3	A	G
rhod frag. 2	66	G	C
rhod frag. 2	67	T	G
rhod frag. 2	69	T	A
rhod frag. 2	93	C	G
rhod frag. 2	136	T	C
334 (Myobatrachidae)			
H1 frag. 11	27	G	A
H1 frag. 11	622	C	A
H1 frag. 11	778	C	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 11	887	A	T
H1 frag. 12	112	G	A
H1 frag. 13	125	A	C
H1 frag. 14	208	T	A
H1 frag. 16	614	T	A
H1 frag. 17	107	—	G
H1 frag. 17	182	T	—
H1 frag. 17	251	T	C
H1 frag. 18	322	C	T
H1 frag. 18	378	C	A
H1 frag. 18	838	A	T
H1 frag. 2	32	A	G
H1 frag. 2	218	A	C
H1 frag. 2	301	C	A
H1 frag. 2	407	A	T
H1 frag. 21	155	T	A
H1 frag. 23	40	C	A
H1 frag. 23	236	A	G
H1 frag. 23	283	A	C
H1 frag. 23	623	A	—
H1 frag. 23	1060	C	T
H1 frag. 23	1226	T	C
H1 frag. 23	1342	A	T
H1 frag. 23	1348	A	C
H1 frag. 23	1627	A	T
H1 frag. 23	1919	A	—
H1 frag. 3	108	A	C
H1 frag. 3	214	T	C
H1 frag. 4	232	A	C
H1 frag. 6	167	A	—
H3 frag. 1	12	C	T
H3 frag. 1	105	G	T
SIA frag. 2	44	C	G
SIA frag. 2	48	T	C
SIA frag. 4	88	T	C
348 (Nobleobatrachia)			
H1 frag. 1	40	T	A
H1 frag. 10	101	G	A
H1 frag. 11	89	C	T
H1 frag. 11	126	C	T
H1 frag. 11	439	C	—
H1 frag. 11	1017	—	T
H1 frag. 11	1170	—	T
H1 frag. 12	52	C	T
H1 frag. 13	97	A	T
H1 frag. 14	9	G	A
H1 frag. 14	238	A	T
H1 frag. 16	36	T	—
H1 frag. 16	201	T	—
H1 frag. 16	313	C	A
H1 frag. 16	359	C	T
H1 frag. 16	386	—	T
H1 frag. 16	467	G	A
H1 frag. 16	487	—	A
H1 frag. 16	590	A	T
H1 frag. 16	672	A	—
H1 frag. 17	58	A	T
H1 frag. 17	196	—	A
H1 frag. 18	185	C	T
H1 frag. 18	514	A	—
H1 frag. 18	868	A	T
H1 frag. 18	872	A	T
H1 frag. 18	883	C	T
H1 frag. 19	403	C	A
H1 frag. 19	651	T	—
H1 frag. 19	749	C	T
H1 frag. 19	814	—	T
H1 frag. 2	196	T	A
H1 frag. 2	301	C	—
H1 frag. 23	173	—	T
H1 frag. 23	250	G	A
H1 frag. 23	283	A	T
H1 frag. 23	623	A	T
H1 frag. 23	997	A	—
H1 frag. 23	1041	T	C
H1 frag. 23	1181	C	A
H1 frag. 23	1221	C	T
H1 frag. 23	1303	C	A
H1 frag. 23	1342	A	T
H1 frag. 23	1364	A	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 23	1781	C	T
H1 frag. 23	1951	A	—
H1 frag. 23	1962	A	T
H1 frag. 24	5	T	C
H1 frag. 24	33	A	G
H1 frag. 3	108	A	T
H1 frag. 3	355	A	G
H1 frag. 4	286	A	T
H1 frag. 4	346	T	C
H1 frag. 4	617	—	C
H1 frag. 6	181	A	C
H1 frag. 7	24	C	—
H1 frag. 7	74	G	A
H1 frag. 8	69	C	T
H1 frag. 8	281	T	C
H1 frag. 8	667	C	T
H1 frag. 9	5	C	T
H1 frag. 9	52	T	C
H1 frag. 9	202	C	A
H1 frag. 9	226	A	G
H1 frag. 9	506	A	C
H1 frag. 9	775	C	T
H1 frag. 9	818	T	C
H3 frag. 1	45	C	T
H3 frag. 1	55	C	A
H3 frag. 1	111	G	T
H3 frag. 1	114	T	A
H3 frag. 1	147	A	G
H3 frag. 1	225	G	C
H3 frag. 1	243	A	G
H3 frag. 2	42	C	G
rhod frag. 1	9	T	C
rhod frag. 1	12	T	A
rhod frag. 1	93	A	C
rhod frag. 1	107	T	G
rhod frag. 1	128	C	T
rhod frag. 2	24	C	T
rhod frag. 2	73	G	A
rhod frag. 2	82	G	C
rhod frag. 2	126	C	T
rhod frag. 2	127	C	G
rhod frag. 2	129	A	T
SIA frag. 1	27	A	G
SIA frag. 2	14	A	C
SIA frag. 2	44	C	G
SIA frag. 3	24	C	A
SIA frag. 3	39	C	T
SIA frag. 3	42	T	C
SIA frag. 3	135	G	A
SIA frag. 3	138	T	A
SIA frag. 4	1	C	T
SIA frag. 4	79	T	G
349 (Meridianura)			
H1 frag. 10	199	C	T
H1 frag. 11	622	C	T
H1 frag. 11	694	C	—
H1 frag. 11	927	A	—
H1 frag. 11	1089	C	A
H1 frag. 11	1294	C	T
H1 frag. 12	14	C	T
H1 frag. 13	8	G	A
H1 frag. 13	169	—	C
H1 frag. 14	208	T	A
H1 frag. 16	152	A	T
H1 frag. 16	429	C	A
H1 frag. 16	658	A	C
H1 frag. 16	683	T	A
H1 frag. 17	46	A	C
H1 frag. 17	47	C	T
H1 frag. 17	182	T	A
H1 frag. 17	383	A	—
H1 frag. 18	322	C	T
H1 frag. 18	358	A	T
H1 frag. 18	821	T	C
H1 frag. 19	376	C	T
H1 frag. 19	668	A	T
H1 frag. 19	695	C	T
H1 frag. 19	771	A	T
H1 frag. 2	171	A	C
H1 frag. 23	224	C	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 23	568	—	T
H1 frag. 23	635	—	C
H1 frag. 23	908	—	T
H1 frag. 23	1027	A	T
H1 frag. 23	1627	A	C
H1 frag. 23	1704	C	A
H1 frag. 23	1754	A	T
H1 frag. 24	17	C	T
H1 frag. 4	169	C	A
H1 frag. 5	12	A	G
H1 frag. 6	167	A	—
H1 frag. 7	96	A	C
H1 frag. 8	523	A	T
H1 frag. 8	722	—	T
H1 frag. 9	93	C	T
H1 frag. 9	333	C	A
H1 frag. 9	788	C	A
H3 frag. 1	3	C	T
H3 frag. 1	48	A	G
H3 frag. 1	193	C	A
H3 frag. 1	195	G	A
rhod frag. 1	36	A	G
rhod frag. 1	104	T	C
rhod frag. 2	118	T	C
350 (Brachycephalidae)			
28S frag. 2	330	G	C
28S frag. 2	787	G	A
H1 frag. 11	457	A	—
H1 frag. 11	1268	C	T
H1 frag. 12	8	G	A
H1 frag. 12	163	A	—
H1 frag. 13	39	A	—
H1 frag. 14	109	C	A
H1 frag. 14	129	C	T
H1 frag. 14	146	A	G
H1 frag. 14	149	G	A
H1 frag. 15	54	G	A
H1 frag. 16	16	G	A
H1 frag. 16	25	C	T
H1 frag. 17	231	A	—
H1 frag. 18	488	T	A
H1 frag. 18	604	A	T
H1 frag. 18	830	C	T
H1 frag. 19	331	G	—
H1 frag. 19	356	C	—
H1 frag. 19	439	G	—
H1 frag. 19	453	A	—
H1 frag. 19	460	A	—
H1 frag. 19	635	C	T
H1 frag. 2	407	A	T
H1 frag. 21	277	C	T
H1 frag. 22	53	C	T
H1 frag. 22	63	G	A
H1 frag. 23	490	T	C
H1 frag. 23	1256	T	A
H1 frag. 23	1348	A	T
H1 frag. 23	1444	G	C
H1 frag. 8	148	C	T
H1 frag. 8	369	C	T
H1 frag. 8	536	G	A
H1 frag. 9	545	C	—
H1 frag. 9	725	C	A
rhod frag. 1	21	C	T
rhod frag. 1	51	T	C
rhod frag. 1	162	T	C
SIA frag. 3	84	A	C
tyr frag. 1	7	G	A
tyr frag. 1	12	A	C
tyr frag. 2	128	G	A
tyr frag. 2	222	T	C
tyr frag. 2	234	C	T
tyr frag. 2	266	A	G
tyr frag. 3	98	C	T
tyr frag. 3	153	A	G
358 (*Syrrhophus*)			
28S frag. 2	405	—	G
28S frag. 2	406	—	G
28S frag. 2	480	—	C
28S frag. 2	573	—	G
28S frag. 2	574	—	G

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Br/Taxon/Frag	Pos	Anc	Der
28S frag. 2	575	—	G
28S frag. 2	578	—	G
28S frag. 2	630	—	C
28S frag. 3	97	—	C
28S frag. 3	204	—	C
28S frag. 3	208	—	C
28S frag. 3	210	—	C
28S frag. 3	211	—	C
28S frag. 3	221	—	T
28S frag. 3	222	—	T
28S frag. 3	313	—	C
28S frag. 3	314	—	C
28S frag. 3	317	—	C
28S frag. 3	484	—	G
28S frag. 3	485	—	G
28S frag. 4	131	T	C
H1 frag. 11	57	A	—
H1 frag. 11	96	C	T
H1 frag. 11	1191	C	T
H1 frag. 11	1259	T	C
H1 frag. 13	33	C	T
H1 frag. 13	93	—	A
H1 frag. 13	97	T	A
H1 frag. 14	51	A	G
H1 frag. 14	102	T	C
H1 frag. 15	28	G	A
H1 frag. 16	191	C	A
H1 frag. 16	266	C	T
H1 frag. 16	414	C	A
H1 frag. 17	52	A	T
H1 frag. 17	160	C	A
H1 frag. 17	296	C	A
H1 frag. 17	407	C	T
H1 frag. 18	615	C	A
H1 frag. 18	648	C	T
H1 frag. 18	707	T	A
H1 frag. 19	15	A	—
H1 frag. 19	61	G	T
H1 frag. 19	91	C	A
H1 frag. 19	245	—	C
H1 frag. 19	278	C	T
H1 frag. 19	695	T	A
H1 frag. 2	420	A	G
H1 frag. 21	161	—	C
H1 frag. 23	102	A	T
H1 frag. 23	140	T	A
H1 frag. 23	577	—	A
H1 frag. 23	623	T	A
H1 frag. 23	1146	—	A
H1 frag. 23	1338	C	A
H1 frag. 23	1451	—	G
H1 frag. 23	1824	T	—
H1 frag. 23	1974	C	T
H1 frag. 24	38	T	C
H1 frag. 25	90	T	C
H1 frag. 3	47	C	T
H1 frag. 4	64	T	A
H1 frag. 4	343	G	A
H1 frag. 4	346	C	A
H1 frag. 8	37	C	T
H1 frag. 8	62	T	C
H1 frag. 8	722	T	—
H1 frag. 9	47	G	A
H1 frag. 9	51	C	T
H1 frag. 9	151	—	A
H1 frag. 9	226	G	A
rhod frag. 1	9	C	T
rhod frag. 2	136	T	C
tyr frag. 2	105	G	A
tyr frag. 2	131	T	C
tyr frag. 3	73	C	T
tyr frag. 3	88	A	T
361 (*Craugastor*)			
28S frag. 2	240	C	T
28S frag. 2	262	—	T
28S frag. 2	264	—	G
28S frag. 2	490	—	G
28S frag. 2	491	—	T
28S frag. 2	584	G	—
28S frag. 2	671	G	C

Br/Taxon/Frag	Pos	Anc	Der
28S frag. 2	719	C	—
28S frag. 2	762	—	A
H1 frag. 10	7	A	G
H1 frag. 11	40	G	—
H1 frag. 11	83	—	A
H1 frag. 11	1113	A	C
H1 frag. 12	80	A	T
H1 frag. 12	126	—	A
H1 frag. 13	69	C	A
H1 frag. 13	127	A	T
H1 frag. 13	156	T	C
H1 frag. 14	208	A	—
H1 frag. 15	33	A	C
H1 frag. 16	1	A	G
H1 frag. 16	450	A	T
H1 frag. 17	4	A	G
H1 frag. 17	33	A	C
H1 frag. 17	274	A	T
H1 frag. 18	254	C	A
H1 frag. 18	433	C	A
H1 frag. 18	821	T	A
H1 frag. 18	838	A	C
H1 frag. 19	61	G	C
H1 frag. 19	123	A	T
H1 frag. 19	307	A	—
H1 frag. 19	318	G	—
H1 frag. 19	338	A	—
H1 frag. 19	449	C	A
H1 frag. 2	171	C	A
H1 frag. 2	187	C	T
H1 frag. 2	196	A	T
H1 frag. 20	20	T	A
H1 frag. 20	54	A	T
H1 frag. 20	77	A	G
H1 frag. 23	5	A	T
H1 frag. 23	24	A	T
H1 frag. 23	38	T	C
H1 frag. 23	559	A	C
H1 frag. 23	823	—	T
H1 frag. 23	1154	C	—
H1 frag. 23	1245	T	C
H1 frag. 23	1322	C	T
H1 frag. 23	1393	—	C
H1 frag. 23	1684	T	A
H1 frag. 3	26	A	C
H1 frag. 4	526	—	G
H1 frag. 5	17	C	A
H1 frag. 6	226	A	C
H1 frag. 7	9	G	A
H1 frag. 7	55	C	T
H1 frag. 7	74	A	T
H1 frag. 8	369	T	C
H1 frag. 8	714	A	G
H1 frag. 9	28	A	G
H1 frag. 9	49	T	C
H1 frag. 9	98	T	C
H1 frag. 9	409	T	C
H1 frag. 9	652	T	C
H3 frag. 1	126	T	G
rhod frag. 1	10	A	G
rhod frag. 1	12	A	C
tyr frag. 1	25	G	A
tyr frag. 2	62	T	G
tyr frag. 2	68	C	T
tyr frag. 2	171	T	C
tyr frag. 3	38	A	G
tyr frag. 3	82	T	C
tyr frag. 3	119	C	T
366 (Cladophrynia)			
28S frag. 2	172	—	C
28S frag. 2	518	—	G
28S frag. 2	570	—	G
28S frag. 2	768	C	A
28S frag. 3	337	—	G
28S frag. 3	344	—	G
28S frag. 3	345	—	G
H1 frag. 11	27	G	A
H1 frag. 11	53	T	G
H1 frag. 11	279	—	A
H1 frag. 11	505	A	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 11	1049	—	A
H1 frag. 11	1071	C	A
H1 frag. 13	69	C	T
H1 frag. 13	82	C	A
H1 frag. 13	151	C	—
H1 frag. 16	191	C	T
H1 frag. 16	386	T	A
H1 frag. 17	413	—	T
H1 frag. 18	349	C	A
H1 frag. 18	654	A	—
H1 frag. 18	656	G	—
H1 frag. 18	717	C	T
H1 frag. 18	732	C	T
H1 frag. 18	822	—	A
H1 frag. 18	838	A	T
H1 frag. 19	808	C	A
H1 frag. 2	438	T	A
H1 frag. 22	61	A	G
H1 frag. 23	316	—	C
H1 frag. 23	350	—	T
H1 frag. 23	362	—	T
H1 frag. 23	379	—	C
H1 frag. 23	387	—	A
H1 frag. 23	397	—	C
H1 frag. 23	762	C	A
H1 frag. 23	807	—	T
H1 frag. 23	811	—	T
H1 frag. 23	1154	C	T
H1 frag. 23	1329	—	T
H1 frag. 23	1382	—	A
H1 frag. 3	20	T	A
H1 frag. 4	94	C	T
H1 frag. 4	529	C	A
H1 frag. 4	617	C	A
H1 frag. 4	619	C	T
H1 frag. 6	199	C	A
H1 frag. 8	37	C	T
H1 frag. 8	628	C	T
H1 frag. 8	727	—	C
H1 frag. 9	48	C	T
H1 frag. 9	506	C	T
SIA frag. 1	3	C	T
SIA frag. 1	21	G	A
tyr frag. 1	75	T	C
tyr frag. 2	207	C	A
tyr frag. 3	73	C	T
tyr frag. 3	181	G	T
367 (Cryptobatrachidae)			
H1 frag. 11	23	T	C
H1 frag. 11	264	C	G
H1 frag. 11	713	—	T
H1 frag. 11	887	A	C
H1 frag. 11	1333	T	C
H1 frag. 13	156	T	C
H1 frag. 13	159	T	A
H1 frag. 13	163	A	C
H1 frag. 14	28	C	T
H1 frag. 15	43	A	G
H1 frag. 16	398	A	T
H1 frag. 18	164	T	C
H1 frag. 18	254	T	A
H1 frag. 18	325	—	A
H1 frag. 18	494	C	T
H1 frag. 19	203	A	C
H1 frag. 19	286	C	T
H1 frag. 19	788	A	C
H1 frag. 20	20	T	A
H1 frag. 22	15	A	G
H1 frag. 23	72	C	T
H1 frag. 23	89	G	A
H1 frag. 23	173	T	A
H1 frag. 23	213	A	G
H1 frag. 23	902	C	A
H1 frag. 23	908	T	C
H1 frag. 6	26	A	—
H1 frag. 8	74	A	T
H1 frag. 8	122	A	C
H1 frag. 8	139	C	T
H1 frag. 8	300	A	G
H1 frag. 8	544	A	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 8	828	A	T
H1 frag. 9	791	—	T
368 (Tinctanura)			
28S frag. 2	243	T	G
28S frag. 2	254	A	C
28S frag. 2	339	—	T
28S frag. 2	692	G	C
28S frag. 3	370	C	A
28S frag. 3	385	T	—
28S frag. 3	424	G	—
H1 frag. 1	36	A	G
H1 frag. 1	72	C	T
H1 frag. 11	421	—	C
H1 frag. 11	541	—	T
H1 frag. 11	910	C	—
H1 frag. 11	1113	A	T
H1 frag. 13	33	C	A
H1 frag. 16	170	C	—
H1 frag. 16	298	—	T
H1 frag. 18	584	—	T
H1 frag. 18	615	C	T
H1 frag. 18	628	C	T
H1 frag. 19	509	C	T
H1 frag. 19	796	A	T
H1 frag. 2	184	—	T
H1 frag. 2	238	C	T
H1 frag. 2	420	A	G
H1 frag. 23	48	C	T
H1 frag. 23	327	—	T
H1 frag. 23	404	—	T
H1 frag. 23	416	—	T
H1 frag. 23	707	—	A
H1 frag. 23	729	C	A
H1 frag. 23	1338	C	A
H1 frag. 23	1518	A	C
H1 frag. 23	1695	A	G
H1 frag. 23	1759	T	C
H1 frag. 23	1828	C	A
H1 frag. 3	108	T	A
H1 frag. 3	214	T	A
H1 frag. 3	355	G	T
H1 frag. 8	741	A	T
H1 frag. 9	383	C	A
H1 frag. 9	580	C	T
H1 frag. 9	714	—	G
tyr frag. 3	128	C	T
369 (Amphignathodontidae)			
H1 frag. 10	86	A	T
H1 frag. 10	97	T	C
H1 frag. 10	199	T	C
H1 frag. 11	126	T	C
H1 frag. 11	819	C	A
H1 frag. 11	1000	A	—
H1 frag. 11	1071	A	T
H1 frag. 11	1170	T	C
H1 frag. 11	1248	C	T
H1 frag. 13	169	C	A
H1 frag. 14	83	A	T
H1 frag. 16	382	A	C
H1 frag. 16	509	A	C
H1 frag. 17	182	A	C
H1 frag. 17	196	A	C
H1 frag. 18	185	T	C
H1 frag. 18	632	A	—
H1 frag. 19	338	A	—
H1 frag. 19	378	—	C
H1 frag. 19	749	T	C
H1 frag. 23	173	T	G
H1 frag. 23	224	T	C
H1 frag. 23	356	—	C
H1 frag. 23	815	—	A
H1 frag. 23	1233	A	G
H1 frag. 23	1435	—	G
H1 frag. 23	1657	T	C
H1 frag. 8	177	A	G
H1 frag. 8	249	A	C
H1 frag. 8	470	—	C
H1 frag. 8	667	T	C
H1 frag. 9	22	A	G
H1 frag. 9	281	T	A

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Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 9	367	A	T
H1 frag. 9	708	A	C
rhod frag. 1	66	T	C
rhod frag. 1	135	C	T
rhod frag. 2	80	G	A
rhod frag. 2	134	C	A
SIA frag. 3	39	T	C
SIA frag. 3	144	T	C
tyr frag. 1	73	T	A
tyr frag. 2	98	C	T
tyr frag. 2	194	C	A
371 (Athesphatanura)			
28S frag. 2	719	C	—
28S frag. 2	788	—	A
28S frag. 3	54	A	G
28S frag. 3	379	C	—
28S frag. 3	389	C	—
H1 frag. 11	392	C	—
H1 frag. 11	565	C	A
H1 frag. 11	1161	A	T
H1 frag. 11	1191	C	T
H1 frag. 14	250	C	A
H1 frag. 15	42	A	G
H1 frag. 16	388	—	T
H1 frag. 16	547	C	A
H1 frag. 17	118	A	—
H1 frag. 17	296	C	T
H1 frag. 17	333	C	T
H1 frag. 17	407	C	A
H1 frag. 18	648	C	G
H1 frag. 18	830	C	A
H1 frag. 19	147	C	T
H1 frag. 2	437	C	T
H1 frag. 21	139	—	A
H1 frag. 23	379	C	A
H1 frag. 23	883	C	A
H1 frag. 23	1359	G	A
H1 frag. 23	1627	C	A
H1 frag. 23	1754	T	A
H1 frag. 4	169	A	C
H1 frag. 4	286	T	A
H1 frag. 4	548	C	T
H1 frag. 8	29	T	C
H1 frag. 8	281	C	T
H1 frag. 9	52	C	T
H1 frag. 9	798	A	C
H3 frag. 1	168	T	G
rhod frag. 2	127	G	C
rhod frag. 2	129	T	A
SIA frag. 3	84	A	T
tyr frag. 1	12	A	C
tyr frag. 2	222	T	C
tyr frag. 3	88	A	G
372 (Hylidae)			
28S frag. 2	284	T	C
28S frag. 2	358	—	G
28S frag. 2	516	—	G
H1 frag. 12	21	G	A
H1 frag. 14	64	A	T
H1 frag. 17	160	C	T
H1 frag. 17	231	A	T
H1 frag. 17	437	C	T
H1 frag. 18	518	—	A
H1 frag. 18	581	C	T
H1 frag. 18	616	—	C
H1 frag. 18	872	T	A
H1 frag. 19	286	C	T
H1 frag. 23	397	C	T
H1 frag. 23	452	C	T
H1 frag. 23	733	—	T
H1 frag. 23	811	T	A
H1 frag. 4	292	A	G
H1 frag. 4	391	A	T
H1 frag. 4	619	T	A
H1 frag. 8	514	C	T
H1 frag. 8	727	C	T
H1 frag. 9	46	T	A
H1 frag. 9	580	T	A
rhod frag. 2	118	C	T
rhod frag. 2	147	T	A

Br/Taxon/Frag	Pos	Anc	Der
tyr frag. 2	77	C	T
tyr frag. 3	64	A	—
tyr frag. 3	114	T	A
tyr frag. 3	127	A	T
372 (unnamed taxon)			
28S frag. 2	312	C	G
28S frag. 2	453	C	T
28S frag. 2	537	—	T
28S frag. 2	757	G	A
28S frag. 3	281	—	T
28S frag. 3	370	A	T
28S frag. 4	131	T	C
28S frag. 4	138	T	G
H1 frag. 1	72	T	C
H1 frag. 11	53	G	T
H1 frag. 11	393	—	T
H1 frag. 11	536	C	—
H1 frag. 11	887	A	T
H1 frag. 11	1050	—	T
H1 frag. 11	1071	A	T
H1 frag. 11	1248	C	T
H1 frag. 12	139	A	T
H1 frag. 16	4	C	T
H1 frag. 17	38	A	C
H1 frag. 17	47	T	A
H1 frag. 17	161	—	A
H1 frag. 18	24	C	T
H1 frag. 18	322	T	C
H1 frag. 18	433	C	—
H1 frag. 18	530	C	T
H1 frag. 18	604	A	T
H1 frag. 18	648	G	A
H1 frag. 18	717	T	A
H1 frag. 18	750	G	A
H1 frag. 19	140	C	T
H1 frag. 2	180	A	T
H1 frag. 2	184	T	C
H1 frag. 2	277	A	—
H1 frag. 2	439	C	T
H1 frag. 20	7	G	A
H1 frag. 23	417	—	A
H1 frag. 23	419	—	A
H1 frag. 23	490	T	A
H1 frag. 23	902	C	A
H1 frag. 23	1337	A	T
H1 frag. 23	1410	—	T
H1 frag. 23	1828	A	—
H1 frag. 24	5	C	T
H1 frag. 24	33	G	A
H1 frag. 3	22	A	T
H1 frag. 3	327	C	A
H1 frag. 6	199	A	C
H1 frag. 8	37	T	C
H1 frag. 8	667	T	C
H1 frag. 9	281	T	C
H1 frag. 9	409	A	T
H1 frag. 9	818	C	T
H3 frag. 1		T	C
H3 frag. 1	3	T	C
rhod frag. 1	90	T	C
rhod frag. 1	168	C	T
rhod frag. 1	169	A	G
SIA frag. 2	59	C	T
SIA frag. 4	13	C	T
SIA frag. 4	52	C	T
SIA frag. 4	67	T	C
tyr frag. 1	22	T	G
tyr frag. 1	73	T	C
tyr frag. 2	14	A	G
tyr frag. 2	111	C	T
tyr frag. 2	130	A	T
tyr frag. 2	141	G	A
tyr frag. 2	193	C	A
tyr frag. 2	223	G	A
tyr frag. 2	224	A	G
tyr frag. 2	266	A	G
tyr frag. 3	2	C	A
tyr frag. 3	58	—	G
tyr frag. 3	128	T	A

Br/Taxon/Frag	Pos	Anc	Der
tyr frag. 3	161	T	C
tyr frag. 3	170	C	T
377 (Pelodryadinae)			
H1 frag. 11	421	C	A
H1 frag. 11	480	—	C
H1 frag. 12	103	T	A
H1 frag. 14	31	T	A
H1 frag. 17	231	T	C
H1 frag. 17	337	—	A
H1 frag. 18	276	A	—
H1 frag. 18	374	—	G
H1 frag. 18	766	C	T
H1 frag. 18	861	A	—
H1 frag. 19	376	T	A
H1 frag. 19	695	T	A
H1 frag. 19	796	T	C
H1 frag. 2	7	C	A
H1 frag. 2	133	T	—
H1 frag. 2	238	T	C
H1 frag. 20	20	T	A
H1 frag. 20	23	C	A
H1 frag. 23	103	T	C
H1 frag. 23	236	A	T
H1 frag. 23	400	—	A
H1 frag. 23	733	T	A
H1 frag. 23	1245	C	T
H1 frag. 23	1256	T	A
H1 frag. 23	1356	A	G
H1 frag. 23	1444	G	A
H1 frag. 23	1687	A	T
H1 frag. 23	1704	A	T
H1 frag. 3	355	T	A
H1 frag. 4	148	C	A
H1 frag. 4	343	G	A
H1 frag. 6	181	C	A
H1 frag. 8	441	A	T
H1 frag. 8	511	G	A
H1 frag. 8	647	A	T
H1 frag. 9	256	C	—
H3 frag. 2	57	C	T
rhod frag. 1	101	G	A
tyr frag. 2	68	C	T
tyr frag. 2	198	C	G
tyr frag. 2	207	A	C
tyr frag. 3	63	G	A
tyr frag. 3	82	T	C
tyr frag. 3	93	C	G
tyr frag. 3	99	T	C
386 (Hylinae)			
28S frag. 3	187	G	C
28S frag. 3	344	G	C
28S frag. 3	487	G	C
H1 frag. 11	279	A	T
H1 frag. 12	148	T	A
H1 frag. 14	93	A	T
H1 frag. 16	382	A	T
H1 frag. 16	563	A	C
H1 frag. 17	182	A	—
H1 frag. 19	635	C	A
H1 frag. 21	113	A	T
H1 frag. 23	365	—	C
H1 frag. 23	855	—	C
H1 frag. 23	1687	A	G
H1 frag. 23	1763	T	C
H1 frag. 4	386	T	A
H1 frag. 4	401	T	C
H1 frag. 4	548	T	—
H1 frag. 8	582	T	C
H1 frag. 9	28	A	G
H1 frag. 9	48	T	C
H1 frag. 9	343	A	C
H1 frag. 9	609	A	C
H3 frag. 2	29	C	T
rhod frag. 2	16	T	C
SIA frag. 3	48	A	T
tyr frag. 1	76	T	A
tyr frag. 2	67	T	C
tyr frag. 2	225	C	A
tyr frag. 2	273	T	C

Br/Taxon/Frag	Pos	Anc	Der
tyr frag. 3	62	—	C
tyr frag. 3	155	A	G
442 (Telmatobiinae)			
H1 frag. 10	199	T	C
H1 frag. 11	505	T	C
H1 frag. 11	887	T	C
H1 frag. 11	1012	C	T
H1 frag. 11	1117	—	G
H1 frag. 11	1266	A	C
H1 frag. 12	9	C	A
H1 frag. 12	90	T	C
H1 frag. 12	148	T	C
H1 frag. 13	97	T	A
H1 frag. 13	132	G	A
H1 frag. 13	156	T	C
H1 frag. 13	172	C	T
H1 frag. 13	179	C	T
H1 frag. 14	93	A	C
H1 frag. 15	33	A	C
H1 frag. 15	40	C	T
H1 frag. 16	21	T	A
H1 frag. 16	31	A	G
H1 frag. 16	57	A	G
H1 frag. 16	152	T	C
H1 frag. 16	333	A	T
H1 frag. 16	547	A	C
H1 frag. 16	590	T	C
H1 frag. 16	671	T	C
H1 frag. 17	54	A	C
H1 frag. 17	81	A	T
H1 frag. 17	85	A	C
H1 frag. 17	182	A	C
H1 frag. 17	255	—	A
H1 frag. 17	279	T	C
H1 frag. 18	45	T	A
H1 frag. 18	615	T	C
H1 frag. 18	632	A	T
H1 frag. 18	838	T	C
H1 frag. 18	887	A	T
H1 frag. 19	147	T	C
H1 frag. 19	148	G	A
H1 frag. 19	201	C	A
H1 frag. 19	403	A	T
H1 frag. 19	509	T	A
H1 frag. 19	729	A	C
H1 frag. 19	823	C	T
H1 frag. 21	243	T	C
H1 frag. 21	251	C	A
H1 frag. 23	54	A	G
H1 frag. 23	86	G	T
H1 frag. 23	182	A	G
H1 frag. 23	224	T	A
H1 frag. 23	387	T	C
H1 frag. 23	903	A	T
H1 frag. 23	1233	A	T
H1 frag. 23	1256	T	C
H1 frag. 23	1337	A	T
H1 frag. 23	1434	—	C
H1 frag. 23	1824	T	C
H1 frag. 23	1825	T	C
H1 frag. 4	394	—	C
H1 frag. 8	249	A	T
H1 frag. 8	727	C	T
H1 frag. 9	281	T	C
H1 frag. 9	367	A	T
H3 frag. 1	6	A	G
H3 frag. 1	84	G	C
H3 frag. 1	102	C	T
H3 frag. 1	124	C	A
H3 frag. 1	126	T	G
H3 frag. 1	192	G	A
H3 frag. 2	66	C	T
rhod frag. 2	139	T	A
424 (Leptodactyliformes)			
28S frag. 2	190	C	—
28S frag. 2	202	C	—
28S frag. 2	203	G	—
28S frag. 2	243	G	—
28S frag. 2	518	G	—
28S frag. 2	519	G	—

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Br/Taxon/Frag	Pos	Anc	Der
28S frag. 2	521	G	—
28S frag. 2	570	G	—
28S frag. 2	584	G	—
28S frag. 2	675	C	—
28S frag. 3	345	G	C
H1 frag. 1	73	T	A
H1 frag. 11	421	C	A
H1 frag. 11	626	—	G
H1 frag. 11	957	—	A
H1 frag. 17	279	—	T
H1 frag. 18	371	A	—
H1 frag. 18	637	—	T
H1 frag. 2	210	A	G
H1 frag. 2	389	T	C
H1 frag. 2	407	A	T
H1 frag. 23	404	T	A
H1 frag. 4	672	C	T
tyr frag. 3	22	A	G
425 (Diphyabatrachia)			
28S frag. 2	339	T	G
28S frag. 2	535	G	—
28S frag. 3	344	G	C
H1 frag. 1	57	T	A
H1 frag. 11	368	A	C
H1 frag. 11	505	T	A
H1 frag. 11	819	C	A
H1 frag. 12	9	C	A
H1 frag. 15	33	A	G
H1 frag. 16	127	G	A
H1 frag. 16	292	A	C
H1 frag. 16	388	T	A
H1 frag. 16	487	A	—
H1 frag. 16	658	C	T
H1 frag. 17	182	A	T
H1 frag. 17	413	T	C
H1 frag. 18	324	—	G
H1 frag. 18	411	T	C
H1 frag. 18	494	C	—
H1 frag. 2	328	T	A
H1 frag. 23	89	G	A
H1 frag. 23	381	—	C
H1 frag. 23	408	—	C
H1 frag. 23	1461	—	A
H1 frag. 23	1714	A	G
H1 frag. 23	1748	T	C
H1 frag. 4	603	A	T
H1 frag. 8	57	T	C
H1 frag. 8	200	A	C
H1 frag. 8	554	A	G
H1 frag. 9	633	C	—
H1 frag. 9	755	C	A
H1 frag. 9	775	T	C
SIA frag. 3	90	C	T
tyr frag. 3	161	T	C
426 (Centrolenidae)			
H1 frag. 1	22	G	A
H1 frag. 11	92	T	C
H1 frag. 11	634	—	T
H1 frag. 11	1017	T	—
H1 frag. 11	1049	A	C
H1 frag. 11	1191	T	C
H1 frag. 11	1327	A	C
H1 frag. 12	80	A	C
H1 frag. 13	55	A	T
H1 frag. 13	168	A	C
H1 frag. 18	209	A	G
H1 frag. 18	254	T	A
H1 frag. 18	322	T	C
H1 frag. 18	629	—	A
H1 frag. 18	637	T	A
H1 frag. 19	203	A	C
H1 frag. 19	729	A	C
H1 frag. 23	103	T	C
H1 frag. 23	792	—	T
H1 frag. 23	908	T	—
H1 frag. 23	1154	T	A
H1 frag. 23	1607	T	A
H1 frag. 23	1798	T	A
H1 frag. 25	22	A	G
H1 frag. 3	26	T	C

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 3	384	T	C
H1 frag. 5	9	A	G
H1 frag. 6	25	T	C
H1 frag. 8	40	T	A
H1 frag. 9	281	T	C
H1 frag. 9	333	A	C
rhod frag. 1	93	C	T
rhod frag. 1	107	G	A
rhod frag. 1	171	C	A
rhod frag. 2	79	C	T
rhod frag. 2	92	A	T
rhod frag. 2	103	C	T
rhod frag. 2	109	C	T
rhod frag. 2	118	C	T
SIA frag. 3	126	C	T
SIA frag. 4	73	G	A
427 (Centroleninae)			
H1 frag. 10	93	A	G
H1 frag. 10	266	C	T
H1 frag. 11	12	G	A
H1 frag. 11	146	C	T
H1 frag. 11	953	C	A
H1 frag. 11	1116	—	C
H1 frag. 12	132	—	C
H1 frag. 12	187	G	A
H1 frag. 14	64	A	C
H1 frag. 14	83	A	C
H1 frag. 16	21	T	A
H1 frag. 16	25	C	T
H1 frag. 16	565	—	C
H1 frag. 17	16	C	A
H1 frag. 17	47	T	C
H1 frag. 17	54	A	C
H1 frag. 17	103	T	C
H1 frag. 17	251	T	—
H1 frag. 17	279	T	C
H1 frag. 17	333	T	C
H1 frag. 17	407	A	T
H1 frag. 17	446	T	A
H1 frag. 18	52	A	T
H1 frag. 18	411	C	A
H1 frag. 18	553	—	C
H1 frag. 18	866	A	G
H1 frag. 18	868	T	A
H1 frag. 19	124	—	C
H1 frag. 19	356	C	T
H1 frag. 19	496	T	C
H1 frag. 19	673	—	A
H1 frag. 19	788	A	T
H1 frag. 19	808	A	G
H1 frag. 2	238	T	C
H1 frag. 2	308	—	C
H1 frag. 2	360	T	A
H1 frag. 20	1	A	C
H1 frag. 21	113	A	T
H1 frag. 23	350	T	C
H1 frag. 23	387	T	A
H1 frag. 23	811	T	C
H1 frag. 23	854	A	C
H1 frag. 23	1027	T	C
H1 frag. 23	1074	T	A
H1 frag. 23	1627	A	C
H1 frag. 23	1687	A	T
H1 frag. 23	1743	A	C
H1 frag. 23	1750	T	C
H1 frag. 23	1754	A	C
H1 frag. 23	1763	T	C
H1 frag. 4	67	—	C
H1 frag. 4	232	A	T
H1 frag. 4	386	T	G
H1 frag. 4	391	A	C
H1 frag. 4	499	T	C
H1 frag. 4	672	T	C
H1 frag. 6	181	C	A
H1 frag. 7	84	T	C
H1 frag. 8	28	A	C
H1 frag. 8	120	—	A
H1 frag. 9	31	C	A
H1 frag. 9	343	A	C
H1 frag. 9	432	T	A

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 9	506	T	A
H1 frag. 9	511	T	A
rhod frag. 1	9	C	T
rhod frag. 1	169	A	G
430 (Leptodactylidae)			
28S frag. 2	187	A	G
28S frag. 2	284	T	C
28S frag. 2	671	G	C
28S frag. 3	115	T	A
H1 frag. 11	421	A	T
H1 frag. 11	762	A	C
H1 frag. 11	957	A	C
H1 frag. 12	21	G	A
H1 frag. 13	82	A	T
H1 frag. 15	50	A	C
H1 frag. 16	563	A	C
H1 frag. 18	433	C	T
H1 frag. 18	542	—	C
H1 frag. 18	615	T	A
H1 frag. 19	201	C	A
H1 frag. 19	403	A	T
H1 frag. 19	496	T	A
H1 frag. 19	544	—	T
H1 frag. 21	155	T	—
H1 frag. 23	224	T	C
H1 frag. 23	807	T	—
H1 frag. 23	1321	G	A
H1 frag. 23	1825	T	C
H1 frag. 4	223	A	T
H1 frag. 5	17	C	A
H1 frag. 6	81	A	T
H1 frag. 9	739	A	T
H1 frag. 9	798	C	T
H3 frag. 1	108	A	T
rhod frag. 2	126	T	C
436 (*Leptodactylus*)			
28S frag. 2	488	—	G
28S frag. 2	505	C	G
28S frag. 3	219	—	T
28S frag. 3	337	G	C
H1 frag. 1	57	G	T
H1 frag. 1	73	A	T
H1 frag. 10	125	—	A
H1 frag. 11	415	—	A
H1 frag. 11	595	A	T
H1 frag. 11	626	G	T
H1 frag. 11	722	—	T
H1 frag. 11	887	A	T
H1 frag. 11	1017	T	—
H1 frag. 11	1170	T	A
H1 frag. 12	60	A	T
H1 frag. 14	83	A	C
H1 frag. 14	89	T	C
H1 frag. 16	16	A	G
H1 frag. 16	691	A	G
H1 frag. 17	4	A	G
H1 frag. 17	5	T	C
H1 frag. 17	52	A	T
H1 frag. 17	333	T	C
H1 frag. 17	350	A	G
H1 frag. 18	209	A	G
H1 frag. 18	474	A	T
H1 frag. 18	530	C	A
H1 frag. 18	707	T	A
H1 frag. 18	822	A	T
H1 frag. 19	668	T	—
H1 frag. 19	771	T	A
H1 frag. 2	389	C	T
H1 frag. 21	139	C	T
H1 frag. 23	312	—	C
H1 frag. 23	379	A	T
H1 frag. 23	416	T	A
H1 frag. 23	795	C	A
H1 frag. 23	854	A	C
H1 frag. 23	927	—	A
H1 frag. 23	1627	A	C
H1 frag. 23	1717	A	G
H1 frag. 4	22	A	T
H1 frag. 4	64	T	A
H1 frag. 4	94	T	G

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 4	271	T	C
H1 frag. 4	386	T	A
H1 frag. 4	434	A	G
H1 frag. 7	84	T	A
H1 frag. 8	200	C	—
H1 frag. 8	544	A	T
H1 frag. 9	652	T	A
H3 frag. 2	36	G	C
rhod frag. 1	104	C	G
rhod frag. 1	169	A	G
rhod frag. 2	42	G	A
tyr frag. 2	136	G	T
tyr frag. 2	141	G	A
tyr frag. 2	183	C	T
tyr frag. 3	14	G	T
tyr frag. 3	67	T	C
tyr frag. 3	93	C	G
440 (Chthonobatrachia)			
H1 frag. 11	315	A	C
H1 frag. 11	631	—	A
H1 frag. 11	887	A	T
H1 frag. 13	55	A	C
H1 frag. 14	64	A	C
H1 frag. 18	530	C	T
H1 frag. 23	96	A	T
H1 frag. 23	173	T	A
H1 frag. 23	335	—	A
H1 frag. 23	903	—	A
H1 frag. 23	1245	C	T
H1 frag. 3	58	C	T
H3 frag. 1	162	G	C
H3 frag. 1	174	T	G
H3 frag. 2	42	G	C
SIA frag. 3	84	T	C
SIA frag. 4	70	T	C
tyr frag. 2	273	T	C
441 (Ceratophryidae)			
28S frag. 2	172	C	—
28S frag. 2	567	C	—
28S frag. 3	344	G	T
28S frag. 3	487	G	—
H1 frag. 1	68	T	C
H1 frag. 10	217	T	A
H1 frag. 11	16	A	G
H1 frag. 11	778	A	T
H1 frag. 11	1049	A	T
H1 frag. 17	103	T	A
H1 frag. 17	210	T	A
H1 frag. 17	254	—	A
H1 frag. 17	335	—	A
H1 frag. 18	13	A	G
H1 frag. 18	256	—	G
H1 frag. 18	276	A	T
H1 frag. 18	349	A	T
H1 frag. 18	488	T	A
H1 frag. 18	606	—	C
H1 frag. 19	376	T	A
H1 frag. 19	753	—	A
H1 frag. 23	100	A	T
H1 frag. 23	102	A	T
H1 frag. 23	409	—	T
H1 frag. 23	464	—	T
H1 frag. 23	811	T	A
H1 frag. 3	214	A	G
H1 frag. 3	384	T	C
H1 frag. 6	115	A	T
H1 frag. 8	93	C	T
H1 frag. 9	708	A	C
H1 frag. 9	798	C	T
H3 frag. 1	108	A	T
H3 frag. 1	129	G	A
444 (Ceratophryinae)			
28S frag. 2	187	A	—
H1 frag. 11	264	C	A
H1 frag. 11	290	—	T
H1 frag. 11	368	A	T
H1 frag. 11	421	A	T
H1 frag. 13	163	A	T
H1 frag. 15	56	T	C
H1 frag. 16	388	T	A

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Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 18	539	A	C
H1 frag. 19	286	C	T
H1 frag. 20	7	G	A
H1 frag. 23	452	C	A
H1 frag. 23	1154	T	C
H1 frag. 23	1338	A	T
H1 frag. 23	1554	T	A
H1 frag. 23	1754	A	T
H1 frag. 4	202	—	A
H1 frag. 6	181	C	A
H1 frag. 9	580	T	C
H3 frag. 1	3	T	C
H3 frag. 2	57	C	T
SIA frag. 3	141	C	T
445 (Batrachylini)			
28S frag. 2	330	G	A
28S frag. 2	339	T	C
28S frag. 2	714	G	—
28S frag. 3	295	—	C
28S frag. 3	353	—	A
28S frag. 3	354	—	A
28S frag. 3	416	C	A
28S frag. 3	453	C	A
H1 frag. 1	57	T	A
H1 frag. 11	72	C	T
H1 frag. 11	953	C	T
H1 frag. 11	1217	A	—
H1 frag. 12	52	T	C
H1 frag. 12	153	A	T
H1 frag. 13	39	A	T
H1 frag. 13	55	C	T
H1 frag. 13	159	T	A
H1 frag. 14	28	C	A
H1 frag. 14	238	T	A
H1 frag. 16	535	C	A
H1 frag. 17	168	—	T
H1 frag. 17	296	T	A
H1 frag. 17	413	T	C
H1 frag. 18	433	C	A
H1 frag. 18	491	—	C
H1 frag. 18	530	T	C
H1 frag. 18	563	A	C
H1 frag. 18	637	T	—
H1 frag. 18	830	A	G
H1 frag. 19	278	C	A
H1 frag. 19	596	C	T
H1 frag. 21	139	A	T
H1 frag. 22	61	G	A
H1 frag. 23	794	—	C
H1 frag. 23	908	T	—
H1 frag. 23	1060	C	T
H1 frag. 23	1329	T	A
H1 frag. 4	191	T	A
H1 frag. 4	211	A	C
H1 frag. 4	403	—	A
H1 frag. 4	672	T	C
H1 frag. 6	26	A	C
H1 frag. 6	62	A	T
H1 frag. 7	19	G	A
H1 frag. 8	511	G	A
H1 frag. 9	755	C	T
rhod frag. 1	96	C	T
rhod frag. 1	99	T	A
rhod frag. 2	6	C	G
rhod frag. 2	93	C	G
rhod frag. 2	126	T	G
SIA frag. 1	3	T	C
SIA frag. 3	126	C	T
SIA frag. 3	168	A	C
446 (Ceratophyrini)			
28S frag. 2	182	C	T
28S frag. 2	283	—	T
28S frag. 2	671	G	T
28S frag. 2	788	A	—
28S frag. 2	790	T	C
28S frag. 3	54	G	A
28S frag. 3	344	T	—
28S frag. 3	370	A	—
28S frag. 3	577	—	C
H1 frag. 1	41	A	G
H1 frag. 11	36	T	C
H1 frag. 11	778	T	—
H1 frag. 11	1170	T	A
H1 frag. 12	74	A	T
H1 frag. 13	8	A	G
H1 frag. 14	31	T	C
H1 frag. 14	250	A	C
H1 frag. 15	33	A	G
H1 frag. 16	221	A	T
H1 frag. 16	266	A	T
H1 frag. 16	292	A	T
H1 frag. 16	509	A	C
H1 frag. 16	576	C	T
H1 frag. 17	47	T	C
H1 frag. 18	494	C	A
H1 frag. 18	628	T	A
H1 frag. 18	717	T	C
H1 frag. 18	761	T	A
H1 frag. 19	271	C	T
H1 frag. 19	376	A	C
H1 frag. 2	277	A	G
H1 frag. 25	22	A	G
H1 frag. 25	40	T	C
H1 frag. 3	258	A	T
H1 frag. 3	376	—	C
H1 frag. 3	391	T	C
H1 frag. 4	169	C	A
H1 frag. 4	415	—	G
H1 frag. 4	499	T	C
H1 frag. 6	81	A	C
H1 frag. 6	213	A	C
H1 frag. 8	116	T	A
H1 frag. 9	432	T	A
H1 frag. 9	633	C	—
H1 frag. 9	710	—	A
rhod frag. 1	125	T	C
448 (Hesticobatrachia)			
28S frag. 2	339	T	C
28S frag. 2	532	—	G
28S frag. 2	533	—	G
28S frag. 3	347	—	A
28S frag. 3	376	—	C
H1 frag. 11	53	G	T
H1 frag. 11	72	C	T
H1 frag. 11	663	A	C
H1 frag. 13	82	A	C
H1 frag. 16	292	A	T
H1 frag. 16	576	C	T
H1 frag. 17	160	C	T
H1 frag. 17	350	A	—
H1 frag. 18	822	A	T
H1 frag. 19	271	C	T
H1 frag. 19	356	C	T
H1 frag. 19	600	C	T
H1 frag. 2	218	T	A
H1 frag. 23	105	A	T
H1 frag. 23	902	C	T
H1 frag. 23	1669	C	T
H1 frag. 4	94	T	C
H1 frag. 4	211	A	—
H1 frag. 6	25	T	C
H1 frag. 9	580	T	A
H1 frag. 9	755	C	T
SIA frag. 3	39	T	C
SIA frag. 3	48	A	G
SIA frag. 3	180	C	T
tyr frag. 3	155	A	C
449 (Cycloramphidae)			
H1 frag. 11	852	C	T
H1 frag. 11	983	T	C
H1 frag. 12	103	T	A
H1 frag. 13	33	A	—
H1 frag. 16	535	C	A
H1 frag. 17	140	—	C
H1 frag. 18	276	A	—
H1 frag. 18	563	A	T
H1 frag. 19	752	—	C
H1 frag. 2	328	T	—
H1 frag. 21	57	A	—
H1 frag. 23	904	—	T
H1 frag. 4	280	C	T
H3 frag. 2	5	C	T
rhod frag. 1	60	T	C
rhod frag. 2	6	C	G
SIA frag. 3	141	C	T
tyr frag. 2	195	A	G
tyr frag. 3	65	A	G
tyr frag. 3	181	T	G
450 (Hylodinae)			
H1 frag. 11	16	A	C
H1 frag. 11	457	A	T
H1 frag. 11	565	A	T
H1 frag. 12	163	A	T
H1 frag. 13	6	A	—
H1 frag. 13	55	C	—
H1 frag. 14	4	G	A
H1 frag. 14	38	A	C
H1 frag. 14	51	A	G
H1 frag. 15	11	G	A
H1 frag. 16	191	T	C
H1 frag. 16	633	—	G
H1 frag. 16	691	A	T
H1 frag. 17	296	T	C
H1 frag. 17	429	A	T
H1 frag. 18	139	—	C
H1 frag. 18	191	—	C
H1 frag. 18	488	T	A
H1 frag. 19	24	G	T
H1 frag. 19	42	A	T
H1 frag. 19	668	T	C
H1 frag. 19	749	T	C
H1 frag. 23	72	C	T
H1 frag. 23	89	G	A
H1 frag. 23	173	A	—
H1 frag. 23	318	—	T
H1 frag. 23	379	A	T
H1 frag. 23	404	A	T
H1 frag. 23	416	T	A
H1 frag. 23	559	A	C
H1 frag. 23	729	A	T
H1 frag. 23	1256	T	A
H1 frag. 23	1444	G	—
H1 frag. 23	1627	A	T
H1 frag. 25	30	C	T
H1 frag. 4	191	T	C
H1 frag. 4	262	A	G
H1 frag. 4	441	C	A
H1 frag. 4	493	C	T
H1 frag. 4	499	T	C
H1 frag. 9	367	A	T
H1 frag. 9	409	A	C
H1 frag. 9	708	A	T
H1 frag. 9	775	T	A
H3 frag. 1	69	C	G
H3 frag. 1	96	C	T
H3 frag. 1	111	T	A
H3 frag. 1	192	G	C
rhod frag. 1		A	G
rhod frag. 1	39	A	C
rhod frag. 1	87	A	G
rhod frag. 1	97	T	C
rhod frag. 1	125	T	C
rhod frag. 2	12	A	G
rhod frag. 2	16	T	C
rhod frag. 2	113	G	A
SIA frag. 3	126	C	A
SIA frag. 3	129	C	T
SIA frag. 4	76	T	G
tyr frag. 1	76	T	C
tyr frag. 2	19	A	G
tyr frag. 2	29	C	T
tyr frag. 2	44	T	C
tyr frag. 2	50	T	C
tyr frag. 2	225	C	G
tyr frag. 2	266	A	G
tyr frag. 3	47	T	G
tyr frag. 3	63	G	C
tyr frag. 3	73	T	C
tyr frag. 3	98	C	T
452 (Cycloramphinae)			
H1 frag. 11	368	A	C
H1 frag. 11	663	C	—
H1 frag. 11	1095	—	T
H1 frag. 11	1248	C	T
H1 frag. 12	160	T	A
H1 frag. 17	198	—	T
H1 frag. 18	358	T	A
H1 frag. 18	451	—	A
H1 frag. 18	520	—	T
H1 frag. 19	788	A	T
H1 frag. 23	1754	A	T
H1 frag. 4	126	C	T
H1 frag. 7	6	A	T
H1 frag. 9	633	C	T
H3 frag. 1	15	A	C
H3 frag. 1	108	A	G
rhod frag. 1	169	A	G
rhod frag. 2	93	C	G
tyr frag. 3	82	T	C
453 (Cycloramphini)			
28S frag. 2	246	G	T
28S frag. 2	567	C	G
28S frag. 3	54	G	A
28S frag. 3	337	G	—
28S frag. 3	344	G	—
28S frag. 3	345	C	T
28S frag. 3	347	A	T
H1 frag. 11	53	T	G
H1 frag. 11	541	T	A
H1 frag. 14	89	T	C
H1 frag. 16	386	A	C
H1 frag. 17	140	C	T
H1 frag. 17	160	T	A
H1 frag. 17	251	T	—
H1 frag. 17	372	T	A
H1 frag. 18	539	A	C
H1 frag. 19	350	A	G
H1 frag. 2	342	A	C
H1 frag. 20	182	T	C
H1 frag. 21	243	T	A
H1 frag. 23	10	C	T
H1 frag. 23	48	T	C
H1 frag. 23	362	T	A
H1 frag. 24	19	C	A
H1 frag. 25	17	T	C
H1 frag. 3	26	T	C
H1 frag. 4	94	C	T
H1 frag. 4	316	C	T
H1 frag. 4	614	A	C
H1 frag. 6	27	G	A
H1 frag. 6	62	A	T
H1 frag. 8	93	C	T
H1 frag. 8	122	A	T
H1 frag. 8	272	T	A
H1 frag. 8	511	G	A
H1 frag. 9	618	A	C
H1 frag. 9	798	C	T
H3 frag. 1	42	C	T
H3 frag. 1	99	C	T
H3 frag. 1	168	G	T
H3 frag. 1	240	G	A
H3 frag. 2	42	C	G
454 (Alsodini)			
28S frag. 2	206	—	G
28S frag. 2	209	—	C
28S frag. 2	703	—	C
28S frag. 3	487	G	C
H1 frag. 11	505	T	C
H1 frag. 11	1012	C	T
H1 frag. 11	1049	A	T
H1 frag. 12	139	A	T
H1 frag. 14	250	A	C
H1 frag. 18	474	A	T
H1 frag. 18	604	A	—
H1 frag. 18	830	A	C
H1 frag. 19	376	T	G
H1 frag. 23	807	T	C
H1 frag. 23	903	A	C
H1 frag. 23	1519	—	T

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Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 5	9	A	G
H1 frag. 9	315	A	—
rhod frag. 2	69	T	C
rhod frag. 2	139	T	A
SIA frag. 1	12	T	G
SIA frag. 1	39	T	G
SIA frag. 2	8	T	C
SIA frag. 4	22	G	A
tyr frag. 2	273	C	T
tyr frag. 3	91	A	G
tyr frag. 3	140	A	G
tyr frag. 3	155	C	A
460 (*Agastorophrynia*)			
28S frag. 2	330	G	—
28S frag. 2	494	G	C
28S frag. 3	232	—	G
28S frag. 3	283	—	T
28S frag. 3	284	—	T
28S frag. 3	289	—	C
28S frag. 3	371	—	C
H1 frag. 11	536	C	T
H1 frag. 11	626	G	—
H1 frag. 11	1089	A	C
H1 frag. 13	69	T	—
H1 frag. 16	241	A	C
H1 frag. 16	629	A	—
H1 frag. 17	196	A	T
H1 frag. 18	234	—	T
H1 frag. 18	411	T	C
H1 frag. 18	604	A	C
H1 frag. 18	615	T	A
H1 frag. 18	717	T	A
H1 frag. 19	42	A	C
H1 frag. 2	88	A	T
H1 frag. 21	76	A	T
H1 frag. 23	340	—	T
H1 frag. 23	1634	—	C
H1 frag. 23	1952	—	A
H1 frag. 24	1	C	T
H1 frag. 4	64	T	C
H1 frag. 4	169	C	T
H1 frag. 4	447	A	G
H1 frag. 6	163	C	T
H1 frag. 8	272	T	C
H1 frag. 8	511	G	A
rhod frag. 2	126	T	G
SIA frag. 1	39	T	C
SIA frag. 3	138	A	C
SIA frag. 3	168	A	C
tyr frag. 1	23	T	A
tyr frag. 1	49	G	C
tyr frag. 1	75	C	T
461 (Dendrobatoidea)			
H1 frag. 11	279	A	C
H1 frag. 11	413	—	C
H1 frag. 11	509	—	A
H1 frag. 11	1000	A	—
H1 frag. 11	1071	A	C
H1 frag. 12	21	G	A
H1 frag. 12	74	A	T
H1 frag. 14	93	A	T
H1 frag. 14	208	A	T
H1 frag. 15	33	A	C
H1 frag. 15	56	T	C
H1 frag. 16	535	C	T
H1 frag. 16	683	A	T
H1 frag. 18	641	—	C
H1 frag. 18	830	A	T
H1 frag. 19	146	G	A
H1 frag. 19	147	T	C
H1 frag. 19	148	G	T
H1 frag. 19	203	A	C
H1 frag. 19	286	C	T
H1 frag. 2	223	A	T
H1 frag. 23	25	T	C
H1 frag. 23	199	A	T
H1 frag. 23	213	A	G
H1 frag. 23	452	C	—
H1 frag. 23	521	A	—
H1 frag. 23	568	T	—

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 23	635	C	—
H1 frag. 23	693	A	—
H1 frag. 23	698	G	—
H1 frag. 23	942	T	C
H1 frag. 23	1245	T	C
H1 frag. 23	1554	T	A
H1 frag. 24	19	C	A
H1 frag. 4	94	C	A
H1 frag. 4	265	G	A
H1 frag. 4	392	—	C
H1 frag. 4	484	C	T
H1 frag. 5	8	—	G
H1 frag. 5	16	A	—
H1 frag. 6	23	C	T
H1 frag. 8	122	A	C
H1 frag. 8	260	C	T
H1 frag. 8	369	C	T
H1 frag. 8	545	A	T
H1 frag. 9	432	T	—
H1 frag. 9	672	A	T
H1 frag. 9	755	T	A
H1 frag. 9	775	T	C
H3 frag. 1	162	C	G
H3 frag. 2	42	C	G
469 (Bufonidae)			
28S frag. 2	172	C	—
28S frag. 2	312	C	—
28S frag. 2	613	G	—
28S frag. 2	639	G	—
28S frag. 2	655	G	—
28S frag. 2	769	A	C
28S frag. 3	76	—	T
28S frag. 3	87	—	C
28S frag. 3	347	A	G
H1 frag. 1	41	A	G
H1 frag. 10	101	A	G
H1 frag. 11	27	A	G
H1 frag. 11	88	T	C
H1 frag. 11	89	T	C
H1 frag. 11	827	—	T
H1 frag. 11	830	—	A
H1 frag. 11	1170	T	C
H1 frag. 12	9	C	A
H1 frag. 13	29	T	A
H1 frag. 14	193	T	A
H1 frag. 14	238	T	C
H1 frag. 16	152	T	—
H1 frag. 16	382	A	T
H1 frag. 16	485	T	A
H1 frag. 17	372	T	A
H1 frag. 17	410	—	T
H1 frag. 19	28	—	A
H1 frag. 19	201	C	A
H1 frag. 2	14	A	C
H1 frag. 2	133	T	A
H1 frag. 2	218	A	C
H1 frag. 20	7	G	A
H1 frag. 23	96	T	A
H1 frag. 23	421	—	A
H1 frag. 23	1342	T	C
H1 frag. 23	1714	A	G
H1 frag. 23	1748	T	C
H1 frag. 3	394	—	C
H1 frag. 4	191	T	C
H1 frag. 4	548	T	C
H1 frag. 8	33	C	A
H1 frag. 8	562	G	A
H1 frag. 8	727	C	A
H3 frag. 1	114	A	C
H3 frag. 1	129	G	A
rhod frag. 1	85	A	C
rhod frag. 2	3	A	G
rhod frag. 2	9	A	G
rhod frag. 2	42	G	C
rhod frag. 2	51	T	C
SIA frag. 3	171	G	C
476 (*Rhaebo*)			
28S frag. 2	466	—	T
28S frag. 2	505	C	G
H1 frag. 10	269	C	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 11	7	G	A
H1 frag. 11	126	T	C
H1 frag. 11	1166	—	G
H1 frag. 12	9	A	C
H1 frag. 12	160	T	G
H1 frag. 14	4	G	A
H1 frag. 14	144	A	G
H1 frag. 14	177	T	C
H1 frag. 15	22	T	C
H1 frag. 16	21	A	T
H1 frag. 16	298	T	A
H1 frag. 16	382	T	A
H1 frag. 16	535	C	T
H1 frag. 17	196	T	C
H1 frag. 17	413	T	G
H1 frag. 18	52	A	T
H1 frag. 19	123	A	C
H1 frag. 19	449	T	A
H1 frag. 19	542	C	T
H1 frag. 2	437	T	A
H1 frag. 23	50	C	T
H1 frag. 23	776	—	A
H1 frag. 23	1711	A	C
H1 frag. 23	1793	T	C
H1 frag. 3	20	A	T
H1 frag. 3	299	T	C
H1 frag. 3	391	T	—
H1 frag. 4	316	C	T
H1 frag. 4	373	G	A
H1 frag. 4	386	T	A
H1 frag. 4	461	A	C
H1 frag. 4	603	C	T
H1 frag. 6	34	G	A
H1 frag. 8	161	T	C
H1 frag. 8	488	T	A
H1 frag. 8	601	—	C
H1 frag. 8	628	T	—
H1 frag. 8	647	A	G
H1 frag. 8	721	C	T
H1 frag. 8	809	G	A
H1 frag. 9	315	A	—
H1 frag. 9	321	T	C
H1 frag. 9	714	A	C
H3 frag. 1	111	T	A
H3 frag. 1	162	C	G
H3 frag. 1	213	C	T
rhod frag. 1	102	G	T
rhod frag. 2	79	C	T
491 (*Ingerophrynus*)			
H1 frag. 2	20	T	C
H1 frag. 2	323	—	C
H1 frag. 23	387	A	T
H1 frag. 23	1097	G	A
H1 frag. 23	1796	A	C
H1 frag. 23	1828	C	A
H1 frag. 4	264	A	G
H1 frag. 4	401	T	—
H1 frag. 4	489	T	C
H1 frag. 8	232	C	T
H1 frag. 8	249	A	T
H1 frag. 8	260	A	C
H1 frag. 8	313	C	T
H1 frag. 8	523	C	T
H1 frag. 8	735	C	T
H1 frag. 9	321	T	—
499 (*Bufo*)			
H1 frag. 1	71	A	C
H1 frag. 11	31	T	C
H1 frag. 11	1259	T	C
H1 frag. 13	7	T	—
H1 frag. 13	14	A	—
H1 frag. 13	121	T	C
H1 frag. 13	193	T	C
H1 frag. 14	208	A	G
H1 frag. 15	33	C	T
H1 frag. 16	19	C	T
H1 frag. 16	96	—	G
H1 frag. 16	308	—	A
H1 frag. 16	648	T	C
H1 frag. 18	24	T	C

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 18	79	A	T
H1 frag. 18	109	T	A
H1 frag. 18	237	T	A
H1 frag. 18	254	C	A
H1 frag. 18	349	A	G
H1 frag. 18	571	T	C
H1 frag. 18	868	A	T
H1 frag. 19	145	A	C
H1 frag. 19	181	G	A
H1 frag. 19	203	A	G
H1 frag. 19	209	C	T
H1 frag. 19	771	C	T
H1 frag. 19	808	A	G
H1 frag. 2	88	T	C
H1 frag. 2	171	T	C
H1 frag. 21	133	C	T
H1 frag. 22	55	T	C
H1 frag. 23	224	T	C
H1 frag. 23	274	C	T
H1 frag. 23	283	T	C
H1 frag. 23	335	A	C
H1 frag. 23	416	T	C
H1 frag. 23	421	A	T
H1 frag. 23	789	C	—
H1 frag. 23	811	T	A
H1 frag. 23	902	T	C
H1 frag. 23	1074	A	G
H1 frag. 23	1154	A	G
H1 frag. 23	1233	A	G
H1 frag. 23	1245	T	C
H1 frag. 23	1256	A	G
H1 frag. 23	1364	T	C
H1 frag. 23	1607	T	A
H1 frag. 23	1940	T	C
H1 frag. 24	12	G	A
H1 frag. 6	169	C	—
H1 frag. 8	461	—	A
H1 frag. 9	46	T	C
rhod frag. 1	94	G	A
rhod frag. 1	128	T	A
rhod frag. 2	79	C	G
rhod frag. 2	113	G	A
rhod frag. 2	116	T	C
rhod frag. 2	129	T	C
rhod frag. 2	130	A	C
506 (*Amietophrynus*)			
H1 frag. 23	17	A	G
H1 frag. 23	1337	C	T
H1 frag. 23	1554	T	A
H1 frag. 23	1739	C	A
H1 frag. 23	1781	T	C
H1 frag. 23	1798	T	C
H1 frag. 23	1973	T	G
H1 frag. 6	199	A	T
H1 frag. 8	562	A	G
513 (*Anaxyrus*)			
H1 frag. 1	40	A	G
H1 frag. 11	887	T	C
H1 frag. 11	1089	C	T
H1 frag. 11	1235	—	A
H1 frag. 14	193	A	T
H1 frag. 14	208	A	T
H1 frag. 16	99	C	T
H1 frag. 16	221	A	T
H1 frag. 16	648	T	C
H1 frag. 17	333	A	C
H1 frag. 18	741	A	C
H1 frag. 19	376	A	C
H1 frag. 19	668	T	C
H1 frag. 23	103	A	T
H1 frag. 23	1214	A	T
H1 frag. 3	108	C	A
H1 frag. 7	39	T	C
H1 frag. 7	84	T	C
H1 frag. 7	96	C	A
H1 frag. 8	313	C	T
H1 frag. 8	523	C	T
rhod frag. 2	80	G	A

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Br/Taxon/Frag	Pos	Anc	Der
519 (*Cranopsis*)			
H1 frag. 11	1161	T	A
H1 frag. 12	148	A	G
H1 frag. 12	186	C	A
H1 frag. 14	93	A	T
H1 frag. 16	221	A	C
H1 frag. 16	648	T	A
H1 frag. 16	678	C	A
H1 frag. 17	333	A	T
H1 frag. 17	372	A	T
H1 frag. 17	411	—	T
H1 frag. 18	322	C	A
H1 frag. 18	539	T	A
H1 frag. 18	581	A	T
H1 frag. 18	707	C	T
H1 frag. 18	732	C	T
H1 frag. 2	88	T	A
H1 frag. 21	139	T	C
H1 frag. 23	1074	A	T
H1 frag. 23	1181	A	T
H1 frag. 3	130	T	C
H1 frag. 4	452	A	G
H1 frag. 4	672	C	T
H1 frag. 8	69	T	C
H1 frag. 8	735	T	C
H1 frag. 9	708	A	T
522 (*Chaunus*)			
28S frag. 2	453	C	T
H1 frag. 11	1170	C	T
H1 frag. 13	8	T	A
H1 frag. 14	193	A	G
H1 frag. 16	127	T	C
H1 frag. 16	590	A	G
H1 frag. 17	310	—	C
H1 frag. 20	23	C	T
H1 frag. 21	76	A	C
H1 frag. 23	224	T	C
H1 frag. 23	335	A	—
H1 frag. 23	362	C	—
H1 frag. 23	397	C	A
H1 frag. 23	888	—	C
H1 frag. 23	1233	A	G
H1 frag. 23	1321	G	A
H1 frag. 23	1973	A	C
H1 frag. 4	246	A	T
H1 frag. 6	181	C	T
H1 frag. 8	444	—	A
H1 frag. 9	43	C	A
rhod frag. 1	51	T	C
Amolops/Amolops hongkongensis			
H1 frag. 10	55	A	—
H1 frag. 11	86	A	—
H1 frag. 11	89	C	—
H1 frag. 11	91	A	—
H1 frag. 11	92	T	—
H1 frag. 11	95	T	—
H1 frag. 11	96	T	—
H1 frag. 11	120	G	—
H1 frag. 11	130	T	—
H1 frag. 11	134	A	—
H1 frag. 11	138	A	—
H1 frag. 11	139	A	—
H1 frag. 11	146	C	—
H1 frag. 11	155	A	—
H1 frag. 11	160	G	—
H1 frag. 11	213	C	—
H1 frag. 11	230	C	—
H1 frag. 11	264	C	—
H1 frag. 11	315	A	—
H1 frag. 11	368	C	—
H1 frag. 11	409	C	—
H1 frag. 11	425	A	—
H1 frag. 11	439	C	—
H1 frag. 11	505	C	—
H1 frag. 11	565	C	—
H1 frag. 11	600	G	—
H1 frag. 11	622	A	—
H1 frag. 11	663	A	—
H1 frag. 11	668	C	—
H1 frag. 11	852	T	—

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 11	963	C	—
H1 frag. 11	983	C	—
H1 frag. 11	1000	C	—
H1 frag. 11	1113	G	—
H1 frag. 11	1135	C	—
H1 frag. 11	1161	C	—
H1 frag. 11	1191	C	—
H1 frag. 11	1232	A	—
H1 frag. 11	1327	T	A
H1 frag. 11	1333	T	C
H1 frag. 12	9	C	T
H1 frag. 12	103	A	T
H1 frag. 12	128	C	T
H1 frag. 12	148	T	C
H1 frag. 12	173	C	T
H1 frag. 12	177	G	—
H1 frag. 12	186	T	C
H1 frag. 13	82	T	C
H1 frag. 13	116	C	T
H1 frag. 13	141	A	—
H1 frag. 13	167	—	T
H1 frag. 13	168	C	A
H1 frag. 13	172	C	T
H1 frag. 14	12	C	T
H1 frag. 14	35	A	—
H1 frag. 14	51	A	G
H1 frag. 14	63	A	G
H1 frag. 14	86	C	G
H1 frag. 14	89	T	C
H1 frag. 14	102	T	C
H1 frag. 14	158	C	—
H1 frag. 14	242	G	A
H1 frag. 14	260	G	T
H1 frag. 15	36	T	C
H1 frag. 15	43	G	A
H1 frag. 15	50	C	T
H1 frag. 16	127	T	A
H1 frag. 16	170	T	A
H1 frag. 16	266	T	A
H1 frag. 16	429	C	T
H1 frag. 16	464	A	T
H1 frag. 16	535	A	T
H1 frag. 16	576	C	G
H1 frag. 16	614	T	C
H1 frag. 17	20	G	A
H1 frag. 17	22	T	C
H1 frag. 17	81	A	T
H1 frag. 17	231	G	A
H1 frag. 17	383	T	A
H1 frag. 17	446	A	C
H1 frag. 18	79	A	G
H1 frag. 18	106	—	C
H1 frag. 18	107	—	A
H1 frag. 18	108	—	A
H1 frag. 18	109	T	C
H1 frag. 18	411	C	T
H1 frag. 18	447	T	A
H1 frag. 18	514	T	—
H1 frag. 18	530	T	A
H1 frag. 18	628	C	T
H1 frag. 18	667	—	C
H1 frag. 18	866	G	A
H1 frag. 19	24	A	T
H1 frag. 19	54	T	A
H1 frag. 19	91	T	A
H1 frag. 19	148	A	T
H1 frag. 19	154	A	G
H1 frag. 19	159	—	A
H1 frag. 19	203	A	C
H1 frag. 19	211	A	G
H1 frag. 19	349	—	A
H1 frag. 19	453	A	—
H1 frag. 19	518	T	A
H1 frag. 19	531	A	C
H1 frag. 19	578	A	T
H1 frag. 19	729	C	A
H1 frag. 19	796	A	G
H1 frag. 19	819	T	C
H1 frag. 20	16	T	C
H1 frag. 20	146	T	C

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 21	57	A	T
H1 frag. 21	90	T	C
H1 frag. 21	218	C	T
H1 frag. 22	62	G	A
H1 frag. 23	21	G	A
H1 frag. 23	24	A	G
H1 frag. 23	163	C	—
H1 frag. 23	182	T	G
H1 frag. 23	199	A	—
H1 frag. 23	238	T	C
H1 frag. 23	274	C	A
H1 frag. 23	942	C	A
H1 frag. 23	1214	T	C
H1 frag. 23	1226	T	—
H1 frag. 23	1256	T	C
H1 frag. 23	1270	A	G
H1 frag. 23	1288	T	C
H1 frag. 23	1342	T	C
H1 frag. 23	1518	T	A
H1 frag. 23	1711	C	A
H1 frag. 23	1726	C	T
H1 frag. 23	1732	T	G
H1 frag. 24	24	G	A
H1 frag. 25	50	T	—
H1 frag. 6	81	C	T
H1 frag. 6	163	C	T
H1 frag. 6	199	C	T
H1 frag. 7	15	T	C
H1 frag. 7	91	—	T
H1 frag. 7	92	C	T
H1 frag. 8	29	T	C
H1 frag. 8	109	—	T
H1 frag. 8	116	C	T
H1 frag. 8	139	T	C
H1 frag. 8	159	G	A
H1 frag. 8	161	A	C
H1 frag. 8	249	T	A
H1 frag. 8	344	—	G
H1 frag. 8	350	—	T
H1 frag. 8	351	—	T
H1 frag. 8	387	T	A
H1 frag. 8	501	—	A
H1 frag. 8	503	C	A
H1 frag. 8	514	T	C
H1 frag. 8	525	C	T
H1 frag. 8	551	G	A
H1 frag. 8	626	T	C
H1 frag. 8	628	T	G
H1 frag. 8	665	—	T
H1 frag. 8	696	A	G
H1 frag. 8	714	A	G
H1 frag. 8	816	T	—
H1 frag. 9	66	—	T
H1 frag. 9	67	C	G
H1 frag. 9	71	C	T
H1 frag. 9	81	C	T
H1 frag. 9	281	A	—
H1 frag. 9	367	C	A
H1 frag. 9	467	G	A
H1 frag. 9	528	—	T
H1 frag. 9	615	—	T
H1 frag. 9	652	A	—
H1 frag. 9	693	C	T
H1 frag. 9	775	C	T
Aquixalus/Aquixalus gracilipes			
H1 frag. 1	36	A	T
H1 frag. 1	38	T	C
H1 frag. 1	72	C	T
H1 frag. 10	19	A	G
H1 frag. 10	24	A	G
H1 frag. 10	43	A	—
H1 frag. 10	269	C	T
H1 frag. 11	7	G	A
H1 frag. 11	31	T	C
H1 frag. 11	36	T	C
H1 frag. 11	79	A	G
H1 frag. 11	86	A	G
H1 frag. 11	282	—	G
H1 frag. 11	505	C	T
H1 frag. 11	819	T	A

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 11	852	C	T
H1 frag. 11	933	—	C
H1 frag. 11	1057	—	C
H1 frag. 11	1089	T	G
H1 frag. 11	1232	A	C
H1 frag. 11	1245	A	C
H1 frag. 11	1248	A	G
H1 frag. 11	1333	T	C
H1 frag. 12	74	T	C
H1 frag. 12	125	T	A
H1 frag. 12	153	A	G
H1 frag. 12	187	G	A
H1 frag. 13	4	T	C
H1 frag. 13	33	T	C
H1 frag. 13	125	A	C
H1 frag. 13	127	T	C
H1 frag. 14	9	G	A
H1 frag. 14	63	A	G
H1 frag. 14	64	C	T
H1 frag. 14	65	G	A
H1 frag. 14	80	—	C
H1 frag. 14	102	T	C
H1 frag. 14	238	A	G
H1 frag. 14	250	C	T
H1 frag. 15	12	A	G
H1 frag. 15	15	A	T
H1 frag. 15	45	C	T
H1 frag. 15	50	C	T
H1 frag. 16	8	G	A
H1 frag. 16	10	A	G
H1 frag. 16	127	C	T
H1 frag. 16	201	T	C
H1 frag. 16	359	C	T
H1 frag. 16	563	A	C
H1 frag. 17	23	A	T
H1 frag. 17	429	A	G
H1 frag. 18	433	T	C
H1 frag. 18	494	C	T
H1 frag. 18	741	C	T
H1 frag. 18	883	C	T
H1 frag. 19	54	T	A
H1 frag. 19	119	A	G
H1 frag. 19	154	A	G
H1 frag. 19	197	A	C
H1 frag. 19	203	A	C
H1 frag. 19	211	A	C
H1 frag. 19	213	T	C
H1 frag. 19	216	T	C
H1 frag. 19	356	T	A
H1 frag. 19	514	—	T
H1 frag. 19	542	A	G
H1 frag. 19	600	C	T
H1 frag. 19	612	T	C
H1 frag. 19	749	A	C
H1 frag. 2	42	C	A
H1 frag. 2	328	A	C
H1 frag. 2	420	A	G
H1 frag. 2	424	A	C
H1 frag. 20	1	T	C
H1 frag. 20	16	T	C
H1 frag. 21	57	A	C
H1 frag. 21	76	T	C
H1 frag. 21	124	A	G
H1 frag. 21	251	A	T
H1 frag. 22	10	C	A
H1 frag. 22	11	C	A
H1 frag. 22	23	G	A
H1 frag. 23	559	C	A
H1 frag. 23	1060	C	T
H1 frag. 23	1169	C	A
H1 frag. 23	1181	A	C
H1 frag. 23	1221	C	A
H1 frag. 23	1226	T	C
H1 frag. 23	1316	T	C
H1 frag. 23	1342	T	C
H1 frag. 23	1478	A	G
H1 frag. 23	1607	A	G
H1 frag. 23	1726	C	T
H1 frag. 23	1750	T	C
H1 frag. 23	1865	G	A

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Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 23	1882	A	T
H1 frag. 23	1968	C	—
H1 frag. 25	17	T	C
H1 frag. 25	32	G	A
H1 frag. 3	16	G	A
H1 frag. 3	20	T	A
H1 frag. 3	176	A	G
H1 frag. 3	184	A	G
H1 frag. 3	342	T	A
H1 frag. 3	402	T	A
H1 frag. 4	24	A	G
H1 frag. 4	26	A	G
H1 frag. 4	94	T	G
H1 frag. 4	169	A	—
H1 frag. 4	274	A	G
H1 frag. 4	283	T	C
H1 frag. 4	292	T	A
H1 frag. 4	298	A	G
H1 frag. 4	404	C	T
H1 frag. 4	408	T	C
H1 frag. 4	461	A	G
H1 frag. 4	477	T	A
H1 frag. 4	565	—	A
H1 frag. 4	627	—	T
H1 frag. 4	637	C	A
H1 frag. 4	663	T	C
H1 frag. 5	5	G	A
H1 frag. 6	31	C	T
H1 frag. 6	62	A	T
H1 frag. 6	81	C	T
H1 frag. 6	137	C	—
H1 frag. 6	181	A	C
H1 frag. 8	37	C	G
H1 frag. 8	41	T	C
H1 frag. 8	69	C	T
H1 frag. 8	97	—	T
H1 frag. 8	181	A	G
H1 frag. 8	232	T	C
H1 frag. 8	321	A	G
H1 frag. 8	550	G	A
H1 frag. 8	551	A	G
H1 frag. 8	569	A	—
H1 frag. 8	611	A	G
H1 frag. 8	711	T	C
H1 frag. 9	5	T	A
H1 frag. 9	14	A	G
H1 frag. 9	22	A	C
H1 frag. 9	46	A	C
H1 frag. 9	57	T	C
H1 frag. 9	73	T	C
H1 frag. 9	367	A	T
H1 frag. 9	506	A	C
H1 frag. 9	812	A	G
rhod frag. 1	21	T	C
rhod frag. 1	85	A	C
rhod frag. 1	87	G	A
rhod frag. 1	104	C	T
rhod frag. 1	107	C	T
rhod frag. 2	86	C	A
rhod frag. 2	97	C	A
rhod frag. 2	98	C	A
rhod frag. 2	100	C	G
rhod frag. 2	113	G	A
rhod frag. 2	115	A	C
rhod frag. 2	126	A	C
rhod frag. 2	130	G	A
Duttaphrynus/Bufo melanostictus			
28S frag. 4	40	G	A
H1 frag. 1	20	A	G
H1 frag. 10	86	T	A
H1 frag. 11	91	A	G
H1 frag. 11	536	T	C
H1 frag. 11	622	T	—
H1 frag. 11	663	T	G
H1 frag. 11	1009	—	C
H1 frag. 11	1049	A	C
H1 frag. 11	1316	A	T
H1 frag. 12	59	T	—
H1 frag. 12	153	A	C
H1 frag. 12	160	T	C

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 13	33	A	C
H1 frag. 13	47	T	A
H1 frag. 13	121	T	C
H1 frag. 13	159	T	A
H1 frag. 13	169	C	A
H1 frag. 14	78	T	A
H1 frag. 14	166	C	T
H1 frag. 14	244	G	A
H1 frag. 15	54	A	G
H1 frag. 16	1	A	T
H1 frag. 16	11	A	G
H1 frag. 16	100	T	—
H1 frag. 16	127	T	—
H1 frag. 16	279	—	A
H1 frag. 16	292	C	A
H1 frag. 16	398	T	A
H1 frag. 16	443	—	T
H1 frag. 16	537	T	C
H1 frag. 16	590	A	T
H1 frag. 16	648	A	G
H1 frag. 16	691	A	T
H1 frag. 17	372	A	G
H1 frag. 17	413	T	C
H1 frag. 18	1	G	C
H1 frag. 18	83	T	A
H1 frag. 18	138	A	G
H1 frag. 18	254	C	—
H1 frag. 18	357	—	C
H1 frag. 18	727	C	A
H1 frag. 18	822	T	C
H1 frag. 19	54	A	C
H1 frag. 19	63	—	A
H1 frag. 19	140	T	C
H1 frag. 19	195	C	T
H1 frag. 19	203	A	G
H1 frag. 19	244	A	G
H1 frag. 19	403	A	T
H1 frag. 19	668	T	C
H1 frag. 2	32	A	G
H1 frag. 2	63	—	T
H1 frag. 2	100	A	T
H1 frag. 2	133	C	A
H1 frag. 2	184	C	A
H1 frag. 2	277	G	A
H1 frag. 2	437	T	C
H1 frag. 2	439	T	C
H1 frag. 20	7	A	G
H1 frag. 20	20	T	A
H1 frag. 20	129	A	C
H1 frag. 20	182	T	C
H1 frag. 21	155	T	C
H1 frag. 23	87	G	A
H1 frag. 23	199	C	A
H1 frag. 23	213	A	G
H1 frag. 23	359	—	T
H1 frag. 23	404	A	—
H1 frag. 23	416	T	G
H1 frag. 23	623	T	C
H1 frag. 23	811	T	C
H1 frag. 23	854	A	C
H1 frag. 23	912	A	T
H1 frag. 23	1068	—	C
H1 frag. 23	1181	A	C
H1 frag. 23	1245	T	C
H1 frag. 23	1270	A	C
H1 frag. 23	1329	C	T
H1 frag. 23	1554	T	G
H1 frag. 23	1607	T	C
H1 frag. 23	1781	T	A
H1 frag. 23	1793	T	G
H1 frag. 23	1940	T	A
H1 frag. 23	1962	C	T
H1 frag. 3	22	A	T
H1 frag. 3	26	T	C
H1 frag. 3	401	—	A
H1 frag. 4	126	T	A
H1 frag. 4	169	T	G
H1 frag. 4	265	G	A
H1 frag. 4	401	T	—
H1 frag. 4	408	A	G

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 4	430	A	G
H1 frag. 4	447	A	G
H1 frag. 4	484	C	T
H1 frag. 4	529	A	T
H1 frag. 7	74	A	G
H1 frag. 8	40	T	C
H1 frag. 8	59	T	C
H1 frag. 9	367	A	G
H1 frag. 9	490	—	G
H3 frag. 1	75	T	C
H3 frag. 1	138	C	T
H3 frag. 1	213	C	T
H3 frag. 2	81	G	C
rhod frag. 1	42	A	G
rhod frag. 1	94	G	T
rhod frag. 1	96	T	G
rhod frag. 2	69	T	C
rhod frag. 2	80	A	G
rhod frag. 2	112	C	T
rhod frag. 2	118	C	A
rhod frag. 2	130	A	T
SIA frag. 2	32	A	G
SIA frag. 2	53	A	C
SIA frag. 4	76	T	G
Meristogenys/Meristogenys orphnocnemis			
H1 frag. 10	6	T	G
H1 frag. 10	80	—	C
H1 frag. 10	217	T	A
H1 frag. 11	57	T	A
H1 frag. 11	79	A	G
H1 frag. 11	368	C	T
H1 frag. 11	392	A	T
H1 frag. 11	446	—	T
H1 frag. 11	595	A	—
H1 frag. 11	762	C	T
H1 frag. 11	819	C	T
H1 frag. 11	887	C	T
H1 frag. 11	963	C	T
H1 frag. 11	983	C	T
H1 frag. 11	1205	—	T
H1 frag. 11	1333	T	C
H1 frag. 12	106	—	C
H1 frag. 21	133	A	T
H1 frag. 21	178	C	T
H1 frag. 22	62	G	A
H1 frag. 23	299	C	T
H1 frag. 23	506	—	G
H1 frag. 23	963	T	A
H1 frag. 23	1003	—	T
H1 frag. 23	1015	A	C
H1 frag. 23	1077	G	—
H1 frag. 23	1303	A	G
H1 frag. 23	1342	T	C
H1 frag. 23	1427	C	T
H1 frag. 23	1951	T	A
H1 frag. 24	17	C	T
H1 frag. 25	20	C	A
H1 frag. 6	25	C	T
H1 frag. 6	31	C	A
H1 frag. 6	62	A	T
H1 frag. 6	126	—	T
H1 frag. 6	167	A	—
H1 frag. 6	181	A	T
H1 frag. 6	213	C	T
H1 frag. 7	6	A	C
H1 frag. 7	78	C	T
H1 frag. 8	29	T	C
H1 frag. 8	69	C	T
H1 frag. 8	85	—	C
H1 frag. 8	161	A	G
H1 frag. 8	181	G	A
H1 frag. 8	352	A	G
H1 frag. 8	514	T	C
H1 frag. 8	550	G	A
H1 frag. 8	553	A	G
H1 frag. 8	568	T	A
H1 frag. 8	626	T	A
H1 frag. 8	714	A	G
H1 frag. 8	735	A	G

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 8	748	G	C
H1 frag. 8	772	—	C
H1 frag. 8	773	T	C
H1 frag. 8	796	T	C
H1 frag. 8	838	C	A
H1 frag. 9	1	T	C
H1 frag. 9	22	A	G
H1 frag. 9	27	A	G
H1 frag. 9	28	A	G
H1 frag. 9	48	T	C
H1 frag. 9	52	T	C
H1 frag. 9	84	T	A
H1 frag. 9	90	G	A
H1 frag. 9	367	C	G
H1 frag. 9	481	T	A
H1 frag. 9	507	—	T
H1 frag. 9	580	C	A
H1 frag. 9	637	—	T
H1 frag. 9	672	T	A
H1 frag. 9	755	T	C
H1 frag. 9	840	T	C
rhod frag. 1	45	C	T
Opisthodon/Limnodynastes ornatus			
28S frag. 2	448	—	C
28S frag. 2	473	T	C
28S frag. 2	492	—	G
28S frag. 2	493	—	T
28S frag. 3	389	C	T
H1 frag. 1	22	G	T
H1 frag. 1	33	C	T
H1 frag. 11	368	C	T
H1 frag. 11	392	C	T
H1 frag. 11	409	T	G
H1 frag. 11	536	C	T
H1 frag. 11	681	—	G
H1 frag. 11	682	A	T
H1 frag. 11	849	—	T
H1 frag. 11	1079	A	—
H1 frag. 11	1161	A	T
H1 frag. 11	1336	C	T
H1 frag. 12	96	—	C
H1 frag. 13	91	T	C
H1 frag. 13	117	C	T
H1 frag. 13	141	A	C
H1 frag. 16	382	T	A
H1 frag. 16	429	C	T
H1 frag. 16	547	A	G
H1 frag. 16	654	—	G
H1 frag. 16	681	C	T
H1 frag. 17	12	C	T
H1 frag. 17	38	A	G
H1 frag. 17	52	A	T
H1 frag. 17	118	G	—
H1 frag. 17	160	C	A
H1 frag. 17	423	G	A
H1 frag. 18	185	C	T
H1 frag. 18	377	—	T
H1 frag. 18	378	A	T
H1 frag. 18	388	C	T
H1 frag. 18	411	C	A
H1 frag. 18	512	—	A
H1 frag. 18	550	A	T
H1 frag. 18	563	C	A
H1 frag. 18	628	T	—
H1 frag. 18	727	A	T
H1 frag. 18	767	T	C
H1 frag. 18	830	C	T
H1 frag. 18	838	A	C
H1 frag. 18	861	A	G
H1 frag. 18	872	C	A
H1 frag. 18	878	T	C
H1 frag. 19	119	C	T
H1 frag. 19	197	A	C
H1 frag. 19	415	C	T
H1 frag. 19	439	G	T
H1 frag. 19	542	C	T
H1 frag. 19	796	A	G
H1 frag. 2	16	C	T
H1 frag. 2	65	T	C
H1 frag. 2	328	C	T

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Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 2	438	A	G
H1 frag. 20	25	G	A
H1 frag. 20	115	T	C
H1 frag. 21	113	A	G
H1 frag. 23	224	C	T
H1 frag. 23	547	—	A
H1 frag. 23	652	—	C
H1 frag. 23	654	T	C
H1 frag. 23	693	A	G
H1 frag. 23	729	C	T
H1 frag. 23	942	T	A
H1 frag. 23	1233	G	A
H1 frag. 3	214	T	C
H1 frag. 4	169	A	C
H1 frag. 4	254	C	T
H1 frag. 4	502	—	A
H1 frag. 4	503	—	A
H1 frag. 6	163	C	T
H3 frag. 1	108	C	T
rhod frag. 1	3	T	C
rhod frag. 1	36	A	G
rhod frag. 2	85	G	A
rhod frag. 2	94	C	T
SIA frag. 1	4	T	C
SIA frag. 1	12	T	C
SIA frag. 1	21	A	G
SIA frag. 2	47	C	G
SIA frag. 2	53	A	C
SIA frag. 2	71	G	C
SIA frag. 3	3	A	G
SIA frag. 3	48	C	T
SIA frag. 3	69	C	G
SIA frag. 3	96	G	A
SIA frag. 3	144	T	C
SIA frag. 3	156	A	G
SIA frag. 4	19	T	C
SIA frag. 4	37	T	C
SIA frag. 4	67	T	C
Phrynoidis/Bufo asper			
H1 frag. 1	38	A	C
H1 frag. 1	50	A	G
H1 frag. 1	57	A	T
H1 frag. 10	86	T	A
H1 frag. 10	101	G	A
H1 frag. 11	23	T	C
H1 frag. 11	488	—	T
H1 frag. 11	565	A	T
H1 frag. 11	887	T	C
H1 frag. 11	1046	—	A
H1 frag. 11	1217	T	A
H1 frag. 11	1232	T	C
H1 frag. 11	1294	T	C
H1 frag. 11	1327	T	C
H1 frag. 11	1336	C	T
H1 frag. 12	52	T	C
H1 frag. 12	125	T	C
H1 frag. 12	143	C	T
H1 frag. 12	148	A	G
H1 frag. 13	117	A	T
H1 frag. 14	35	A	C
H1 frag. 14	59	A	G
H1 frag. 14	78	T	A
H1 frag. 14	90	T	C
H1 frag. 14	113	T	C
H1 frag. 16	3	T	C
H1 frag. 16	19	T	A
H1 frag. 16	388	A	—
H1 frag. 16	439	—	C
H1 frag. 16	547	A	T
H1 frag. 16	652	—	C
H1 frag. 17	58	T	C
H1 frag. 17	333	C	G
H1 frag. 17	413	T	C
H1 frag. 17	437	C	T
H1 frag. 18	24	T	C
H1 frag. 18	45	T	C
H1 frag. 18	138	A	G
H1 frag. 18	570	T	C
H1 frag. 18	821	A	C
H1 frag. 18	830	A	G

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 19	135	A	G
H1 frag. 19	137	T	C
H1 frag. 19	231	T	C
H1 frag. 19	254	A	G
H1 frag. 19	600	T	A
H1 frag. 19	662	—	C
H1 frag. 19	729	A	—
H1 frag. 19	826	A	T
H1 frag. 2	73	T	C
H1 frag. 2	180	T	A
H1 frag. 2	184	C	A
H1 frag. 2	218	C	A
H1 frag. 2	277	A	G
H1 frag. 2	420	A	G
H1 frag. 20	7	A	G
H1 frag. 20	10	T	C
H1 frag. 21	113	T	A
H1 frag. 21	133	C	A
H1 frag. 23	48	T	C
H1 frag. 23	67	A	G
H1 frag. 23	100	A	C
H1 frag. 23	103	A	C
H1 frag. 23	274	C	T
H1 frag. 23	623	T	C
H1 frag. 23	693	T	C
H1 frag. 23	799	T	A
H1 frag. 23	902	T	C
H1 frag. 23	908	T	A
H1 frag. 23	1041	T	C
H1 frag. 23	1329	C	T
H1 frag. 23	1333	T	C
H1 frag. 23	1356	A	G
H1 frag. 23	1359	G	A
H1 frag. 23	1595	—	A
H1 frag. 23	1643	—	A
H1 frag. 23	1793	T	C
H1 frag. 23	1798	T	C
H1 frag. 23	1828	C	T
H1 frag. 23	1919	A	T
H1 frag. 23	1940	T	C
H1 frag. 23	1962	C	A
H1 frag. 24	10	A	G
H1 frag. 24	17	C	T
H1 frag. 3	22	A	C
H1 frag. 3	55	G	A
H1 frag. 3	58	C	T
H1 frag. 3	124	C	A
H1 frag. 3	327	C	T
H1 frag. 3	368	A	T
H1 frag. 4	239	—	C
H1 frag. 4	417	—	G
H1 frag. 4	473	A	G
H1 frag. 6	27	G	A
H1 frag. 6	163	A	G
H1 frag. 8	139	C	T
H1 frag. 8	177	A	C
H1 frag. 8	316	T	C
H1 frag. 8	582	T	C
H1 frag. 9	47	G	A
H1 frag. 9	321	T	C
H1 frag. 9	511	T	C
H1 frag. 9	672	A	C
H1 frag. 9	775	A	G
H3 frag. 1	15	C	A
H3 frag. 1	69	C	G
H3 frag. 1	114	C	A
H3 frag. 1	195	A	G
rhod frag. 2	42	C	T
SIA frag. 4	76	T	A
Pseudepidalea/Bufo viridis			
28S frag. 3	133	C	A
H1 frag. 10	93	A	G
H1 frag. 10	199	C	T
H1 frag. 10	217	C	A
H1 frag. 11	31	T	C
H1 frag. 11	36	C	T
H1 frag. 11	79	A	T
H1 frag. 11	86	A	G
H1 frag. 11	95	T	C
H1 frag. 11	1008	—	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 11	1048	—	T
H1 frag. 11	1049	A	T
H1 frag. 11	1071	A	C
H1 frag. 11	1170	C	T
H1 frag. 11	1248	A	T
H1 frag. 13	14	A	T
H1 frag. 13	116	A	G
H1 frag. 13	156	T	C
H1 frag. 14	35	A	G
H1 frag. 14	56	A	G
H1 frag. 14	193	A	G
H1 frag. 15	60	T	A
H1 frag. 16	14	C	T
H1 frag. 16	40	G	A
H1 frag. 16	118	—	C
H1 frag. 16	119	—	C
H1 frag. 16	127	T	C
H1 frag. 16	216	—	T
H1 frag. 16	221	A	G
H1 frag. 16	311	—	C
H1 frag. 16	398	T	C
H1 frag. 16	590	A	G
H1 frag. 16	671	C	T
H1 frag. 17	16	C	A
H1 frag. 17	58	T	C
H1 frag. 17	210	C	A
H1 frag. 18	322	C	A
H1 frag. 18	501	C	T
H1 frag. 18	604	T	A
H1 frag. 18	707	C	T
H1 frag. 18	741	A	G
H1 frag. 18	822	T	A
H1 frag. 19	153	A	T
H1 frag. 19	197	A	T
H1 frag. 19	376	T	C
H1 frag. 19	823	C	T
H1 frag. 2	171	T	C
H1 frag. 20	23	C	A
H1 frag. 23	224	T	C
H1 frag. 23	387	A	T
H1 frag. 23	421	A	T
H1 frag. 23	807	A	T
H1 frag. 23	902	T	C
H1 frag. 23	1088	G	A
H1 frag. 23	1233	A	G
H1 frag. 23	1256	A	G
H1 frag. 23	1518	A	C
H1 frag. 23	1793	T	C
H1 frag. 3	327	C	T
H1 frag. 4	191	C	A
H1 frag. 4	223	C	A
H1 frag. 4	254	C	A
H1 frag. 4	286	A	G
H1 frag. 4	452	A	T
H1 frag. 4	592	A	T
H1 frag. 4	670	A	C
H1 frag. 7	6	A	T
H1 frag. 8	57	T	C
H1 frag. 8	200	C	T
H1 frag. 8	232	C	A
H1 frag. 8	316	T	C
H1 frag. 8	446	—	A
H1 frag. 8	554	A	G
H1 frag. 9	27	G	A
H1 frag. 9	281	T	—
H1 frag. 9	618	A	G
H1 frag. 9	693	A	C
H3 frag. 1	6	A	G
rhod frag. 1	3	C	T
rhod frag. 2	136	C	T
SIA frag. 1	36	C	T
SIA frag. 1	42	G	C
SIA frag. 3	90	C	T
Rhinella/Bufo margaritifer			
H1 frag. 19	151	A	T
H1 frag. 19	153	A	G
H1 frag. 19	244	A	C
H1 frag. 19	307	C	T
H1 frag. 19	424	G	A
H1 frag. 19	623	C	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 20	54	A	T
H1 frag. 21	76	A	G
H1 frag. 21	133	C	T
H1 frag. 21	139	C	T
H1 frag. 23	11	C	T
H1 frag. 23	25	T	C
H1 frag. 23	48	T	C
H1 frag. 23	70	C	T
H1 frag. 23	103	A	C
H1 frag. 23	335	A	G
H1 frag. 23	693	T	A
H1 frag. 23	1154	A	G
H1 frag. 23	1181	A	G
H1 frag. 23	1245	T	C
H1 frag. 23	1303	T	C
H1 frag. 23	1322	C	T
H1 frag. 23	1358	T	C
H1 frag. 23	1359	G	A
H1 frag. 23	1427	A	C
H1 frag. 23	1714	G	A
H1 frag. 23	1739	A	T
H1 frag. 23	1748	C	T
H1 frag. 23	1750	T	A
H1 frag. 23	1828	C	T
H1 frag. 8	10	C	T
H1 frag. 8	93	T	C
H1 frag. 8	172	T	C
H1 frag. 8	232	C	T
H1 frag. 8	268	—	C
H1 frag. 8	272	T	A
H1 frag. 8	281	T	C
H1 frag. 8	298	G	A
H1 frag. 8	313	C	T
H1 frag. 8	520	A	C
H1 frag. 8	544	A	T
H1 frag. 8	556	T	A
H1 frag. 8	569	G	A
H1 frag. 8	611	T	C
H1 frag. 8	628	T	C
H1 frag. 8	727	C	—
H1 frag. 8	787	C	T
H1 frag. 9	5	C	A
H1 frag. 9	281	T	C
H1 frag. 9	362	—	C
H1 frag. 9	545	C	T
H1 frag. 9	632	—	T
H1 frag. 9	633	C	T
H1 frag. 9	672	A	T
H1 frag. 9	693	A	T
H1 frag. 9	714	G	A
H1 frag. 9	775	A	C
H1 frag. 9	818	C	T
Salamandrinae/*Salamandra salamandra*			
H1 frag. 10	23	A	G
H1 frag. 10	250	G	A
H1 frag. 11	86	G	A
H1 frag. 11	210	—	C
H1 frag. 11	211	—	C
H1 frag. 11	212	—	A
H1 frag. 11	499	—	T
H1 frag. 11	593	—	C
H1 frag. 11	818	—	T
H1 frag. 11	1161	A	T
H1 frag. 11	1266	C	T
H1 frag. 11	1342	T	A
H1 frag. 12	41	T	C
H1 frag. 12	45	T	A
H1 frag. 12	59	A	C
H1 frag. 13	97	A	T
H1 frag. 13	116	A	G
H1 frag. 13	168	A	C
H1 frag. 13	172	C	T
H1 frag. 14	146	A	G
H1 frag. 14	238	A	G
H1 frag. 15	21	T	C
H1 frag. 15	33	A	G
H1 frag. 16	8	G	A
H1 frag. 16	127	T	C
H1 frag. 16	201	T	A

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Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 16	232	—	T
H1 frag. 16	382	A	—
H1 frag. 16	509	A	T
H1 frag. 17	120	T	A
H1 frag. 17	231	A	G
H1 frag. 18	121	A	—
H1 frag. 18	138	A	T
H1 frag. 18	254	A	C
H1 frag. 18	276	C	T
H1 frag. 18	366	C	A
H1 frag. 18	514	A	C
H1 frag. 18	563	A	T
H1 frag. 18	707	C	—
H1 frag. 18	872	T	C
H1 frag. 19	42	A	G
H1 frag. 19	153	A	T
H1 frag. 19	195	A	T
H1 frag. 19	203	A	C
H1 frag. 19	237	A	G
H1 frag. 19	439	A	C
H1 frag. 19	715	A	C
H1 frag. 19	823	C	T
H1 frag. 20	51	T	A
H1 frag. 20	107	A	G
H1 frag. 21	23	C	T
H1 frag. 21	57	A	C
H1 frag. 21	90	A	T
H1 frag. 21	218	C	T
H1 frag. 21	243	T	C
H1 frag. 23	54	A	T
H1 frag. 23	61	G	A

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 23	70	C	T
H1 frag. 23	140	T	A
H1 frag. 23	556	—	T
H1 frag. 23	920	A	G
H1 frag. 23	1015	A	G
H1 frag. 23	1081	A	T
H1 frag. 23	1088	A	T
H1 frag. 23	1090	C	T
H1 frag. 23	1338	A	G
H1 frag. 23	1752	A	G
H1 frag. 23	1763	T	C
H1 frag. 23	1776	A	G
H1 frag. 24	34	T	A
H1 frag. 25	16	A	G
H1 frag. 25	20	A	C
H1 frag. 7	35	A	T
H1 frag. 7	78	C	T
H1 frag. 8	545	T	G
H1 frag. 8	554	A	G
H1 frag. 8	562	G	A
H1 frag. 8	710	A	T
H1 frag. 8	714	A	G
H1 frag. 8	792	A	—
H1 frag. 9	90	G	A
H1 frag. 9	283	—	T
H1 frag. 9	284	—	T
H1 frag. 9	294	—	A
H1 frag. 9	629	—	G
H1 frag. 9	633	A	T
H1 frag. 9	672	A	C
H1 frag. 9	708	A	G

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 9	775	A	G
H1 frag. 9	788	A	T
H3 frag. 1	37	C	T
H3 frag. 1	63	C	T
H3 frag. 1	99	C	T
H3 frag. 1	105	G	C
H3 frag. 1	219	C	T
rhod frag. 1	10	G	A
rhod frag. 1	78	G	C
rhod frag. 1	129	C	T
rhod frag. 1	140	C	T
rhod frag. 1	153	G	T
rhod frag. 2	27	C	T
rhod frag. 2	33	G	C
rhod frag. 2	39	G	T
rhod frag. 2	46	G	T
Stephopaedes			
H1 frag. 23	22	T	C
H1 frag. 23	70	C	T
H1 frag. 23	86	G	A
H1 frag. 23	102	A	T
H1 frag. 23	140	T	C
H1 frag. 23	340	C	T
H1 frag. 23	362	T	—
H1 frag. 23	404	A	—
H1 frag. 23	568	T	C
H1 frag. 23	762	T	C
H1 frag. 23	799	A	C
H1 frag. 23	807	T	C
H1 frag. 23	917	C	A
H1 frag. 23	1124	A	T

Br/Taxon/Frag	Pos	Anc	Der
H1 frag. 23	1154	A	T
H1 frag. 23	1303	T	C
H1 frag. 23	1321	G	A
H1 frag. 23	1329	C	A
H1 frag. 23	1333	T	C
H1 frag. 23	1358	T	C
H1 frag. 23	1364	T	C
H1 frag. 23	1695	G	A
H1 frag. 23	1732	T	C
H1 frag. 23	1759	C	T
H1 frag. 23	1824	T	C
H1 frag. 24	17	T	C
H1 frag. 24	19	C	A
H1 frag. 25	20	C	T
Vandijkophrynus			
H1 frag. 22	55	T	C
H1 frag. 23	5	T	C
H1 frag. 23	73	C	T
H1 frag. 23	199	T	C
H1 frag. 23	557	—	C
H1 frag. 23	789	C	A
H1 frag. 23	1071	—	T
H1 frag. 23	1072	—	T
H1 frag. 23	1108	T	C
H1 frag. 23	1181	A	C
H1 frag. 23	1342	T	C
H1 frag. 23	1549	—	C
H1 frag. 23	1627	A	T
H1 frag. 23	1745	G	A

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APPENDIX 6

NOMENCLATURAL NOTES

AMPHIBIA: Amphibia in the sense that we use it (Gray, 1825; de Queiroz and Gauthier, 1992; Cannatella and Hillis, 1993) corresponds reasonably closely to Lissamphibia of recent authors, although our concept excludes all fossil taxa outside of the living crown group, and is identical to the meaning of the term as used by the vast majority of scientists in day-to-day discourse. Lissamphibia was originally conceived of by Haeckel (1866) to include salamanders and frogs, but specifically excluded caecilians, making it synonymous with Batrachii Latreille (1800) and Batrachia of Rafinesque (1814) (which were Latinizations of the French vernacular Batraciens Brongniart, 1800a; Dubois, 2004b).[35] Gadow (1901) subsequently transferred caecilians into his Lissamphibia, and this concept of the taxon has persisted (e.g., Parsons and Williams, 1963), even as the familiar name ''Amphibia'' has had its intended meaning concomitantly eroded through its variable use for very different concepts of living and fossil groups (e.g., Huxley, 1863; Cope, 1880; Romer, 1933; Milner, 1993; Laurin and Reisz, 1997; Laurin, 2002; Ruta et al., 2003). We think, as did de Queiroz and Gauthier (1992) and Cannatella and Hillis (1993), that by restricting the name Amphibia to the best-known group (living amphibians; the concept of Gray, 1825, *not* of Linnaeus, 1758, the latter a heterogeneous taxon containing various amphibians and reptiles) will stabilize nomenclature without putting undue restraint on the formulation of systematic hypotheses. Dubois (2004b) has suggested that the name Amphibia should be attributed to de Blainville (1816). This attribution would require that one arbitrarily choose between two uses by de Blainville in the original paper. On page 107 of his *Prodromus*, he uses the term ''Amphybiens'' as a French colloquial equivalent of his equally French Nudipellifères. On page 111, he uses the name ''Amphibiens'' for an order containing solely ''Protees et les Sirens'' (proteids and sirenids), rendering Amphibiens de Blainville a synonym of Perennibranchia Latreille (1825). We follow de Blainville in his use of the term as a formal taxon name—in other words, as a synonym of Perennibranchia Latreille (1825).

Another synonym of Amphibia, as we employ it, is Neobatrachii, coined by Sarasin and Sarasin (1890: 245) as a subclass for all living amphibians. If one is unwilling to accept ''Amphibia'' as restricted to crown-group amphibians because of the rather large paleontological literature construing this term to early tetrapods, then Neobatrachii, unlike Lissamphibia, is the taxonomic name of choice because it is untroubled by variable application (Dubois, 2004b). (It is, however, homonymous with Neobatrachia Reig, 1958, a taxon of frogs [Dubois, 2004b], so should this become a communication problem in the future, a new name must be selected to replace Neobatrachia Reig.)

GYMNOPHIONA AND APODA: The names Apoda and Gymnophiona have been used more-or-less interchangeably for the taxon of caecilians for a long time. The first use of the name Apoda above the family group was by Linnaeus (1758) for a group of fishes, thereby making all subsequent uses of Apoda above the family group in Amphibia junior homonyms (although homonymy in above-family-group nomenclature does not have agreed-upon procedures to address it, and homonymy above the family-group level is considered by many to be a nonproblem). Oppel (1810) proposed the name Apoda explicitly as a family for caecilians, rendering his use of this name unavailable for above-family taxonomy under the provisions of the current International Code of Zoological Nomenclature (Dubois, 1984a: 112; ICZN, 1999; but see Dubois, 2004b). Fischer von Waldheim (1813) applied the name as a composite taxon containing caecilians, amphisbaenians, and snakes. Merrem (1820) was the first to use the name Apoda, as have many subsequent authors, in the modern sense as an order for caecilians. Dubois (2004b) regarded the homonymy of Apoda Linnaeus, 1758, and Apoda Merrem, 1820, as good reason to reject use of Apoda Merrem, 1820. Although there are no rules in unregulated nomenclature, we agree with Dubois (2004b) for a slightly different reason: that the name Apoda has been used—recently—in confusing ways in influential publications. Trueb and Cloutier (1991) considered the name Apoda Merrem, 1820, to apply to the living crown group of caecilians and the name Gymnophiona to apply to Apoda + *Eocaecilia* (a fossil form). Cannatella and Hillis (1993) and S.E. Evans and Sigogneau-Russell (2001) subsequently considered the name Gymnophiona to apply to the living crown group and the name Apoda to apply to their Gymnophiona + *Eocaecilia*, and Dubois (2005) treated Gymnophiona as including both the living crown group (his epifamily Caecilioidia) and *Eocaecilia*

[35] Although in regulated nomenclature the coining of certain vernacular (i.e., non-Latinized) names can be regarded as constituting the coining of a new scientific names (e.g., Art. 11.7.2; ICZN, 1999), we see no reason to extend that practice to unregulated nomenclature.

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(his epifamily Eocaecilioidia). This is problematic, and for this reason we provide the name Parabatrachia (etymology: para- [Greek: beside, resembling] + batrachos [Greek: frog, i.e., with reference to Batrachia]) for the taxon composed of living caecilians + *Eocaecilia* Jenkins and Walsh, 1993. The diagnosis of Parabatrachia is identical to Gymnophiona, except that limbs are retained (Trueb and Cloutier, 1991).

Gymnophia Rafinesque (1814: 104) is the oldest name available for the living crown-group taxon, and this was assumed (Dubois, 1984a, 2004b) to have been emended to Gymnophiona by J. Müller (1832: 198), although there is no evidence in Müller's paper that he was aware of the publication of Rafinesque (1814). It appears that J. Müller (1831) published the name Gymnophidia as alternative name for his Coeciliae (presumably a subsequent usage of Caeciliae Wagler, 1830) in ignorance of Rafinesque's (1814) earlier paper, and provided the name Gymnophiona J. Müller, 1832, as a replacement name for his earlier Gymnophidia. Gymnophia Rafinesque, 1814, is an earlier name, but predominant usage favors Gymnophiona J. Müller, 1832. Other names that are available for this taxon are: (1) Nuda Fitzinger, 1826; (2) Caeciliae Wagler, 1830; (3) Gymnophidia J. Müller, 1831; and (4) Pseudo-ophidia de Blainville, 1835 (a Latinization of Pseudophidiens de Blainville, 1816). Gymnodermia Rafinesque, 1815, is not available for this taxon, having originally been formed as a family-group taxon composed of caecilians and amphisbaenians.

BATRACHIA: As a concept, Batrachia extends from Batraciens Brongniart (1800a), a French vernacular name for salamanders plus frogs, but specifically excludes caecilians. This was subsequently Latinized (brought into scientific nomenclature in our view) by Latreille (1800) as Batrachii and as Batrachia of Rafinesque (1814). Trueb and Cloutier (1991) applied the name Batrachia to the clade composed of salamanders plus frogs, which is, in fact, the original content of the taxon so named (Dubois, 2004b). As early as Merrem (1820) the content of the group called Batrachia was expanded to include all living amphibians. Other available names for this taxon (in terms of implied content), although all junior to Batrachia Latreille, 1800, are Achelata Fischer von Waldheim, 1813; Dipnoa Leuckart, 1821; Amphibia Latreille, 1825; Caducibranchia Berthold, 1827; Astatodipnoa Wagler, 1828; Lissamphibia Haeckel, 1866; and Paratoidia Gardiner, 1982. Paratoidea de Queiroz and Gauthier, 1992 (an apparently incorrect subsequent spelling of Paratoidia Gardiner, 1982), was defined as Batrachia plus all fossil relatives more closely related to Batrachia than to Gymnophiona, and is therefore not synonymous.

CAUDATA: Caudata Scopoli (1777) originally included several reptile taxa as well as salamanders and clearly referred to a taxon quite different from that with which it is associated today. Duméril (1806: 94) used the name Caudati as the Latin equivalent of his Urodèles (but as an explicit family and therefore unavailable for use in unregulated nomenclature—contra Dubois, 2004b). This was likely a subsequent use of Scopoli's Caudata, but redefined, excluding the reptile taxa, and with a new content. Oppel (1810) used Caudata in the modern sense of content, but followed earlier authors in its application as a family-group taxon, rendering it unavailable for use above the family-group level (contra Dubois, 2004b). Fischer von Waldheim (1813: 58) treated Caudati as an unranked taxon, above the family group, for salamanders and as a synonym of his Urodeli, and it is this author to whom should be attributed Caudata in the sense that we now use it. Stejneger (1907) used the name Caudata in its modern usage, but attributed the name/concept to Scopoli.

Urodèles Duméril (1806), unfortunately, was also coined as a family for salamanders and is therefore unavailable for above-family-group nomenclature. It also was not Latinized, although some such family-group and genus-group names are protected in regulated nomenclature. Fischer von Waldheim (1813) was the first user of the name Caudati as an order, but he applied the name as a synonym of his Urodeli.

The nomenclatural question here is not one of priority. Clearly, Caudata Scopoli does not apply to the taxon of salamanders, and Fischer von Waldheim (1813) named Urodeli and Caudati as synonyms, with all uses of these names prior to Fischer von Waldheim (1813) being applied as families and therefore unavailable under the current Code. We therefore accept Caudati Fischer von Waldheim (1813), as emended to Caudata, as the name for crown-group salamanders, because this is the usage preferred by most working amphibian systematists (e.g., Duellman and Trueb, 1986).

Trueb and Cloutier (1991) and Cannatella and Hillis (1993) applied the name Urodela to the larger group of fossil and living salamanders. This was a novel application and the first time that Urodela and Caudata (named originally as objective synonyms) were explicitly construed to apply to different taxa. Should this usage be accepted, the authorship of Urodela in this sense should be attributed to Trueb and Cloutier (1991), who provided both the concept and the underyling diag-

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nosis, although the name would be a homonym of all earlier uses.

Another name of note in this discussion is Gradientia, which has had some use for the taxon of salamanders, but as originally conceived (Laurenti, 1768) the taxon was heterogeneous, containing salamanders, crocodiles, at least one frog, and several lizards (Dubois, 2004b). It was not until Merrem (1820) that Gradientia was used as an order for salamanders. But, importantly in our view, Gradientia does not enjoy any current usage.

Names that are synonymous with Caudata in our sense (and that of Fischer von Waldheim, 1813) are Urodelia Rafinesque, 1815; Gradientia Merrem, 1820 (*not* Gradientia Laurenti, 1768); Batrachoidei Mayer, 1849; Saurobatrachii Fatio, 1872; Mecodonta Wiedersheim, 1877; and Neocaudata Cannatella and Hillis, 1993 (at least under their cladographic definition as applied to our topology).

CRYPTOBRANCHOIDEI: Dunn (1922) first recognized this monophyletic group as a superfamily, Cryptobranchoidea, which was shortly thereafter (Noble, 1931) regarded as a suborder, albeit retaining the superfamily name ending. Tamarunov (1964b) first changed the name ending to avoid implying a regulated superfamily rank, an emendation that we follow.

DIADECTOSALAMANDROIDEI: The name Salamandroidea (as an above-family-group name) has been applied by different authors to several different concepts: (1) all salamanders, excluding *Amphiuma* (Sarasin and Sarasin, 1890); (2) Salamandridae + Amphiumidae + Plethodontidae (Noble, 1931; following Dunn, 1922, who used the name as a superfamily for Ambystomatidae [sensu lato], Salamandridae, and Plethodontidae); (3) restricted to the family Salamandridae (Regal, 1966; Laurent, 1986 ''1985''; Dubois, 2005); (4) Salamandridae, Amphiumidae, Plethodontidae, and Brachosauroididae (fossil taxon; Tamarunov, 1964b, as Salamandroidei); and (5) all salamanders, excluding Sirenidae and Cryptobranchoidea (Duellman and Trueb, 1986).

We could have redefined ''Salamandroidea'' for a sixth time, this time to include sirenids. Rather than do this, and extend the confusion, we provide a new name to correspond to a new taxonomic concept, Diadectosalamandroidei: all salamanders excluding Cryptobranchoidea.

PERENNIBRANCHIA: Merrem (1820) provided the name Amphipneusta for *Hypochthon* (= *Proteus*) and *Siren*. Unfortunately, he named this taxon as a tribe, between order and genus, thereby implying under the current International Code of Zoological Nomenclature (ICZN, 1999) that it should be considered to be within the family group and therefore unavailable for above-family-group nomenclature. Similarly, Rafinesque (1815) coined the name Meantia as an explicit family-group name (and therefore unavailable) for *Larvarius* (= *Proteus*), *Proteus*, *Exobranchia* (= *Necturus*), and *Sirena* (= *Siren*). The next oldest name that can be legitimately construed to attach to this taxon is Perennibranchia Latreille (1825), which was coined to contain *Siren* and *Proteus*. Other available names that are synonyms are Branchiuromalgaei Ritgen, 1828; Dysmolgae Ritgen, 1828; Diplopneumena Hogg, 1838; Manentibranchia Hogg, 1838; Externibranchia Hogg, 1839b; Branchiata Fitzinger, 1843; Ramibranchia A.H.A. Duméril, 1863; and Perennibranchiata Knauer, 1883.

ANURA: For 60 years (Romer, 1945), Salientia has been considered to contain the fossil taxon Proanura and the extant crown group, Anura. This use has been followed by most workers (e.g., Tamarunov, 1964a, 1964b; Trueb and Cloutier, 1991; Cannatella and Hillis, 1993; Ford and Cannatella, 1993). We accept this usage, although for most of their history the names Salientia and Anura were used interchangeably. Salientia, as first coined (Laurenti, 1768: 24), was the order containing frogs but also sharing *Proteus* with Laurenti's Gradientia. Merrem (1820: 163), in his influential classification, used Salientia for an order of frogs alone and this usage was followed by many subsequent workers (e.g., Wied-Neuwied, 1825; Hogg, 1839a; Gray, 1850a; Günther, 1859 ''1858''). But, if the name Salientia is to be construed as something other than the crown group, it must be given the authorship of Romer (1945), who provided the concept that is current today. Cannatella and Hillis (1993) cladographically defined Salientia to mean a taxon containing Anura and all of its fossil relatives more closely related to it than to Caudata—in other words, Salientia Romer, 1945.

The concept Anura started as anoures (A.M.C. Duméril, 1806: 93), French vernacular for the frog ''famille'' (and therefore unavailable for above-family-group nomenclature, contra Dubois, 2004b), which was subsequently Latinized and ranked as an order as Anuri by Fischer von Waldheim (1813: 58), as Anuria by Rafinesque (1815: 78), as Anoura by Gray (1825: 213), and ultimately as Anura by Hogg (1839a: 270). Synonyms of Anura (and of most uses of Salientia before 1945) are Ecaudata Scopoli, 1777: 464; Ecaudati Fischer von Waldheim, 1813: 58; Acaudata Knauer, 1883: 100; Batrachia Tschudi, 1838: 25; Heteromorpha Fitzinger, 1835: 107; Miura Van der Hoeven, 1833: 307; Pygomolgaei Ritgen, 1828: 278; and Raniformia Hogg, 1839a: 271.

LEIOPELMATIDAE: Had we retained two monotypic familes for *Ascaphus* (Ascaphidae) and

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Leiopelma (Leiopelmatidae), the name Amphicoela Noble, 1931, would have been available for this taxon in unregulated nomenclature. Subsequent authors (e.g., Romer, 1945; Reig, 1958) have extended the concept of this taxon to various fossil groups, and it remains an open question whether these taxa are internal or external to the original implied clade.

LALAGOBATRACHIA: The names available for this taxon demonstrate the illusion of precision that can result from retaining cladographically optimized taxonomic names when the underlying topology changes in ways that require a substantial reconceptualization of diagnosis and content. The taxon whose cladographic position as defined by Ford and Cannatella (1993) that corresponds to Lalagobatrachia in content and most closely approximates it in diagnostic features is Discoglossanura (Discoglossidae and all frogs other than *Leiopelma* and *Ascaphus*, the most recent common ancestor of this group and all of its descendants), as understood on the preferred tree of Ford and Cannatella (1993). The name that their cladographic definition would require to be applied is Pipanura (Pipimorpha + Neobatrachia), although the resulting content of this application is substantially different from that intended and the diagnosis is entirely different.

XENOANURA: The name Pipoidea Ford and Cannatella (1993) had its placement defined cladographically as including Pipidae and Rhinophrynidae, their most recent common ancestor, and all of its descendants (which likely includes Paleobatrachidae, a fossil taxon), while Xenoanura Savage (1973: 352) had as its original content Pipidae, Rhinophrynidae, and Paleobatrachidae. Therefore these two names are subjective synonyms. We employ the older name.

SOKOLANURA: The cladographically defined names Bombinanura and Discoglossanura provided by Ford and Cannatella (1993) optimize definitionally on this branch, so in one sense they are synonyms of our Sokolanura, except that the content and diagnoses of Bombinanura and Discoglossanura under this optimization are significantly different from that which was originally proposed. Rather than engender considerable confusion we coin a new name.

COSTATA: As originally coined (Nicholls, 1916: 86), Opisthocoela contained solely Discoglossidae (= Bombinatoridae and Alytidae in our usage), rendering it a synonym of Costati Lataste, 1879. Opisthocoela was subsequently used to contain Leiopelmatidae, Discoglossidae, and Pipidae (Ahl, 1930: 83) or Discoglossidae and Pipidae (Noble, 1931: 486). The original use of Costati (Lataste, 1879: 339) was as a taxon containing Discoglossidae and Alytidae (equivalent in content to Bombinatoridae and Alytidae in our usage), rendering Costati and Opisthocoela synonyms in their original forms. We employ the older name as emended by Stejneger (1907).

ALYTIDAE: Within the framework of regarding Discoglossidae and Bombinatoridae to be subfamilies of a larger Discoglossidae, Dubois (1987) explained the nomenclatural issues as well as the history of his 1982 appeal to the International Commission of Zoological Nomenclature to give Discoglossidae precedence over Bombinatoridae (as well as over Alytae and Bombitatores). Dubois (2005) used the older name, Alytidae, for this taxon formerly known as Discoglossidae, noting the use of Alytini by Sanchíz (1984), among others. We follow this usage as consistent with the International Code of Zoological Nomenclature (ICZN, 1999).

ACOSMANURA: Acosmanura is identical in content with Ranoidei Dubois (1983), which is a junior homonym of Ranoidei Sokol (1977) (= Acosmanura + Xenoanura). Sokol applied the name Ranoidei to the group containing all frogs excluding his Discoglossoidei (Leiopelmatidae and Discoglossidae, both sensu lato).

NEOBATRACHIA: Sarasin and Sarasin (1890: 245) coined a new taxon name, Neobatrachii, as a subclass for all living amphibians. This name is homonymous with Neobatrachia Reig, which was coined by Reig as a taxon of frogs (Dubois, 2004b, 2005). Because Neobatrachii Sarasin and Sarasin, 1890, is so unfamiliar, we see little chance that this homonymy will cause any confusion (contra Dubois, 2004b, 2005). Regardless, should homonymy become an issue in unregulated taxonomic names, this taxon will require a new name.

BATRACHOPHRYNIDAE: If *Batrachophrynus* is not closely allied with *Caudiverbera* and *Telmatobufo*, it is nomenclaturally unfortunate because Batrachophrynidae Cope, 1875, is the oldest name for the inclusive taxon as long as *Batrachophrynus* is considered to be a member of the family group. We suspect that additional work will show *Batrachophrynus* to attach elsewhere in the general cladogram, which will render the name of the family containing only *Telmatobufo* and *Caudiverbera* as Calyptocephalellidae Reig, 1960.

BUFONIDAE: A number of the generic names used in our work require comment.

Chascax Ritgen, 1828 (type species: *Bombinator strumosus* Merrem, 1820), is a senior name for *Peltophryne* Fitzinger, 1843, but is a *nomen oblitum* under Article 23.9 of the International Code of Zoological Nomenclature (ICZN, 1999).

Epidalea Cope, 1864. *Calamita* Oken, 1816, is a senior synonym of *Epidalea* Cope, 1864. How-

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ever, *Calamita* Oken, 1816, is unavailable according to Opinion 417 (Anonymous, 1956).

Rhinella Fitzinger, 1826. Other names that are available for *Rhinella* Fitzinger, 1826 (type species: *Bufo* (*Oxyrhynchus*) *proboscideus* Spix, 1824, by monotypy); *Otilophus* Cuvier, 1829 (type species: *Rana margaritifera* Laurenti, 1768, by original designation); *Eurhina* Fitzinger, 1843 (type species: *Bufo* (*Oxyrhynchus*) *proboscideus* Spix, 1824, by original designation); and *Trachycara* Tschudi, 1845 (type species: *Trachycara fusca* Tschudi, 1834, by original designation). *Oxyrhynchus* Spix, 1824 (no type species designated) is not available for this taxon because it is a junior homonym of *Oxyrhynchus* Leach, 1818 (a fish).

Rhaebo Cope, 1862. A senior synonym of *Rhaebo* Cope, 1862, is *Phrynomorphus* Fitzinger, 1843: 32 (type species: *Bufo leschenaulti* Duméril and Bibron, 1841 [= *Bufo guttatus* Schneider, 1799]), which is a junior homonym of *Phrynomorphus* Curtis, 1831, an insect genus.

RANOIDES: Two other names are available for this taxon: Diplasiocoela Nicholls, 1916 (which was coined as a synonym of Firmisternia *sensu* Boulenger, 1882), and Firmisternia Boulenger, 1882. Surprisingly, the first use of the name Firmisternia (Cope, 1875: 8) explicitly excluded Raniformia (ranids, rhacophorids, petropedetids, hyperoliids, and *Leptopelis* in Cope's sense) and Gastrechmia (Hemisotidae), and included only Phryniscidae, Dendrobatidae (excluding Colostethidae), Engystomidae, and Brevicipitidae. If the name Firmisternia were to be applied to this branch in the cladogram, the intended content would have to to come from Firmisternia Boulenger, 1882, not Firmisternia Cope, 1875.

Complicating the application of this name is Ranoidei Sokol, 1977. Sokol (1977) named Ranoidei as a suborder to include all taxa not in his Discoglossoidea (in his usage, composed of Discoglossidae [sensu lato, including Bombinatoridae] and Leiopelmatidae [including *Ascaphus*]). In other words, Ranoidei Sokol, 1977, is composed of our Acosmanura + Xenoanura. Subsequently, Dubois (1983) applied the name Ranoidei to all frogs, excluding his Pipoidei (= Xenoanura + Anomocoela of our usage) and Discoglossoidei. This renders Ranoidei Dubois, 1983, a synonym of Acosmanura.

Our inclination is to preserve as closely as possible the near-universal vernacular term for this group, ''ranoid''. We also would have liked to use the form ''Ranoidei'', but, unfortunately, this would have engendered confusion with Ranoidei Sokol and Ranoidei Dubois. We therefore have formed the name as Ranoides, a taxon name explicitly above regulated nomenclature. To maintain parallel spelling in its sister taxon, we also form the new name for the old Hyloidea as Hyloides.

APPENDIX 7

NEW AND REVIVED COMBINATIONS AND CLARIFICATIONS REGARDING TAXONOMIC CONTENT

Because many users of this work will not be familiar with gender agreement and other arcana of nomenclature, we present here the names of species affected by generic changes made (and, in some cases referenced) within this paper. In some places (noted) we provide the entire content of certain taxa for clarity.

CAUDATA

PLETHODONTIDAE

(1) *Eurycea* Rafinesque, 1822. The synonymy of *Haideotriton* Carr, 1939, with *Eurycea* Rafinesque, 1822, results in *Eurycea wallacei* (Carr, 1939) new combination.

(2) *Pseudoeurycea* Taylor, 1944. The synonymy of *Ixalotriton* Wake and Johnson, 1989, with *Pseudoeurycea* Taylor, 1944, results in two name changes: *Pseudoeurycea nigra* (Wake and Johnson, 1989) new combination; *Pseudoeurycea parva* Lynch and Wake, 1989. Synonymy of *Lineatriton* Tanner, 1950, with *Pseudoeurycea* Taylor, 1944, results in the three name changes: *Pseudoeurycea lineola* (Cope, 1865) new combination; *P. orchileucos* (Brodie, Mendelson, and Campbell, 2002) new combination; and *P. orchimelas* (Brodie, Mendelson, and Campbell, 2002) new combination.

ANURA

SOOGLOSSIDAE

(1) *Sooglossus* Boulenger, 1906. The placement of *Nesomantis* Boulenger, 1909, into the synonymy of *Sooglossus* Boulenger, 1906, results in one name change: *Sooglossus thomasseti* (Boulenger, 1909) new combination.

LIMNODYNASTIDAE

(1) *Opisthodon* Steindachner, 1867. Recognition of the *Limnodynastes ornatus* group as the

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genus *Opisthodon* Steindachner, 1867, results in two resurrected combinations: *Opisthodon ornatus* (Gray, 1842); and *O. spenceri* (Parker, 1940).

Brachycephalidae

(1) The partition of former *Eleutherodactylus* Duméril and Bibron, 1841, into the genera *Craugastor*, ''*Eleutherodactylus*'', ''*Euhyas*'', ''*Pelorius*'', and *Syrrhophus*, results in the following new or revived combinations.

(a) *Craugastor* Cope, 1862 (all combinations previously made by implication by Crawford and Smith, 2005). *Craugastor adamastus* (Campbell, 1994) new combination; *C. alfredi* (Boulenger, 1898) new combination; *C. amniscola* (Campbell and Savage, 2000) new combination; *C. anciano* (Savage, McCranie, and Wilson, 1988) new combination; *C. andi* (Savage, 1974) new combination; *C. angelicus* (Savage, 1975) new combination; *C. anomalus* (Boulenger, 1898) new combination; *C. aphanus* (Campbell, 1994) new combination; *C. augusti* (Dugès In Brocchi, 1879) new combination; *C. aurilegulus* (Savage, McCranie, and Wilson, 1988) new combination; *C. azueroensis* (Savage, 1975) new combination; *C. biporcatus* (Peters, 1863) new combination; *C. bocourti* (Brocchi, 1877) new combination; *C. bransfordii* (Cope, 1886) new combination; *C. brevirostris* (Shreve, 1936) new combination; *C. brocchi* (Boulenger *In* Brocchi, 1882) new combination; *C. bufoniformis* (Boulenger, 1896) new combination; *C. catalinae* (Campbell and Savage, 2000) new combination; *C. cerasinus* (Cope, 1875 ''1876'') new combination; *C. chac* (Savage, 1987) new combination; *C. charadra* (Campbell and Savage, 2000) new combination; *C. cheiroplethus* (Lynch, 1990) new combination; *C. chrysozetetes* (McCranie, Savage, and Wilson, 1989) new combination; *C. coffeus* (McCranie and Köhler, 1999) new combination; *C. crassidigitus* (Taylor, 1952) new combination; *C. cruzi* (McCranie, Savage, and Wilson, 1989) new combination; *C. cuaquero* (Savage, 1980) new combination; *C. daryi* (Ford and Savage, 1984) new combination; *C. decoratus* (Taylor, 1942) new combination; *C. emcelae* (Lynch, 1985) new combination; *C. emleni* (Dunn and Emlen, 1932) new combination; *C. epochthidius* (McCranie and Wilson, 1997) new combination; *C. escoces* (Savage, 1975) new combination; *C. fecundus* (McCranie and Wilson, 1997) new combination; *C. fitzingeri* (Schmidt, 1857) new combination; *C. fleischmanni* (Boettger, 1892) new combination; *C. galacticorhinus* (Canseco-Márquez and Smith, 2004) new combination; *C. glaucus* (Lynch, 1967) new combination; *C. gollmeri* (Peters, 1863) new combination; *C. greggi* (Bumzahem, 1955) new combination; *C. guerreroensis* (Lynch, 1967) new combination; *C. gulosus* (Cope, 1875 ''1876'') new combination; *C. hobartsmithi* (Taylor, 1937) new combination; *C. inachus* (Campbell and Savage, 2000) new combination; *C. jota* (Lynch, 1980) new combination; *C. laevissimus* (Werner, 1896) new combination; *C. laticeps* (Duméril, 1853) new combination; *C. lauraster* (Savage, McCranie, and Espinal, 1996) new combination; *C. lineatus* (Brocchi, 1879) new combination; *C. loki* (Shannon and Werler, 1955) new combination; *C. longirostris* (Boulenger, 1898) new combination; *C. matudai* (Taylor, 1941) new combination; *C. megacephalus* (Cope, 1875 ''1876'') new combination; *C. megalotympanum* (Shannon and Werler, 1955) new combination; *C. melanostictus* (Cope, 1875) new combination; *C. merendonensis* (Schmidt, 1933) new combination; *C. mexicanus* (Brocchi, 1877) new combination; *C. milesi* (Schmidt, 1933) new combination; *C. mimus* (Taylor, 1955) new combination; *C. monnichorum* (Dunn, 1940) new combination; *C. myllomyllon* (Savage, 2000) new combination; *C. necerus* (Lynch, 1975) new combination; *C. noblei* (Barbour and Dunn, 1921) new combination; *C. obesus* (Barbour, 1928) new combination; *C. occidentalis* (Taylor, 1941) new combination; *C. olanchano* (McCranie and Wilson, 1999) new combination; *C. omiltemanus* (Günther, 1900) new combination; *C. omoaensis* (McCranie and Wilson, 1997) new combination; *C. opimus* (Savage and Myers, 2002) new combination; *C. palenque* (Campbell and Savage, 2000) new combination; *C. pechorum* (McCranie and Wilson, 1999) new combination; *C. pelorus* (Campbell and Savage, 2000) new combination; *C. persimilis* (Barbour, 1926) new combination; *C. phasma* (Lips and Savage, 1996) new combination; *C. podiciferus* (Cope, 1875) new combination; *C. polymniae* (Campbell, Lamar, and Hillis, 1989) new combination; *C. polyptychus* (Cope, 1886) new combination; *C. pozo* (Johnson and Savage, 1995) new combination; *C. psephosypharus* (Campbell, Savage, and Meyer, 1994) new combination; *C. punctariolus* (Peters, 1863) new combination; *C. pygmaeus* (Taylor, 1937) new combination; *C. raniformis* (Boulenger, 1896) new combination; *C. ranoides* (Cope, 1886) new combination; *C. rayo* (Savage and DeWeese, 1979) new combination; *C. rhodopis* (Cope, 1867) new combination; *C. rhyacobatrachus* (Campbell and Savage, 2000) new combination; *C. rivulus* (Campbell and Savage, 2000) new combination; *C. rostralis* (Werner, 1896) new combination; *C. rugosus* (Peters, 1873) new combination; *C. rugulosus* (Cope, 1870) new combination; *C. rupinius* (Campbell and Savage, 2000) new combination; *C. sabrinus* (Campbell and Savage, 2000) new combination; *C. saltuar-*

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ius (McCranie and Wilson, 1997) new combination; *C. sandersoni* (Schmidt, 1941) new combination; *C. sartori* (Lynch, 1965) new combination; *C. silvicola* (Lynch, 1967) new combination; *C. spatulatus* (Smith, 1939) new combination; *C. stadelmani* (Schmidt, 1936) new combination; *C. stejnegerianus* (Cope, 1893) new combination; *C. stuarti* (Lynch, 1967) new combination; *C. tabasarae* (Savage, Hollingsworth, Lips, and Jaslow, 2004) new combination; *C. talamancae* (Dunn, 1931) new combination; *C. tarahumaraensis* (Taylor, 1940) new combination; *C. taurus* (Taylor, 1958) new combination; *C. taylori* (Lynch, 1966) new combination; *C. trachydermus* (Campbell, 1994) new combination; *C. uno* (Savage, 1984) new combination; *C. vocalis* (Taylor, 1940) new combination; *C. vulcani* (Shannon and Werler, 1955) new combination; *C. xucanebi* (Stuart, 1941) new combination; *C. yucatanensis* (Lynch, 1965) new combination; *C. zygodactylus* (Lynch and Myers, 1983) new combination.

(b) ''*Euhyas*'' Fitzinger, 1843: ''*Euhyas*'' *acmonis* (Schwartz, 1960) new combination; ''*E.*'' *adela* (Diaz, Cadiz, and Hedges, 2003) new combination; ''*E.*'' *albipes* (Barbour and Shreve, 1937) new combination; ''*E.*'' *alcoae* (Schwartz, 1971); ''*E.*'' *alticola* (Lynn, 1937) new combination; ''*E.*'' *amadeus* (Hedges, Thomas, and Franz, 1987) new combination; ''*E.*'' *andrewsi* (Lynn, 1937) new combination; ''*E.*'' *apostates* (Schwartz, 1973) new combination; ''*E.*'' *armstrongi* (Noble and Hassler, 1933) new combination; ''*E.*'' *atkinsi* (Dunn, 1925) new combination; ''*E.*'' *briceni* (Boulenger, 1903) new combination; ''*E.*'' *caribe* (Hedges and Thomas, 1992) new combination; ''*E.*'' *casparii* (Dunn, 1926) new combination; ''*E.*'' *cavernicola* (Lynn, 1954) new combination; ''*E.*'' *corona* (Hedges and Thomas, 1992) new combination; ''*E.*'' *counouspea* (Schwartz, 1964) new combination; ''*E.*'' *cubana* (Barbour, 1942) new combination; ''*E.*'' *cuneata* (Cope, 1862) new combination; ''*E.*'' *dimidiatus* (Cope, 1862) new combination; ''*E.*'' *dolomedes* (Hedges and Thomas, 1992) new combination; ''*E.*'' *emiliae* (Dunn, 1926) new combination; ''*E.*'' *etheridgei* (Schwartz, 1958) new combination; ''*E.*'' *furcyensis* (Shreve and Williams, 1963) new combination; ''*E.*'' *fusca* (Lynn and Dent, 1943) new combination; ''*E.*'' *glandulifer* (Cochran, 1935) new combination; ''*E.*'' *glanduliferoides* (Shreve, 1936) new combination; ''*E.*'' *glaphycompus* (Schwartz, 1973) new combination; ''*E.*'' *glaucoreia* (Schwartz and Fowler, 1973) new combination; ''*E.*'' *goini* (Schwartz, 1960) new combination; ''*E.*'' *gossei* (Dunn, 1926) new combination; ''*E.*'' *grabhami* (Dunn, 1926) new combination; ''*E.*'' *grahami* (Schwartz, 1979) new combination; ''*E.*'' *greyi* (Dunn, 1926) new combination; ''*E.*'' *griphus* (Crombie, 1986) new combination; ''*E.*'' *guanahacabibes* Estrada and Rodriguez, 1985 new combination; ''*E.*'' *gundlachi* (Schmidt, 1920) new combination; ''*E.*'' *iberia* (Estrada and Hedges, 1996) new combination; ''*E.*'' *intermedia* (Barbour and Shreve, 1937) new combination; ''*E.*'' *jamaicensis* (Barbour, 1910) new combination; ''*E.*'' *jaumei* (Estrada and Alonso, 1997) new combination; ''*E.*'' *jugans* (Cochran, 1937) new combination; ''*E.*'' *junori* (Dunn, 1926) new combination; ''*E.*'' *karlschmidti* (Grant, 1931) new combination; ''*E.*'' *klinikowskii* (Schwartz, 1959) new combination; ''*E.*'' *leoncei* (Shreve and Williams, 1963) new combination; ''*E.*'' *limbata* (Cope, 1862); ''*E.*'' *lucioi* (Schwartz, 1980) new combination; ''*E.*'' *luteola* (Gosse, 1851) new combination; ''*E.*'' *maestrensis* (Díaz, Cádiz, and Navarro, 2005) new combination; ''*E.*'' *minuta* Noble, 1923 new combination; ''*E.*'' *monensis* (Meerwarth, 1901) new combination; ''*E.*'' *nubicola* Dunn, 1926 new combination; ''*E.*'' *orcutti* (Dunn, 1928); ''*E.*'' *orientalis* (Barbour and Shreve, 1937) new combination; ''*E.*'' *oxyrhynca* (Duméril and Bibron, 1841) new combination; ''*E.*'' *pantoni* (Dunn, 1926); ''*E.*'' *parabates* (Schwartz, 1964) new combination; ''*E.*'' *paulsoni* (Schwartz, 1964) new combination; ''*E.*'' *pentasyringos* (Schwartz and Fowler, 1973) new combination; ''*E.*'' *pezopetra* (Schwartz, 1960) new combination; ''*E.*'' *pictissima* (Cochran, 1935) new combination; ''*E.*'' *pinarensis* (Dunn, 1926) new combination; ''*E.*'' *planirostris* (Cope, 1862) new combination; ''*E.*'' *rhodesi* (Schwartz, 1980) new combination; ''*E.*'' *richmondi* (Stejneger, 1904) new combination; ''*E.*'' *ricordii* (Duméril and Bibron, 1841); ''*E.*'' *rivularis* (Diaz, Estrada, and Hedges, 2001) new combination; ''*E.*'' *schmidti* (Noble, 1923) new combination; ''*E.*'' *sciagraphus* (Schwartz, 1973) new combination; ''*E.*'' *semipalmata* (Shreve, 1936) new combination; ''*E.*'' *simulans* (Diaz and Fong, 2001); ''*E.*'' *sisyphodemus* (Crombie, 1977) new combination; ''*E.*'' *symingtoni* (Schwartz, 1957) new combination; ''*E.*'' *tetajulia* (Estrada and Hedges, 1996) new combination; ''*E.*'' *thomasi* (Schwartz, 1959) new combination; ''*E.*'' *thorectes* (Hedges, 1988) new combination; ''*E.*'' *toa* (Estrada and Hedges, 1991) new combination; ''*E.*'' *tonyi* (Estrada and Hedges, 1997) new combination; ''*E.*'' *turquinensis* (Barbour and Shreve, 1937) new combination; ''*E.*'' *varleyi* (Dunn, 1925) new combination; ''*E.*'' *ventrilineata* (Shreve, 1936) new combination; ''*E.*'' *warreni* (Schwartz, 1976); ''*E.*'' *weinlandi* (Barbour, 1914) new combination; ''*E.*'' *zeus* (Schwartz, 1958) new combination; ''*E.*'' *zugi* (Schwartz, 1958) new combination.

(c) ''*Pelorius*'' Hedges, 1989. ''*Pelorius*'' *chlo-*

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rophenax (Schwartz, 1976) new combination; ''*P.*'' *hypostenor* (Schwartz, 1965) new combination; ''*P.*'' *inoptatus* (Barbour, 1914) new combination; ''*P.*'' *nortoni* (Schwartz, 1976) new combination; ''*P.*'' *parapelates* (Hedges and Thomas, 1987) new combination; ''*P.*'' *ruthae* (Noble, 1923) new combination.

(d) *Syrrhophus* Cope, 1878 (all resurrected combinations either previously formed or implied by prior authors). *Syrrhophus angustidigitorum* (Taylor, 1940); *S. cystignathoides* (Cope, 1877); *S. dennisi* Lynch, 1970; *S. dilatus* (Davis and Dixon, 1955); *S. dixoni* (Lynch, 1991); *S. grandis* (Dixon, 1957); *S. guttilatus* (Cope, 1879); *S. interorbitalis* Langebartel and Shannon, 1956; *S. leprus* Cope, 1879; *S. longipes* (Baird, 1859); *S. marnockii* Cope, 1878; *S. maurus* (Hedges, 1989); *S. modestus* Taylor, 1942; *S. nitidus* (Peters, 1870); *S. nivicolimae* Dixon and Webb, 1966; *S. pallidus* Duellman, 1958; *S. pipilans* Taylor, 1940; *S. rubrimaculatus* Taylor and Smith, 1945; *S. rufescens* (Duellman and Dixon, 1959); *S. saxatilis* (Webb, 1962); *S. syristes* (Hoyt, 1965); *S. teretistes* Duellman, 1958; *S. verrucipes* Cope, 1885; *S. verruculatus* (Peters, 1870).

Hylidae: Pelodryadinae

(1) *Litoria* Tschudi, 1838: The synonymy of *Nyctimystes* Stejneger, 1916, and *Cyclorana* Steindachner, 1867 (with retention of *Cyclorana* as a subgenus within *Litoria*), with *Litoria* Tschudi, 1838, results in the following new or revived combinations.

(a) *Cyclorana* Steindachner, 1867. *Litoria* (*Cyclorana*) *alboguttata* (Günther, 1867); *L.* (*C.*) *australis* (Gray, 1842) new combination; *L.* (*C.*) *brevipes* (Peters, 1871) new combination; *L.* (*C.*) *cryptotis* (Tyler and Martin, 1977) new combination; *L.* (*C.*) *cultripes* (Parker, 1940) new combination; *L.* (*C.*) *longipes* (Tyler and Martin, 1977) new combination; *L.* (*C.*) *maculosa* (Tyler and Martin, 1977) new combination; *L.* (*C.*) *maini* (Tyler and Martin, 1977) new combination; *L.* (*C.*) *manya* (van Beurden and McDonald, 1980) new combination; *L.* (*C.*) *novaehollandiae* (Steindachner, 1867) new combination; *L.* (*C.*) *platycephala* (Günther, 1873) new combination; *L.* (*C.*) *vagita* (Tyler, Davies, and Martin, 1981) new combination; *L.* (*C.*) *verrucosa* (Tyler and Martin, 1977) new combination.

(b) *Nyctimystes* Stejneger, 1916. *Litoria avocalis* (Zweifel, 1958) new combination; *L. cheesmanae* (Tyler, 1964) new combination; *L. dayi* (Günther, 1897) new combination; *L. daymani* (Zweifel, 1958) new combination; *L. disrupta* (Tyler, 1963) new combination; *L. fluviatilis* (Zweifel, 1958) new combination; *L. foricula* (Tyler, 1963) new combination; *L. granti* (Boulenger, 1914) new combination; *L. gularis* (Parker, 1936) new combination; *L. humeralis* (Boulenger, 1912) new combination; *L. kubori* (Zweifel, 1958) new combination; *L. michaeltyleri* new name;[36] *L. montana* (Peters and Doria, 1878) new combination; *L. narinosa* (Zweifel, 1958) new combination; *L. obsoleta* (Lönnberg, 1900) new combination; *L. oktediensis* (Richards and Johnston, 1993) new combination; *L. papua* (Boulenger, 1897) new combination; *L. perimetri* (Zweifel, 1958) new combination; *L. persimilis* (Zweifel, 1958) new combination; *L. pulchra* (Wandolleck, 1911 ''1910'') new combination; *L. rueppelli* (Boettger, 1895) new combination; *L. semipalmata* (Parker, 1936) new combination; *L. trachydermis* (Zweifel, 1983) new combination; *L. zweifeli* (Tyler, 1967) new combination.

Leptodactylidae

(1) *Leptodactylus* Fitzinger, 1826. The placement of *Adenomera* Steindachner, 1867, as a synonym of *Lithodytes* Fitzinger, 1843, and *Lithodytes* as a subgenus of *Leptodactylus*, as well as the placement of *Vanzolinius* Heyer, 1974, as a synonym of *Leptodactylus*, results in the new or revived combinations.

(a) *Adenomera* Steindachner, 1867, and *Lithodytes* Fitzinger, 1843. *Leptodactylus* (*Lithodytes*) *andreae* Müller, 1923; *L.* (*L.*) *araucarius* (Kwet and Angulo, 2002) new combination; *L.* (*L.*) *bokermanni* Heyer, 1973; *L.* (*L.*) *diptyx* Boettger, 1885; *L.* (*L.*) *hylaedactylus* (Cope, 1868); *L.* (*L.*) *lineatus* (Schneider, 1799); *L.* (*L.*) *lutzi* (Heyer, 1975) new combination; *L.* (*L.*) *marmoratus* (Steindachner, 1867); *L.* (*L.*) *martinezi* (Bokermann, 1956).

(b) *Vanzolinius* Heyer, 1974. *Leptodactylus discodactylus* Boulenger, 1884 ''1883''.

Dendrobatidae

Ameerega Bauer, 1986. Although *Ameerega* Bauer, 1986, is an older name for the clade currently referred to by other authors as *Epipedobates* Myers, 1987, an extensive revision of Dendrobatidae is under way, rendering a much different generic taxonomy from that employed in this paper (Grant et al., in press). For this reason we do not provide a list of new combinations for species of former *Epipedobates*.

[36] When placed in *Litoria*, *Nyctimystes tyleri* Zweifel, 1983, becomes a secondary homonym of *Litoria tyleri* Martin, Watson, Gartside, Littlejohn, and Loftus-Hills, 1979 ''1978''. Although we expect that ongoing work will correct this nomenclatural anomaly, we propose *Litoria michaeltyleri* nomen novum to replace *Nyctimystes tyleri* Zweifel, 1983.

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BUFONIDAE

The extensive generic rearrangements result in many name changes:

(1) *Altiphrynoides* Dubois, 1987 ''1986''. The synonymy of *Altiphrynoides* Dubois, 1987 ''1986'', and *Spinophrynoides* Dubois, 1987 ''1986'', results in a single name change: *Altiphrynoides osgoodi* (Loveridge, 1932) new combination.

(2) *Amietophrynus* new genus. The components of *Amietophrynus* come from several former species groups of ''*Bufo*'', all exhibiting the 20-chromosome condition, with the exception of the *A. pardalis* group, which has reversed to the 22-chromosome condition (Cunningham and Cherry, 2004): *A. asmarae* (Tandy, Bogart, Largen, and Feener, 1982) new combination; *A. blanfordii* (Boulenger, 1882) new combination; *A. brauni* (Nieden, 1911) new combination; *A. buchneri* (Peters, 1882) new combination; *A. camerunensis* (Parker, 1936) new combination; *A. chudeaui* (Chabanaud, 1919); *A. cristiglans* (Inger and Menzies, 1961) new combination; *A. danielae* (Perret, 1977) new combination; *A. djohongensis* (Hulselmans, 1977) new combination; *A. fuliginatus* (de Witte, 1932) new combination; *A. funereus* (Bocage, 1866) new combination; *A. garmani* (Meek, 1897) new combination; *A. gracilipes* (Boulenger, 1899) new combination; *A. gutturalis* (Power, 1927) new combination; *A. kassasii* (Baha El Din, 1993) new combination; *A. kerinyagae* (Keith, 1968) new combination; *A. kisoloensis* (Loveridge, 1932) new combination; *A. langanoensis* (Largen, Tandy, and Tandy, 1978) new combination; *A. latifrons* (Boulenger, 1900) new combination; *A. lemairii* (Boulenger, 1901) new combination; *A. maculatus* (Hallowell, 1854) new combination; *A. pantherinus* (Smith, 1828) new combination; *A. pardalis* (Hewitt, 1935) new combination; *A. perreti* (Schiøtz, 1963) new combination; *A. poweri* (Hewitt, 1935) new combination; *A. rangeri* (Hewitt, 1935) new combination; *A. reesi* (Poynton, 1977) new combination; *A. regularis* (Reuss, 1833) new combination; *A. steindachneri* (Pfeffer, 1893) new combination; *A. superciliaris* (Boulenger, 1888) new combination; *A. taiensis* (Rödel and Ernst, 2000) new combination (including *Bufo amieti* Tandy and Perret, 2000, according to S. Stuart, personal commun.); *A. togoensis* (Ahl, 1924) new combination; *A. tuberosus* (Günther, 1858) new combination; *A. turkanae* (Tandy and Feener, 1985) new combination; *A. urunguensis* (Loveridge, 1932) new combination; *A. villiersi* (Angel, 1940) new combination; *A. vittatus* (Boulenger, 1906) new combination; *A. xeros* (Tandy, Tandy, Keith, and Duff-MacKay, 1976) new combination.

(3) *Anaxyrus* Tschudi, 1845. Recognition of this major clade of Nearctic ''*Bufo*'' as a genus requires a number of new name combinations: *Anaxyrus americanus* (Holbrook, 1836) new combination; *A. baxteri* (Porter, 1968) new combination; *A. boreas* (Baird and Girard, 1852) new combination; *A. californicus* (Camp, 1915) new combination; *A. canorus* (Camp, 1916) new combination; *A. cognatus* (Say *in* James, 1823) new combination; *A. compactilis* (Wiegmann, 1833) new combination; *A. debilis* (Girard, 1854) new combination; *A. exsul* (Myers, 1942) new combination; *A. fowleri* (Hinckley, 1882) new combination; *A. hemiophrys* (Cope, 1886) new combination; *A. houstonensis* (Sanders, 1953) new combination; *A. kelloggi* (Taylor, 1938) new combination; *A. mexicanus* (Brocchi, 1879) new combination; *A. microscaphus* (Cope, 1867) ''1866'' new combination; *A. nelsoni* (Stejneger, 1893) new combination; *A. punctatus* (Baird and Girard, 1852) new combination; *A. quercicus* (Holbrook, 1840) new combination; *A. retiformis* (Sanders and Smith, 1951) new combination; *A. speciosus* (Girard, 1854) new combination; *A. terrestris* (Bonnaterre, 1789) new combination; *A. woodhousii* (Girard, 1854) new combination.

(4) *Bufo* Laurent, 1768. This taxon is *Bufo* (sensu stricto). All other species in *Bufo* (sensu lato) should have the generic name *Bufo* placed in quotation marks (i.e., ''*Bufo*'') inasmuch as they are not part of the clade formally called *Bufo*, sensu stricto. Members of *Bufo* sensu stricto are *Bufo andrewsi* Schmidt, 1925; *B. aspinius* (Yang, Liu, and Rao, 1996); *B. bankorensis* Barbour, 1908; *B. bufo* (Linnaeus, 1758); *B. gargarizans* Cantor, 1842; *B. japonicus* Temminck and Schlegel, 1838; *B. kabischi* Herrmann and Kühnel, 1997; *B. minshanicus* Stejneger, 1926; *B. spinosus* Daudin, 1803; *B. tibetanus* Zarevskij, 1926; *B. torrenticola* Matsui, 1976; *B. tuberculatus* Zarevskij, 1926; *B. verrucosissimus* (Pallas, 1814); *B. wolongensis* Herrmann and Kühnel, 1997.

(5) Former ''*Bufo*'' species not allocated to genus (see discussion under ''Taxonomy'' and above under *Bufo*) are:

(a) Nomina dubia. ''*Bufo*'' *brevirostris* Rao, 1937; ''*B.*'' *simus* Schmidt, 1857.

(b) Unassigned to group. ''*B.*'' *koynayensis* Soman, 1963; ''*B.*'' *ocellatus* Günther, 1858.

(c) ''*Bufo*'' *arabicus* group, ''*Bufo*'' *arabicus* Heyden, 1827; ''*B.*'' *dhufarensis* Parker, 1931; ''*B.*'' *dodsoni* Boulenger, 1895; ''*B.*'' *scorteccii* Balletto and Cherchi, 1970.

(d) ''*Bufo*'' *mauritanicus* group: ''*Bufo*'' *mauritanicus* Schlegel, 1841).

(e) ''*Bufo*'' *pentoni* group, ''*Bufo*'' *pentoni* Anderson, 1893; ''*B.*'' *tihamicus* Balletto and Cherchi, 1973.

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(f) ''*Bufo*'' *scaber* group: ''*Bufo*'' *atukoralei* Bogert and Senanayake, 1966; ''*B.*'' *kotagamai* Fernando, Dayawansa, and Siriwardhane, 1994; ''*B.*'' *parietalis* Boulenger, 1882; ''*B.*'' *scaber* Schneider, 1799; ''*B.*'' *silentvalleyensis* Pillai, 1981.

(g) ''*Bufo*'' *stejnegeri* group. ''*Bufo*'' *ailaoanus* Kou, 1984; ''*B.*'' *cryptotympanicus* Liu and Hu, 1962; ''*B.*'' *pageoti* Bourret, 1937; ''*B.*'' *stejnegeri* Schmidt, 1931.

(h) ''*Bufo*'' *stomaticus* group. ''*Bufo*'' *beddomii* Günther, 1876; ''*B.*'' *hololius* Günther, 1876; ''*B.*'' *olivaceus* Blanford, 1874; ''*B.*'' *stomaticus* Lütken, 1864; ''*B.*'' *stuarti* Smith, 1929; ''*B.*'' *sumatranus* Peters, 1871 (provisional allocation); ''*B.*'' *valhallae* Meade-Waldo, 1909 (provisionally allocated).

(6) *Chaunus* Wagler, 1828: Recognition of this major clade of predominantly Neotropical ''*Bufo*'' (excluding *Rhinella*) as a genus requires a number of new name combinations. Although we do not reject the use of species groups (see Blair, 1972a; Duellman and Schulte, 1992), we think that these require considerable reevaluation regarding their monophyly and utility. Recommended changes are *Chaunus abei* (Baldissera, Caramaschi, and Haddad, 2004) new combination; *C. achalensis* (Cei, 1972) new combination; *C. achavali* (Maneyro, Arrieta, and de Sá, 2004) new combination; *C. amabilis* (Pramuk and Kadivar, 2003) new combination; *C. amboroensis* (Harvey and Smith, 1993) new combination; *C. arborescandens* (Duellman and Schulte, 1992) new combination; *C. arenarum* (Hensel, 1867) new combination; *C. arequipensis* (Vellard, 1959) new combination; *C. arunco* (Molina, 1782) new combination; *C. atacamensis* (Cei, 1962) new combination; *C. beebei* (Gallardo, 1965) new combination; *C. bergi* (Céspedez, 2000) new combination; *C. chavin* (Lehr, Köhler, Aguilar, and Ponce, 2001) new combination; *C. cophotis* (Boulenger, 1900) new combination; *C. corynetes* (Duellman and Ochoa-M., 1991) new combination; *C. crucifer* (Wied-Neuwied, 1821) new combination; *C. diptychus* (Cope, 1862) new combination; *C. dorbignyi* (Duméril and Bibron, 1841) new combination; *C. fernandezae* (Gallardo, 1957) new combination; *C. fissipes* (Boulenger, 1903) new combination; *C. gallardoi* (Carrizo, 1992) new combination; *C. gnustae* (Gallardo, 1967) new combination; *C. granulosus* (Spix, 1824) new combination; *C. henseli* (Lutz, 1934) new combination; *C. icterricus* (Spix, 1824) new combination; *C. inca* (Stejneger, 1913) new combination; *C. jimi* (Stevaux, 2002) new combination; *C. justinianoi* (Harvey and Smith, 1994) new combination; *C. limensis* (Werner, 1901) new combination; *C. marinus* (Linnaeus, 1758) new combination; *C. nesiotes* (Duellman and Toft, 1979) new combination; *C. ornatus* (Spix, 1824) new combination; *C. poeppigii* (Tschudi, 1845) new combination; *C. pombali* (Baldissera, Caramaschi, and Haddad, 2004) new combination; *C. pygmaeus* (Myers and Carvalho, 1952) new combination; *C. quechua* (Gallardo, 1961) new combination; *C. rubescens* (Lutz, 1925) new combination; *C. rubropunctatus* (Guichenot, 1848) new combination; *C. rumbolli* (Carrizo, 1992) new combination; *C. schneideri* (Werner, 1894) new combination; *C. spinulosus* (Wiegmann, 1834) new combination; *C. vellardi* (Leviton and Duellman, 1978) new combination; *C. veraguensis* (Schmidt, 1857) new combination.

(7) *Cranopsis* Cope, 1875. Recognition of the Middle American clade of ''*Bufo*'' as *Cranopsis* Cope, 1875, renders the following new or revived combinations: *Cranopsis alvaria* (Girard in Baird, 1849) new combination; *C. aucoinae* (O'Neill and Mendelson, 2004) new combination; *C. bocourti* (Brocchi, 1877) new combination; *C. campbelli* (Mendelson, 1994) new combination; *C. canalifera* (Cope, 1877) new combination; *C. cavifrons* (Firschein, 1950) new combination; *C. coccifer* (Cope, 1866) new combination; *C. conifera* (Cope, 1862) new combination; *C. cristata* (Wiegmann, 1833) new combination; *C. cycladen* (Lynch and Smith, 1966) new combination; *C. fastidiosa* (Cope, 1875) new combination; *C. gemmifer* (Taylor, 1940) new combination; *C. holdridgei* (Taylor, 1952) new combination; *C. ibarrai* (Stuart, 1954) new combination; *C. leucomyos* (McCranie and Wilson, 2000) new combination; *C. luetkenii* (Boulenger, 1891) new combination; *C. macrocristata* (Firschein and Smith, 1957) new combination; *C. marmorea* (Wiegmann, 1833) new combination; *C. mazatlanensis* (Taylor, 1940) new combination; *C. melanochlora* (Cope, 1877) new combination; *C. nebulifer* (Girard, 1854) new combination; *C. occidentalis* (Camerano, 1879) new combination; *C. periglenes* (Savage, 1967); *C. peripatetes* (Savage, 1972) new combination; *C. perplexa* (Taylor, 1943) new combination; *C. pisinna* (Mendelson, Williams, Sheil, and Mulcahy, 2005) new combination; *C. porteri* (Mendelson, Williams, Sheil, and Mulcahy, 2005) new combination; *C. signifera* (Mendelson, Williams, Sheil, and Mulcahy, 2005) new combination; *C. spiculata* (Mendelson, 1997) new combination; *C. tacanensis* (Smith, 1852) new combination; *C. tutelaria* (Mendelson, 1997) new combination; *C. valliceps* (Wiegmann, 1833) new combination.

(8) *Duttaphrynus* new genus. Recognition of the former ''*Bufo*'' *melanostictus* group as a genus requires the following name changes: *Duttaphrynus crocus* (Wogan, Win, Thin, Lwin, Shein, Kyi, and Tun, 2003) new combination; *D. cyphosus*

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(Ye, 1977) new combination; *D. himalayanus* (Günther, 1864) new combination; *D. melanostictus* (Schneider, 1799) new combination; *D. microtympanum* (Boulenger, 1882) new combination; *D. noellerti* (Manamendra-Arachchi and Pethiyagoda, 1998) new combination.

(9) *Epidalea* Cope, 1864. Recognition as a genus of the former ''*Bufo*'' *calamita* group renders one revived name: *Epidalea calamita* (Laurenti, 1768).

(10) *Ingerophrynus* new genus. Recognition of the former ''*Bufo*'' *biporcatus* group + allies results in the following new combinations: *Ingerophrynus biporcatus* (Gravenhorst, 1829) new combination; *I. celebensis* (Günther, 1859 ''1858'') new combination; *I. claviger* (Peters, 1863) new combination; *I. divergens* (Peters, 1871) new combination; *I. galeatus* (Günther, 1864) new combination; *I. kumquat* (Das and Lim, 2001) new combination; *I. macrotis* (Boulenger, 1887) new combination; *I. parvus* (Boulenger, 1887) new combination; *I. philippinicus* (Boulenger, 1887) new combination; *I. quadriporcatus* (Boulenger, 1887) new combination.

(11) *Mertensophryne* Tihen, 1960. Placing *Stephopaedes* Channing, 1979 ''1978'' (as a subgenus) and the ''*Bufo*'' *taitanus* group within *Mertensophryne* provides the following new combinations.

(a) *Mertensophryne*, unassigned to subgenus (the former ''*Bufo*'' *taitanus* group): *Mertensophryne lindneri* (Mertens, 1955) new combination; *M. lonnbergi* (Andersson, 1911) new combination; *M. melanopleura* (Schmidt and Inger, 1959) new combination; *M. micranotis* (Loveridge, 1925) new combination; *M. mocquardi* (Angel, 1924) new combination; *M. nyikae* (Loveridge, 1953) new combination; *M. schmidti* (Grandison, 1972); *M. taitana* Peters, 1878 new combination; *M. uzunguensis* (Loveridge, 1932) new combination.

(b) *Mertensophryne*, subgenus *Stephopaedes*: *Mertensophryne* (*Stephopaedes*) *anotis* (Boulenger, 1907) new combination; *M.* (*S.*) *howelli* (Poynton and Clarke, 1999) new combination; *M.* (*S.*) *loveridgei* (Poynton, 1991) new combination; *Mertensophryne* (*Stephopaedes*) *usambarae* (Poynton and Clarke, 1999).

(12) *Nannophryne* Günther, 1870: With the resurrection of *Nannophryne*, the single species, *Nannophryne variegata* Günther, 1870, takes its original form.

(13) *Peltophryne* Fitzinger, 1843. Resurrection of *Peltophryne* results in the following names being revived: *Peltophryne cataulaciceps* (Schwartz, 1959); *P. empusa* Cope, 1862; *P. fluviatica* (Schwartz, 1972); *P. fracta* (Schwartz, 1972); *P. fustiger* (Schwartz, 1960); *P. guentheri* (Cochran, 1941); *P. gundlachi* (Ruibal, 1959); *P. lemur* Cope, 1869 ''1868''; *P. longinasus* (Stejneger, 1905); *P. peltocephala* (Tschudi, 1838); *P. taladai* (Schwartz, 1960).

(14) *Phrynoidis* Fitzinger, 1843. Recognition of the former ''*Bufo*'' *asper* group as *Phrynoidis* results in two new combinations: *Phrynoidis aspera* (Gravenhorst, 1829); *P. juxtaspera* (Inger, 1964) new combination.

(15) *Poyntonophrynus* new genus. Recognition of the former ''*Bufo*'' *vertebralis* group as a genus results in the following new combinations: *Poyntonophrynus beiranus* (Loveridge, 1932) new combination; *P. damaranus* (Mertens, 1954) new combination; *P. dombensis* (Bocage, 1895) new combination; *P. fenoulheti* (Hewitt and Methuen, 1912) new combination; *P. grandisonae* (Poynton and Haacke, 1993) new combination; *P. hoeschi* (Ahl, 1934) new combination; *P. kavangensis* (Poynton and Broadley, 1988) new combination; *P. lughensis* (Loveridge, 1932) new combination; *P. parkeri* (Loveridge, 1932) new combination; *P. vertebralis* (Smith, 1848) new combination.

(16) *Pseudepidalea* new genus. Recognition of the former ''*Bufo*'' *viridis* group as a genus results in the following new combinations: *Pseudepidalea brongersmai* (Hoogmoed, 1972) new combination; *P. latastii* (Boulenger, 1882) new combination; *P. luristanica* (Schmidt, 1952) new combination; *P. oblonga* (Nikolskii, 1896) new combination; *P. pewzowi* (Bedriaga, 1898) new combination; *P. pseudoraddei* (Mertens, 1971) new combination; *P. raddei* (Strauch, 1876) new combination; *P. surda* (Boulenger, 1891) new combination; *P. taxkorensis* (Fei, 1999) new combination; *P. viridis* (Laurenti, 1768) new combination.

(17) *Rhaebo* Cope, 1862. Recognition of the former ''*Bufo*'' *guttatus* group results in the following name changes: *Rhaebo anderssoni* (Melin, 1941) new combination; *R. blombergi* (Myers and Funkhouser, 1951) new combination; *R. caeruleostictus* (Günther, 1859) new combination [placed here on the basis of comments by Hoogmoed, 1989a]; *R. glaberrimus* (Günther, 1869) new combination; *R. guttatus* (Schneider, 1799) new combination; *R. haematiticus* (Cope, 1862); *R. hypomelas* Boulenger, 1913 (placed here provisionally).

(18) *Rhinella* Fitzinger, 1826. Recognition of the former ''*Bufo*'' *margaritifer* group as the genus *Rhinella* results in the following name changes: *Rhinella acutirostris* (Spix, 1824) new combination; *R. alata* (Thominot, 1884) new combination; *R. castaneotica* (Caldwell, 1991) new combination; *R. ceratophrys* (Boulenger, 1882) new combination; *R. cristinae* (Vélez-Rodriguez and Ruiz-Carranza, 2002) new combination; *R.*

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dapsilis (Myers and Carvalho, 1945) new combination; *R. intermedia* (Günther, 1858) new combination; *R. iserni* Jiménez de la Espada, 1875; *R. margaritifer* (Laurenti, 1768) new combination; *R. nasica* (Werner, 1903) new combination; *R. proboscidea* (Spix, 1824); *R. roqueana* (Melin, 1941) new combination; *R. scitula* (Caramaschi and Niemeyer, 2003) new combination; *R. sclerocephala* (Mijares-Urrutia and Arends-R., 2001) new combination; *R. stanlaii* (Lötters and Köhler, 2000) new combination; *R. sternosignata* (Günther, 1858).

(19) *Vandijkophrynus* new genus. Recognition of the former ''*Bufo*'' *angusticeps* group as *Vandijkophrynus* results in the following name changes: *Vandijkophrynus amatolicus* (Hewitt, 1925) new combination; *V. angusticeps* (Smith, 1848) new combination; *V. gariepensis* (Smith, 1848) new combination; *V. inyangae* (Poynton, 1963) new combination; *V. robinsoni* (Branch and Braacke, 1996) new combination.

Microhylidae: Asterophryinae

(1) *Xenorhina* Peters, 1863. The synonymy of *Xenobatrachus* Peters and Doria, 1878, with *Xenorhina* Peters, 1863, results in the following changes: *Xenorhina anorbis* (Blum and Menzies, 1989 ''1988'') new combination; *X. arfakiana* (Blum and Menzies, 1989 ''1988'') new combination; *X. bidens* van Kampen, 1909; *X. fuscigula* (Blum and Menzies, 1989 ''1988'') new combination; *X. gigantea* van Kampen, 1915; *X. huon* (Blum and Menzies, 1989 ''1988'') new combination; *X. macrops* van Kampen, 1913; *X. mehelyi* (Boulenger, 1898) new combination; *X. multisica* (Blum and Menzies, 1989 ''1988'') new combination; *X. obesa* (Zweifel, 1960) new combination; *X. ocellata* van Kampen, 1913; *X. ophiodon* (Peters and Doria, 1878) new combination; *X. rostrata* (Méhely, 1898); *X. scheepstrai* (Blum and Menzies, 1989 ''1988'') new combination; *X. schiefenhoeveli* (Blum and Menzies, 1989 ''1988'') new combination; *X. subcrocea* (Menzies and Tyler, 1977) new combination; *X. tumula* (Blum and Menzies, 1989 ''1988'') new combination; *X. zweifeli* (Kraus and Allison, 2002) new combination.

Microhylidae: Cophylinae

(1) *Rhombophryne* Boettger, 1880. Transfer of several species of ''*Plethodontohyla*'' Boulenger, 1882, into *Rhombophryne* Boettger, 1880, renders the following name changes: *Rhombophryne alluaudi* (Mocquard, 1901) new combination; *Rhombophryne coudreaui* (Angel, 1938) new combination; *Rhombophryne laevipes* (Mocquard, 1895) new combination.

Arthroleptidae

(1) *Arthroleptis* Smith, 1849. The synonymy of *Schoutedenella* de Witte, 1921, with *Arthroleptis* Smith, 1849, results in the following revived combinations: *Arthroleptis crusculum* Angel, 1950; *A. discodactyla* (Laurent, 1954); *A. hematogaster* (Laurent, 1954); *A. lameerei* de Witte, 1921; *A. loveridgei* de Witte, 1933; *A. milletihorsini* Angel, 1922; *A. mossoensis* (Laurent, 1954); *A. nimbaensis* Angel, 1950; *A. phrynoides* (Laurent, 1976); *A. pyrrhoscelis* Laurent, 1952; *A. schubotzi* Nieden, 1911 ''1910''; *A. spinalis* Boulenger, 1919; *A. sylvatica* (Laurent, 1954); *A. troglodytes* Poynton, 1963; *A. vercammeni* (Laurent, 1954); *A. xenochirus* Boulenger, 1905; *A. xenodactyla* Boulenger, 1909; *A. xenodactyloides* Hewitt, 1933; *A. zimmeri* Ahl, 1925 ''1923''.

Hyperoliidae

(1) *Hyperolius* Rapp, 1842. The synonymy of *Nesionixalus* Perret, 1976, with *Hyperolius* Rapp, 1842 (and recognition of *Nesionixalus* as a subgenus), results in the following revived combinations: *Hyperolius* (*Nesionixalus*) *molleri* (Bedriaga, 1892); *Hyperolius* (*Nesionixalus*) *thomensis* Bocage, 1886.

Ceratobatrachidae

(1) *Ingerana* Dubois, 1987 ''1986''. Treatment of *Liurana* Dubois, 1987 ''1986'', as a synonym of *Ingerana* results in three name changes: *Ingerana alpina* (Huang and Ye, 1997) new combination; *I. medogensis* (Fei, Ye, and Huang, 1997) new combination; *I. reticulata* (Zhao and Li, 1984) new combination.

Phrynobatrachidae

(1) *Phrynobatrachus* Günther, 1862. Placing *Dimorphognathus* Boulenger, 1906, into the synonymy of *Phrynobatrachus* Günther, 1862, renders *Phrynobatrachus africanus* (Hallowell, 1858 ''1857'') new combination. Placing *Phrynodon* Parker, 1935, into the synonymy of *Phrynobatrachus* Günther, 1862, renders *Phrynobatrachus sandersoni* (Parker, 1935) new combination.

Pyxicephalidae

(1) *Amietia* Dubois, 1987 ''1986''. Placing *Afrana* Dubois, 1992, into the synonymy of *Amietia* Dubois, 1987 ''1986'', results in the following name changes: *Amietia amieti* (Laurent, 1976) new combination; *A. angolensis* (Bocage, 1866) new combination; *A. desaegeri* (Laurent, 1972) new combination; *A. dracomontana* (Channing, 1978) new combination; *A. fuscigula* (Duméril

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and Bibron, 1841) new combination; *A. inyangae* (Poynton, 1966) new combination; *A. johnstoni* (Günther, 1894 ''1893'') new combination; *A. ruwenzorica* (Laurent, 1972) new combination; *A. vandijki* (Visser and Channing, 1997) new combination.

Dicroglossidae: Dicroglossinae

(1) *Annandia* Dubois, 1992. Treatment as a genus produces a single new combination: *Annandia delacouri* (Angel, 1928) new combination. (This combination was implied by Dubois, 2005.)

(2) *Eripaa* Dubois, 1992. Treatment as a genus produces a single new combination: *Eripaa fasciculispina* (Inger, 1970) new combination.

(3) *Nanorana* Günther, 1896. Placement of *Chaparana* Bourret, 1939, and *Paa* Dubois, 1975, into the synonymy of *Nanorana* Günther, 1896, provides the following name changes: *Nanorana aenea* (Smith, 1922) new combination; *N. annandalii* (Boulenger, 1920) new combination; *N. arnoldi* (Dubois, 1975) new combination; *N. barmoachensis* (Khan and Tasnim, 1989) new combination; *N. blanfordii* (Boulenger, 1882) new combination; *N. bourreti* (Dubois, 1987 ''1986'') new combination; *N. chayuensis* (Ye, 1977) new combination; *N. conaensis* (Fei and Huang, 1981) new combination; *N. ercepeae* (Dubois, 1974 ''1973'') new combination; *N. fansipani* (Bourret, 1939) new combination; *N. feae* (Boulenger, 1887) new combination; *N. hazarensis* (Dubois and Khan, 1979) new combination; *N. liebigii* (Günther, 1860) new combination; *N. liui* (Dubois, 1987 ''1986'') new combination; *N. maculosa* (Liu, Hu, and Yang, 1960) new combination; *N. medogensis* (Fei and Ye, 1999) new combination; *N. minica* (Dubois, 1975) new combination; *N. mokokchungensis* (Das and Chanda, 2000) new combination; *N. polunini* (Smith, 1951) new combination; *N. quadranus* (Liu, Hu, and Yang, 1960) new combination; *N. rarica* (Dubois, Matsui, and Ohler, 2001) new combination; *N. robertingeri* (Wu and Zhao, 1995) new combination; *N. rostandi* (Dubois, 1974 ''1973'') new combination; *N. sternosignata* (Murray, 1885) new combination; *N. taihangnica* (Chen and Jiang, 2002) new combination; *N. unculuanus* (Liu, Hu, and Yang, 1960) new combination; *N. vicina* (Stoliczka, 1872) new combination; *N. yunnanensis* (Anderson, 1879 ''1878'') new combination.

(4) *Ombrana* Dubois, 1992. Treatment as a genus produces a single new combination: *Ombrana sikimensis* (Jerdon, 1870) new combination.

Dicroglossidae: Occidozyginae

(1) *Occidozyga* Kuhl and Van Hasselt, 1822. Replacement of *Phrynoglossus* Peters, 1867, into the synonymy of *Occidozyga* Kuhl and Van Hasselt, 1822, presents the following revived combinations: *Occidozyga baluensis* (Boulenger, 1896); *O. borealis* (Annandale, 1912); *O. celebensis* Smith, 1927; *O. diminutivus* (Taylor, 1922); *O. floresianus* Mertens, 1927; *O. laevis* (Günther, 1858); *O. magnapustulosus* (Taylor and Elbel, 1958); *O. martensii* (Peters, 1867); *O. semipalmatus* Smith, 1927; *O. sumatrana* (Peters, 1877); *O. vittatus* (Andersson, 1942).

Rhacophoridae

(1) *Chiromantis* Peters, 1854. The synonymy of *Chirixalus* Boulenger, 1893, with *Chiromantis* Peters, 1854, presents the following new combinations: *Chiromantis cherrapunjiae* (Roonwal and Kripalani, 1966 ''1961'') new combination; *C. doriae* (Boulenger, 1893) new combination; *C. dudhwaensis* (Ray, 1992) new combination; *C. hansenae* (Cochran, 1927) new combination; *C. laevis* (Smith, 1924); *C. nongkhorensis* (Cochran, 1927) new combination; *C. punctatus* (Wilkinson, Win, Thin, Lwin, Shein, and Tun, 2003) new combination; *C. shyamrupus* (Chanda and Ghosh, 1989) new combination; *C. simus* (Annandale, 1915) new combination; *C. vittatus* (Boulenger, 1887) new combination.

(2) *Feihyla* new genus. We place only *Philautus palpebralis* Smith, 1924, into *Feihyla*, as *Feihyla palpebralis* (Smith, 1924), although we expect other species to be placed in this genus as data emerge.

(3) *Kurixalus* Ye, Fei, and Dubois, 1999. Because the content of *Kurixalus* is controversial (see Delorme et al., 2005), we list the species we regard as being in this monophyletic group: *Kurixalus eiffingeri* (Boettger, 1895); *K. idiootocus* (Kuramoto and Wang, 1987) new combination; and provisionally *Kurixalus verrucosus* (Boulenger, 1893) new combination (based on the tree, data undisclosed, presented by Delorme et al., 2005).

Ranidae

Because of the extensive changes in ranid taxonomy, we provide a listing of all recognized genera and species, noting new combinations.

(1) *Amolops* Cope, 1865. *Amolops bellulus* Liu, Yang, Ferraris, and Matsui, 2000; *A. chakrataensis* Ray, 1992; *A. chunganensis* (Pope, 1929); *A. cremnobatus* Inger and Kottelat, 1998; *A. daiyunensis* (Liu and Hu, 1975); *A. formosus* (Günther, 1876 ''1875''); *A. gerbillus* (Annandale, 1912); *A. granulosus* (Liu and Hu, 1961); *A. hainanensis* (Boulenger, 1900 ''1899''); *A. himalayanus* (Boulenger, 1888); *A. hongkongensis* (Pope and Romer, 1951); *A. jaunsari* Ray, 1992; *A. jinjiangensis*

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Su, Yang, and Li, 1986; *A. kangtingensis* (Liu, 1950); *A. kaulbacki* (Smith, 1940); *A. larutensis* (Boulenger, 1899); *A. liangshanensis* (Wu and Zhao, 1984); *A. lifanensis* (Liu, 1945); *A. loloensis* (Liu, 1950); *A. longimanus* (Andersson, 1939 ''1938''); *A. mantzorum* (David, 1872 ''1871''); *A. marmoratus* (Blyth, 1855); *A. mengyangensis* Wu and Tian, 1995; *A. monticola* (Anderson, 1871); *A. nepalicus* Yang, 1991; *A. ricketti* (Boulenger, 1899); *A. spinapectoralis* Inger, Orlov, and Darevsky, 1999; *A. tormotus* (Wu, 1977); *A. torrentis* (Smith, 1923); *A. tuberodepressus* Liu and Yang, 2000; *A. viridimaculatus* (Jiang, 1983); *A. wuyiensis* (Liu and Hu, 1975).

(2) *Babina* Thompson, 1912. *Babina adenopleura* (Boulenger, 1909) new combination; *B. caldwelli* (Schmidt, 1925) new combination; *B. chapaensis* (Bourret, 1937) new combination; *B. daunchina* (Chang, 1933) new combination; *B. holsti* (Boulenger, 1892) new combination; *B. lini* (Chou, 1999) new combination; *B. pleuraden* (Boulenger, 1904) new combination; *B. psaltes* (Kuramoto, 1985) new combination; *B. subaspera* (Barbour, 1908).

(3) *Clinotarsus* Mivart, 1869. *Clinotarsus curtipes* (Jerdon, 1854 ''1853'').

(4) *Glandirana* Fei, Ye, and Huang, 1991 ''1990''. *Glandirana emeljanovi* (Nikolskii, 1913) new combination; *G. minima* (Ting and T'sai, 1979); *G. rugosa* (Temminck and Schlegel, 1838) new combination; *R. tientaiensis* (Chang, 1933 ''1933–1934'') new combination.

(5) *Huia* Yang, 1991. *Huia absita* Stuart and Chan-ard, 2005; *H. amamiensis* (Matsui, 1994) new combination; *H. andersonii* (Boulenger, 1882) new combination; *H. anlungensis* (Liu and Hu, 1973) new combination; *H. archotaphus* (Inger and Chan-ard, 1997) new combination; *H. bacboensis* (Bain, Lathrop, Murphy, Orlov, and Ho, 2003) new combination; *H. banaorum* (Bain, Lathrop, Murphy, Orlov, and Ho, 2003) new combination; *H. cavitympanum* (Boulenger, 1893); *Huia chapaensis* (Bourret, 1937) new combination; *H. chloronota* (Günther, 1876 ''1875'') new combination; *H. daorum* (Bain, Lathrop, Murphy, Orlov, and Ho, 2003) new combination; *H. exiliversabilis* (Li, Ye, and Fei, 2001) new combination; *H. grahami* (Boulenger, 1917) new combination; *H. graminea* (Boulenger, 1900 ''1899'') new combination; *H. hainanensis* (Fei, Ye, and Li, 2001) new combination; *H. hejiangensis* (Deng and Yu, 1992) new combination; *H. hmongorum* (Bain, Lathrop, Murphy, Orlov, and Ho, 2003) new combination; *H. hosii* (Boulenger, 1891) new combination; *H. iriodes* (Bain and Nguyen, 2004) new combination; *H. ishikawae* (Stejneger, 1901) new combination; *H. jingdongensis* (Fei, Ye, and Li, 2001) new combination; *H. junlianensis* (Huang, Fei, and Ye, 2001) new combination; *H. khalam* (Stuart, Orlov, and Chan-ard, 2005) new combination; *H. kuangwuensis* (Liu and Hu, 1966) new combination; *H. leporipes* (Werner, 1930) new combination; *H. livida* (Blyth, 1856 ''1855'') new combination; *H. lungshengensis* (Liu and Hu, 1962) new combination; *H. margaretae* (Liu, 1950) new combination; *H. masonii* (Boulenger, 1884); *H. megatympanum* (Bain, Lathrop, Murphy, Orlov, and Ho, 2003) new combination; *H. melasma* Stuart and Chan-ard, 2005; *H. modiglianii* (Doria, Salvidio, and Tavano, 1999); *H. morafkai* (Bain, Lathrop, Murphy, Orlov, and Ho, 2003) new combination; *H. narina* (Stejneger, 1901) new combination; *H. nasica* (Boulenger, 1903); *H. nasuta* Li, Ye, and Fei, 2001 new combination; *H. schmackeri* (Boettger, 1892) new combination; *H. sinica* (Ahl, 1927 ''1925'') new combination; *H. sumatrana* Yang, 1991; *H. supranarina* (Matsui, 1994) new combination; *H. swinhoana* (Boulenger, 1903) new combination; *H. tabaca* (Bain and Nguyen, 2004) new combination; *H. tiannanensis* (Yang and Li, 1980) new combination; *H. trankieni* (Orlov, Ngat, and Ho, 2003) new combination; *H. utsunomiyaorum* (Matsui, 1994) new combination; *H. versabilis* (Liu and Hu, 1962) new combination; *H. wuchuanensis* (Xu, 1983) new combination.

(6) *Humerana* Dubois, 1992. *Humerana humeralis* (Boulenger, 1887) new combination; *Humerana miopus* (Boulenger, 1918) new combination; *Humerana oatesii* (Boulenger, 1892) new combination.

(7) *Hydrophylax* Fitzinger, 1843. *Hydrophylax albolabris* (Hallowell, 1856); *H. albotuberculatus* (Inger, 1954) new combination; *H. amnicola* (Perret, 1977) new combination; *H. asperrima* (Perret, 1977) new combination; *H. chalconotus* (Schlegel, 1837) new combination; *H. crassiovis* (Boulenger, 1920) new combination; *H. darlingi* (Boulenger, 1902) new combination; *H. everetti* (Boulenger, 1882) new combination; *H. galamensis* (Duméril and Bibron, 1841); *H. igorotus* (Taylor, 1922) new combination; *H. kampeni* (Boulenger, 1920) new combination; *H. lemairei* (de Witte, 1921) new combination; *H. lepus* (Andersson, 1903) new combination; *H. longipes* (Perret, 1960) new combination; *H. luzonensis* (Boulenger, 1896) new combination; *H. macrops* (Boulenger, 1897) new combination; *H. malabaricus* (Tschudi, 1838); *H. occidentalis* (Perret, 1960) new combination; *H. parkerianus* (Mertens, 1938); *H. raniceps* (Peters, 1871) new combination; *H. tipanan* (Brown, McGuire, and Diesmos, 2000) new combination.

(8) *Hylarana* Tschudi, 1838. *Hylarana erythraea* (Schlegel, 1837); *H. guentheri* (Boulenger, 1882); *H. macrodactyla* Günther, 1858; *H. taipe-*

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hensis (Van Denburgh, 1909) new combination; *Hylarana tytleri* Theobald, 1868.

(9) *Lithobates* Fitzinger, 1843. *L. areolatus* (Baird and Girard, 1852) new combination; *Lithobates berlandieri* (Baird, 1859) new combination; *Lithobates blairi* (Mecham, Littlejohn, Oldham, Brown, and Brown, 1973) new combination; *Lithobates brownorum* (Sanders, 1973); *L. bwana* (Hillis and de Sá, 1988) new combination; *L. capito* (LeConte, 1855) new combination; *L. catesbeianus* (Shaw, 1802) new combination; *L. chichicuahutla* (Cuellar, Méndez-De La Cruz, and Villagrán-Santa Cruz, 1996) new combination; *L. chiricahuensis* (Platz and Mecham, 1979) new combination; *L. clamitans* (Latreille, 1801) new combination; *L. dunni* (Zweifel, 1957) new combination; *L. fisheri* (Stejneger, 1893) new combination; *L. forreri* (Boulenger, 1883) new combination; *L. grylio* (Stejneger, 1901) new combination; *L. heckscheri* (Wright, 1924) new combination; *L. johni* (Blair, 1965) new combination; *L. juliani* (Hillis and de Sá, 1988) new combination; *L. lemosespinali* (Smith and Chiszar, 2003) new combination; *L. macroglossa* (Brocchi, 1877) new combination; *L. maculatus* (Brocchi, 1877) new combination; *L. magnaocularis* (Frost and Bagnara, 1974) new combination; *L. megapoda* (Taylor, 1942) new combination; *L. miadis* (Barbour and Loveridge, 1929) new combination; *L. montezumae* (Baird, 1854) new combination; *L. neovolcanicus* (Hillis and Frost, 1985) new combination; *L. okaloosae* (Moler, 1985) new combination; *L. omiltemanus* (Günther, 1900) new combination; *L. onca* (Cope, 1875) new combination; *L. palmipes* (Spix, 1824); *L. palustris* (LeConte, 1825) new combination; *L. pipiens* (Schreber, 1782) new combination; *L. psilonota* (Webb, 2001) new combination; *L. pueblae* (Zweifel, 1955) new combination; *L. pustulosus* (Boulenger, 1883) new combination; *L. septentrionalis* (Baird, 1854) new combination; *L. sevosus* (Goin and Netting, 1940) new combination; *L. sierramadrensis* (Taylor, 1939 ''1938'') new combination; *L. spectabilis* (Hillis and Frost, 1985) new combination; *L. sphenocephalus* (Cope, 1886) new combination; *L. sylvaticus* (LeConte, 1825) new combination; *L. tarahumarae* (Boulenger, 1917) new combination; *L. taylori* (Smith, 1959) new combination; *L. tlaloci* (Hillis and Frost, 1985) new combination; *L. vaillanti* (Brocchi, 1877) new combination; *L. vibicarius* (Cope, 1894) new combination; *L. virgatipes* (Cope, 1891) new combination; *L. warszewitschii* (Schmidt, 1857) new combination; *L. yavapaiensis* (Platz and Frost, 1984) new combination; *L. zweifeli* (Hillis, Frost, and Webb, 1984) new combination.

(10) *Meristogenys* Yang, 1991: *Meristogenys amoropalamus* (Matsui, 1986); *M. jerboa* (Günther, 1872); *M. kinabaluensis* (Inger, 1966); *M. macrophthalmus* (Matsui, 1986); *M. orphnocnemis* (Matsui, 1986); *M. phaeomerus* (Inger and Gritis, 1983); *M. poecilus* (Inger and Gritis, 1983); *M. whiteheadi* (Boulenger, 1887).

(11) *Nasirana* Dubois, 1992. *Nasirana alticola* (Boulenger, 1882) new combination.

(12) *Pelophylax* Fitzinger, 1843.[37] *Pelophylax bedriagae* (Camerano, 1882 ''1881'') new combination; *P. bergeri* (Günther, 1986) new combination; *P. cerigensis* (Beerli, Hotz, Tunner, Heppich, and Uzzell, 1994) new combination; *P. chosenicus* (Okada, 1931) new combination; *P. cretensis* (Beerli, Hotz, Tunner, Heppich, and Uzzell, 1994) new combination; *P. demarchii* (Scortecci, 1929) new combination; *P. epeiroticus* (Schneider, Sofianidou, and Kyriakopoulou-Sklavounou, 1984) new combination; *P. fukienensis* (Pope, 1929) new combination; *P. hubeiensis* (Fei and Ye, 1982); *P. kurtmuelleri* (Gayda, 1940 ''1939''); *P. lateralis* (Boulenger, 1887) new combination; *P. lessonae* (Camerano, 1882 ''1881'') new combination; *P. nigrolineatus* (Liu and Hu, 1960 ''1959''); *P. nigromaculatus* (Hallowell, 1861 ''1860''); *P. perezi* (Seoane, 1885); *P. plancyi* (Lataste, 1880) new combination; *P. porosus* (Cope, 1868) new combination; *P. ridibundus* (Pallas, 1771); *P. saharicus* (Boulenger, 1913) new combination; *P. shqipericus* (Hotz, Uzzell, Günther, Tunner, and Heppich, 1987) new combination; *P. shuchinae* (Liu, 1950); *P. tenggerensis* (Zhao, Macey, and Papenfuss, 1988) new combination; *P. terentievi* (Mezhzherin, 1992) new combination.

(13) *Pterorana* Kiyasetuo and Khare, 1986. *Pterorana khare* Kiyasetuo and Khare, 1986.

(14) *Pulchrana* Dubois, 1992. *P. banjarana* (Leong and Lim, 2003) new combination; *P. baramica* (Boettger, 1900) new combination; *P. debussyi* (van Kampen, 1910) new combination; *P. glandulosa* (Boulenger, 1882) new combination; *P. grandocula* (Taylor, 1920) new combination; *P. laterimaculata* (Barbour and Noble, 1916) new combination; *P. luctuosa* (Peters, 1871) new combination; *P. mangyanum* (Brown and Guttman, 2002) new combination; *P. melanomenta* (Taylor, 1920) new combination; *P. moellendorffi* (Boettger, 1893) new combination; *P. picturata* (Boulenger, 1920) new combination; *P. siberu* (Dring,

[37] We concur with Bogart (2003) that named hybridogens/kleptons are composed of hybrids, not covered by regulated Linnaean nomenclature. This does not mean that we reject the utilitarian naming conventions suggested by Dubois (1982: e.g., *Pelophylax* kl. *esculentus*, *Pelophylax* kl. *grafi*), for denoting kinds of frog, only that these names do not represent taxa in any evolutionary/phylogenetic sense, but instead are ''kinds'' of frogs.

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McCarthy, and Whitten, 1990) new combination; *P. signata* (Günther, 1872) new combination; *P. similis* (Günther, 1873) new combination.

(15) *Rana* Linnaeus, 1758. *Rana amurensis* Boulenger, 1886; *R. arvalis* Nilsson, 1842; *R. asiatica* Bedriaga, 1898; *R. aurora* Baird and Girard, 1852; *R. boylii* Baird, 1854; *R. camerani* Boulenger, 1886; *R. cascadae* Slater, 1939; *R. chaochiaoensis* Liu, 1946; *R. chensinensis* David, 1875; *R. chevronta* Hu and Ye, 1978; *R. dalmatina* Fitzinger *In* Bonaparte, 1839; *R. draytonii* Baird and Girard, 1852; *R. dybowskii* Günther, 1876; *R. graeca* Boulenger, 1891; *R. holtzi* Werner, 1898; *R. huanrenensis* Fei, Ye, and Huang, 1991 ''1990''; *R. iberica* Boulenger, 1879; *R. italica* Dubois, 1987 ''1985''; *R. japonica* Boulenger, 1879; *R. johnsi* Smith, 1921; *R. kukunoris* Nikolskii, 1918; *R. kunyuensis* Lu and Li, 2002; *R. latastei* Boulenger, 1879; *R. longicrus* Stejneger, 1898; *R. luteiventris* Thompson, 1913; *R. macrocnemis* Boulenger, 1885; *R. multidenticulata* Chou and Lin, 1997; *R. muscosa* Camp, 1917; *R. okinavana* Boettger, 1895; *R. omeimontis* Ye and Fei, 1993; *R. ornativentris* Werner, 1903; *R. pirica* Matsui, 1991; *R. pretiosa* Baird and Girard, 1853; *R. pyrenaica* Serra-Cobo, 1993; *Rana sakuraii* Matsui and Matsui, 1990; *R. sangzhiensis* Shen, 1986; *R. sauteri* Boulenger, 1909; *R. tagoi* Okada, 1928; *R. temporaria* Linnaeus, 1758; *R. tsushimensis* Stejneger, 1907; *R. weiningensis* Liu, Hu, and Yang, 1962; *R. zhengi* Zhao, 1999; *R. zhenhaiensis* Ye, Fei, and Matsui, 1995.

(16) *Sanguirana* Dubois, 1992. *Sanguirana sanguinea* (Boettger, 1893). new combination; *S. varians* (Boulenger, 1894) new combination.

(17) *Staurois* Cope, 1865. *Staurois latopalmatus* (Boulenger, 1887); *S. natator* (Günther, 1858); *S. nubilis* (Mocquard, 1890); *S. tuberilinguis* Boulenger, 1918.

(18) *Sylvirana* Dubois, 1992. *Sylvirana arfaki* (Meyer, 1875 ''1874'') new combination; *S. attigua* (Inger, Orlov, and Darevsky, 1999) new combination; *S. aurantiaca* (Boulenger, 1904) new combination; *S. aurata* (Günther, 2003) new combination; *S. bannanica* (Rao and Yang, 1997) new combination; *S. celebensis* (Peters, 1872) new combination; *S. chitwanensis* (Das, 1998) new combination; *S. cubitalis* (Smith, 1917) new combination; *S. daemeli* (Steindachner, 1868) new combination; *S. danieli* (Pillai and Chanda, 1977) new combination; *S. elberti* (Roux, 1911) new combination; *S. faber* (Ohler, Swan, and Daltry, 2002) new combination; *S. florensis* (Boulenger, 1897) new combination; *S. garoensis* (Boulenger, 1920) new combination; *S. garritor* (Menzies, 1987) new combination; *S. gracilis* (Gravenhorst, 1829) new combination; *S. grisea* (van Kampen, 1913) new combination; *S. jimiensis* (Tyler, 1963) new combination; *S. kreffti* (Boulenger, 1882) new combination; *S. latouchii* (Boulenger, 1899) new combination; *S. leptoglossa* (Cope, 1868) new combination; *S. maosonensis* (Bourret, 1937) new combination; *S. margariana* (Anderson, 1879 ''1878'') new combination; *S. milleti* (Smith, 1921) new combination; *S. moluccana* (Boettger, 1895) new combination; *S. montivaga* (Smith, 1921) new combination; *S. mortenseni* (Boulenger, 1903) new combination; *S. nigrotympanica* (Dubois, 1992) new combination; *S. nigrovittata* (Blyth, 1856 ''1855'') new combination; *S. novaeguineae* (van Kampen, 1909) new combination; *S. papua* (Lesson, 1831) new combination; *S. persimilis* (van Kampen, 1923) new combination; *S. spinulosa* (Smith, 1923) new combination; *S. supragrisea* (Menzies, 1987) new combination; *S. temporalis* (Günther, 1864) new combination; *S. volkerjane* (Günther, 2003) new combination.

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Fig. 50. Consensus of four most parsimonious trees, showing old and new family-group taxonomy.

Frost, D.R., et al. 2006. The amphibian tree of life.
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